# Trade-offs Between Wood Density and Radial Growth in the Region H White Spruce Controlled Parentage Program, Alberta, Canada

**by**

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## Abstract

Trade-offs between wood density and radial growth rate in white spruce were investigated. Decreases in wood density associated with increased radial growth rate have been well documented in several tree species, including white spruce (*Picea glauca* (Moench) Voss). One of the goals of the Region H white spruce Controlled Parentage Program is to increase stem volume at rotation; however, the Forest Genetic Resource Conservation and Management Standards of Alberta (2016) require program proponents to consider the indirect selection of correlated traits, including wood density, when selecting for increased growth rates.

Resistograph drilling resistance (%), Pilodyn penetration depth (mm), wood specific gravity and diameter inside bark (mm) at breast height were measured in 40 different families from three progeny test sites at age 26. Two to eight trees/family/site were selected for drilling resistance and diameter at breast height measurements, two to eight trees/family for two sites were selected for penetration depth and two to seven trees/family across all three sites were selected for wood specific gravity assessment. Analyses included phenotypic and genotypic correlations between the various traits, regression analyses for estimating wood specific gravity using drilling resistance and penetration depth measurements and calculation of narrow sense heritability and breeding values for drilling resistance, penetration depth and diameter inside bark. These breeding values were plotted against the breeding values for height (cm) at age 25, which were provided by the Government of Alberta.

A paired t-test showed that significant differences existed between drilling resistance measurements taken from the north and east aspects of individual trees, but a significant difference was not found between penetration depth for the same trees. Significant differences existed between sites for all four traits; however, significant differences existed only for drilling resistance between families. Additionally, coefficients of variation showed that the variation in diameter was two to three times greater compared to any of the wood density measurements. Phenotypic correlations between the various quantitative traits were typically moderate in strength ($r \sim 0.5$) at both the individual- and family-level and all were significant. The relative standard error was approximately 5-10% of the respective correlation coefficient. Multiple linear regression showed that both drilling resistance and penetration depth were relatively poor predictors ($r^2 \sim 0.4$) of wood specific gravity at both the individual- and family-level. There was no genotype-by-environment interaction detected for drilling resistance or Resistograph, but there was for both penetration depth and diameter inside bark. Narrow sense heritabilities were generally low for diameter at breast height ($h^2 < 0.15$) and higher ($h^2 > 0.3$) for drilling resistance and penetration depth, except for Hay River, which showed the opposite response for drilling resistance ($h^2 = 0.11$) and diameter inside bark ($h^2 = 0.42$). The relative standard error associated with each heritability estimate was generally high (30-150% of the heritability). Genetic correlations for all traits were significant and weak to moderate ($0.3 < r > 0.7$) at the individual-level and very weak ($r < 0.15$) and not significant at the family level.

At the phenotypic level, there is some evidence that increased radial growth rate is associated with a decrease in wood density; however, the decrease in wood density is very small (< 10%) and the variation in wood density is much lower than that found in diameter. Additionally, the range of wood density and level of variation in the Region H white spruce Controlled Parentage Program was similar to wild stands in Quebec, indicating that there was no loss in wood density through selection for height. Resistograph appears to be a more sensitive measurement for assessing wood density compared to Pilodyn, as it was able to delineate significant differences even at the family level and provided the highest estimates of heritability with relatively lower associated standard errors. The genetic correlation between drilling resistance and diameter inside bark was virtually non-existent ($r_g$ = -0.08). Forest companies should monitor the wood density of natural and artificially-regenerated stands on an ongoing basis and assess wood density within each tree improvement program and each generation within a respective program to ensure that mean wood density does not decline compared to natural stands over time.

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## List of Abbreviations

**BV:** Breeding value

**CoV:** Coefficient of variation

**CPP:** Controlled Parentage Program

**DR:** Drilling resistance (%)

**DIB:** Diameter inside bark (mm) at breast height (1.3 m)

**FGRMS:** Alberta’s Forest Genetic Resource Management and Conservation Standards (2016).

**GoA:** Government of Alberta

**Ne:** Effective population size

**PD:** Penetration depth (mm)

**Sw:** White spruce

**TI:** Tree improvement

**WD:** Wood density

**WSG:** Wood specific gravity

# Glossary of Terms

**Annual allowable cut:** The volume of timber ($m^3$) that a forest company is granted to harvest from a specific region of publicly-owned (Crown) land in Alberta by the Government of Alberta.

**Alberta Agriculture and Forestry:** A branch of the Government of Alberta that regulates forestry activities on Crown land in Alberta.

**Allowable cut effect:** Describes the uplift in annual allowable cut through various management activities, including tree improvement.

**Bleached chemi-thermomechanical pulp:** A grade of pulp that is produced by impregnating hot wood chips with chemicals followed by mechanical refining. The refining process shears fibres from one other. This is a high-yield (~90%) process that preserves all components present in wood (cellulose, hemicellulose and lignin). Typically used to produce printing and writing grades of paper and boxboard products.

**Best linear unbiased predictor:** A method used to predict random effects (e.g. family breeding values, heritability) that is often used in the analysis of quantitative genetic experiments. May be used to determine breeding values at either the individual (i.e. progeny) or family (i.e. parent) levels.

**Breeding value:** A numerical representation of the additive genetic component of a phenotype, typically given as a percent deviation from the population mean, though it may also be expressed in the units a measurement was taken. Any breeding values given in the present study will be as a percent deviation. May be given at the individual-, family- level or program-level.

**Controlled Parentage Program:** A species-specific breeding/clonal program and its associated deployment region in Alberta. Includes aspects of genetic testing, deployment of genetic material (wild or improved), breeding and diversity monitoring, among other requirements.

**Detailed Forest Management Plan:** A management plan forest companies with Forest Management Agreements are required to submit to the Government of Alberta. These documents detail harvest volumes and areas, long-term planning, reforestation programs, research programs (including tree improvement) and management for non-timber values (e.g. recreation and conservation). Publicly available on the Government of Alberta website.

**Drilling resistance:** The measurement taken using the Resistograph device. An indirect measure of wood density. Sometimes referred to as drilling amplitude in the literature.

**Diameter inside bark:** The diameter inside bark (mm) at breast height (1.3 m) as measured using the Resistograph device.

**Earlywood:** Wood that is formed early in the growing season (i.e. spring). In conifers, earlywood is composed primarily of tracheids with thin cell walls and large lumens that facilitate mass water transport. Typically has a lighter appearance and lower wood density compared to latewood.

**Alberta’s Forest Genetic Resource Management and Conservation Standards:** The standards by which tree improvement and deployment of forest genetic material (i.e. trees and shrubs) is regulated in Alberta.

**Forest Management Agreement:** A form of renewable forest tenure in Alberta whereby a forest company is given access to large supplies of publicly-owned timber in exchange for assuming most management duties associated with planning, harvesting and reforestation. Typically forest companies are granted an annual allowable cut (in $m^3$) in a specific area of the Province for a period of 20 years.

**Government of Alberta:** The Provincial Government of the Province of Alberta, Canada. The Government of Alberta has a responsibility to manage Crown lands, including forests.

**IQR*1.5 rule:** A method used to screen for outliers in a data set.

**Juvenile wood:** Wood that is grown under the influence of the crown. Typically found adjacent to the pith in the lower stem but may compose the outer wood in the upper stem where live crown persists. Typically possesses less traits, including lower wood density, compared to mature wood.

**Latewood:** Wood that is formed late in the growing season (i.e. summer). In conifers, latewood is composed primarily of tracheids with thick cell walls and small lumens that provide structural strength to the tree. Typically has a darker appearance and higher wood density compared to earlywood.

**Modulus of elasticity:** A measure of the stiffness of a material (i.e. resistance to elastic deformation under load). Positively correlated with wood density.

**Modulus of rupture:** A measure of strength of material (i.e. resistance to material failure under load). Positively correlated with wood density.

**Mature wood:** Wood that is not grown under the influence of the live crown. Typically composes the outer wood of the lower stem or where there is a lack of live crown. Typically possess more desirable properties, including higher wood density, compared to juvenile wood.

**Northern bleached softwood Kraft:** A grade of softwood (i.e. conifer) pulp composed primarily of chemically digested cellulose fibres. Yields using this process typically do not exceed ~50% due to being limited by the proportion of cellulose present in the wood. Typically used in high-quality products where strength is desired (e.g. magazine, writing and tissue papers). Sometimes referred to as chemical pulp.

**Effective population size:** It is calculated using the relative contributions of each genotype within a breeding population to a specific seed or vegetative lot. For a program possessing no relatedness between clones/parents, the maximum Ne is equal to the number of parents/clones, though this assumes equal contributions among clones/parents.

**Penetration depth:** The measurement taken using the Pilodyn device. An indirect measure of wood density.

**Tree improvement:** Refers in general to the process of genetic improvement of tree populations through breeding, selection and testing for specific traits. In Alberta, the most commonly improved trait is height (as an indirect selection for increased volume at rotation age).

**Thermomechanical pulp:** A grade of pulp produced via mechanical refining of hot wood chips. This is a high-yield process (~90%) due to the preservation of the cellulose, hemicellulose and lignin present in the wood. Often used to produce low grade paper products, including newsprint.

**Wood density:** Refers in general to wood density or related indirect measures of the trait (e.g. drilling resistance or Pilodyn).

**Wood specific gravity:** A measure of the relative density of wood compared to water and which is technically unitless. Determined using green volume and constant weight for this project. The wood specific gravity measurements taken in this study are equivalent to green wood density (in $kg/m^3$). Various protocols to determine wood specific gravity exist and may not be equivalent between studies (e.g. basic wood specific gravity *versus* 12% wood specific gravity).

# Chapter 1: Literature Review

## 1.1 – Introduction

Across the globe forests are being managed more intensively, including in Alberta. Pressure on Alberta's land base is increasing through climate change (Gray and Hamann 2015), increases to other resource dispositions (e.g. oil and gas development [AER 2018]) and conservation, particularly for woodland caribou throughout Alberta's forested ecoregions (Schneider and Pendlebury 2016; GoA 2017). Many jurisdictions are increasingly utilizing improved varieties of trees to realize greater volume productivity in terms of both per unit of land area and per unit of time. Using more productive varieties allows forest companies to either harvest larger trees for the same rotation length or to harvest trees of the same size with a shorter rotation. Both scenarios allow for the maximization of the land's productivity. In addition to increasing pressure on the land base, there is demand for wood that is harvested legally and sustainably. Various sustainable forestry initiatives (e.g. Sustainable Forestry Initiative Forest Management Standard from SFI Inc.) certify that wood is sourced in a manner that is ethical and which does not compromise the health of the forest or the productive capacity of the land (SFI Inc. 2015). Tree improvement (TI) is an important activity for meeting these objectives despite competing values and pressures. Many of Alberta's TI programs seek to increase productivity while maintaining high genetic diversity, climatic adaptability and wood quality (ATISC 2007; ATISC 2008). However, increased growth rate has often been shown to be negatively correlated with wood density in many tree species (Zhang 1995), including white spruce (*Picea glauca*

[Moench] Voss - Middleton and Munro 2002; Pike and Montgomery 2017). Further complicating this are Alberta's Forest Genetic Resource Management and Conservation Standards (FGRMS – AAF 2016a), which establishes the collection and deployment of forest genetic material, as well as the requirements for TI programs. The intent of the present study is to investigate trade-offs between radial growth rate and wood density (WD) in Alberta's Region H white spruce (Sw) Controlled Parentage Program (CPP) and the implications of this relationship on the management and deployment of material from this program.

## 1.2 – Distribution, Ecology and Utilization of White Spruce in Alberta

White spruce is a widely-distributed (Figure 1.1) coniferous tree species occurring throughout the boreal forest with an essentially continuous distribution from Alaska, sweeping eastwards across the prairie provinces of Canada into Ontario, Quebec and the Maritime Provinces. In Alberta, Sw may be found in every forested ecoregion of the province (AAF 2016b) and comprises approximately half of the merchantable coniferous timber (FCC 2006). Approximately 46% of the seedlings produced for reforestation in Alberta are spruce (AAF 2017a), most of which are Sw, with minor contributions from black (*Picea mariana* (Mill.) B.S.P) and Engelmann spruce (*Picea engelmannii* Parry ex Engelm.). White spruce is a relatively slow growing (Lieffers *et al.,* 1996), long-lived (typically 100-250 years - Abrahamson 2015), species that naturally occurs as a component of mixedwoods, but is often planted as a pure-species during reforestation of harvested stands in Alberta (Man and Lieffers 1999). Mature Sw attains typical sizes of 25-30 m in height and 60-90 cm in diameter (Abrahamson 2015). White spruce is typically a mid-late successional species (Peters *et al.,* 2006) that will occupy the understory of quaking aspen (*Populus tremuloides* Michx.) dominated mixedwoods, eventually overtopping the aspen after several decades (~100 years - Lieffers *et al.,* 1996). This characteristic also makes Sw amenable to being managed in mixedwood stands where the aspen overstory is harvested and the Sw understory is protected (Grover *et al.,* 2014).

**Figure 1.1: Distribution map of white spruce (*Picea glauca* [Moench] Voss). Available from Natural Resources Canada, Canadian Forest Service (2015).**

Although Sw is widely distributed and occurs throughout many different environments, the focus will be on its ecology in Alberta. White spruce occurs naturally throughout all of Alberta's ecoregions (Figure 1.2), with the exception of the Grassland Natural Region and its associated Subregions in the Southeast corner of the province (NRC 2006). In general, Sw in Alberta experiences relatively long and cold winters, short, hot summers and low levels of precipitation, though this varies greatly by the respective Natural Region/Subregion (NRC 2006). White spruce forms a major component of the forest in the Boreal Forest and Foothills Natural Regions (NRC

2006), which form the core part of the ‘Green Area’ in Alberta, which are public lands largely managed for natural resource development and extraction, including forestry (AAF 2017b). Historically, the Foothills and Boreal Forest Natural Regions have an average annual temperature ($^0$C) of approximately 2 and -1.5, respectively and an average annual precipitation (mm) of approximately 600 and 400, respectively (NRC 2006). The continentality of the Boreal Forest Natural Region is greater compared to the Foothills Natural Regions due to experiencing both higher average summer and lower average winter temperatures (NRC 2006). Additionally, drought stress, as indicated by summer moisture index (calculated as growing degree days > 5 $^0$C divided by growing season average precipitation [mm]), is greater in the Boreal Forest Natural Region (NRC 2006). In short, Sw growing in Alberta is exposed to relatively harsh and highly variable climates. Furthermore, the climates of these regions are expected to be modified under current climate change scenarios, which may increase climatic variability and increase drought stress (Gray and Hamann 2015).

White spruce is a highly-valued commercial species in Alberta and is largely harvested to produce lumber and pulp, with a smaller proportion being allocated to plywood production (FCC 2006; AWP 2013a). There are several major mills in Alberta that consume softwood fibre as part of their operations, including 20 sawmills producing lumber and boards, four pulp mills producing northern bleached softwood Kraft, bleached chemi-thermomechanical pulp and newsprint, and several others that produce specialty products including, plywood, glue laminated timber, medium density fibreboard and laminated veneer lumber (AWP 2013b). In 2012, lumber, pulp and panel products shipped from Alberta totaled approximately $1 billion, $1.8 billion and $550 million in value, respectively (GoA 2013).

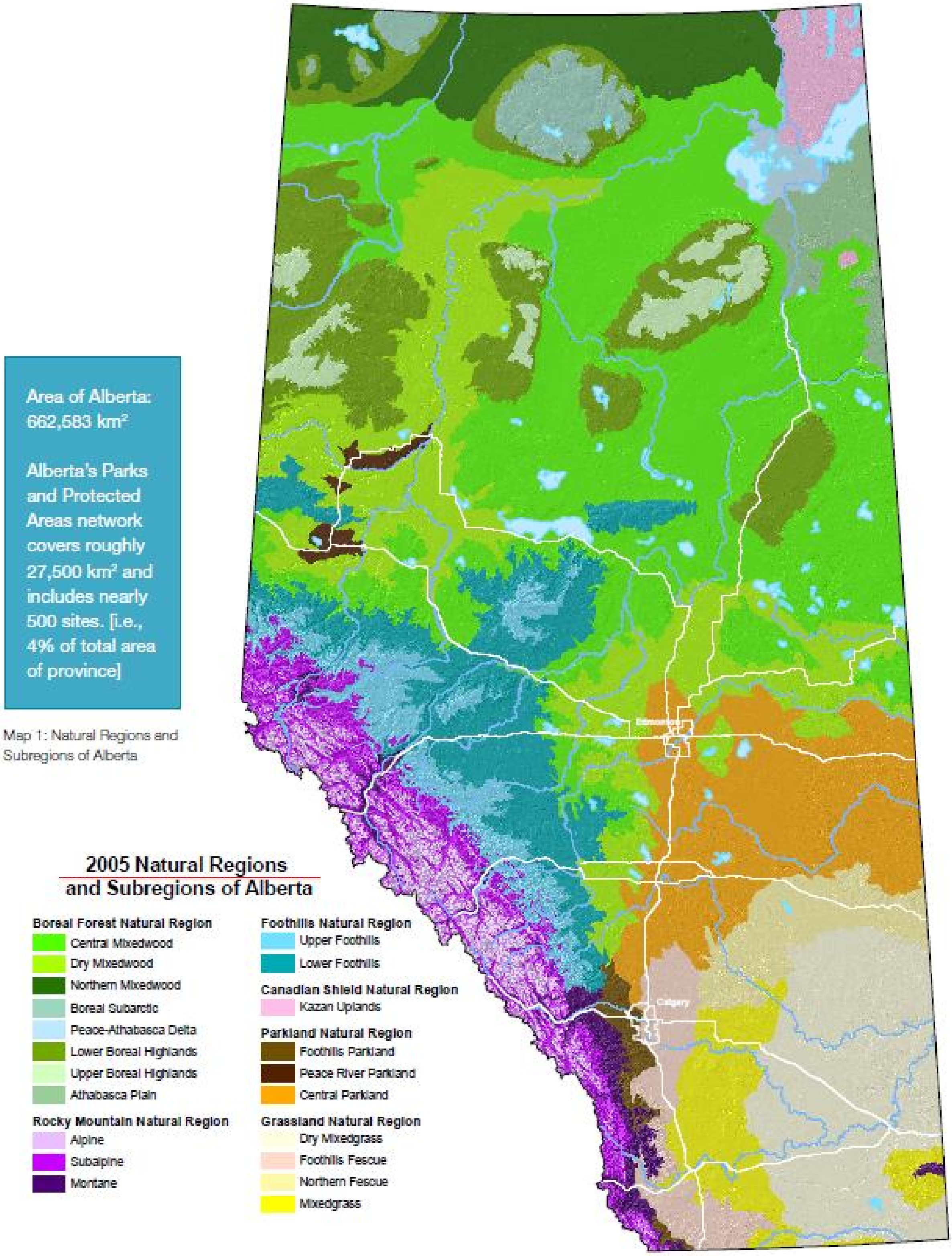

**Figure 1.2: A map of Alberta's Natural Regions and Subregions as of 2005. The Boreal Forest and Foothills Natural Regions are largely managed for natural resource extraction, including forestry. Available from Alberta Parks (2015).**

### 1.3 – Wood Quality in White Spruce

The definition of ‘wood quality’ varies greatly based upon the intended end-use of the fibre and the value of the product. Jozsa and Middleton (1994) defined wood quality as all of the attributes that affect the suitability of wood fibre for a specific application, while Zhang’s (2003) definition included factors that affect the value-recovery chain. A useful definition of wood quality for industry is a combination of the above definitions. For the purposes of the present study, wood quality will be defined as ‘those factors which affect the suitability of wood fibre for a specific end-use and which affects the value of that product’.

There are many characteristics that affect wood quality, and which are defined as either physical or mechanical properties. Physical properties include WD, tree height, tree diameter, growth rate, tree form, grain orientation, microfibril angle, and the presence of knots and/or abnormal wood (e.g. compression wood). Mechanical properties include modulus of elasticity, modulus of rupture, compressive strength, transverse strength, shearing strength and hardness. It is important to note that mechanical properties are critical for the purposes of engineering (e.g. building a house) and are a result of the wood’s physical properties. Wood density is useful as an indicator for modulus of elasticity and modulus of rupture because both traits are strongly and positively correlated with WD (Cown and Hutchison 1983; Burdon *et al.,* 2001) and WD is easily measured in standing timber using various tools. Most modulus of elasticity and modulus of rupture testing requires destructive sampling of the tree, which is not conducive to testing in TI programs. Additionally, it would be sensible to assess mechanical properties at the intended rotation age. However, due to the length of rotation for boreal species in Alberta, which ranges from 80-100 years (Rweyongeza 2013; Rweyongeza 2016), WD serves as a useful early indicator for these important traits.

It is also important to consider how wood quality varies within a tree, including inter- and intra-annual differences. Because of the annual nature of tree growth, each successive year of growth results in a 'new' tree enveloping the previous one. Not only is there the possibility for variation in the physical characteristics of the wood between years, the general nature of wood changes as it transitions from juvenile to mature wood. Juvenile wood, which is grown under the influence of the crown, is of lower quality and density, compared to mature wood (Alteyrac *et al.,* 2006). Specifically, juvenile wood is less dense, contains shorter fibres and is more prone to other physical defects, including checking, shrinking and warping (Cown *et al.,* 1996; Alteyrac *et al.,* 2006). Each of these factors have the potential to decrease value-recovery through either lowering yields of high-grade lumber or through culling.

Compounding the above issue is the intensive management of forest resources. In general, rotation lengths for managed forest plantations are decreasing, increasing the ratio of juvenile wood:mature wood (Alteyrac *et al.,* 2006). According to McKeever (1997), mean stem diameter has steadily decreased in publicly- and privately-owned timberlands in the United States over the past 70 years to the point where most logs are 15-30 cm in diameter when harvested. Additionally, these logs likely have a higher proportion of juvenile wood compared to old-growth stands, which suffers from increased rates of warping, shrinking and decreased WD (Cown *et al.,* 1996). Combined, these deficiencies will lead to a decrease in wood quality, as well as decreased forest value. For example, loblolly pine (*Pinus taeda* L. – commonly grown in the Southeastern United States) and radiata pine (*Pinus radiata* D. Don – commonly grown in

New Zealand, Australia and South America) are both grown as short rotation tree species with rotation lengths of 20-30 and 25-35 years, respectively, which have been shown to have reduced wood quality (e.g. lower WD, higher juvenile wood: mature wood ratio) relative to wild trees (Clark *et al.,* 1996: Cown and McConchie 1982). The transition from juvenile wood to mature wood in loblolly pine is estimated to be between 5.5 to over 20 years, depending on the site (Clark *et al.,* 2006). The North Carolina State University Cooperative Tree Improvement Program, which works with loblolly pine, has integrated a 'Performance Rating System' into their program, which includes aspects of growth rate, disease resistance, cold tolerance and wood quality, into their program so that cooperators may select families that will maximize return on investment when planted in a particular area (NCSU 2018). The Performance Rating System data is based on young progeny test data (assessed at age four to six – NCSU 2018), and will be composed almost exclusively of juvenile wood (Clark *et al.,* 2006); however, because the rotation lengths are short (20-30 years [Clark *et al.,* 1996]), and juvenile wood is of lower quality compared to mature wood (Cown *et al.,* 1996; Alteyrac *et al.,* 2006), wood quality measurements at this age should represent the 'minimum' expected WD and wood quality. Thus, while the value of the end-use product may be diminished through lower WD, overall forest value may increase through an increase in fibre yield, and therefore, product yield.

In Alberta, however, the length of rotation is much longer, owing to the relatively slow growth rate of Sw (Grover *et al.,* 2014) and relatively short growing season (typically 100-140 days – GoA 2014), though the growing season is projected to increase under current climate change scenarios (Gray and Hamann 2015). Typically, stands will not be harvested until they are at least 80 years old and are often much older (Rweyongeza 2013). Hinton Wood Products, for example, has reported that most of the timber harvested within their Forest Management Agreement area is approximately 130 years old (WFM 2017). Due to the long rotations, Alberta's trees are likely to maintain relatively low juvenile wood:mature wood ratios and relatively high wood quality. This may change, however, as these stands in Alberta are replaced through reforestation with improved stock from TI programs, and, subsequently, rotation lengths may be reduced from the current 80-100 years (Rweyongeza 2013). It is not known to what extent wood quality in Alberta's forests may be compromised by this change. Mvolo *et al.,* (2015) estimated that the transition age for juvenile to mature wood in Sw was between 11-27 years at breast height with a juvenile wood proportion of 15.3-47.5% in approximately 80-year-old trees in Ontario, Canada. It is reasonable to expect that wild Sw trees growing in Alberta will have a similar transition age and ratio of juvenile wood:mature wood for any given age.

A second factor affecting overall WD is the ratio of earlywood to latewood in each growth ring. Earlywood, which is formed early in the growing season (i.e. spring), is composed of individual fibres that have thin walls and large lumens (Jozsa and Middleton 1994) and facilitate mass water transport (Domec and Gartner 2002). Latewood, which is formed later in the growing season (i.e. summer), is characterized by cells with thicker cell walls and smaller lumens (Jozsa and Middleton 1994) and imparts much greater strength and stiffness to wood than does earlywood (Buyuksari *et al.,* 2017). Past research has shown that rapid growth in trees is negatively correlated with WD in several tree species (Zhang 1995), including Sw (Middleton and Munro 2002; Pike and Montgomery 2017). This reduction in WD is largely associated with increased earlywood:latewood ratios, resulting in a decrease in overall WD (Makinen and Hynynen 2014; Rossi *et al.,* 2015). White spruce has a relatively high earlywood proportion (approximately 80-90% - Lenz *et al.,* 2013) and a slow transition from earlywood to latewood (Micko *et al.,* 1982), leading to moderately low wood density. Corriveau *et al.,* (1987) found that the average WD of juvenile wood and mature wood in wild Sw populations in Quebec was 0.353 and 0.328 kg/dm$^3$, respectively, while Duchesne and Zhang (2003) determined that the mean WD of 35 fast growing families across two sites in Quebec was 0.325-0.330 kg/dm$^3$. Several studies have documented density ranges of 0.26-0.524 kg/dm$^3$ (Wang *et al.,* 1982; Micko *et al.,* 1982; Corriveau 1987). Three industry sources indicate Sw WD is between 0.35-0.38 kg/dm$^3$, which is a useful benchmark value (Alemdag 1984; FCC 2006; USDA 2010). It should be noted that 1 kg/dm$^3$ is equivalent to 1000 kg/m$^3$, with the former being used frequently in primary literature and the latter being used primarily in industry or other secondary sources. It is clear that WD varies considerably throughout the stem, even in relatively small areas (Plate 1.1). Wood density not only varies with tree age and its position relative to the crown, but also by the time of year that it is formed. Both juvenile wood:mature wood and earlywood:latewood ratios have the potential to be modified via silviculture, including through TI.

Tree improvement is one of several silvicultural tools used to obtain an increase in the growth rate of trees. Other treatments include spacing, thinning (precommercial and commercial), fertilization and site preparation. Yang (2002) found that wider spacing resulted in higher growth rates and lower WD in Sw. Spacing treatments of 1.8 x 1.8 m, 2.7 x 2.7 m and 3.6 x 3.6 m resulted in average growth ring widths of 3.20, 5.18 and 5.98 mm and WSG of 0.376, 0.336 and 0.330 in juvenile wood, respectively. Additionally, the coefficient of variation (CoV) for ring width was higher compared to wood density by a factor of approximately 2-2.5 (Yang 2002).

Nyakuengama *et al.,* (2002) found that fertilizer treatments (control, nitrogen, phosphorus and nitrogen/phosphorus) resulted in larger ring widths (4.47, 5.08, 5.13 and 5.72 mm, respectively) seven years after treatment in radiata pine, and that the WD of these four treatments was 587, 578, 564, 555 kg/m$^3$, respectively. Peltola *et al.,* (2007) found that thinning treatments resulted in increased ring widths and higher proportions of earlywood in Scots pine (*Pinus sylvestris* L.). Additionally, Peltola *et al.,* (2007) found that the density of juvenile wood tended to decrease with heavier thinning treatments, while mature wood density increased slightly, regardless of treatment. White spruce responds well to thinning, which acts as a release treatment by increasing light availability (Grover *et al.,* 2014). Grover *et al.,* (2014) observed an increase of 152% in diameter growth for Sw 10 years after harvesting the quaking aspen component of mixedwood stands in Alberta. In general, the overall result of suppression is that the core of juvenile wood is relatively small in diameter, decreasing the juvenile wood:mature wood ratio, while greater volumes of mature wood develop after the release treatment (Renninger *et al.,* 2006). Renninger *et al.,* (2006) also reported that the WD of suppressed versus released Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) were reduced from 0.57 to 0.47 g/cm$^3$ and 0.50 to 0.45 g/cm$^3$, respectively; however, these decreases in WD were relatively dwarfed by the associated increase in growth ring width from 0.54 to 1.99 mm and 0.94 to 2.91 mm, respectively. Clark and Edwards (1999) found that increasingly intensive methods of site preparation, including chopping, discing and herbicide treatments, resulted in greater radial growth rates and lower WD in loblolly pine, though the differences in WSG, which ranged from 0.43-0.46 across all treatments, were not significant. In all cases, the relative changes in WD were between 3-7%. In summary, silvicultural treatments (including TI) that increase growth rate will result in somewhat diminished WD. What is interesting however, is that the relative decrease in WD tends to be much lower than the relative increase in diameter growth associated with application of these treatments.

The above silvicultural interventions differ greatly from TI in one important aspect – the effects of these treatments do not alter gene frequencies of subsequent generations. The foundation of TI is that practitioners should be able to produce a population-level change in a characteristic (e.g. tree height) through an increase in the occurrence of favourable genotypes. Decreases in WD associated with height selection (and thereby indirectly selecting for volume) are well documented in TI programs for several Canadian conifer species, including interior spruce (*Picea engelmannii* Parry Engelm. x *Picea glauca* [Moench] Voss [Yanchuk and Kiss 1993]), black spruce (Zhang *et al.*, 1996) and Douglas-fir (Stoehr *et al.,* 2009), though relative decreases in WD were smaller than the respective increase in growth rate. Zhang *et al.,* (1996) noted that correlations between WD and growth rate in black spruce were generally negative at the family-level, but some families showed no effect or even the opposite trend. Because the heritability of radial growth rate is low, while the heritability of WD is high (Cornelius 1994) and the range of WD in natural Sw stands is narrow (Wang *et al.,* 1982; Micko *et al.,* 1982; Corriveau 1987), a similar response is expected in SW. Limited information regarding the effect of height or volume selection on WD in subsequent generations of TI programs appears to be available but will become an important consideration as Alberta's TI programs mature from their first-generation selections to more advanced generations.

## 1.4 – Effects of Wood Quality on End-use Product Quality

The quality of the end-use product is innately linked to the quality of the fibre from which that product was manufactured. It is in the interest of forest companies and the GoA to maintain high wood quality not only to produce the highest-quality product possible, thereby increasing profitability, but it is also a requirement under the current genetic standards (AAF 2016a), which will be discussed in the next section.

Dimensional lumber, which is typically used for construction purposes, is one of Alberta's key softwood products, accounting for over $1 billion in shipments (3.39 billion bdft or ~8 million $m^3$) in 2012 (GoA 2013). Canadian lumber is graded according to the National Lumber Grade Association Standard Grading Rules for Canadian Lumber (NLGA 2017). Most dimensional lumber destined for structural applications will be visually graded, essentially equating appearance (e.g. number and size of knots, amount of compression wood, slope of grain) with strength (NLGA 2017). Lumber that may be utilized for more specialized engineered purposes (e.g. pre-engineered roof trusses, glulam beams) will be both visually graded and stress rated (NLGA 2017). In general, high-quality logs will be composed of wood that has few and small knots, possesses grain that runs parallel to the longitudinal plane of the lumber, contains little to no compression wood, are large in diameter and are composed primarily of mature wood (Cown *et al.,* 1996; NLGA 2017). Knots, for example, reduce the overall strength and stiffness of wood (Zhong *et al.,* 2016), while lumber that contains a high proportion of juvenile wood suffers from higher rates of distortion (Cown *et al.,* 1996). Both conditions may lead to diminished lumber value or possible culling. Under the NLGA (2017) grading rules, the No. 3 structural grade allows knots with a maximum diameter of 3/4" (~1.9 cm) on a 2" (~5 cm) board, while the No. 2 structural grade allows only a 5/8" (~1.6 cm) maximum knot diameter for the same size board. The No. 3 grade is worth significantly less than the No. 2 and better grade, which held values of $412 and $556 USD/1000 bdft (~2.23 m$^3$), respectively, as of April 27, 2018 (NRCAN 2018).

Alberta's second major forest product is pulp, totalling approximately $1.8 billion in shipments from Alberta in 2012 (GoA 2013). Of concern to this project are the following three processes: 1) Thermomechanical pulp; 2) bleached chemi-thermomechanical pulp; and 3) northern bleached softwood Kraft, each of which produce very different pulp products. The thermomechanical process uses heat and a mechanical refiner (a large rotating metal disk) to produce a pulp that is composed of fibres that are shorn from the log. This process results in a high yield (80-90%), low-strength pulp that is commonly used to produce newsprint (Awada *et al.,* 2015). The bleached chemi-thermomechanical pulp process first heats the wood fibres, impregnates them with chemicals, mechanically separates the fibres using a refiner and finally bleaches the resulting pulp. This process also results in high yields but produces a white pulp of higher strength compared to the thermomechanical process due to caustic treatments during the bleaching process (Li *et al*., 2010). For both the thermomechanical and bleached chemi-thermomechanical processes, the hemicellulose and lignin content of the wood is preserved, which leads to higher yields and bulk, but lower strength due to reduced inter-fibre bonding (Li *et al.,* 2010). The northern bleached softwood Kraft process uses a multi-step chemical process that dissolves the lignin and hemicelluloses present in the wood, preserving primarily cellulose fibres. Compared to mechanically-produced pulps, the strength of northern bleached softwood Kraft pulp is much higher due to enhanced bonding between fibres (Tavast *et al.,* 2015), though the yield is reduced to approximately 40-50% because of the removal of the lignin and hemicellulose components (MacLeod 2007). Both bleached chemi-thermomechanical and northern bleached softwood Kraft pulps are used in the manufacture of printing, writing and specialty paper, paperboard and tissue and towel products (WFM 2019; MW 2019). A discussion of the effects of wood quality on pulp quality and value would be lengthy given the different possible intended end-uses of the above processes and the complexity of pulping processes; therefore, northern bleached softwood Kraft will be used as an example. In 2009, Alberta's six pulp mills produced a total of 2.26 million tonnes of pulp (FPI 2010). Alberta's three northern bleached softwood Kraft mills have a combined annual production capacity of between 750,000-1,500,000 metrics tonnes (AWP 2013c, AWP 2013d, AWP 2013e).

Both wood density and tracheid length are positively correlated with the strength of Kraft pulp, while WD and compression wood proportions are positively and negatively correlated with pulp yield, respectively (Cown and Kibblewhite 1980). Furthermore, Cown and Kibblewhite (1980) suggest that in New Zealand, where there is a regional cline and WD decreases from north to south, fibre should be partitioned based on the strength required for the intended end-use. While it is possible that a similar cline may exist in Alberta, Corriveau *et al.,* (1987) found that there was no correlation between WD and latitude in wild Sw populations in Quebec. The values of northern bleached softwood Kraft and bleached chemi-thermomechanical pulp as of March 2018 were $1270 and $625/metric tonne, respectively (NRCAN 2018). Because pulp may be manufactured to specific customer specifications (i.e. specialty grades [MW 2019}), the effect of wood quality on commodity value is not as evident; rather, increases in process efficiency is the primary method through which mills maximize fibre value. For example, the

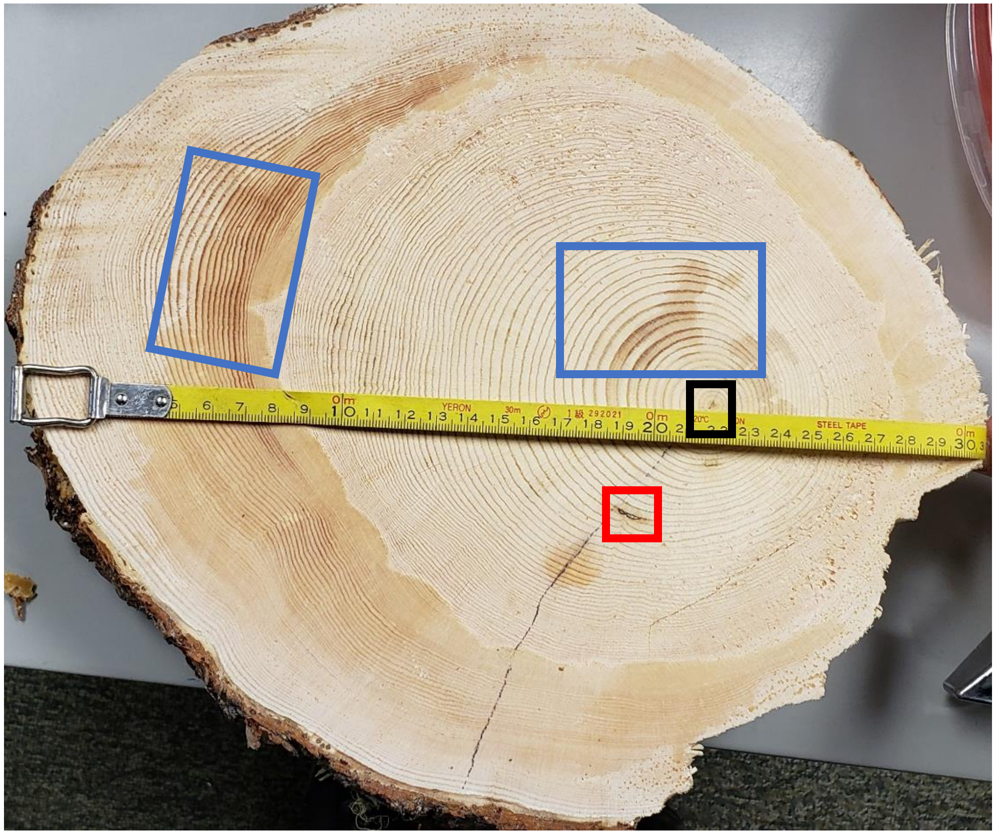

**Plate 1.1: A wood cookie taken from the butt of a mature (estimated at 115 years) white spruce log harvested on the Hinton Wood Products Forest Management Agreement area. This cookie exemplifies how wood quality can vary greatly across the stem of a tree, even within a relatively small area. This stem was highly eccentric. The pith is highlighted with a black box. There is a trend of decreasing ring width as distance from the pith (i.e. age) increases. Some of the juvenile wood rings (i.e. close to the pith) are up to 4 mm wide, whereas some of the mature wood rings, especially on the right side, are so narrow that they cannot be discriminated by the unaided eye. Although not assessed for this example, the ratio of earlywood to latewood appears to be quite variable and appears to decrease somewhat with age. There is also visible compression wood (highlighted with a blue box). Hidden defects, such as wounds (highlighted by a red box) may also be present in the stem. For reference, the length of the measuring tape across the cookie is approximately 30.5 cm.**

waste stream of sawmills is often utilized as feedstock (e.g. for pulp or fibreboard) or hog fuel (to generate energy), making use of otherwise wasted (i.e. low-value) fibre to maximize revenue; however, ensuring WD of improved populations is maintained relative to natural populations will ensure that pulp yields, and profitability, will not decline.

## 1.5 – Tree Improvement in Alberta

Forest Management Agreements are a type of forest tenure (20-year duration and renewable) whereby a forest company becomes responsible for assuming most forest management activities in exchange for access to large volumes of publicly-owned timber, while the Government of Alberta provides regulatory oversight and approval (AAF 2017c). Some of these management activities include assembling comprehensive Detailed Forest Management Plans that address sustainable harvest levels, reforestation activities and timetables, as well as ecosystem, conservation and recreation values (AAF 2017d). A Detailed Forest Management Plan may also address a company's participation in TI programs within their Forest Management Agreement area. For example, Hinton Wood Products 2014 Detailed Forest Management Plan details their plans for deployment of improved seed, conservation of forest genetic resources, the number of TI and research trials to be installed within their Forest Management Agreement area and their active research programs (WFM 2017). Approximately half of the TI programs in Alberta are cooperative efforts between forest companies and the Government of Alberta (GoA) where the forest companies create, manage and implement the programs with the GoA providing regulatory oversight. In other cases, there may be several forest companies participating in a single program or a program may be entirely managed by the GoA (AFGRC 2004).

One of the most important responsibilities that forest companies assume under their Forest Management Agreements is the responsibility to reforest the land after harvesting. Alberta's Forest Genetic Resource Management and Conservation Standards (AAF 2016a) outlines many of the standards pertaining to reforestation of Crown (i.e. publicly-owned) land. During the 2014/15 planting season, nearly 58,000 hectares were artificially reforested with over 80 million seedlings (AAF 2017a). Such an effort obviously requires a vast amount of seed, but where is this seed sourced from? Seed (or other propagules) are classified as either Stream 1 or Stream 2 material with these designations being determined by the source of the material (AAF 2016a).

Material gathered from wild sources, artificially regenerated stands or Stream 1 seed orchards is known as Stream 1 material (AAF 2016a). There are 90 seed zones within Alberta which are delineated based on geography, elevation and natural regions/subregions (AAF 2016a). Stream 1 material may either be collected using a point or seed zone collection (AAF 2016a). Seedlots are required to be collected from a minimum of 30 individuals for both types of collections for unrestricted (i.e. no variances required if deployment is otherwise in keeping with GoA standards) registration of seedlots. The major differences between point and seed zone collections is that a point collection gathers all the seed from within a 2 km radius area and 100 m elevation range, whereas a seed zone collection may occur throughout an entire seed zone. Point collections also have a standing variance that allows for deployment up to 1 km outside of a seed zone boundary, so long as the collection was taken from within 100 m of the elevation of the intended deployment area and wider deployment may be considered if a variance is requested from the GoA. It is important to note that seed zones are not species specific and currently apply to all tree and shrub species native to Alberta (AAF 2016a). Seed may be gathered using several methods, including ground or aerial picking. Seed gathered from wild parents via aerial picking is often gathered from parents with phenotypically superior performance (i.e. tall) but with no understanding of the underlying genetics, while seed picked from the ground will tend to better represent the average performance of the stand.

Material gathered from approved production facilities is known as Stream 2 material. Stream 2 material differs from Stream 1 material in several important aspects. Firstly, deployment of Stream 2 material is more tightly regulated than that of Stream 1 material. For example, the amount of Stream 2 material that may be deployed is determined by the effective population size (Ne) of the seed or vegetative lot, which itself is calculated from the relative contributions of each parent to a specific seed or vegetative lot, rather than requiring a minimum number of parents as with Stream 1 material (AAF 2016a). In order to meet the requirements for unrestricted registration, Stream 2 seedlots must have an Ne of at least 18. When Ne is between 18 to 29 a maximum of 25% of the targeted land base may be reforested using Stream 2 material, with Stream 1 material making up the remaining 75%. When the Ne ≥ 54, 100% of the targeted land base may be reforested using Stream 2 material (AAF 2016a). Secondly, deployment areas for Stream 2 material are much larger than seed zones and are species specific. These regions are referred to as CPP regions and are defined as “a program to produce Stream 2 material for deployment within the associated CPP region” (AAF 2016a). Thirdly, the genetic identity of individual trees is known within a CPP (AAF 2016a). Individuals incorporated into a CPP are assigned unique identifiers, making it possible to conduct genetic tests on the progeny of the production populations since pedigrees are maintained. As part of a CPP, a minimum of three progeny trials are required to be planted throughout a CPP region to test environmental adaptability and family performance for traits of interest (e.g. height - AAF 2016a). Controlled Parentage Programs may be used to generate populations that are improved for a specific trait (e.g. height growth, tree form) compared to wild populations (AAF 2016a). Increases in the mean population value of these traits due to breeding and selection are referred to as genetic gain and are specific to an intended rotation length (e.g. 80 years) and CPP population (AAF 2016a). In an ideal world, genetic gain for traits would be estimated at age of rotation, but this is not practical for Alberta due to the long rotation lengths (80-100 years - Rweyongeza 2013). Instead, age-age correlations are used to estimate height gain at rotation using measurements taken at younger ages (AAF 2016a). This will be discussed further below.

One of the major motivations for undertaking TI activities in Alberta is the possibility for an increase in the annual allowable cut, which is defined as “the annual amount of timber that can be harvested on a sustainable basis within a defined forest area” (AAF 2017e). Increases to the annual allowable cut through silvicultural practices (including TI) is referred to as the allowable cut effect (Hegan and Luckert 2000). Because of the type of tenure system practiced in Alberta, forest companies can use TI as a tool to increase their current annual allowable cut by planting trees that will be more productive than the trees that are currently being harvested (i.e. increasing timber volume yield/unit land area for the next rotation). In comparison, the type of forest tenure practiced in British Columbia which has a heavier emphasis on timber sales and short-term, non-renewable tenures, means that forest companies generally do not benefit as greatly from direct investment into TI (BC 2012); therefore, most TI activities in British Columbia are pursued at the government, rather than industry level (FGC 2005). Currently, increases to the annual allowable cut are calculated based on genetic gain for volume at rotation age, which is estimated via breeding values (BVs) for height (Figure 1.3) measured at a selection age and adjusted using the appropriate age-age correlation, as well as other parameters (e.g. supplemental mass pollination, pollen contamination) for deployed seedlots (AAF 2016a). Genetic gain for height is converted to genetic gain for volume by using a factor of two (AAF 2016a). Genetic gain for a specific CPP region must then be approved by the GoA (AAF 2016a).

Age-age correlations for Alberta's TI programs are available for selection ages ranging from 10-50 years with a minimum selection age of 14 years for spruce (AAF 2016a; Rweyongeza 2016). It should be noted that the significance of this relationship increases quite dramatically as the age of assessment approaches the intended rotation age (AAF 2016a; Rweyongeza 2016). For example, age-age correlations for height in Sw at a rotation age of 100 years with assessments conducted at 10, 30 and 50 years are 0.375, 0.826 and 0.990, respectively (AAF 2016a). Previously, age-age correlations used for TI in Alberta were based on the work of Lambeth (1980) (Rweyongeza 2016), as is done in British Columbia (Xie and Yanchuk 2003). However, an important distinction now exists between the ways Alberta and British Columbia integrate age-age correlations into their respective TI programs. Alberta uses a phenotypic age-age correlation based on the work of Rweyongeza (2016) (AAF 2016a), whereas British Columbia uses a genetic age-age correlation (Xie and Yanchuk 2003), which are typically stronger than their phenotypic counterparts (White *et al.,* 2007). Rweyongeza (2016) posits that the large standard errors associated with genetic age-age correlations makes predictions less reliable. Thus, Rweyongeza (2016) proposes that phenotypic age-age correlations are a practical substitute which makes conservative estimates of genetic gain. Genetic gain describes the average increase in performance for a specific trait (e.g. height) at the program-level (i.e. across all sites and families being deployed in a CPP region), while BVs describe the performance for a specific trait for an individual or family, which taken together will impact genetic gain. The age-age correlation is viewed as a risk-mitigation tool that ensures forest companies are not rewarded with an increase in their current annual allowable cut if an actual increase in timber volume is not realized through an increase in forest productivity on Crown land in future rotations (Rweyongeza 2016).

Making selections in TI programs is further complicated because forest companies must consider correlated traits that may be indirectly selected for along with increased growth rates, including WD (AAF 2016a). Although not explicitly stated in FGRMS (AAF 2016a), both the GoA (March 2018 personal communication with A Benowicz – GoA) and industry representatives (July 2018 personal communication with D Renaud) interpret this to mean that WD of improved families should, on average, be equivalent to their wild counterparts. As noted previously, past research has shown that growth rate and WD are negatively correlated in many tree species (Zhang 1995), including Sw (Middleton and Munro 2002; Pike and Montgomery 2017). Pike and Montgomery (2017) have also shown that some Sw families combine high growth potential with only minor decreases in WD, while Duchesne and Zhang (2003) found that growth rate and WD were not significantly correlated in fast-growing Sw families in Quebec. Other research has shown a moderately negative, or sometimes positive, correlation between growth rate and wood density in black spruce, a closely related species (Zhang *et al.,* 1994).

It is obvious that TI programs will incur large expenses to forest companies; therefore, some benefit must exist to offset this investment. A systematic review of TI programs has shown that TI yields consistently produce positive economic gains under a variety of conditions, in several different countries and with programs using many different tree species, though conifers are best represented (Chang *et al.,* 2019). Additionally, Schreiber and Thomas (2017) have shown, using an Alberta-specific TI investment model, that increases to the annual allowable cut (and thereby, return-on-investment) is highest when improved seed, even with moderate levels of genetic gain, is deployed extensively. This should encourage forest companies in Alberta to maintain high genetic diversity (i.e. high Ne) within their programs, even at the expense of some genetic gain, to maximize potential deployment area, particularly in first-generation programs which may be subject to low levels of genetic gain. Additionally, each CPP is associated with a specific geographic region, each of which spans multiple seed zones, allowing for flexible and wide-spread deployment of improved material compared to Stream 1 material. Stream 2 material may be planted up to 50 km outside of the associated CPP region without the need to apply for a variance, so long as the deployment occurs within 100 m and 50 m of the upper and lower CPP elevation limits, respectively (AAF 2016a). However, other variances for deploying Stream 2 outside of a CPP region are currently not permitted, except where an emergency exists (AAF 2016a). Improved seed is also harvested from a centralized population (i.e. a seed orchard), simplifying the task of collecting high-quality seed. Together, the benefits of an uplift in the current annual allowable cut, expanded deployment areas and simplified access to seed create a strong value proposition for forest companies in Alberta to pursue TI.

## 1.6 – White Spruce Genetics

Like other conifers, Sw possesses a large genome that is approximately 20 Gbp in size (Warren *et al*., 2015) – approximately 6.5 times the size of the human genome (Venter *et al*., 2001). Despite the size of the Sw genome, this diploid species possesses only 24 chromosomes (Nkongolo 1996). Additionally, conifers are primarily outcrossing and highly heterozygous, lending to their ability to adapt to local conditions (Prunier *et al*., 2016). Outcrossing is also necessary in conifer populations because they tend to carry a high genetic load and are, therefore, highly intolerant to inbreeding (Fowler and Park 1983). Fowler and Park (1983) found that the number of lethal equivalents in three Sw populations ranged from 8.0-12.9. Genetic load and lethal equivalents are related concepts. A lethal equivalent is a combination of deleterious alleles in an individual that may result in death while genetic load would be the sum of these deleterious alleles present in a population (Redei 2008). For example, if four deleterious alleles each had a 25% probability of causing death, the sum would be a lethal equivalent of one. Compared to outcrossed individuals, inbred Sw trees possess lower proportions of filled seed (reductions of up to 90%), decreased survival rates (up to six times lower), and approximately 50% reduced height and diameter growth, though germination rates of viable seed were nearly equal (Fowler and Park 1983). In terms of TI programs, intolerance to inbreeding is a useful tool. Because of the desire to produce seed that is of high quality and that will result in vigorous seedlings, intolerance to inbreeding acts as a natural filter that will remove most inbred individuals from a population, increasing the value of collected seedlots. Conifer orchard design emphasizes placing unrelated clones or individuals in proximity to each other to maximize outcrossing, reducing the deleterious effects of inbreeding (van Buittenen 1971; Lstiburek and El-Kassaby 2010). Additionally, the minimum diversity requirements (Ne = 18 for Stream 2 material, 30 parents for Stream 1 collections) were implemented to ensure that inbreeding in artificially regenerated stands would not exceed the levels of inbreeding present in open-pollinated wild stands for at least three generations should human interference cease (AAF 2016a).

## 1.7 – Trait Heritability

In the simplest terms, heritability describes the degree to which offspring resemble their parents. Specifically, heritability is an estimate of the proportion of the phenotypic variance component that is due to the genetic variance component and varies between 0-1 (Redei 2008). The phenotypic variance component is the sum of the genetic variance and environmental variance (including error) components (Redei 2008). The genetic variance component is the sum of the additive, dominance and epistatic variance components (Redei 2008). Narrow sense heritability ($h^2$) is defined as the proportion of phenotypic variation that is due to the additive genetic variance component (Redei 2008). The additive genetic effect is essentially the proportion of phenotypic expression (e.g. height) that is due to inheritance and generally exerts more influence than other genetic effects (i.e. dominance and epistatic effects

- Hill *et al.,* 2008). Traits with a higher heritability (i.e. the genetic effect is relatively higher) will result in higher estimated BVs (Postma 2005). Maximizing estimated BVs is important to TI programs because this will increase the level of potential genetic gain for a given trait and program. Heritability is population, site, and trait specific (Kiss and Yeh 2011). Narrow sense heritability tends to underestimate the additive genetic effect, particularly for traits with low heritability (i.e. growth traits) (Viana *et al.,* 2009). Heritabilities < 0.3 are generally considered to be low, while 0.3-0.5 is moderate and values > 0.5 indicate high heritability (Cornelius 1994).

Heritability varies greatly among different traits. Each of the following examples are given for narrow sense heritability in Sw. The heritability of piceol and pungenol, defence chemicals that play a role in spruce budworm resistance, were estimated to be 0.67 and 0.65, respectively, while the heritability of *Pgβglu*-1, a gene that moderates the release of these chemicals, was 0.58 (Parent *et al.,* 2017). Each of these traits are controlled by only a few genes (Parent *et al.,* 2017) and will not be greatly affected by the environment, lending to their high heritability. Conversely, estimates for the heritability of diameter growth are extremely low, ranging from 0.04-0.14 in a study conducted by Merrill and Mohn (1985). Growth traits, including height and diameter, are quantitative traits and will be affected by a great number of genes, each of which exerts only a small effect on the overall phenotype, while environment will exert a huge influence (Jiang *et al.,* 2016). For example, spacing can exert a large influence on diameter growth (Yang 2002) while shading negatively impacts both height and diameter growth (Grover *et al.,* 2014), both of which can mask the genetic effect. Another consideration for estimating heritabilities is the effect of time. A study conducted by Kiss and Yeh (2011) estimated that the heritability of height in Sw was 0.52, 0.36 and 0.29 at ages three, six and ten, respectively.

Interestingly, the heritability of height decreased over time and will likely stabilize at some point. This pattern of change in heritability may be partly due to the continued influence of the environment over time, resulting in increasing variation in the progeny (i.e. the progeny within a single family vary more as the environment exerts its influence over a greater span of time) or differential expression of the genes underlying the trait over time.

The traits of greatest interest to forest companies are growth traits, which tend to have quite low heritabilities, as shown above. The narrow sense heritability of WSG in Sw was estimated to be 0.447 in a study conducted in Quebec (Beaulieu *et al.,* 2006) and is generally considered to be moderately heritable in conifers (Zobel and Jett 1995; Hong *et al.,* 2015; Fundova *et al.,* 2018). In a review of the heritability of seven different traits, Corenlius (1994) found that the median narrow sense heritability for height, diameter and WSG were 0.25, 0.19 and 0.48, respectively. Overall, it appears that it may be possible to select for WD as a secondary trait with relatively small losses in WD as volume increases, which is supported by the literature (Zhang *et al*., 1995; Wang *et al.,* 2003). It seems likely that WD has a physiological ‘floor.’ Previous research has shown that there is a negative correlation between WD and tree mortality (Kraft *et al.,* 2010). Specifically, WD is linked to resistance to wind-breakage (Niklas 1992; Curran *et al.,* 2008), drought resistance (Hacke *et al.,* 2001; Jacobsen *et al*., 2005) and pathogen resistance (Augspurger and Kelly 1984; Romero and Bolker 2008), indicating that higher WD may also impart some level of increased fitness. Individuals with lower WD may be at higher risk of early mortality, and therefore, may not pass their genes onto subsequent generations. Conversely, fast-growing trees may not present a clear fitness advantage (Mailly *et al.,* 2009). Specifically, the mortality rates of dominant trees are similar to those of codominant trees (Mailly *et al.,* 2009), dominant trees are less resistant to drought stress than are suppressed trees (Grote *et al.,* 2016) and fast-growing trees may be more likely to experience early mortality (Bigler 2016).

Breeding values are perhaps the most important value estimated as part of Alberta's TI programs. Specifically, BVs for height are used to compare the growth performance of parents, families and individuals, inform management decisions about orchards, influence both backward and forward selections and ultimately determine the level of genetic gain in height at rotation which is possible in a program (AAF 2016a). Simply put, BVs represent the level of performance of a trait (e.g. height) for an individual or family compared to the mean performance within a population that is due to the genetic effect (Xie and Yankchuk 2003; AAF 2016a). In Alberta, BVs are typically represented in relative terms as a percent deviation from the mean value (i.e. 0) of that trait for a population (AAF 2016a). The expectation is that progeny from families with high BVs for a specific trait will perform better than progeny from families with low BVs in the same environment as a portion of this performance (i.e. the additive genetic portion) is heritable (Xie and Yanchuk 2003). Since BVs are directly influenced by the heritability of a trait (Xie and Yanchuk 2003), BVs will also be specific to the environment and time that the trait was measured. Breeding values may be estimated using a variety of methods (Xie and Yanchuk 2003) but best linear unbiased predictions, which is supported by FGRMS (AAF 2016a), will be used for the present study.

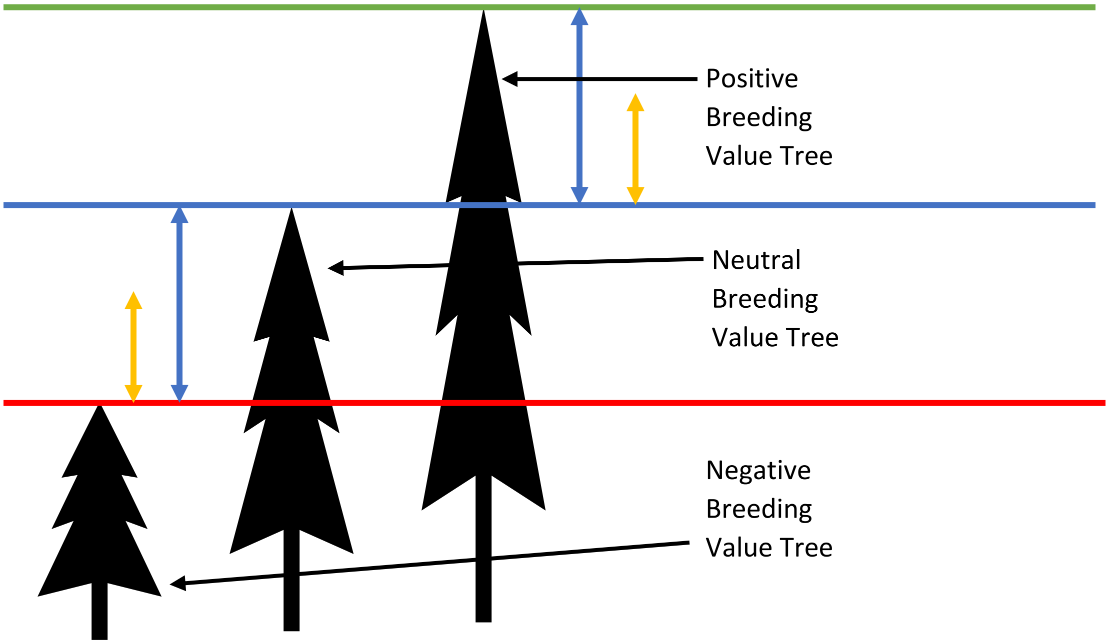

**Figure 1.3: A visualization of breeding values. The blue line represents the average height performance for the population, while the green and red lines represent the height performance of the respective individual trees. The difference between the blue line and the green and red lines represents the difference in phenotypic performance for height (blue arrows). This parameter includes the genetic and phenotypic variance components, as well as the error term. If the narrow sense heritability for height was 0.5 for this population, the additive genetic component (i.e. the breeding value) for height for that individual would be half of the phenotypic performance difference (yellow arrow). The breeding value of a parent can then be estimated using the breeding values for several of its progeny because of their shared genetics.**

## 1.8 – Objectives and Hypotheses

The objectives of this study are as follows:

1. Establish a correlation between diameter inside bark at breast height and wood specific gravity (and associated indirect measures) for the Region H white spruce CPP;
2. Calculate narrow sense heritabilities and breeding values for drilling resistance, penetration depth and diameter inside bark at breast height for the Region H white spruce CPP;

3. Perform and compare phenotypic and genotypic correlations for wood specific gravity, drilling resistance, penetration depth and diameter inside bark at breast height; and
4. Compare methods for rapidly measuring wood density in standing trees for Alberta's white spruce tree improvement programs and make recommendations for use in other tree species utilized in Alberta.

The associated hypotheses for this study are as follows:

1. Differences in performance for wood density traits (i.e. drilling resistance, penetration depth and wood specific gravity) and diameter inside bark exists between sites, breeding value categories for height at age 18 (used to select families to be assessed in the present study) and families;
2. The range of wood specific gravity is similar to that of natural white spruce populations described in the literature due to the relatively high heritability of WD and because the Region H white spruce CPP is currently composed of only wild (i.e. unimproved) selections;
3. Drilling resistance is positively and significantly correlated with wood specific gravity, while penetration depth will be negatively and significantly correlated with wood specific gravity. Drilling resistance will be a more sensitive measurement for showing differences in wood density between sites, breeding value categories for height at age 18 and families than penetration depth;
4. Drilling resistance is negatively and significantly correlated with diameter inside bark at breast height, while penetration depth will be positively and significantly correlated with diameter inside bark at breast height;

5. Any genetic effects associated with the wood density traits or diameter inside bark at breast height are smaller than the associated environmental effects; and
6. The narrow sense heritability of wood density traits are higher than those for either diameter inside bark at breast height or height while estimated breeding values will be lower for wood density traits than for either of the growth traits.

### 1.9 – Summary

White spruce is one of the most important commercial trees species in Alberta and Canada. It is well-suited to a variety of end-uses, including lumber, pulp and plywood – all of which are produced in Alberta. Because of its high utilization, forest companies are pursuing genetic improvement of Sw as one method to maximize the current annual allowable cut on their respective Forest Management Agreement area's. Although the increase in volume is only obtained at rotation once the trees have been harvested, the GoA allows for increases in current annual allowable cut through the allowable cut effect. This potential increase in annual allowable cut is the main driving factor for investment in TI programs, though other tangible benefits also exist. These benefits include a centralized production population for seed, higher quality seed, and more extensive deployment permitted compared to Stream 1 material and their associated seed zones. Additionally, an Alberta-specific financial model shows that even moderate investments in TI can generate positive economic benefits (Schreiber and Thomas 2017). The Forest Genetic Resource Management and Conservation Standards (AAF 2016a) control the collection and deployment of both wild and improved material, as well as the establishment and management of TI programs, in Alberta. Important concepts enshrined in this document include Ne (minimum Ne = 18 for unrestricted deployment of Stream 2 materials for the first 25% of the target strata deployment area), deployment limits for improved material (which are determined by Ne), parental collections and procedures for claims of genetic gain and how this affects the annual allowable cut. White spruce possesses significant genetic variability that may be exploited in TI programs. Although the heritability of growth traits is relatively low, incorporating large and diverse populations into TI programs improves possible outcomes. For example, starting with a large genetic base allows for a high selection differential to be applied (while maintaining diversity requirements), allowing for higher genetic gain during the early stages of a program. What is promising, however, is the higher heritability of WD compared to growth traits. Wood density is likely to be less variable than diameter or height performance owing to the high heritability of WD (i.e. environment exerts less influence on phenotype – Cornelius 1994) and because WD possess clear links to tree survival and fitness (Kraft *et al.,* 2010).

# Chapter 2: Materials and Methods

## 2.1 – Region H White Spruce Controlled Parentage Program Description and Climate Summary

### 2.1.1 – Region H White Spruce Controlled Parentage Program (CPP) and Progeny Test Site Descriptions

The Region H white spruce CPP occupies the Northwestern Boreal Lowlands Natural Region in Alberta and is characterized by mixedwood forests (AAF 2016a). The region covers an area of approximately five million hectares, and has a longitudinal range of 114-120 $^{o}$W, a latitudinal range of 56.77-59.30 $^{o}$N, and an operational elevation range of 250-550 meters (AAF 2016a). The Region H CPP is owned by the GoA and managed by Alberta Agriculture and Forestry. Three progeny trials were established, forming the G154 test series, using 2-year old seedlings in May 1994: Chinchaga (57.50 $^{o}$N, 118.12 $^{o}$W, 470 m), Hay River (59.08 $^{o}$N, 117.34 $^{o}$W, 370 m) and Red Earth Creek (56.34 $^{o}$N, 115.19 $^{o}$W, 518 m) (AAF 1994a; AAF 1994b; AAF 1994c). Together, these three progeny tests form the G154 test series. It should be noted that the Red Earth Creek and Chinchaga test sites are physically located within the Region D1 and G2 CPP boundaries, respectively (Figure 2.1). Seed lots gathered from phenotypically superior wild parents were planted from several CPP regions, including 50 from H, one from the E/E1 overlap area, four from D, as well as six bulk control lots (AAF 1994a; AAF 1994b; AAF 1994c). The purpose of this set of trials is to assess the family performance and adaptability of the selected seed lots for deployment within the Region H CPP area. The experimental design of the three progeny trials consists of randomized complete blocks with seven replicates of each family/site and a single tree border row around the entire plot (AAF 1994a; AAF 1994b; AAF 1994c). Each family row plot within each replicate is comprised of either four or five trees using 2.5 m x 2.5 m spacing between trees (AAF 1994a; AAF 1994b; AAF 1994c). All WD and diameter inside bark (DIB) measurements were taken at age 26 during the spring and summer of 2017.

### 2.1.2 – Summary of Climate Data for the Region H White Spruce Controlled Parentage Program

Annual climate data for the Region H Sw CPP were taken from the Alberta Agriculture and Forestry Climate Almanac for Alberta (2019) for the period of 1994-2017. This time period encompasses from the time of planting to the time of sampling in the present study for the G154 test series. The climate data used were taken from the nearest available weather station to each of the three test sites and are as follows: Chinchaga data were taken from the Keg River Auto station, Hay River data were taken from the Ponderosa Auto Station and Red Earth Data were taken from the Red Earth Auto station (not to be confused with the nearby Red Earth station – AAF 2019). The following four types of data were extracted: 1) seasonal precipitation (mm); 2) growing degree days > 5 $^0$C; 3) frost free period (number of consecutive days where temperature > 0 $^0$C; and 4) summer moisture index (calculated as described in Chapter 1 Section 1.2 from Alberta and Agriculture and Forestry's data – an indicator of summer drought-stress). The climate data were also summarized by site (Table 2.1, Figure 2.2). Temperature data were not available from the Climate Almanac for Alberta (2019).

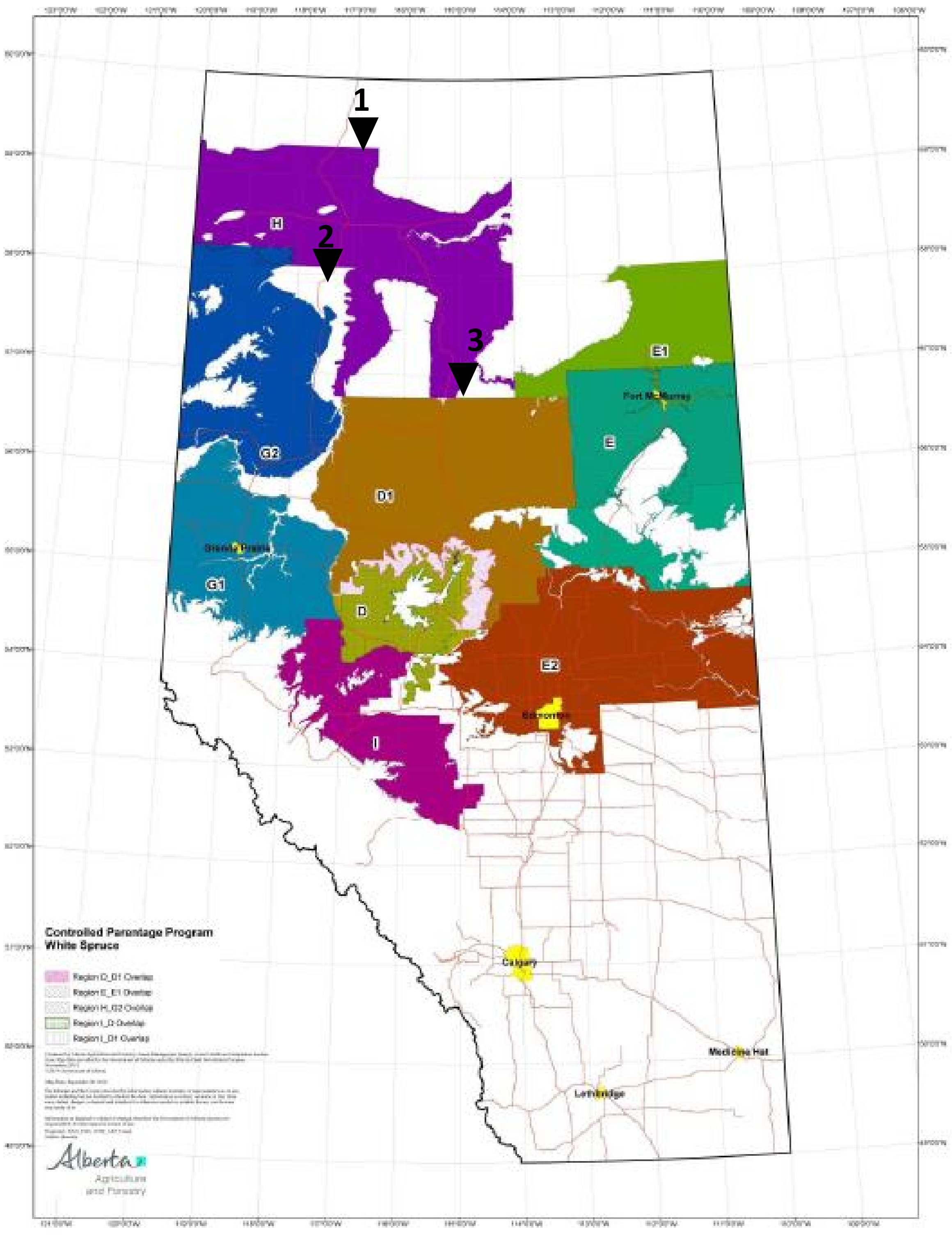

**Figure 2.1: White spruce (*Picea glauca* [Moench] Voss) Controlled Parentage Program (CPP) map, including markers (▼) for the Region H test sites. The Region H white spruce CPP is located in the Northwestern corner of the Province (purple region). The base map was provided by Alberta Agriculture and Forestry (AAF 2016a). The test sites are labelled as follows:**

**1 – Chinchaga; 2 – Hay River; 3 – Red Earth Creek**

Chinchaga and Red Earth are generally similar to each other in climate. Specifically, the number of growing degree days, the frost free period were very similar to one another, though Chinchaga experiences lower drought-stress, as indicated by precipitation and summer moisture index (Table 2.1, Figures 2.2A-D). Seasonal precipitation varies considerable between sites (Table 2.1) and between years (Figure 2.2A). There is a trend of increasing growing degree days for all sites from 2007-2017, though the sites rank order generally remain the same relative to one another (Figure 2.2B). The frost free period appears to experience very high annual variation and follows no clear trend (Figure 2.2C). The summer moisture index trend remained relatively flat between years, though there is some evidence of a recent increase in recent years (2013-2017 – Figure 2.2D).

**Table 2.1: Mean seasonal precipitation (mm), growing degree days > 5 $^0$C, frost free days (number of days where temperature > 0 $^0$C) and summer moisture index (growing degree days/seasonal precipitation) by site for the Region H white spruce Controlled Parentage Program for 1994-2017. The data are summarized from Alberta Agriculture and Forestry's Climate Almanac for Alberta (2019).**

| Site/Climate Factor | Seasonal Precipitation (mm) | Growing Degree Days > 5 $^0$C | Frost Free Days | Summer Moisture Index |
|---|---|---|---|---|
| **Chinchaga** | 297.3 | 1072.4 | 111.0 | 3.9 |
| **Hay River** | 258.8 | 1024.5 | 85.4 | 4.7 |
| **Red Earth** | 345.6 | 1066.3 | 113.8 | 3.3 |

## 2.2 – Family and Tree Selection

### 2.2.1 – Family Selection

A total of 40 families were selected for WD assessment. The family BV for height at 18 years, which was provided by Alberta and Agriculture and Forestry, was used to select the 15 best performing families, the 15 worst performing families, as well as 10 average performing families. These will be referred to as 'high,' 'low,' and 'medium' breeding value categories, respectively. The BVs for height at age 18 were the most up-to-date BVs available for the Region H Sw CPP at the time of family selection. These BVs have since been superseded by the BVs for height at age 25 which have also been provided by Alberta and Agriculture and Forestry and will be used for any genetic analyses as they represent the most recent assessment of family performance for height growth. Breeding values for Alberta's CPP's are an integrated measure of family-level genetic performance across the various test sites and series for a specific region (e.g. Region H) and are weighted by various factors, including family performance at each site, site quality, differences in family survival and representation and genotype-environment interactions (March 2019 email communication with A Benowicz - GoA).

Families were selected across BVs to capture the extremes on either side of the distribution, while facilitating comparisons to average families (i.e. medium BV category), which serves as the control group. It was hypothesized that high BV families will possess higher DIB and lower WD compared to low BV families, while medium BV families should fall between the previous two groups both for DIB and WD. The extreme values on either side of the distribution are of great interest to TI programs because high-performing families will be selected and retained in programs, while poor-performing families will typically be removed ('rogued') from the population, both with the goal of increasing a program's overall mean performance for height, and thereby, increasing genetic gain for volume. Breeding values in the present study are given as a percentage deviation from the mean performance for that trait of the population, which is, by definition, 0%. Table 2.2 and Figure 2.3 show the range in variability captured among families within the respective breeding value categories.

**Table 2.2: Breeding value category summary for the Region H white spruce Controlled Parentage Program family selection.**

| Breeding Value Category | Number of Families | Mean Family BV for Height at 18 Years (%) | Standard Deviation |
|---|---|---|---|
| **High** | 15 | 11.70 | 3.21 |
| **Medium** | 10 | -0.83 | 1.02 |
| **Low** | 15 | -10.41 | 3.64 |

### 2.2.2 – Tree Selection

A list of the trees established at each test site was provided by Alberta and Agriculture and Forestry. This list was then filtered to remove any trees that were dead and/or missing during the Alberta and Agriculture and Forestry's most recent round of measurements (conducted at age 25). Originally, eight trees/family/site were selected at random from the remaining trees for assessment in the present study; however, a combination of mortality, a lack of site maintenance and being unfamiliar with the site resulted in some trees being extremely difficult to positively identify. Because identification is key to progeny tests and maintaining quality

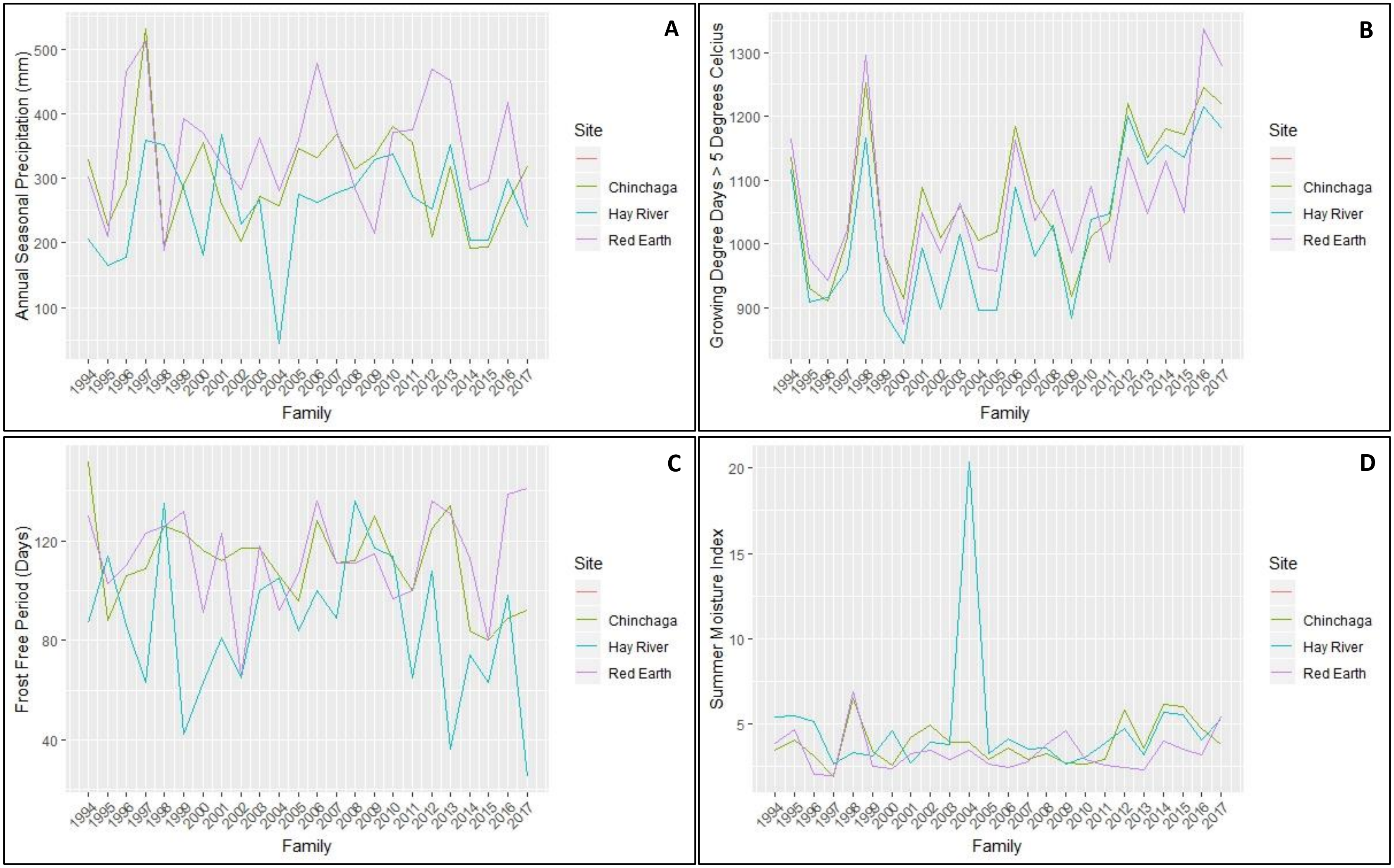

**Figure 2.2: Climate data summary by site for the three Region H white spruce Controlled Parentage Program from years 1994-2017, including annual seasonal precipitation (A), growing degree days (hours where temperature > 5 $^{0}$C) (B), frost free period (number of consecutive days where temperature > 0 $^{0}$C) (C) and summer moisture index (growing degree days/annual seasonal precipitation) (D). Site is coded by colour where Chinchaga is green, Hay River is blue and Red Earth is purple.**

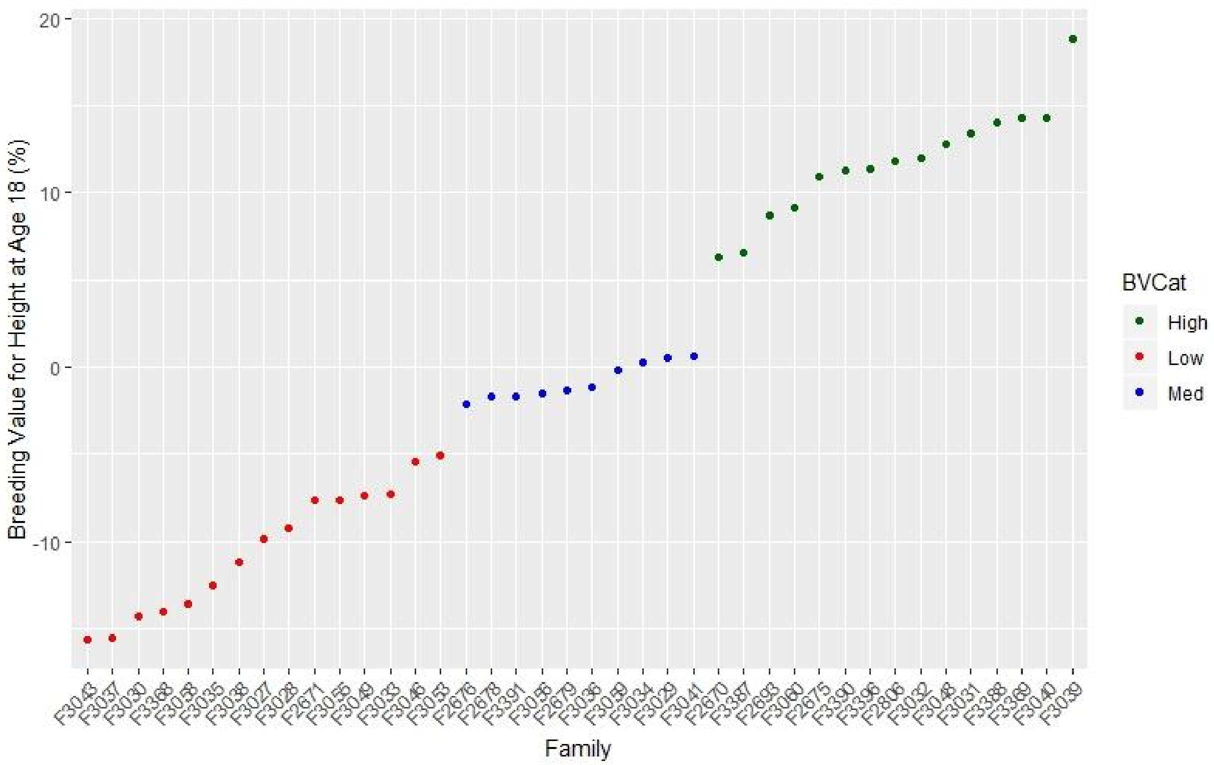

**Figure 2.3: Family mean breeding values for height at age 18 for the Region H white spruce Controlled Parentage Program. Only the 40 families selected for this study of the 55 families represented in the program are shown. The three breeding value categories (BVCat - high, medium, low) are coded by colour.**

data, trees that could not be clearly identified as part of a particular family were discarded from sampling at the Chinchaga and Red Earth Creek test sites. A complete record of trees discarded for this reason may be found in Appendix 1. Due to this difficulty in identifying families, a range from two to eight trees/family/site were ultimately sampled.

## 2.3 – Quantitative Trait Assessment

Four quantitative traits were assessed in this study: Drilling resistance (DR - %) and diameter inside bark (DIB - mm) using a Resistograph Series 6 Scientific (Rinntech), penetration depth (PD

- mm) using a Pilodyn 6J (Hylec Controls) and wood specific gravity (WSG) using Alberta and Agriculture and Forestry's volumetric density method using water displacement with minor adjustments (ATISC 2000). Increment cores were extracted using a 5 mm increment borer (Haglof). A brief description of each method may be found below. All measurements and samples were taken at breast height (1.3 m +/- 15 cm). Measurements were taken as close to each other as possible while ensuring that measurements did not interfere with one another (within approximately 5-10 cm). All four measurements were collected from each individual tree at the same time to eliminate any temporal effects and in one to two days per site and under similar weather conditions in Spring and Summer 2017.

### 2.3.1 – Resistograph

Resistograph is a rapid, non-destructive method (Plate 2.1) for collecting information about wood characteristics in timber, including live standing trees. The Resistograph Series 6 device drives a 3 mm brad point drill bit at a pre-selected speed through the stem. The amount of torque applied to the drill is varied to maintain the selected speed (Rinn *et al.,* 1996, Rinn 2012). The result is that more torque is required to maintain the selected drilling speed in higher density wood, which is referred to as drilling amplitude or drilling resistance (Rinn *et al.,* 1996; Rinn 2012). Drilling resistance will be the term used for the present study. The standard output is given as DR, expressed as a percentage of the maximum motor output, against the current drilling depth which is measured in millimeters (Rinn *et al.,* 1996; Rinn 2012). A measurement is taken every 0.01 mm (Rinntech [date unknown]), which returns a high-resolution graph showing variations in WD across the profile (Rinn 2012). See Figure 2.4 for an example of a delineated Resistograph profile. Ultimately, Resistograph returns a relative measure of WD, as DR is an indirect measure of WD and has no reference to actual WD. This means that DR can be compared easily within a single site but comparisons between sites or programs are somewhat confounded. However, it is possible to calibrate DECOM, the matching analysis software, using either volumetric or X-ray densitometry measurements to return an estimate of actual wood density (Rinntech 2017), or to simply use standard regression analysis to do the same. Rinntech [date unknown] claims that the correlation between DR and WD is positive and very strong ($r^2 > 0.9$). Previous research reflects the utility of Resistograph for selection purposes in TI programs (Isik and Li 2003; Fundova *et al.,* 2018). Isik and Li (2003) and Fundova *et al.,* (2018) suggest a single Resistograph measurement is sufficient for selection purposes, so long as the sampled area is free of knots or other defects. Two measurements/tree were collected in this study to reduce the probability of measurement error and to better represent the WD of each tree.

Two bark-to-bark Resistograph profiles were taken at breast height (1.3 m +/- 15 cm) from each tree (2-8 trees/family/site, n = 704) using a drilling speed of 20 mm/second: the first starting on the north aspect of the tree and the second from the east aspect. The mean value of the two measurements, both for DR and DIB, were calculated and used to perform all subsequent analyses. Profiles were collected from areas free of branches and other defects (e.g. flat spots, crooks) whenever possible to ensure profiles would be clear and well-delineated; however, due to the young age of the trees, avoiding branches completely was not possible. If a tree was deemed to be unsuitable for sampling the next available tree from the same row plot was sampled instead (e.g. substituting tree 4 for 3). Drill bits were replaced regularly after approximately 300 drillings. Although, this exceeded the recommended interval (200 drillings) by Rinntech (date unknown) the trees in this study were of small diameter (average DIB ~10 cm); therefore, this was not expected to introduce any additional error into the measurements. In an investigation of the effect of bit sharpness on Resistograph measurement biases, Ukrainetz and O'Neill (2010) found no evidence of measurement bias after 350 drillings in interior spruce. The bits were regularly inspected to monitor sharpness in the present study and at no point did the bits appear to be dull.

### 2.3.2 – Pilodyn

Pilodyns, which were originally developed to detect rot in utility poles (Hansen 2000), are a simple and rapid method to assess WD in standing timber. The device thrusts a pin into the wood using a precisely calibrated spring-loaded mechanism (Cown 1978). Penetration depth is negatively correlated with WD and Pilodyns have been utilized successfully in several studies for selection purposes in TI programs, dating back to the 1970's (Cown 1978; Hansen 2000; Fundova *et al.,* 2018). Additionally, a Pilodyn may also be useful for estimating modulus of elasticity (Wu *et al.,* 2010). Unlike Resistograph, Pilodyn can only estimate WD in the outermost wood as the penetration depth is limited to 40 mm. A comparison between the Resistograph and Pilodyn methods was requested by our industry partners as Pilodyn has been used to assess WD in Alberta's TI programs in the past. Cown (1982) and Hansen (2000) suggest that two measurements/stem are sufficient for selection purposes in TI programs.

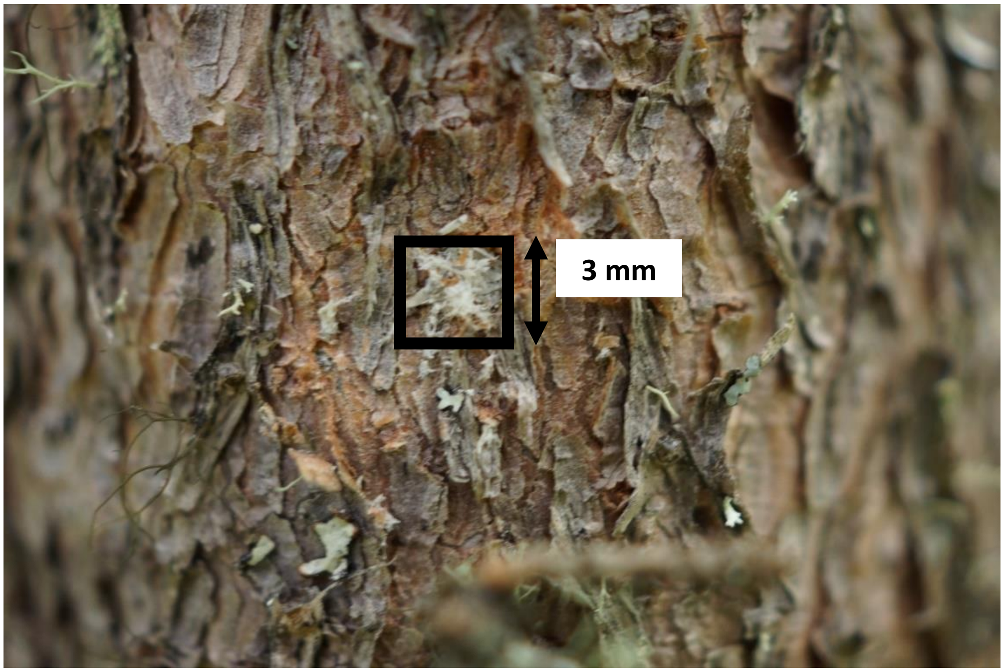

**Plate 2.1: An example of the impact left by Resistograph drilling in white spruce. The only evidence left is a small borehole (3 mm) from the drill bit. As the bit is removed, the hole is filled with the drilling chaff. The borehole is highlighted by the black box.**

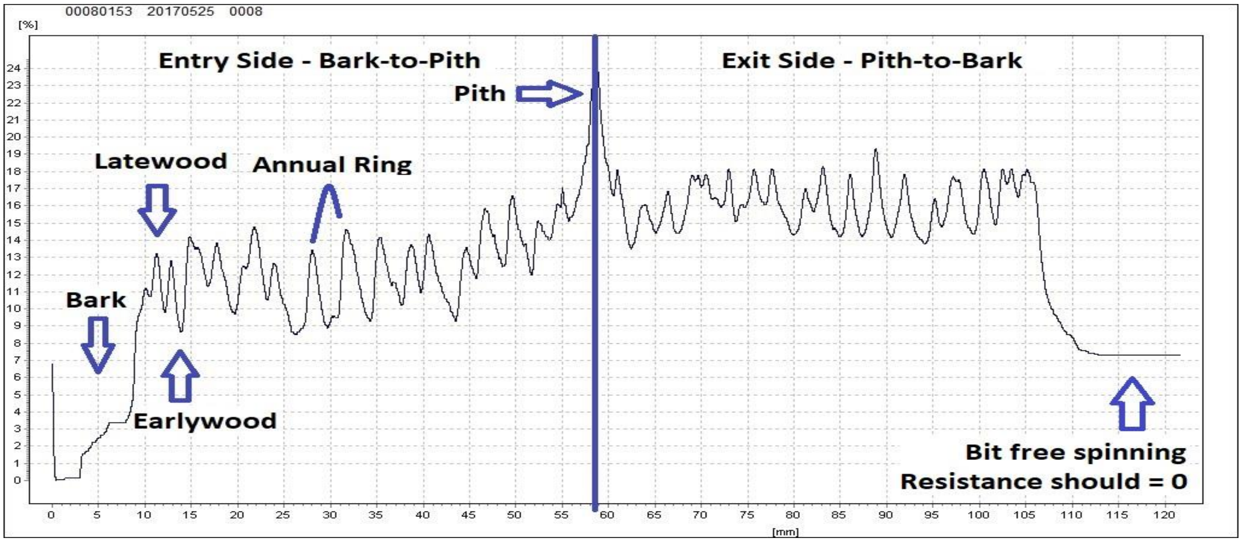

**Figure 2.4: An example of a delineated bark-to-bark Resistograph profile taken from a tree in the Region H white spruce Controlled Parentage Program. Drilling resistance (%) is given on the y-axis and drilling depth (mm) on the x-axis. This profile, which is read left-to-right, has clear signals for the bark (~8 mm, ~110 mm), latewood (peaks), earlywood (troughs), annual rings (space between consecutive peaks), pith (~58 mm) and the bit exit point (~110 mm). This profile also shows a trend of increasing drilling resistance as drilling depth increases.**

Two Pilodyn readings were taken from each tree in the Chinchaga and Hay River test sites (2-8 trees/family/site, n = 474) in the same manner as the Resistograph. The average of the two measurements was used for further analyses. Pilodyn readings were taken within approximately 10 cm of where the Resistograph measurements were taken to ensure wood structure was as similar as possible. It was only possible to sample two of the three sites (Chinchaga and Hay River) due device failure at the Red Earth test site.

### 2.3.3 – Increment Cores

Increment cores are a useful way to not only observe wood morphology and anatomy directly, they may also be used to estimate WD using simple instruments. Increment cores were collected to perform a regression analysis, allowing for the estimation of WSG from DR and PD.

A single 5 mm bark-to-bark increment core was collected using an increment borer from the north aspect in the same manner as the Resistograph and Pilodyn; however, only the north half of each profile was retained for WD measurement as the south halves were consistently of lower quality (e.g. breakage, rough edges). A subset of selected trees was used (2-7 cores/family, n = 191) due to the labour-intensive and damaging nature of increment core sampling. The cores were stored in plastic straws in a cooler containing ice in the field and then stored in a domestic freezer at approximately -18 $^{o}$C once back at the University of Alberta until analysis. The cores were then processed in accordance with ATISC's (2000) volumetric WD procedure, except for decreasing the drying temperature (from 100 $^{o}$C to 71 $^{o}$C) and extending the drying time due to equipment limitations. This minor change in procedure was not expected to appreciably alter the results.

First, cores were hydrated to fibre saturation point (~30% moisture) using distilled water under vacuum for a period of approximately 24 hours (Plate 2.2). The moisture content was confirmed using an MM4DE digital moisture meter (General Instruments). Next, the volume of the cores was determined using volumetric displacement. The apparatus is a simple combination of an SLF303 top-loading balance (Fisher Scientific, readability = +/- 0.001 g, linearity = +/- 0.005 g), a test tube holder, a dissecting probe and a graduated cylinder filled with distilled water (Plate 2.3). The cores were carefully submerged in the cylinder, ensuring that the core did not contact either the bottom or sides of the cylinder. The readout on the balance in grams is equal to the core volume in millilitres. The cores were then dried to constant weight using an 80-litre commercial dehydrator (Model No. 28-0301, Cabela's Outfitters) set at a temperature of 71 $^{o}$C for a period of 48-72 hours. After drying, the cores were then weighed using the same balance as for the displacement measurements and wood specific gravity was calculated by dividing the weight in grams by the volume displaced in millilitres.

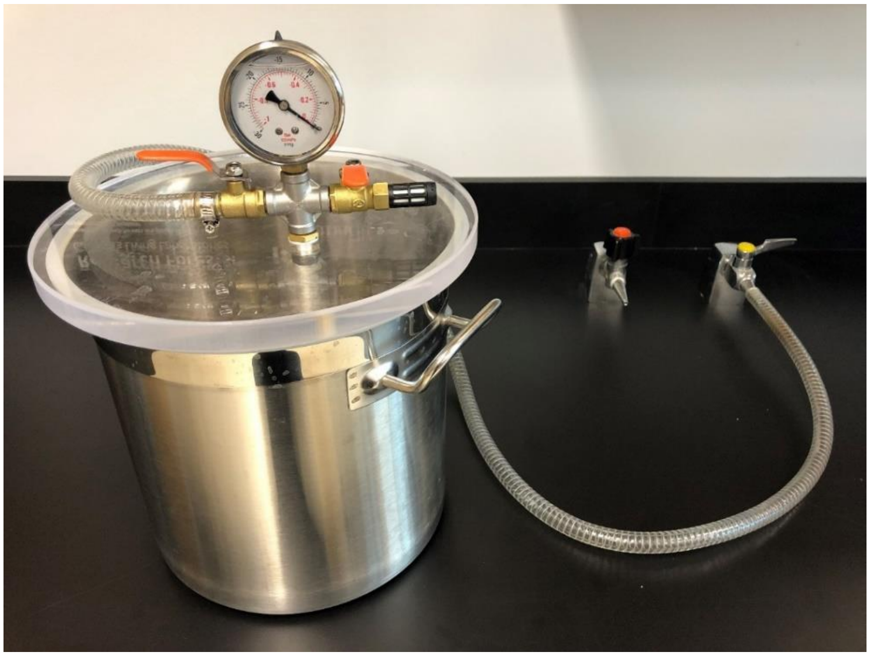

**Plate 2.2: The vacuum chamber used to saturate the white spruce cores collected in the present study to fibre saturation point (moisture content > 30%). Cores were labelled and processed in bulk. This chamber can accommodate many cores or larger pieces, such as wedges or disks. This picture was provided by Morgan Randall from the University of Alberta.**

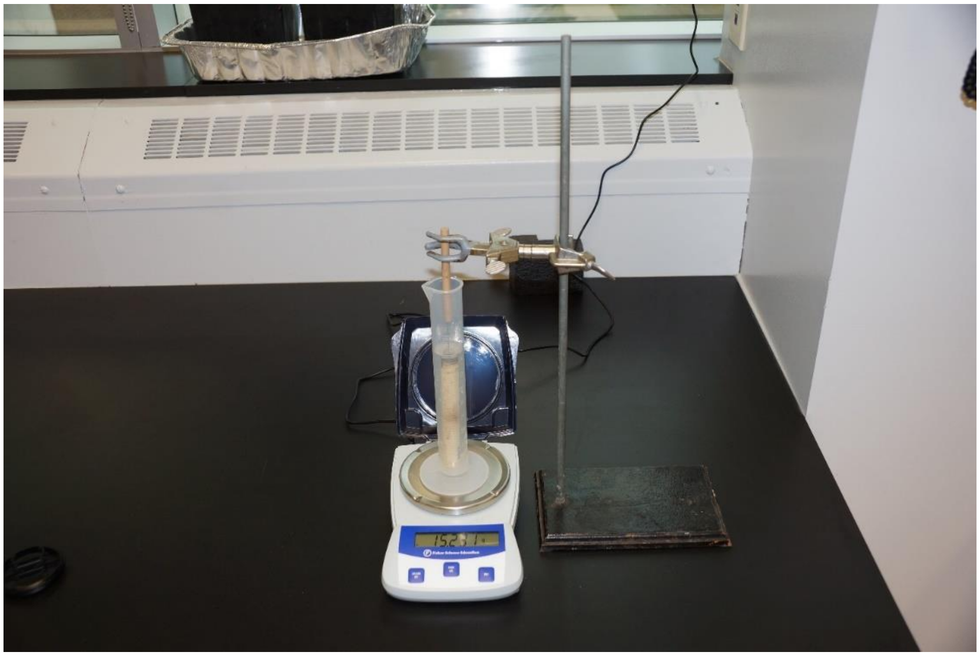

**Plate 2.3: The apparatus used to measure the volume of a 5 mm increment core extracted from white spruce. The volume of the core (in ml) is equal to the mass of water displaced, which is 15.231 g in this example.**

### 2.4 – Data Processing and Quality Control

An important component of utilizing Resistograph data is processing the profiles into usable sections. The raw profiles include extraneous data - bark in particular - that decreased the average drilling resistance across the profile and must be removed prior to analysis for best results. Profiles were processed using the DECOM 2.36i program (Rinntech 2017). DECOM is specialized software that is supplied with the Resistograph device for profile analysis. Software features include profile processing (trimming), math functions (calculating DR), marking defects (voids, rot, compression wood) and WD calibration (Rinntech 2017).

#### 2.4.1 – Resistograph Profile Trimming

Profiles were trimmed to remove the bark portions located at the beginning and end of each profile (Figure 2.5). There are consistent cues within profiles that indicate the transition between bark and wood tissues. The beginning of a typical profile contains a sudden increase in density approximately 8-12 mm into the profile, indicating the point where the bit first encounters wood tissue. However, the delineation between wood and bark tissue is not as clear at the end (exit point) of a profile. In a typical profile, there is a rather abrupt change in the slope of the profile, which indicates the transition from bark to wood and wood to bark tissues on either end (e.g. entry and exit) of the profile. A measurement of DIB was also extracted from this data. In some cases, the ends of the profiles did not have clear exit points, thus a reasonable approximation was made based on cues contained in the profiles, as well as the second profile recorded from the same tree.

It was noted during profile processing that there appeared to be differences in the DR of the entry and exit halves of a single profile. In general, it appeared that the DR of the first half of a profile (from bark-to-pith) was lower than in the second half of the same profile (from pith-to-bark). A similar observation was made by Oliviera *et al.,* (2017) and Fundova *et al.,* (2018). See Figure 2.4 for an example of this phenomenon. Further examples of this trend, as well as a brief analysis of differences in DR between the profile halves, may be found in Appendix 2. This change in DR from one side of a profile to the other held true regardless of which site or aspect a profile was recorded from in the present study. Fundova *et al.,* (2018) detrended profiles assuming a linear relationship between the DR at the start and end of each individual profile. While this method appears to be sound, it would also be onerous and time consuming. Profiles in this study were simply truncated, as suggested by Oliviera *et al.,* (2017), preserving the first half of the profile for analysis (bark-to-pith). Profile truncation is preferable to the detrending method used by Fundova *et al.,* (2018) because each point was adjusted based on a linear model for that specific profile, which would result in introducing error for each individual measurement (of which there are several thousand) within a single profile. Figure 2.4 shows an example of a processed profile from this project that will be used to calculate DR for that particular profile.

### 2.4.2 – Screening for Measurement Error

Data which are considered to represent outliers have a major effect on regression and correlation analyses (Stevens 1984), which formed a major part of the data analysis. Therefore, an intensive screening process was implemented to identify and remove potential outliers attributed to measurement error. It is recognized that outliers are a natural occurrence in a normal distribution (Dawson 2011) and the family selection process used in the present study was likely to bias the data towards producing outliers (i.e. selecting families occurring in the tails of the distribution for BVs for height). The purpose of this process was not to remove data that appeared to be an outlier but to remove data that were not representative of the actual WD of a single tree (i.e. were the result of measurement error).

It was assumed that differences between DR and PD measurements for the north and east aspects should be relatively small (Bouffier *et al.,* 2008). Outliers were screened by calculating the percentage deviation between the paired DR and PD measurements for each tree using the following formula:

$$\% \text{ Deviation} = (1-M_{North}/M_{East})*100$$

where % Deviation is the difference between the two respective DR or PD measurements and $M_{North}$ and $M_{East}$ are the DR or PD measurements of the north and east aspects, respectively. By applying this formula to the data, a nearly symmetrical distribution was achieved, making identification of potential outliers very straightforward. The interquartile range*1.5 rule was then used to screen for outliers, which identified where there were large differences between paired measurements. A measurement was determined to be an outlier if the differences between paired measurements was very large (> 30%) or where there were more moderate differences but disagreement between the DR and PD measurements (e.g. DR indicated low WD but PD indicated high WD in the same tree). This resulted in the removal of data that likely suffered from measurement error (by assessing if the various measurements were in agreement), rather than data that were outliers yet representative of the actual WD of that tree. Although not considered the most robust screening method, the IQR*1.5 rule is simple to implement and should provide adequate results (Rousseeuw and Hubert 2018), given that outlier removal did not rely solely on this method. A summary of removed data may be found in Appendix 3.

Wood specific gravity was screened for outliers using a combination of the 1.5*IQR rule and by creating an inclusion range based on Sw WSG from the literature. Studies by Taylor *et al.,* (1982), Corriveau (1987) and Micko *et al.,* (1982) determined the WSG range of Sw to be 0.26-0.42, 0.268-0.450 and 0.33-0.44, respectively. The methods used to determine WSG in these studies were comparable to the method used in the present study, hence they will be the basis for establishing an inclusion range. Additionally, various industry sources indicate that the WSG of Sw is 0.35-0.38 (Alemdag 1984; FCC 2006; USDA 2010). These values were in agreement both with the above studies, as well as the results of the present study (mean WSG across all sites = 0.372). Therefore, a WSG of 0.37 will be considered representative of average Sw WSG, regardless of location. The inclusion range for the purposes of outlier removal was calculated as follows: 0.26-(0.37*0.1) for the lower limit and 0.45+(0.37*0.1) for the upper limit. This resulted in a WSG inclusion range of 0.223-0.487. Any values falling outside of this range were considered outliers and excluded on the basis of likely being the result of measurement error. The inclusion range was much more conservative than the range calculated by the 1.5*IQR rule (WSG = 0.348-0.378). Additionally, any observations removed due to having DR and PD outliers

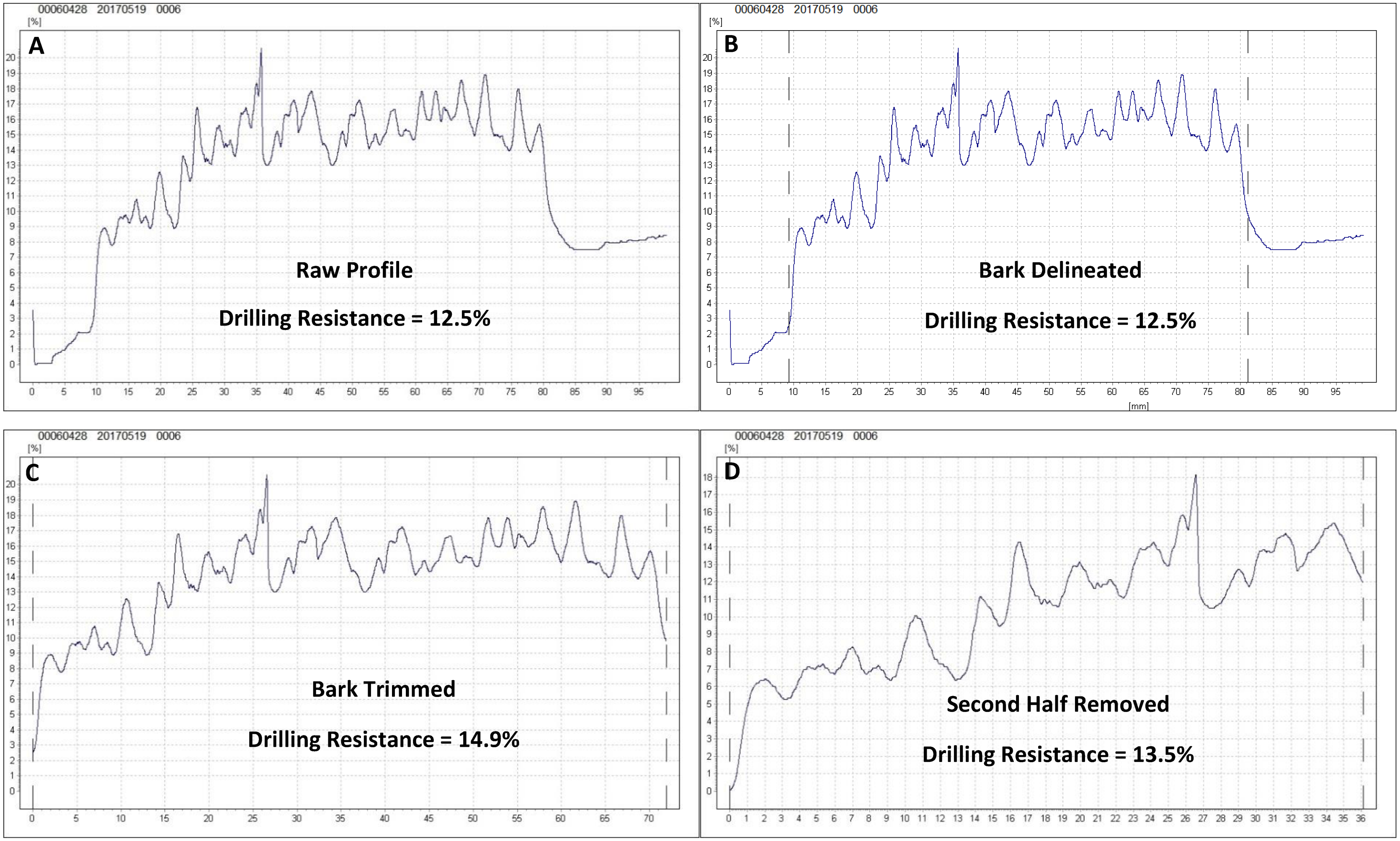

Figure 2.5: An example of a Resistograph profile taken from the Region H white spruce Controlled Parentage Program at different stages of processing. Drilling resistance (%) is on the y-axis and drilling depth (mm) is on the x-axis. The first profile (A) is a raw profile, the second profile (D) has the trim points (i.e. transition from bark to wood) marked on either side of the profile, the third profile (C) has had the bark trimmed and the final profile (D) is the bark-to-pith half of the profile from which the drilling resistance measurement was calculated in the present study. The drilling resistance values in each profile show how the bark and the trend of increasing resistance as drilling depth increases affect the whole profile drilling resistance measurement. For reference, the drilling resistance of the removed half in this example was 16.1%.

as identified by their respective process were automatically removed, as well. A summary of removed data may be found in Appendix 3.

## 2.5 – Data Analysis

Data analyses fall under two general categories: phenotypic and genetic analysis. Phenotypic analyses included phenotypic correlations and regression analysis while genetic analyses included calculating narrow sense heritabilities, BVs and genotypic correlations. All analyses were conducted using a significance level $\alpha \leq 0.05$. All phenotypic analyses, including tests for significant differences between groups (i.e. t-tests, ANOVAs) and analyses for relationships between traits (i.e. correlation, regression) had all sites aggregated together because the strength of correlation and the slope of the regression lines were found to be similar for each site (data not shown). For example, the correlations (r) between DR and DIB for Chinchaga, Hay River and Red Earth were 0.29, 0.47 and 0.27, respectively and regression line slopes of -0.0143, -0.038 and -0.0176, respectively (data not shown). This should be considered appropriate because any selections within the program will ultimately be made at the program-level (i.e. with aggregate data), rather than at the site-level. The only exception to this were the summary statistics and ANOVA conducted by site to assess differences between traits by site. Conversely, all genetic analyses were conducted first by site as the foundation of these analyses is narrow sense heritability, which was expected to vary by site (Kiss and Yeh 2011).

### 2.5.1 – Correlations Between Paired Drilling Resistance and Penetration Depth Measurements

Relationships between the paired (i.e. north and east aspect) DR and PD measurements were analyzed using Pearson's correlation method and differences between the measurements were tested using paired t-tests. Paired t-tests were utilized because the assumption is that because the paired DR and PD measurements were taken from the same tree and at the same time, that they should be similar and do not represent independent observations.

### 2.5.2 – Phenotypic Analyses

Summary statistics, including n, mean, standard error, standard deviation, CoV, minimum (min), maximum (max), skewness (skew) and kurtosis (kurt) were calculated by site (Chinchaga, Hay River and Red Earth), BV category (high, medium, low) for height at age 18 and family for each of the four quantitative traits assessed (DR, PD, WSG and DIB). Differences between groups were analyzed using a one-way ANOVA using the lm() (i.e. linear model) function in R version 3.4.3 (R Core Team 2017). The models were fitted as follows:

$$Y_{ij} = \mu + \tau_i + \varepsilon_{ij}$$

where $y_{ij}$ is the jth observation of the ith treatment, $\mu$ is the sample mean for the respective trait (i.e. DR, PD, WSG, DIB), $\tau_i$ is the effect of the ith treatment (i.e. site, BV category, family) and $\varepsilon_{ij}$ is the error associated with the jth observation on the ith treatment.

Genotype-by-environment interactions for each of the four quantitative traits were tested using two-factor ANOVA using the lm() function using R version 3.4.3 (R Core Team 2017). The models were fitted as follows:

$$Y_{ijk} = \mu + \tau_i + \beta_j + \gamma_{ij} + \varepsilon_{ijk}$$

Where where $y_{ij}$ is the kth observation of the ith and jth treatments, μ is the sample mean for the respective trait (i.e. DR, PD, WSG, DIB), $\tau_i$ is the effect of the ith treatment (i.e. site), $\beta_j$ is the effect of the jth treatment (i.e. family), $\gamma_{ij}$ is the interaction between the two treatments and $\varepsilon_{ijk}$ is the error associated with the kth observation of the ith and jth treatments.

Phenotypic correlations between all quantitative traits (DR, PD, WSG and DIB) were determined using Pearson's correlation method at both the individual- and family-levels using the cor.test() (i.e. correlation test) function in R version 3.4.3, which included an estimate of the standard error for each respective phenotypic correlation.

Multiple linear regression was used to model the predictive relationships between DR or PD and WSG using R version 3.4.3 (R Core Team 2017) with the lm() function. The multiple linear regressions were modeled as follows:

$$Y_i = \beta_0 + \beta_1 x_{i1} + \beta_2 x_{i2} + \varepsilon$$

where $Y_i$ is the value of the ith observation, $\beta_0$ is the model intercept, $\beta_1$ is the regression coefficient of DR or PD, $\beta_2$ is regression coefficient of DIB, $xi_1$ is DR or PD measurement of the ith observation, $xi_2$ is the DIB measurement associated with the ith observation and ε is the error term. Standard errors for each regression model were estimated as follows (Pardoe *et al.,* 2018):

$$\sqrt{SSE}/n-p$$

where SSE is the sum of squared errors for the respective model, n is the number of observations and p is the number of predictive variables (including the intercept) in the respective model. Model quality was evaluated using Akaike's Information Criterion (AIC) and cross-validated using the predicted $r^2$ method with the qpcR package (Spiess 2018). Akaike's Information Criterion was used for model evaluation because it is a common and well-accepted method for evaluating relative model fit (Bozdogan 1987) and predicted $r^2$ was used because it is a useful indicator to evaluate potential overfitting of multiple linear regression models (Colton and Bower 2002). All regression analyses were performed by pooling sites together for the same reason as for the phenotypic correlations.

### 2.5.3 – Genetic Analyses

Narrow sense heritability was calculated by site for each of three quantitative traits (DR, PD, DIB) using ASReml-R version 4.1 (VSNi 2018) and the asremlPlus package (Brien 2018) using R version 3.4.3 (R Core Team 2017). Additive genetic effects (i.e. BVs) for each trait were modeled using a mixed effects model which takes the following general form (Butler *et al.,* 2018):

$$y = X\tau + Z\mu + \varepsilon$$

where y is the vector of observations (i.e. DR, PD, DIB), X is the design matrix associating observations with fixed effects, τ represents the vector of fixed effects (i.e. family) , Z is the design matrix associating observations with random effects, μ represents the vector of random effects (i.e. replicate), and ε represents the vector for residual errors (Butler *et al.,* 2018). Family-level BVs by site were extracted from the model output and used to calculate the mean family BV across the three test sites to provide an integrated family BV for each trait for the entire Region H Sw CPP. Narrow sense heritabilities were calculated using the following formula, which is widely accepted for use in forest trees (Park and Fowler 1987; Perron *et al.*, 2013; Ratcliffe *et al*., 2014):

$$h^2 = 3*\sigma_a^2/(\sigma_a^2+ \sigma_e^2)$$

where $h^2$ is the estimate of narrow sense heritability, $\sigma_a^2$ is the additive genetic variance component from the ASReml-R model output and $\sigma_e^2$ is the environmental variance component, which includes the environmental effect (minus the components of the environmental effect removed through the experimental design – e.g. blocking), the dominance and epistatic genetic effects, as well as the error term. In the above equation, $(\sigma_a^2+ \sigma_e^2)$ is equivalent to the phenotypic variance component, $\sigma_p^2$ (i.e. the sum of all genetic, environmental and error variance components). The coefficient of three in the $3*\sigma_a^2$ term is used to estimate the additive genetic effect when taking into account that the progeny in the Region H white spruce CPP progeny trials are half-sibs, meaning that the mean shared DNA between progeny is 25% (Surles *et al.,* 1990). Theoretically, the coefficient would be four, but three is considered appropriate in forest trees due to inbreeding effects (i.e. sharing more than 25% of DNA between 'half-sibs,' as in the present study) caused by adjacency to and subsequent mating with nearby related individuals (Namkoong 1966). The associated standard error for each heritability estimate was estimated using the pin() function from the sommer package (Covarrubias-Pazaran 2019) using R version 3.4.3 (R Core Team 2017).

Individual-level BVs were calculated using the following formula:

$$BV = h^2(x-\bar{x})$$

where BV is the individual's BV (%) for the respective trait, $h^2$ is the narrow sense heritability calculated for the respective trait and site (e.g. heritability for DR for Chinchaga), where x is the phenotypic observation for the respective individual (e.g. DR for an individual tree from Chinchaga) and where $\bar{x}$ is the sample mean for the respective trait and site (e.g. mean DR for Chinchaga). Genetic correlations at the individual- and family-levels were then calculated using Pearson's correlation method using the cor.test() function in R version 3.4.3 (R Core Team 2017). The standard error for each of the individual-level genetic correlations was estimated using the following formula (Koots and Gibson 1996):

$$1-r_g^2/\surd 2*\surd SE_{h21}*SE_{h22}/h_1^2*h_2^2$$

where $r_g$ is the r value from the respective genetic correlation (i.e. DR and DIB), $SE_{h21}$ and $SE_{h22}$ are the standard errors of the estimates of narrow sense heritabilities for each of the respective traits being correlated, and $h_1^2$ and $h_2^2$ are the estimates of narrow sense heritability for each of the respective traits being correlated. It should be noted that the standard error for the correlations at the family-level were not estimated because trait heritability's were not calculated at the program-level (i.e. by aggregating all site data); however, it is reasonable to assume that family-level standard errors will be inflated relative to the individual-level genetic correlations due to the reduced degrees of freedom (i.e. several hundred individuals *versus* 40 families).

# Chapter 3: Results

## 3.1 – Paired Measurement Correlations

Pearson's correlation coefficients (r) were calculated for the paired DR and PD measurements (i.e. north and east aspects) and DR and PD measurements taken from the same aspect (i.e. $DR_{North}$/$PD_{North}$ and $DR_{East}$/$PD_{East}$ – Table 3.1). Figures 3.1A-B shows boxplots for the four measurements while Figures 3.2A-D shows scatterplots for each respective correlation. The correlations between the paired DR and paired PD measurements were both positive, and moderate and strong, respectively, while the correlation between the DR and PD measurements taken from the same aspect were negative and moderate (Table 3.1). It should be noted that a higher DR indicates higher WD while a lower PD indicates higher WD (i.e. the negative correlation between DR and PD demonstrate agreement). While the mean DR and associated variances were similar for both aspects, a paired t-test revealed that there were significant differences between the two measurements (df = 703, $p < 0.001$); however, a significant difference was not found between the paired PD measurements (df = 473, $p = 0.124$). The relative differences between the mean DR and PD of the paired measurements were 1.94% and 0.53%, respectively, and the level of variation was similar between the both sets of paired measurements. It should be noted that several observations were removed from the data set because they were determined to be outliers using the process described in Chapter 2 Section 2.4.2. See Appendix 3 for a summary of removed data, including justification

**Table 3.1: Pearson's correlation coefficients (r) and associated standard error (+/-, in brackets), p-values and degrees of freedom (in brackets) for the Region H white spruce Controlled Parentage Program across three test sites at age 26 for drilling resistance (%) using Resistograph and penetration depth (mm) using Pilodyn on the north and east aspects.**

| Traits Measured[1] | Correlation Coefficient (SE) | p-value (df) |
|---|---|---|
| $DR_{North}$ ~ $DR_{East}$ | 0.66 (0.03) | < 0.001 (702) |
| $PD_{North}$ ~ $PD_{East}$ | 0.81 (0.03) | < 0.001 (472) |
| $DR_{North}$ ~ $PD_{North}$ | -0.58 (0.04) | < 0.001 (472) |
| $DR_{East}$ ~ $PD_{Easr}$ | -0.51 (0.04) | < 0.001 (472) |

[1] **DR:** Drilling resistance; **PD:** Penetration depth; **SE:** Standard error; **df:** Degrees of freedom

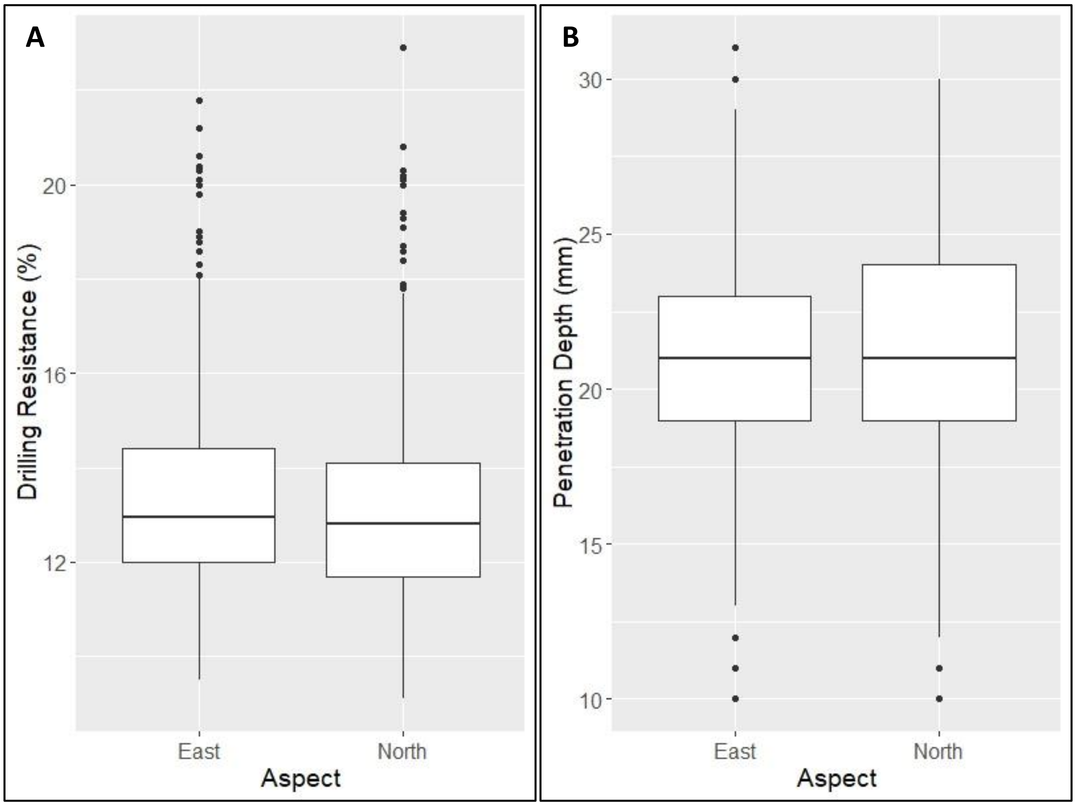

**Figure 3.1: Boxplots for north and east aspect measurements for drilling resistance (%) using Resistograph (A) and penetration depth (mm) using Pilodyn (B) for the Region H white spruce Controlled Parentage Program across three test sites at age 26.**

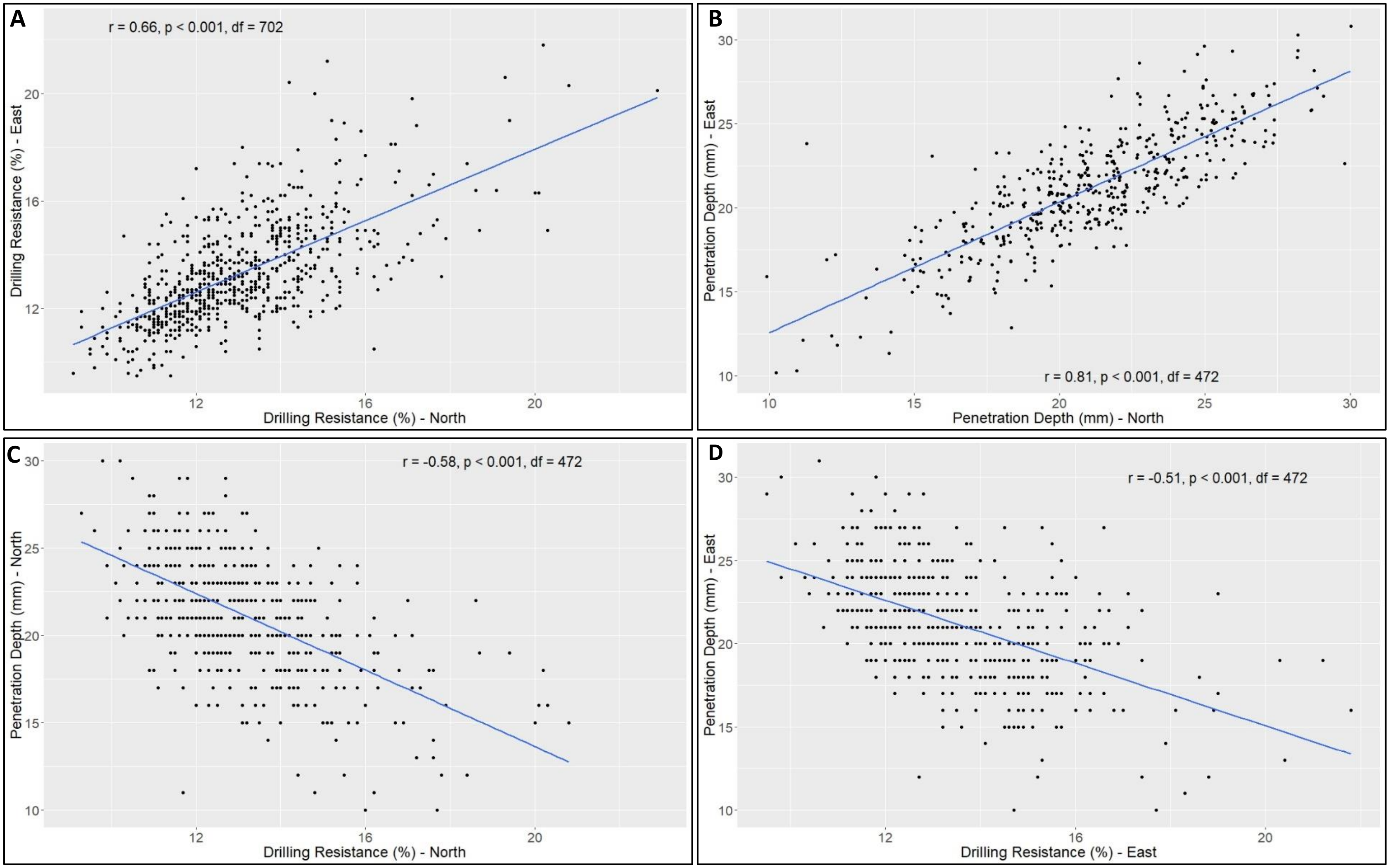

**Figure 3.2: Scatterplots with regression lines for drilling resistance (DR - %) - east vs. DR – north (A), penetration depth (PD - mm) - east vs. PD - north (using a jitter plot to better differentiate individual points - B), DR - north vs. PD – north (C) and DR - east vs. PD - east (D) for the Region H white spruce Controlled Parentage Program averaged across three sites at age 26.**

## 3.2 – Quantitative Trait Summary Statistics

### 3.2.1 – Summary Statistics and ANOVA for Wood Density Traits and Diameter Inside Bark by Site

Overall, the mean for each of the four quantitative traits measured (DR, PD, WSG and DIB) were similar for the Chinchaga and Red Earth sites, while Hay River differed (Figure 3.3A-D). ANOVA for each of the quantitative traits showed that significant differences existed between site trait means for all four traits (Table 3.2). Specifically, Chinchaga and Red Earth were both significantly different from Hay River, but not from one another, for all traits. Wood density, as indicated by all three WD traits (DR, PD and WSG), was lower for Chinchaga and Red Earth compared to Hay River, while DIB showed the opposite response. Summary statistics for each trait by site are presented in Table 3.5. The level of variation for each trait was similar for each site. The level of variation between measurements, as indicated by the coefficient of variation (CoV), was similar for all three WD traits while the amount of variation in DIB was two to three times greater, regardless of site. For example, the CoV for DR, PD and WSG at the Chinchaga test site was 0.10 for all three traits, while the CoV was 0.25 for DIB. In general, the distributions for all traits were near-normal with a couple of caveats. For WD traits, the distributions tended to be moderately skewed towards higher WD (i.e. positively for DR and WSG, negatively for PD), while DIB tended to be only slightly skewed in either direction, depending on site. The kurtosis values showed that the WD traits tended to have more outliers (i.e. more frequent occurrence of data in the tails of the distributions) than DIB, regardless of site.

**Table 3.2: ANOVA summary table for trait measured, F value, degrees of freedom and p-values for drilling resistance (%) using Resistograph, penetration depth (mm) using Pilodyn, wood specific gravity using water displacement and diameter inside bark (mm) at breast height using Resistograph by site for the Region H white spruce Controlled Parentage Program at age 26.**

| Trait Measured | F ($df_b$, $df_w$)[1] | p-value |
|---|---|---|
| **Drilling Resistance (%)** | 44.83 (2, 701) | < 0.001 |
| **Penetration Depth (mm)** | 318.82 (1, 472) | < 0.001 |
| **Wood Specific Gravity** | 12.00 (2, 188) | < 0.001 |
| **Diameter Inside Bark (mm) at Breast Height** | 84.86 (2, 701) | < 0.001 |

[1] **$df_b$:** Degrees of freedom between groups; **$df_w$:** Degrees of freedom within groups.

### 3.2.2 – Summary Statistics and ANOVA for Wood Density Traits and Diameter Inside Bark by Breeding Value Category for Height at 18 Years

Overall, differences in trait means were smaller between BV categories compared to between sites (Figure 3.4A-D). As a reminder, the BV categories represent a simple categorical grouping of families where the high, medium and low categories have positive, near zero and negative BVs for height at age 18, respectively, and were provided by the GoA (Table 2.1). ANOVA showed there are significant differences between BV categories for DR, WSG and DIB, but that significant differences did not exist between BV categories for PD (Table 3.3). Specifically, the medium BV category did not differ significantly from either the low or high categories, but the low and high categories did differ significantly from each other for both DR and DIB. Surprisingly, WSG did not differ significantly between the high and low categories but did differ significantly between the high and medium categories. Summary statistics for all traits by BV category are presented in Table 3.6. In general, WD, as indicated by all three WD traits, was highest for the low BV category while DIB showed the opposite response and was lowest in the low BV category. The high BV category showed the opposite relationship with the medium BV category falling between the former two categories. The patterns of variation were similar to those by site for all of the traits where the relative variation in the WD traits was two to three times lower compared to DIB. The opposite trends were true of the high BV category, with the medium BV category falling in between. The overall trends in skewness and kurtosis were largely similar to those observed by site where there was a greater proportion of the observations occurring in the tails for the WD traits compared to DIB.

**Table 3.3: ANOVA summary table for trait measured, F value, degrees of freedom and p-values for drilling resistance (%) using Resistograph, penetration depth (mm) using Pilodyn, wood specific gravity using water displacement and diameter inside bark (mm) at breast height using Resistograph by breeding value category for the Region H white spruce Controlled Parentage Program at age 26.**

| Trait Measured | F ($df_b$,$df_w$)[1] | p-value |
|---|---|---|
| **Drilling Resistance (%)** | 2.21 (39, 664) | < 0.001 |
| **Penetration Depth (mm)** | 0.62 (2, 471) | 0.538 |
| **Wood Specific Gravity** | 4.37 (2, 188) | 0.014 |
| **Diameter Inside Bark (mm) at Breast Height** | 8.30 (2, 701) | < 0.001 |

[1] **$df_b$:** Degrees of freedom between groups; **$df_w$:** Degrees of freedom within groups.

### 3.2.3 – Summary Statistics and ANOVA for Wood Density Traits and Diameter Inside Bark by Family

Trait variability was much greater by family compared with site or BV category (Figure 3.5). There were no significant differences found between families for PD, WSG or DIB; however, significant differences did exist for DR (Table 3.4). Summary statistics for DR, PD, WSG and DIB are presented in Tables 3.7, 3.8, 3.9 and 3.10, respectively; additionally, statistical groupings for DR are presented in Table 3.7. The patterns of variation were overall similar to the patterns by site and by BV category where the relative density of the WD traits was two to three times lower than the variation in DIB; however, an additional caveat exists. Specifically, it appears that high BV families possess slightly lower relative variation for all traits compared to either medium or low BV families (Tables 3.7-3.10). No discernible pattern was found in skewness or kurtosis by family. In general, the distribution for each individual family appears to be near-normal for all traits except for WSG. Wood specific gravity had far fewer observations/family (2-7) compared to the three other traits (8-21), resulting in less statistical power. Some families (e.g. F2693) did not have enough observations to adequately summarize their WSG.

**Table 3.4: ANOVA summary table for trait measured, F value, degrees of freedom and p-values for drilling resistance (%) using Resistograph, penetration depth (mm) using Pilodyn, wood specific gravity using water displacement and diameter inside bark (mm) at breast height using Resistograph by family for the Region H white spruce Controlled Parentage Program at age 26.**

| Trait Measured | F ($df_b$, $df_w$)[1] | p-value |
|---|---|---|
| **Drilling Resistance (%)** | 2.21 (39, 664) | < 0.001 |
| **Penetration Depth (mm)** | 1.11 (39, 434) | 0.308 |
| **Wood Specific Gravity** | 0.89 (39, 151) | 0.654 |
| **Diameter Inside Bark (mm) at Breast Height** | 1.34 (39, 664) | 0.081 |

**$df_b$:** Degrees of freedom between groups; **$df_w$:** Degrees of freedom within groups.

**Table 3.5: Summary statistics for drilling resistance (%) using Resistograph, penetration depth (mm) using Pilodyn, wood specific gravity using water displacement and diameter inside bark (mm) at breast height using Resistograph by site for the Region H white spruce Controlled Parentage Program at age 26.**

| Stat[1]/Site | Chinchaga | | | | Hay River | | | | Red Earth | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Trait** | **DR (%)** | **PD (mm)** | **WSG** | **DIB (mm)** | **DR (%)** | **PD (mm)** | **WSG** | **DIB (mm)** | **DR (%)** | **PD (mm)** | **WSG** | **DIB (mm)** |
| **Count** | 195 | 195 | 47 | 195 | 279 | 279 | 88 | 279 | 230 | - | 56 | 230 |
| **Mean** | 12.63 | 23.6 | 0.354 | 99.7 | 13.86 | 19.4 | 0.385 | 74.4 | 12.74 | - | 0.365 | 97.9 |
| **SE** | 0.09 | 0.2 | 0.005 | 1.8 | 0.10 | 0.2 | 0.004 | 1.3 | 0.11 | - | 0.005 | 1.7 |
| **StDev** | 1.24 | 2.3 | 0.036 | 25.2 | 1.75 | 2.6 | 0.036 | 21.5 | 1.71 | - | 0.038 | 26.4 |
| **CoV** | 0.10 | 0.10 | 0.10 | 0.25 | 0.13 | 0.14 | 0.09 | 0.29 | 0.13 | - | 0.11 | 0.27 |
| **Min** | 9.70 | 17.5 | 0.231 | 46.0 | 10.50 | 10.0 | 0.320 | 19.5 | 9.35 | - | 0.231 | 28.0 |
| **Max** | 16.70 | 30.5 | 0.451 | 151.0 | 21.00 | 27.0 | 0.486 | 130.0 | 21.50 | - | 0.480 | 154.0 |
| **Skew** | 0.55 | -0.01 | -0.48 | -0.09 | 0.79 | -0.65 | 0.51 | 0.11 | 1.33 | - | 0.14 | -0.41 |
| **Kurt** | 0.45 | -0.10 | 2.34 | -0.87 | 1.23 | 1.01 | 0.03 | -0.54 | 3.94 | - | 2.76 | -0.01 |

[1] **Stat:** Statistic; **DR:** Drilling resistance; **PD:** Penetration depth; **WSG:** Wood specific gravity; **DIB:** Diameter inside bark at breast height; **SE:** Standard error; **StDev:** Standard deviation; **CoV:** Coefficient of variation; **Min:** Minimum; **Max:** Maximum; **Skew:** Skewness; **Kurt:** Kurtosis.

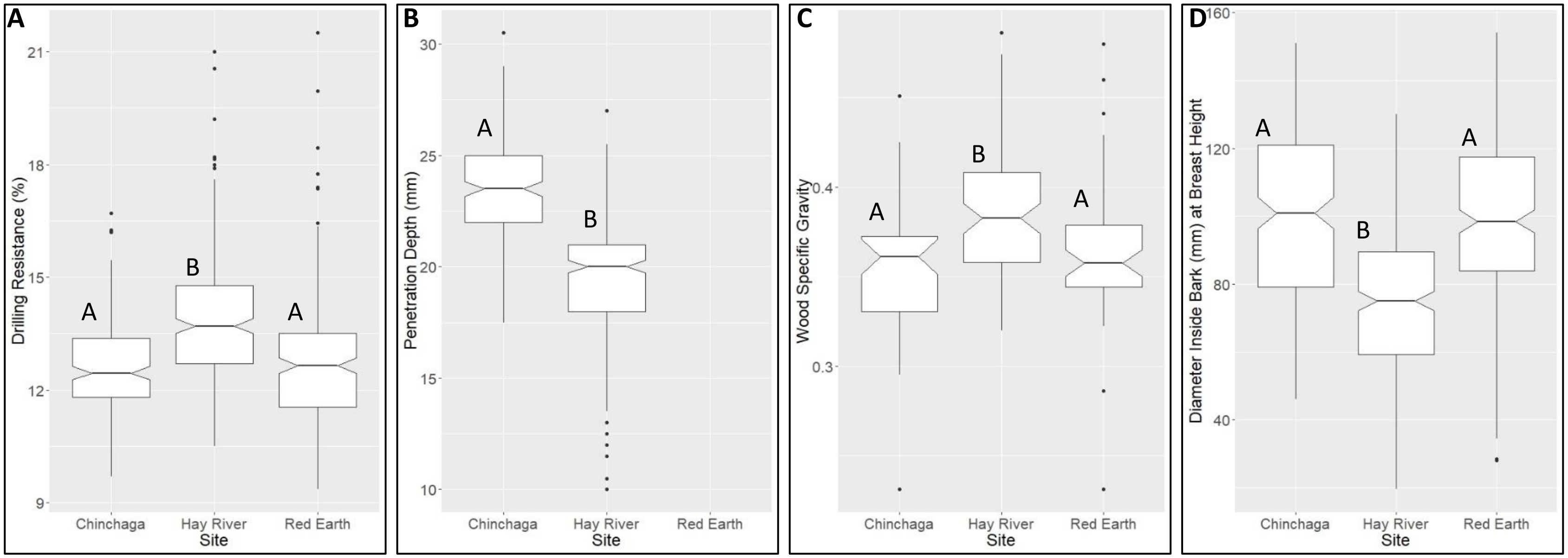

**Figure 3.3: Notched boxplots for drilling resistance (%) using Resistograph (A), penetration depth (mm) using Pilodyn (B), wood specific gravity using water displacement (C) and diameter inside bark (mm) at breast height using Resistograph (D) by site for the Region H white spruce Controlled Parentage Program at age 26. The letters above each individual boxplot indicate statistical groupings (i.e. traits with the same letter were not statistically different).**

**Table 3.6: Summary statistics for drilling resistance (%) using Resistograph, penetration depth (mm) using Pilodyn, wood specific gravity using water displacement and diameter inside bark (mm) at breast height using Resistograph by breeding value category for height at 18 years (provided by the Government of Alberta) for the Region H white spruce Controlled Parentage Program at age 26.**

| Stat/BVCat[1] | High | | | | Medium | | | | Low | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Trait** | **DR (%)** | **PD (mm)** | **WSG** | **DIB (mm)** | **DR (%)** | **PD (mm)** | **WSG** | **DIB (mm)** | **DR (%)** | **PD (mm)** | **WSG** | **DIB (mm)** |
| **Count** | 266 | 178 | 71 | 266 | 182 | 126 | 49 | 182 | 256 | 170 | 71 | 256 |
| **Mean** | 12.87 | 21.2 | 0.362 | 93.6 | 13.13 | 21.3 | 0.382 | 89.4 | 13.47 | 20.9 | 0.374 | 84.1 |
| **SE** | 0.09 | 0.2 | 0.004 | 1.7 | 0.13 | 0.3 | 0.006 | 1.9 | 0.12 | 0.2 | 0.005 | 1.6 |
| **StDev** | 1.40 | 3.2 | 0.033 | 27.8 | 1.73 | 3.4 | 0.043 | 25.5 | 1.93 | 3.2 | 0.041 | 26.4 |
| **CoV** | 0.11 | 0.15 | 0.09 | 0.30 | 0.13 | 0.16 | 0.11 | 0.28 | 0.14 | 0.15 | 0.11 | 0.31 |
| **Min** | 9.35 | 10.5 | 0.231 | 30.0 | 10.00 | 10.0 | 0.302 | 31.5 | 9.90 | 12.0 | 0.231 | 19.5 |
| **Max** | 17.30 | 29.0 | 0.458 | 154.0 | 19.20 | 30.5 | 0.486 | 150.0 | 21.50 | 28.5 | 0.480 | 150.5 |
| **Skew** | 0.52 | -0.19 | -0.37 | -0.02 | 0.66 | -0.37 | 0.47 | 0.04 | 1.12 | -0.19 | -0.26 | 0.00 |
| **Kurt** | 0.42 | 0.30 | 3.32 | -0.71 | 0.59 | 0.77 | 0.08 | -0.60 | 2.19 | 0.00 | 1.48 | -0.55 |

**Stat:** Statistic; **BVCat:** Breeding Value Category for Height at Age 18; **DR:** Drilling resistance; **PD:** Penetration depth; **WSG:** Wood specific gravity; **DIB:** Diameter inside bark at breast height; **SE:** Standard error; **StDev:** Standard deviation; **CoV:** Coefficient of variation; **Min:** Minimum; **Max:** Maximum; **Skew:** Skewness; **Kurt:** Kurtosis.

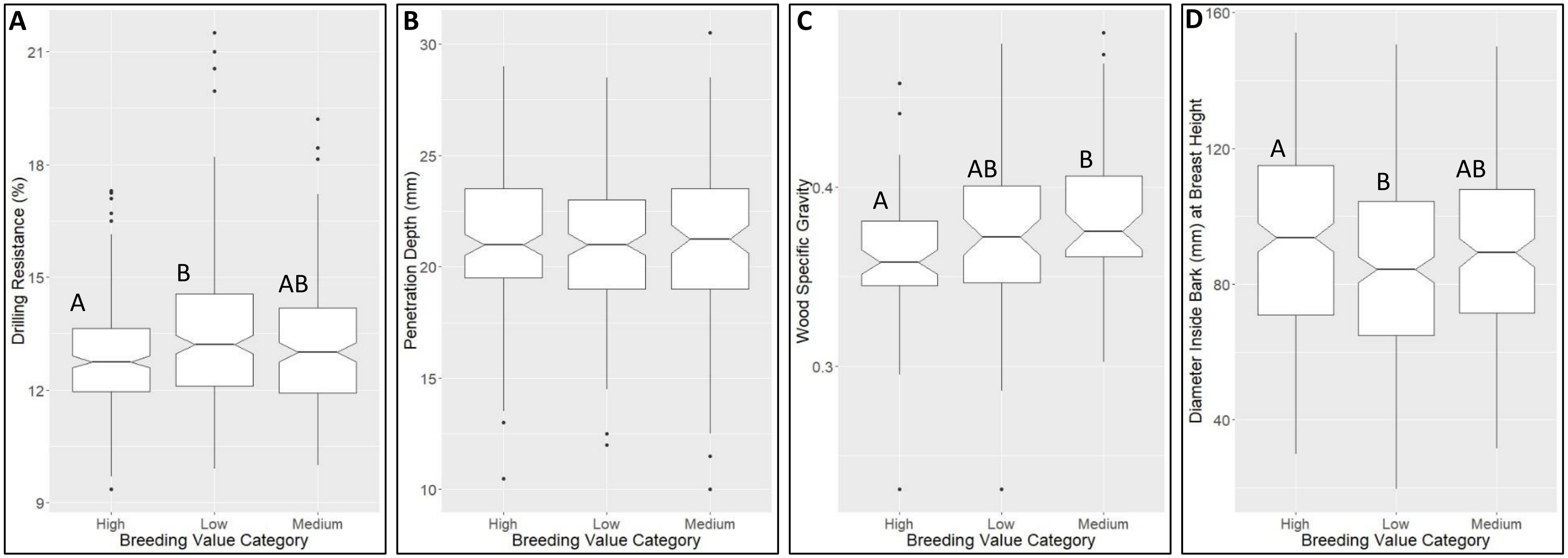

**Figure 3.4: Notched boxplots for drilling resistance (%) using Resistograph (A), penetration depth (mm) using Pilodyn (B), wood specific gravity using water displacement (C) and diameter inside bark (mm) at breast height using Resistograph (D) by breeding value category for height at 18 years for the Region H white spruce Controlled Parentage Program at age 26. The letters above each individual boxplot indicate statistical groupings (i.e. traits with the same letter were not statistically different).**

**Table 3.7: Summary statistics for drilling resistance (%) using Resistograph by family for the Region H white spruce Controlled Parentage Program at age 26. Families are ordered from lowest breeding value for height at 18 years to highest with breeding value categories (low, medium, high) being separated by bolded gridlines. Families sharing a letter in the 'Sig' column do not differ significantly from each other.**

| Fam/Stat[1] | Count | Mean | SE | StDev | CoV | Min | Max | Skew | Kurt | Sig |
|---|---|---|---|---|---|---|---|---|---|---|
| **F3043** | 18 | 13.23 | 0.48 | 2.05 | 0.16 | 10.90 | 18.00 | 1.33 | 1.21 | AB |
| **F3037** | 16 | 13.90 | 0.39 | 1.57 | 0.11 | 11.55 | 17.05 | 0.09 | -0.52 | AB |
| **F3030** | 17 | 13.92 | 0.62 | 2.58 | 0.18 | 9.90 | 21.50 | 1.65 | 4.20 | AB |
| **F3368** | 15 | 12.86 | 0.38 | 1.46 | 0.11 | 11.25 | 16.95 | 1.69 | 3.60 | AB |
| **F3058** | 15 | 14.12 | 0.45 | 1.73 | 0.12 | 11.15 | 17.90 | 0.86 | 1.23 | B |
| **F3035** | 14 | 14.04 | 0.71 | 2.65 | 0.19 | 10.45 | 19.95 | 1.03 | 0.67 | AB |
| **F3038** | 14 | 13.01 | 0.31 | 1.16 | 0.09 | 11.00 | 14.60 | -0.37 | -0.79 | AB |
| **F3027** | 18 | 12.43 | 0.40 | 1.70 | 0.14 | 10.20 | 17.50 | 1.42 | 3.68 | AB |
| **F3028** | 21 | 12.87 | 0.44 | 2.01 | 0.16 | 10.45 | 17.40 | 1.04 | 0.33 | AB |
| **F2671** | 20 | 13.31 | 0.46 | 2.07 | 0.16 | 11.05 | 20.55 | 2.45 | 7.65 | AB |
| **F3055** | 18 | 14.06 | 0.28 | 1.20 | 0.08 | 11.25 | 16.05 | -0.87 | 0.99 | B |
| **F3049** | 19 | 13.16 | 0.38 | 1.67 | 0.13 | 10.50 | 15.55 | 0.01 | -1.35 | AB |
| **F3033** | 18 | 12.79 | 0.30 | 1.27 | 0.10 | 10.20 | 15.10 | -0.32 | 0.14 | AB |
| **F3046** | 15 | 14.45 | 0.61 | 2.36 | 0.16 | 11.25 | 21.00 | 1.33 | 3.63 | B |
| **F3053** | 18 | 14.29 | 0.47 | 2.00 | 0.14 | 11.05 | 18.15 | 0.33 | -0.61 | B |
| **F2676** | 19 | 13.06 | 0.45 | 1.98 | 0.15 | 10.00 | 16.35 | 0.06 | -0.90 | AB |
| **F2678** | 17 | 12.81 | 0.39 | 1.62 | 0.13 | 10.00 | 15.55 | 0.05 | -0.59 | AB |
| **F3391** | 17 | 13.06 | 0.44 | 1.80 | 0.14 | 10.30 | 18.15 | 1.18 | 3.06 | AB |
| **F3056** | 19 | 12.82 | 0.37 | 1.62 | 0.13 | 10.90 | 16.85 | 1.41 | 1.29 | AB |
| **F2679** | 18 | 12.87 | 0.38 | 1.59 | 0.12 | 10.50 | 15.60 | 0.47 | -0.90 | AB |
| **F3036** | 19 | 13.36 | 0.44 | 1.90 | 0.14 | 10.95 | 18.45 | 1.20 | 1.71 | AB |
| **F3059** | 18 | 13.88 | 0.34 | 1.46 | 0.11 | 10.20 | 16.20 | -0.75 | 0.99 | AB |
| **F3034** | 18 | 12.75 | 0.41 | 1.75 | 0.14 | 10.55 | 16.80 | 1.07 | 0.36 | AB |
| **F3029** | 19 | 13.02 | 0.51 | 2.21 | 0.17 | 10.05 | 19.20 | 1.45 | 2.66 | AB |
| **F3041** | 18 | 13.72 | 0.24 | 1.03 | 0.08 | 12.15 | 16.25 | 0.84 | 0.74 | AB |
| **F2670** | 15 | 13.42 | 0.32 | 1.22 | 0.09 | 11.15 | 15.45 | -0.32 | -0.47 | AB |
| **F3387** | 20 | 12.65 | 0.30 | 1.33 | 0.10 | 10.10 | 15.00 | 0.05 | -0.57 | AB |
| **F2693** | 13 | 13.50 | 0.35 | 1.26 | 0.09 | 10.95 | 15.60 | -0.38 | 0.45 | AB |
| **F3060** | 19 | 13.08 | 0.33 | 1.43 | 0.11 | 11.15 | 17.10 | 1.61 | 2.91 | AB |
| **F2675** | 17 | 13.86 | 0.39 | 1.62 | 0.12 | 11.80 | 17.25 | 0.68 | -0.19 | AB |
| **F3390** | 19 | 12.83 | 0.28 | 1.22 | 0.09 | 10.40 | 14.90 | -0.09 | -0.25 | AB |
| **F3396** | 20 | 12.52 | 0.20 | 0.89 | 0.07 | 11.25 | 14.45 | 0.60 | -0.21 | AB |
| **F2806** | 20 | 13.39 | 0.37 | 1.63 | 0.12 | 10.50 | 16.15 | -0.02 | -1.04 | AB |
| **F3032** | 16 | 12.54 | 0.40 | 1.62 | 0.13 | 10.90 | 17.30 | 1.82 | 4.25 | AB |
| **F3048** | 17 | 12.29 | 0.25 | 1.02 | 0.08 | 10.95 | 15.00 | 1.02 | 1.67 | AB |
| **F3031** | 16 | 12.41 | 0.36 | 1.45 | 0.12 | 9.35 | 14.50 | -0.48 | -0.21 | AB |
| **F3388** | 17 | 12.85 | 0.36 | 1.49 | 0.12 | 10.90 | 15.80 | 0.70 | -0.24 | AB |
| **F3369** | 19 | 13.13 | 0.34 | 1.49 | 0.11 | 10.25 | 16.50 | 0.47 | 0.53 | AB |
| **F3040** | 18 | 12.92 | 0.24 | 1.00 | 0.08 | 11.15 | 15.15 | 0.36 | 1.01 | AB |
| **F3039** | 20 | 11.91 | 0.26 | 1.14 | 0.10 | 9.70 | 13.65 | -0.06 | -0.89 | A |

[1] **Stat:** Statistic; **SE:** Standard Error; **StDev:** Standard Deviation; **CoV:** Coefficient of Variation; **Min:** Minimum; **Max:** Maximum; **Skew**: Skewness; **Kurt:** Kurtosis; **Sig:** Statistical grouping.

**Table 3.8: Summary statistics for penetration depth (mm) using Pilodyn by family for the Region H white spruce Controlled Parentage Program at age 26. Families are ordered from lowest breeding value for height at 18 years to highest with breeding value categories (low, medium, high) being separated by bolded gridlines.**

| Fam/Stat[1] | Count | Mean | SE | StDev | CoV | Min | Max | Skew | Kurt |
|---|---|---|---|---|---|---|---|---|---|
| **F3043** | 12 | 21.5 | 1.4 | 4.8 | 0.22 | 12.5 | 28.5 | -0.41 | -0.39 |
| **F3037** | 10 | 19.1 | 1.3 | 4.0 | 0.21 | 12.0 | 25.0 | -0.15 | -0.37 |
| **F3030** | 11 | 19.3 | 0.6 | 1.9 | 0.10 | 16.0 | 21.5 | -0.47 | -1.30 |
| **F3368** | 9 | 21.9 | 0.7 | 2.2 | 0.10 | 19.0 | 25.0 | -0.03 | -1.71 |
| **F3058** | 10 | 18.9 | 1.0 | 3.2 | 0.17 | 12.0 | 22.5 | -1.07 | 1.27 |
| **F3035** | 10 | 21.6 | 1.0 | 3.1 | 0.14 | 16.5 | 26.0 | 0.04 | -0.28 |
| **F3038** | 8 | 20.8 | 0.6 | 1.7 | 0.08 | 19.0 | 23.5 | 0.34 | -1.29 |
| **F3027** | 13 | 22.1 | 0.6 | 2.3 | 0.10 | 18.0 | 25.0 | -0.46 | -0.63 |
| **F3028** | 13 | 21.6 | 1.1 | 3.8 | 0.18 | 15.0 | 27.0 | -0.58 | -0.72 |
| **F2671** | 14 | 21.9 | 0.9 | 3.4 | 0.15 | 17.0 | 28.0 | 0.37 | -1.02 |
| **F3055** | 11 | 20.6 | 0.6 | 2.0 | 0.10 | 17.5 | 25.0 | 0.88 | 1.36 |
| **F3049** | 15 | 22.0 | 0.7 | 2.5 | 0.12 | 18.0 | 25.5 | 0.02 | -1.20 |
| **F3033** | 12 | 21.1 | 0.6 | 2.0 | 0.09 | 17.5 | 25.5 | 0.41 | 1.90 |
| **F3046** | 10 | 20.5 | 1.1 | 3.6 | 0.18 | 14.5 | 27.0 | 0.07 | 0.15 |
| **F3053** | 12 | 19.8 | 1.2 | 4.2 | 0.21 | 15.0 | 27.5 | 0.43 | -1.05 |
| **F2676** | 14 | 21.1 | 1.1 | 4.0 | 0.19 | 14.0 | 27.0 | -0.14 | -0.96 |
| **F2678** | 11 | 21.4 | 0.3 | 1.1 | 0.05 | 19.0 | 23.0 | -0.52 | 1.41 |
| **F3391** | 11 | 22.9 | 1.1 | 3.8 | 0.16 | 18.0 | 28.5 | 0.23 | -1.38 |
| **F3056** | 13 | 20.1 | 1.4 | 5.1 | 0.25 | 10.0 | 26.0 | -0.87 | -0.12 |
| **F2679** | 12 | 21.0 | 0.8 | 2.8 | 0.14 | 17.5 | 26.5 | 0.84 | 0.01 |
| **F3036** | 13 | 21.7 | 0.7 | 2.4 | 0.11 | 18.5 | 26.0 | 0.33 | -0.64 |
| **F3059** | 13 | 22.4 | 0.8 | 2.9 | 0.13 | 19.5 | 30.5 | 1.93 | 4.44 |
| **F3034** | 14 | 20.9 | 1.0 | 3.7 | 0.18 | 12.5 | 25.0 | -1.32 | 0.99 |
| **F3029** | 13 | 21.7 | 1.0 | 3.6 | 0.17 | 16.5 | 27.0 | 0.03 | -1.61 |
| **F3041** | 12 | 19.9 | 0.9 | 3.1 | 0.16 | 15.5 | 24.0 | -0.06 | -1.79 |
| **F2670** | 9 | 20.4 | 1.1 | 3.4 | 0.17 | 15.5 | 27.0 | 0.58 | 0.68 |
| **F3387** | 13 | 20.7 | 1.1 | 4.1 | 0.20 | 10.5 | 27.0 | -0.95 | 2.52 |
| **F2693** | 7 | 20.1 | 1.2 | 3.1 | 0.16 | 16.5 | 24.5 | 0.25 | -1.81 |
| **F3060** | 13 | 22.8 | 0.7 | 2.5 | 0.11 | 18.0 | 26.5 | -0.11 | -0.45 |
| **F2675** | 12 | 20.1 | 0.7 | 2.3 | 0.12 | 16.0 | 22.5 | -0.73 | -0.94 |
| **F3390** | 12 | 22.0 | 0.5 | 1.9 | 0.09 | 19.0 | 25.0 | 0.15 | -0.98 |
| **F3396** | 14 | 21.3 | 1.1 | 4.1 | 0.19 | 15.0 | 28.5 | 0.08 | -0.89 |
| **F2806** | 13 | 19.6 | 0.7 | 2.4 | 0.12 | 15.0 | 24.5 | 0.17 | 0.77 |
| **F3032** | 11 | 21.2 | 0.9 | 3.1 | 0.14 | 15.5 | 26.0 | -0.06 | -0.08 |
| **F3048** | 13 | 21.4 | 0.7 | 2.6 | 0.12 | 17.5 | 26.5 | 0.25 | -0.05 |
| **F3031** | 9 | 21.3 | 1.7 | 5.1 | 0.24 | 13.5 | 29.0 | 0.14 | -0.65 |
| **F3388** | 13 | 21.5 | 0.6 | 2.1 | 0.10 | 19.5 | 25.0 | 0.86 | -0.84 |
| **F3369** | 13 | 20.7 | 1.1 | 3.9 | 0.19 | 13.0 | 25.5 | -0.58 | -0.20 |
| **F3040** | 12 | 22.1 | 1.0 | 3.4 | 0.15 | 15.5 | 27.5 | -0.08 | 0.20 |
| **F3039** | 14 | 22.6 | 0.7 | 2.5 | 0.11 | 17.5 | 26.0 | -0.38 | -0.46 |

[1] **Stat:** Statistic; **SE:** Standard Error; **StDev:** Standard Deviation; **CoV:** Coefficient of Variation; **Min:** Minimum; **Max:** Maximum; **Skew**: Skewness; **Kurt:** Kurtosis.

**Table 3.9: Summary statistics for wood specific gravity using water displacement by family for the Region H white spruce Controlled Parentage Program at age 26. Families are ordered from lowest breeding value for height at 18 years to highest with breeding value categories (low, medium, high) being separated by bolded gridlines.**

| Fam/Stat | Count | Mean | SE | StDev | CoV | Min | Max | Skew | Kurt |
|---|---|---|---|---|---|---|---|---|---|
| **F3043** | 7 | 0.342 | 0.022 | 0.057 | 0.17 | 0.231 | 0.408 | -1.19 | 2.06 |
| **F3037** | 5 | 0.377 | 0.029 | 0.064 | 0.17 | 0.286 | 0.435 | -0.83 | -1.42 |
| **F3030** | 4 | 0.371 | 0.013 | 0.027 | 0.07 | 0.347 | 0.409 | 1.45 | 2.60 |
| **F3368** | 3 | 0.371 | 0.012 | 0.020 | 0.05 | 0.350 | 0.390 | -0.59 | - |
| **F3058** | 4 | 0.392 | 0.017 | 0.034 | 0.09 | 0.356 | 0.429 | 0.05 | -3.67 |
| **F3035** | 3 | 0.395 | 0.028 | 0.049 | 0.12 | 0.362 | 0.451 | 1.65 | - |
| **F3038** | 5 | 0.396 | 0.022 | 0.048 | 0.12 | 0.361 | 0.480 | 1.91 | 3.77 |
| **F3027** | 5 | 0.340 | 0.003 | 0.007 | 0.02 | 0.328 | 0.348 | -1.26 | 2.66 |
| **F3028** | 4 | 0.382 | 0.024 | 0.048 | 0.13 | 0.333 | 0.448 | 1.01 | 2.04 |
| **F2671** | 6 | 0.377 | 0.013 | 0.032 | 0.09 | 0.339 | 0.425 | 0.63 | -0.77 |
| **F3055** | 5 | 0.389 | 0.014 | 0.031 | 0.08 | 0.342 | 0.427 | -0.73 | 1.87 |
| **F3049** | 5 | 0.366 | 0.024 | 0.054 | 0.15 | 0.305 | 0.442 | 0.59 | -0.69 |
| **F3033** | 4 | 0.363 | 0.011 | 0.021 | 0.06 | 0.338 | 0.388 | 0.00 | -0.52 |
| **F3046** | 6 | 0.379 | 0.012 | 0.030 | 0.08 | 0.346 | 0.420 | 0.11 | -1.58 |
| **F3053** | 5 | 0.397 | 0.012 | 0.026 | 0.07 | 0.363 | 0.428 | -0.04 | -1.51 |
| **F2676** | 6 | 0.377 | 0.016 | 0.038 | 0.10 | 0.312 | 0.418 | -0.98 | 1.19 |
| **F2678** | 5 | 0.385 | 0.023 | 0.051 | 0.13 | 0.332 | 0.469 | 1.43 | 3.08 |
| **F3391** | 5 | 0.370 | 0.017 | 0.038 | 0.10 | 0.322 | 0.418 | 0.07 | -1.19 |
| **F3056** | 5 | 0.405 | 0.015 | 0.034 | 0.08 | 0.375 | 0.443 | 0.54 | -3.22 |
| **F2679** | 3 | 0.384 | 0.026 | 0.045 | 0.12 | 0.356 | 0.436 | 1.71 | - |
| **F3036** | 4 | 0.381 | 0.013 | 0.026 | 0.07 | 0.344 | 0.405 | -1.35 | 2.42 |
| **F3059** | 5 | 0.387 | 0.023 | 0.052 | 0.13 | 0.319 | 0.460 | 0.25 | 0.84 |
| **F3034** | 4 | 0.374 | 0.039 | 0.078 | 0.21 | 0.319 | 0.486 | 1.55 | 2.15 |
| **F3029** | 6 | 0.386 | 0.024 | 0.059 | 0.15 | 0.302 | 0.474 | 0.10 | 0.24 |
| **F3041** | 6 | 0.373 | 0.009 | 0.022 | 0.06 | 0.350 | 0.415 | 1.56 | 3.17 |
| **F2670** | 3 | 0.398 | 0.024 | 0.042 | 0.10 | 0.358 | 0.441 | 0.25 | - |
| **F3387** | 7 | 0.355 | 0.022 | 0.059 | 0.17 | 0.231 | 0.403 | -1.94 | 4.19 |
| **F2693** | 2 | 0.379 | 0.012 | 0.019 | 0.05 | 0.365 | 0.392 | - | - |
| **F3060** | 6 | 0.373 | 0.018 | 0.045 | 0.12 | 0.333 | 0.458 | 1.74 | 3.42 |
| **F2675** | 5 | 0.373 | 0.012 | 0.027 | 0.07 | 0.347 | 0.418 | 1.49 | 2.55 |
| **F3390** | 5 | 0.362 | 0.011 | 0.025 | 0.07 | 0.343 | 0.403 | 1.49 | 1.81 |
| **F3396** | 7 | 0.347 | 0.007 | 0.018 | 0.05 | 0.322 | 0.373 | -0.28 | -0.57 |
| **F2806** | 5 | 0.362 | 0.015 | 0.033 | 0.09 | 0.325 | 0.399 | -0.22 | -2.60 |
| **F3032** | 4 | 0.352 | 0.016 | 0.032 | 0.09 | 0.327 | 0.399 | 1.68 | 3.04 |
| **F3048** | 4 | 0.352 | 0.013 | 0.027 | 0.08 | 0.329 | 0.390 | 1.36 | 1.88 |
| **F3031** | 4 | 0.380 | 0.010 | 0.020 | 0.05 | 0.355 | 0.402 | -0.29 | -1.19 |
| **F3388** | 5 | 0.371 | 0.004 | 0.009 | 0.02 | 0.359 | 0.382 | -0.19 | -0.19 |
| **F3369** | 4 | 0.356 | 0.018 | 0.036 | 0.10 | 0.320 | 0.406 | 1.05 | 1.86 |
| **F3040** | 4 | 0.363 | 0.008 | 0.017 | 0.05 | 0.345 | 0.383 | 0.18 | -2.61 |
| **F3039** | 6 | 0.337 | 0.012 | 0.029 | 0.09 | 0.295 | 0.374 | -0.41 | -0.77 |

[1] **Stat:** Statistic; **SE:** Standard Error; **StDev:** Standard Deviation; **CoV:** Coefficient of Variation; **Min:** Minimum; **Max:** Maximum; **Skew**: Skewness; **Kurt:** Kurtosis.

**Table 3.10: Summary statistics for inside-bark diameter at breast height (mm) using Resistograph by family for the Region H white spruce Controlled Parentage Program at age 26. Families are ordered from lowest breeding value for height at 18 years to highest with breeding value categories (low, medium, high) being separated by bolded gridlines.**

| Fam/Stat | Count | Mean | SE | StDev | CoV | Min | Max | Skew | Kurt |
|---|---|---|---|---|---|---|---|---|---|
| **F3043** | 18 | 81.6 | 6.5 | 27.6 | 0.34 | 35.5 | 131.5 | -0.12 | -0.60 |
| **F3037** | 16 | 75.6 | 6.5 | 25.9 | 0.34 | 30.5 | 112.0 | -0.17 | -1.27 |
| **F3030** | 17 | 77.7 | 7.5 | 31.1 | 0.40 | 34.5 | 142.0 | 0.74 | -0.03 |
| **F3368** | 15 | 92.7 | 8.4 | 32.4 | 0.35 | 19.5 | 140.0 | -0.74 | 0.26 |
| **F3058** | 15 | 79.5 | 5.9 | 22.8 | 0.29 | 48.0 | 123.0 | 0.48 | -0.70 |
| **F3035** | 14 | 90.1 | 7.8 | 29.3 | 0.32 | 33.5 | 142.5 | 0.05 | -0.18 |
| **F3038** | 14 | 73.8 | 7.8 | 29.0 | 0.39 | 28.0 | 122.0 | 0.21 | -0.95 |
| **F3027** | 18 | 86.0 | 7.1 | 30.2 | 0.35 | 40.5 | 150.5 | 0.38 | -0.34 |
| **F3028** | 21 | 77.7 | 6.1 | 28.1 | 0.36 | 28.5 | 135.0 | -0.12 | -0.52 |
| **F2671** | 20 | 86.6 | 5.7 | 25.6 | 0.30 | 42.0 | 130.0 | -0.03 | -0.90 |
| **F3055** | 18 | 91.2 | 4.8 | 20.3 | 0.22 | 49.5 | 131.0 | -0.13 | -0.11 |
| **F3049** | 19 | 87.9 | 5.0 | 21.9 | 0.25 | 42.0 | 123.0 | -0.15 | -0.51 |
| **F3033** | 18 | 85.6 | 3.9 | 16.4 | 0.19 | 49.5 | 109.5 | -0.96 | 0.44 |
| **F3046** | 15 | 85.9 | 5.8 | 22.3 | 0.26 | 46.5 | 116.0 | -0.15 | -1.20 |
| **F3053** | 18 | 88.5 | 7.2 | 30.7 | 0.35 | 45.0 | 145.0 | 0.11 | -1.14 |
| **F2676** | 19 | 89.9 | 7.0 | 30.5 | 0.34 | 38.5 | 132.5 | -0.12 | -1.21 |
| **F2678** | 17 | 87.5 | 4.3 | 17.7 | 0.20 | 59.0 | 123.5 | 0.34 | -0.08 |
| **F3391** | 17 | 91.1 | 6.9 | 28.3 | 0.31 | 51.0 | 150.0 | 0.48 | -0.57 |
| **F3056** | 19 | 88.7 | 5.9 | 25.5 | 0.29 | 31.5 | 124.5 | -0.59 | -0.26 |
| **F2679** | 18 | 88.1 | 6.6 | 27.9 | 0.32 | 47.0 | 125.0 | 0.07 | -1.47 |
| **F3036** | 19 | 88.4 | 6.5 | 28.4 | 0.32 | 38.0 | 147.0 | 0.39 | -0.48 |
| **F3059** | 18 | 93.1 | 3.7 | 15.6 | 0.17 | 70.0 | 138.0 | 1.20 | 2.98 |
| **F3034** | 18 | 84.3 | 7.0 | 29.7 | 0.35 | 40.0 | 148.0 | 0.48 | -0.19 |
| **F3029** | 19 | 95.2 | 6.0 | 26.2 | 0.28 | 46.5 | 140.0 | -0.26 | -0.71 |
| **F3041** | 18 | 87.9 | 5.7 | 24.3 | 0.28 | 43.0 | 123.0 | -0.49 | -0.72 |
| **F2670** | 15 | 84.9 | 5.0 | 19.3 | 0.23 | 40.5 | 118.0 | -0.80 | 1.00 |
| **F3387** | 20 | 95.4 | 7.3 | 32.5 | 0.34 | 30.0 | 151.0 | -0.15 | -0.59 |
| **F2693** | 13 | 76.4 | 5.4 | 19.6 | 0.26 | 49.0 | 120.0 | 0.74 | 0.50 |
| **F3060** | 19 | 96.5 | 5.1 | 22.2 | 0.23 | 53.0 | 129.0 | -0.21 | -0.81 |
| **F2675** | 17 | 80.4 | 6.2 | 25.5 | 0.32 | 40.5 | 123.0 | 0.22 | -0.80 |
| **F3390** | 19 | 101.0 | 5.6 | 24.6 | 0.24 | 42.0 | 130.0 | -0.92 | 0.29 |
| **F3396** | 20 | 101.3 | 6.4 | 28.5 | 0.28 | 39.0 | 153.5 | -0.62 | 0.56 |
| **F2806** | 20 | 82.8 | 7.2 | 32.1 | 0.39 | 39.0 | 149.5 | 0.75 | -0.49 |
| **F3032** | 16 | 94.9 | 6.7 | 26.7 | 0.28 | 43.0 | 135.5 | -0.24 | -0.84 |
| **F3048** | 17 | 95.5 | 7.0 | 28.9 | 0.30 | 50.0 | 144.0 | 0.17 | -1.06 |
| **F3031** | 16 | 97.6 | 7.6 | 30.5 | 0.31 | 41.0 | 154.0 | 0.09 | -0.40 |
| **F3388** | 17 | 92.5 | 4.9 | 20.3 | 0.22 | 46.5 | 122.0 | -0.41 | 0.07 |
| **F3369** | 19 | 101.3 | 8.4 | 36.6 | 0.36 | 34.5 | 150.5 | -0.46 | -0.86 |
| **F3040** | 18 | 92.1 | 5.7 | 24.2 | 0.26 | 54.5 | 137.0 | 0.39 | -0.59 |
| **F3039** | 20 | 103.1 | 6.4 | 28.6 | 0.28 | 46.0 | 144.0 | -0.41 | -0.67 |

[1] **Stat:** Statistic; **SE:** Standard Error; **StDev:** Standard Deviation; **CoV:** Coefficient of Variation; **Min:** Minimum; **Max:** Maximum; **Skew**: Skewness; **Kurt:** Kurtosis.

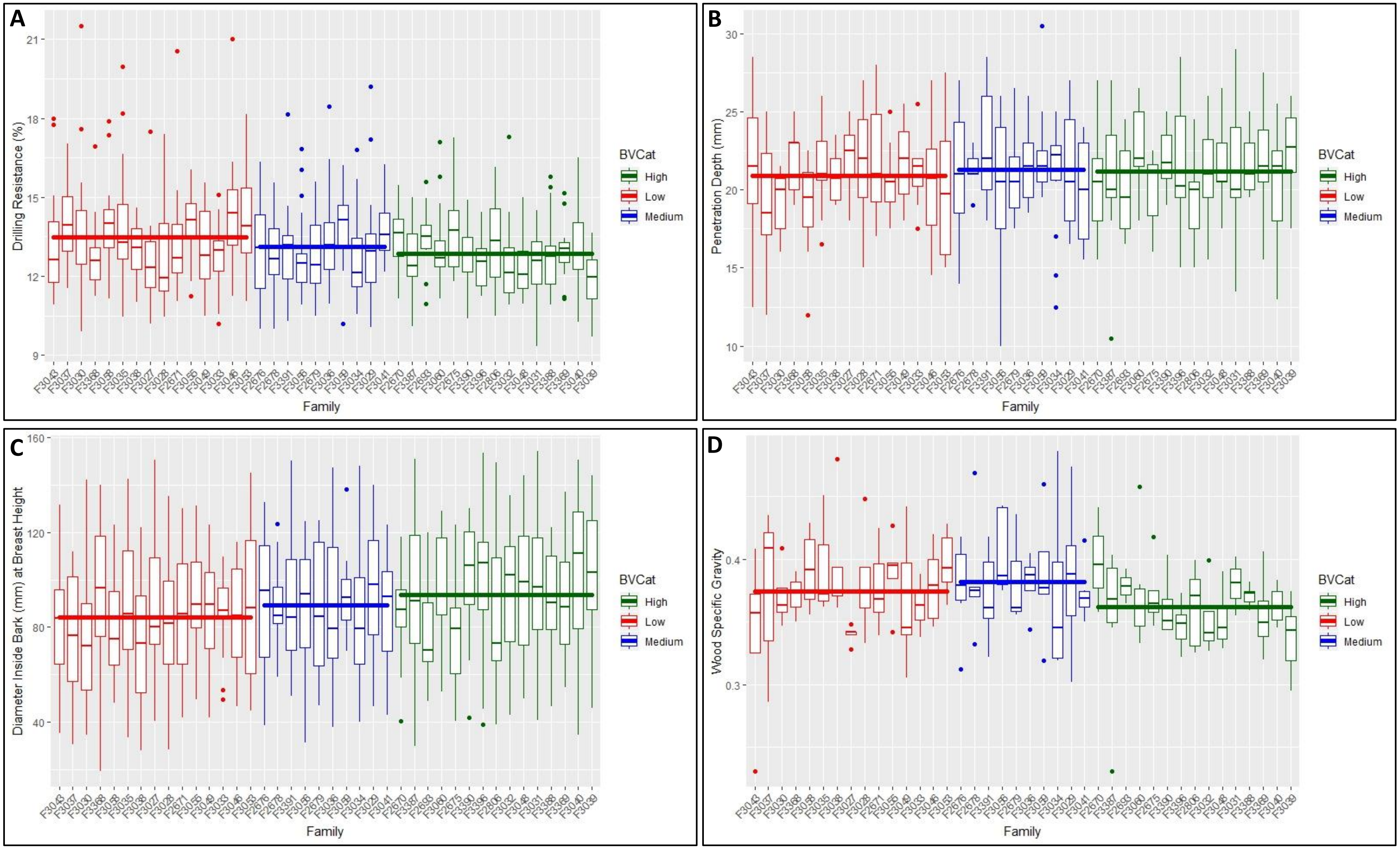

**Figure 3.5: Boxplots for drilling resistance (%) using Resistograph (A), penetration depth (mm) using Pilodyn (B), wood specific gravity using water displacement (C) and diameter inside bark (mm) at breast height using Resistograph (D) by family for the Region H Controlled Parentage Program at age 26. Families are ordered from smallest to largest breeding value for height at 18 years and breeding value category (BVCat - low, medium, high) is indicated by colour. The trait average for each respective breeding value category is indicated by a coloured line.**

### 3.3 – Phenotypic Correlations for Quantitative Traits

Phenotypic correlations between DR, PD, WSG and DIB were calculated both at the individual- and family-levels. Individual-level phenotypic correlations between all traits were all significant and generally moderate in strength and possessing relatively low estimates of standard error (Table 3.11, Figure 3.6A-E). The correlation between PD and DIB was somewhat stronger than the other correlations of WD measurements and DIB (Figure 3.6E, $r_p = 0.76$ versus Figure 3.6D and F, $r_p < 0.50$). In general, the strength of the correlation between any WD trait and DIB were similar in strength and the direction of each indicated a relationship where increasingly large trees possessed lower WD (i.e. negative correlation between DR/WSG and DIB [Figures 3.6D and 3.6F], positive correlation between PD and DIB [Figure 3.6E]). The strength of the correlation between the three WD traits were approximately equal for all three combinations (i.e. DR and PD, DR and WSG and PD and WSG [Table 3.11]). The direction of the correlations all reflected a relationship where increasing WD as indicated by the first trait reflected an increase in WD for the second trait (Figures 3.6D-F).

Family-level phenotypic correlations were generally slightly lower than their individual-level counterparts and the associated estimates of standard error were approximately double compared to the respective individual-level correlation (Table 3.12, Figures 3.7A-E). For example, the correlation between DR and WSG at the individual- and family-levels were $r_p$ = 0.56 and 0.54 with standard errors (+/-) of 0.06 and 0.14, respectively (Tables 3.11 and 3.12, Figures 3.6B and 3.7B). The inflated standard errors associated with the family-level phenotypic correlations are a direct result of the lower number of observations (i.e. there are several hundred individual observations, but only 40 families assessed). Overall, the family-level correlations indicated the same relationships as above and with a similar strength in the relationship, except for PD and DIB, which were somewhat lower compared to individual-level correlations and decreased from $r_p = 0.76$ at the individual-level to $r_p = 0.55$ at the family-level (Figure 3.6E and Figure 3.7E).

**Table 3.11: Individual-level phenotypic correlations ($r_p$) for traits measured and its associated standard error (+/-, in brackets), p-value and degrees of freedom (in brackets) for drilling resistance (%) using Resistograph, penetration depth (mm) using Pilodyn, wood specific gravity using water displacement and diameter inside bark (mm) at breast height using Resistograph for the Region H white spruce Controlled Parentage Program at age 26.**

| Traits Measured | Correlation Coefficient (SE) | p-value (df) |
|---|---|---|
| **DR ~ PD** | -0.61 (0.04) | < 0.001 (472) |
| **DR ~ WSG** | 0.56 (0.06) | < 0.001 (189) |
| **PD ~ WSG** | -0.64 (0.07) | < 0.001 (133) |
| **DR ~ DIB** | -0.44 (0.03) | < 0.001 (702) |
| **PD ~ DIB** | 0.76 (0.03) | < 0.001 (472) |
| **WSG ~ DIB** | -0.49 (0.06) | < 0.001 (189) |

**DR:** Drilling resistance (%); **PD:** Penetration depth (mm); **WSG:** Wood specific gravity; **DIB:** Diameter inside bark (mm) at breast height; **SE:** Standard error; **df:** Degrees of freedom.

**Table 3.12: Family-level phenotypic correlations ($r_p$) for traits measured and its associated standard error (+/-, in brackets), p-value and degrees of freedom (in brackets) for drilling resistance (%) using Resistograph, penetration depth (mm) using Pilodyn, wood specific gravity using water displacement and diameter inside bark (mm) at breast height using Resistograph for the Region H white spruce Controlled Parentage Program at age 26.**

| Traits Measured | Correlation Coefficient (SE) | p-value (df) |
|---|---|---|
| **DR ~ PD** | -0.53 (0.14) | < 0.001 (38) |
| **DR ~ WSG** | 0.54 (0.14) | < 0.001 (38) |
| **PD ~ WSG** | -0.50 (0.14) | 0.001 (38) |
| **DR ~ DIB** | -0.48 (0.14) | 0.002 (38) |
| **PD ~ DIB** | 0.55 (0.12) | < 0.001 (38) |
| **WSG ~ DIB** | -0.42 (0.15) | 0.007 (38) |

**DR:** Drilling resistance (%); **PD:** Penetration depth (mm); **WSG:** Wood specific gravity; **DIB:** Diameter inside bark (mm) at breast height; **SE:** Standard error; **df:** Degrees of freedom.

## 3.4 – Wood Density Regression Analyses

Multiple linear regression analyses were conducted to assess how well DR and PD could predict WSG. Overall, the strength of the predictive relationships were weak to moderate, though both were significant at the individual-level (Table 3.13). The family-level regression models were of approximately the same strength for DR but somewhat weaker for PD, while both were significant (Table 3.14). However, the standard errors associated with each regression model were small at both the individual- (0.03-0.04 – Table 3.13) and family-levels (0.02 – Table 3.14), indicating that although the accuracy of the estimate is moderate, the precision is high.

**Table 3.13: Summary of the multiple linear regression models for drilling resistance (%) using Resistograph plus diameter inside bark (mm) at breast height using Resistograph and penetration depth (mm) using Pilodyn plus diameter inside bark (mm) at breast height using Resistograph at the individual-level for the Region H white spruce Controlled Parentage Program at age 26.**

| Regression Model Statement | Adjusted $r^2$ (SE[1]) | p-value (df) | Regression Equation |
|---|---|---|---|
| WSG ~ DR + DIB | 0.38 (0.04) | < 0.001 (188) | $WSG = 0.29 + 0.01*DR + 5.20*10^{-4}*DIB$ |
| WSG ~ PD + DIB | 0.41 (0.03) | < 0.001 (132) | $WSG = 0.54 – 6.36*10^{-3}*PD – 3.23*10^{-4}*DIB$ |

[1] **SE:** Standard error: **WSG:** Wood specific gravity; **DR:** Drilling resistance (%); **PD:** Penetration depth (mm); **DIB:** Diameter inside bark (mm) at breast height; **df:** Degrees of freedom.

**Table 3.14: Summary of the multiple linear regression models for drilling resistance (%) using Resistograph plus diameter inside bark (mm) at breast height using Resistograph and penetration depth (mm) using Pilodyn plus diameter inside bark (mm) at breast height using Resistograph at the family-level for the Region H white spruce Controlled Parentage Program at age 26.**

| Regression Model Statement | Adjusted $r^2$ (SE[1]) | p-value (df) | Regression Equation |
|---|---|---|---|
| WSG ~ DR + DIB | 0.38 (0.02) | < 0.001 (37) | $WSG = 0.28 + 9.46*10^{-3}*DR + 2.91*10^{-4}*DIB$ |
| WSG ~ PD + DIB | 0.41 (0.02) | = 0.003 (37) | $WSG = 0.48 + 3.45*10^{-3}*PD + 3.50*10^{-4}*DIB$ |

[1] **SE:** Standard error: **WSG:** Wood specific gravity; **DR:** Drilling resistance (%); **PD:** Penetration depth (mm); **DIB:** Diameter inside bark (mm) at breast height; **df:** Degrees of freedom.

## 3.5 – Family Rank Order for Quantitative Traits by Site and Genotype-Environment Interaction

Overall, the family rank order for each of the four quantitative traits (DR, PD, WSG and DIB) was similar between sites (Figure 3.8A-D). In most cases, there were not large changes in family ranking for each individual trait among the three sites. For example, F3039 ranked the lowest for mean family DR at both the Red Earth and Hay River sites and had the 7th lowest rank at the Chinchaga site (Figure 3.8A). Additionally, family rankings for WD (i.e. DR, PD and WSG) traits were generally similar within a single site, though not identical. For example, F2678 ranked second highest for family-level WSG, 13th for DR but ranked 39th for Pilodyn at the Hay River site (Figure 3.8A-C). For example, F3055 at Hay River ranked highly for all four quantitative traits. In summary, it appears that there were relatively low levels of genotype by environment interaction for any of the WD traits and DIB. A two-factor ANOVA showed that there were significant differences between sites for all traits, significant differences between families for all traits except for WSG and a significant interaction between site and family for PD and DIB (Table 3.15). The lower number of observations/family/site for WSG compromised the power of the two-factor ANOVA and likely do not provide robust results (Table 3.15).

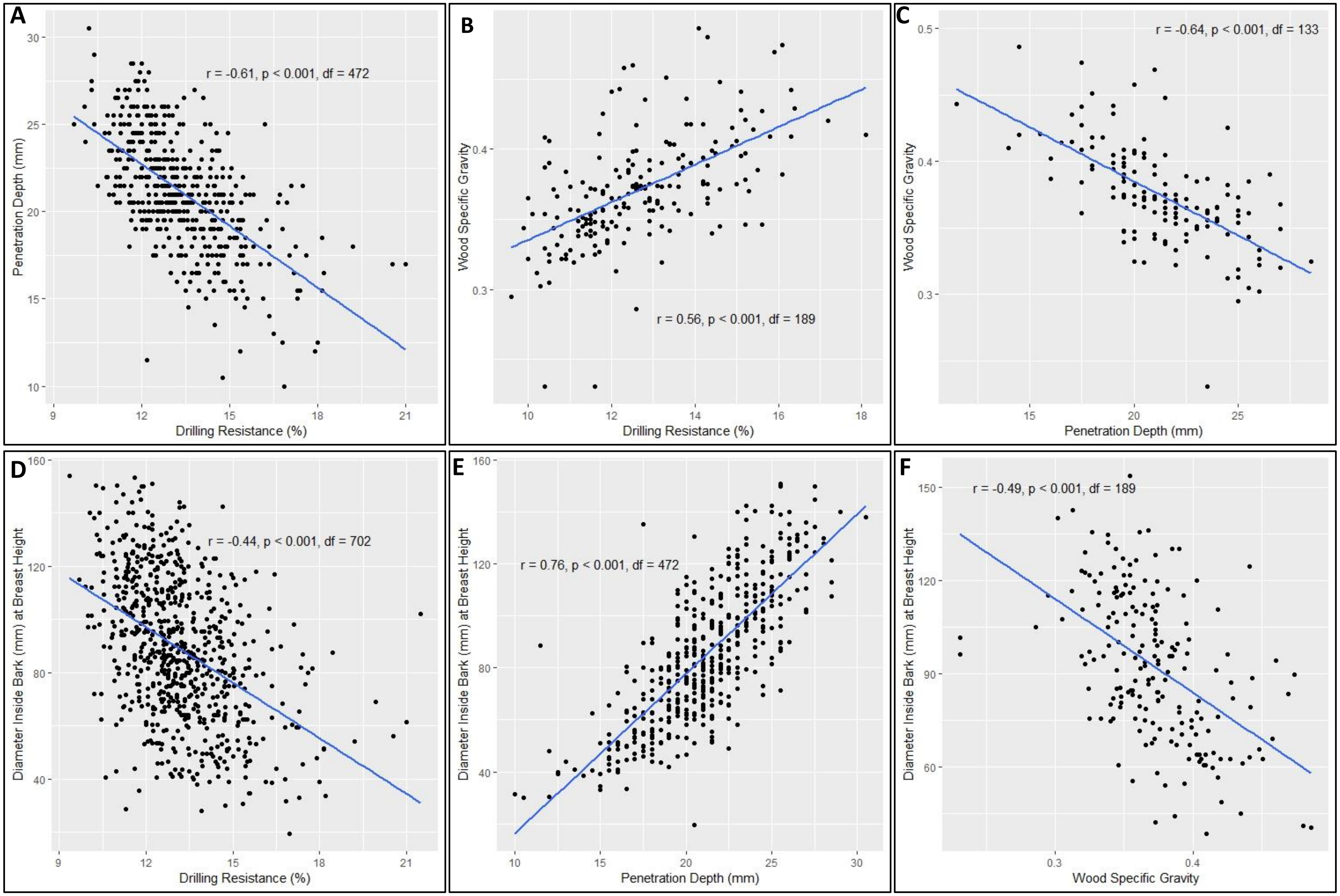

**Figure 3.6: Scatterplots for individual-level phenotypic correlations ($r_p$) with regression lines for drilling resistance (DR - %) and penetration depth (PD – mm) (A), DR and wood specific gravity (WSG) (B), PD and WSG (C), DR and diameter inside bark (mm) at breast height (DIB) (D), PD and DIB (E) and WSG and DIB (F) for the Region H white spruce Controlled Parentage Program at age 26. DR and DIB were measured using Resistograph, PD was measured using Pilodyn and WSG was measured using water displacement.**

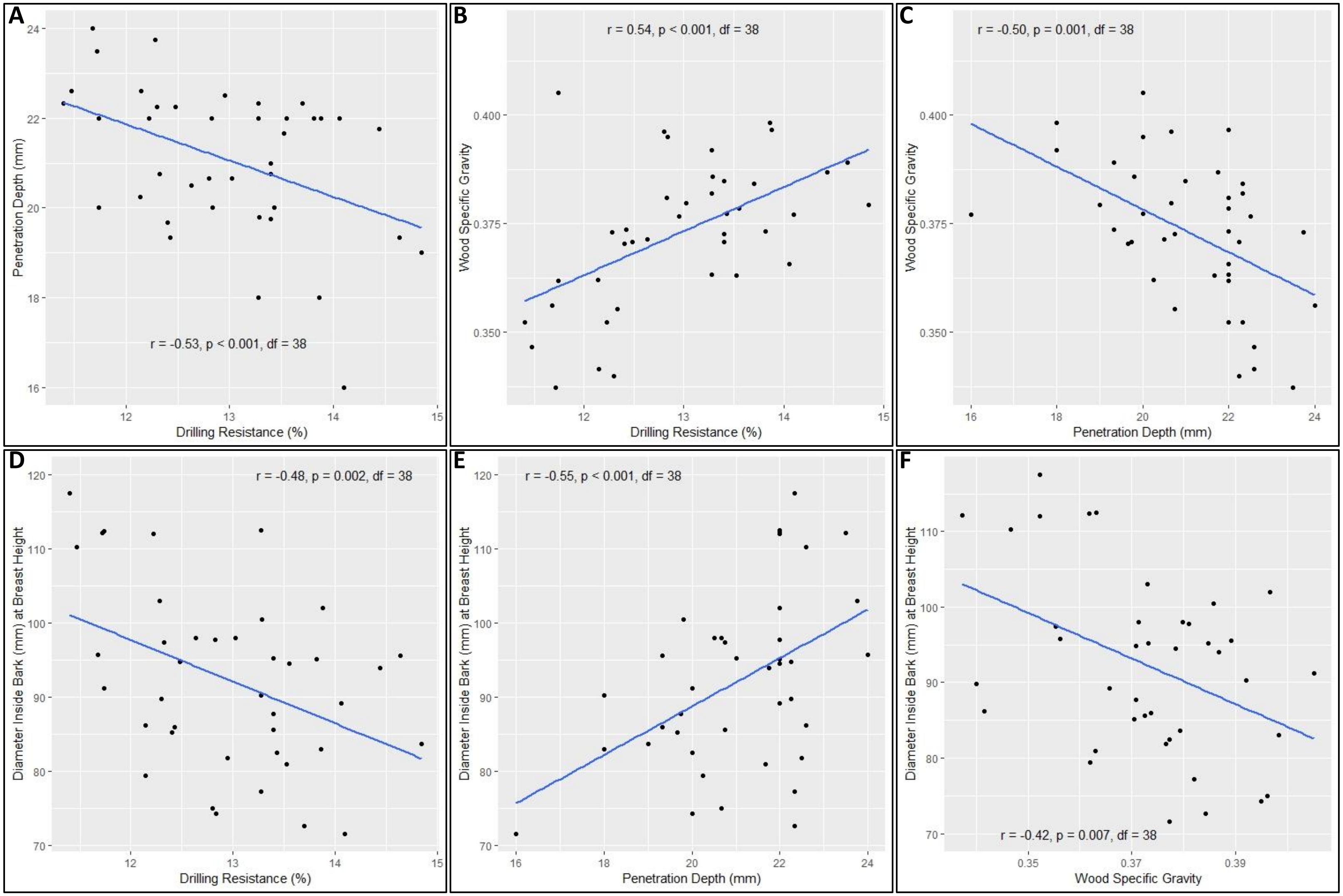

**Figure 3.7: Scatterplots for family-level phenotypic correlations ($r_P$) with regression lines for drilling resistance (DR - %) and penetration depth (PD – mm) (A), DR and wood specific gravity (WSG) (B), PD and WSG (C), DR and diameter inside bark (mm) at breast height (DIB) (D), PD and DIB (E) and DIB and WSG (F) for the Region H white spruce Controlled Parentage Program at age 26. DR and DIB were measured using Resistograph, PD was measured using Pilodyn and WSG was measured using water displacement.**

**Table 3.15: Summary of two-factor ANOVA between site, family and site x family interaction for drilling resistance (%) using Resistograph, penetration depth (mm) using Pilodyn, wood specific gravity using water displacement and diameter inside bark (mm) at breast height using Resistograph across three test sites and 40 families for the Region H white spruce Controlled Parentage Program at age 26.**

| | Trait Measured | | | |
|---|---|---|---|---|
| **Variance Component** | **DR (%)** | **PD (mm)** | **WSG** | **DIB (mm)** |
| **Site (p-value [df])** | < 0.001 (2) | < 0.001 (1) | < 0.001 (2) | < 0.001 (2) |
| **Family (p-value [df])** | < 0.001 (39) | 0.005 (39) | 0.438 (39) | 0.008 (39) |
| **Site x Family (p-value [df])** | 0.522 (78) | 0.009 (39) | 0.253 (64) | 0.035 (78) |
| **Residuals (df)** | 584 | 394 | 85 | 584 |

**DR:** Drilling resistance; **PD:** Penetration depth; **WSG:** Wood specific gravity; **DIB:** Diameter inside bark at breast height; **df:** Degrees of freedom.

### 3.6 – Narrow Sense Heritability for Drilling Resistance, Penetration Depth and Diameter Inside Bark at Breast Height by Site

Overall, the narrow sense heritability of the WD traits (i.e. DR, PD) was higher than the heritability of DIB (Table 3.16); however, both DR and DIB varied greatly between sites. Specifically, the heritability of DR was very low with a large standard error at Hay River ($r_g$ = 0.11 ± 0.12) while DIB was quite high ($r_g$ = 0.42 ± 0.17), while the opposite was true for Chinchaga and Red Earth (Table 3.16). Additionally, the heritability of PD fell between the heritability of DR and DIB and was very similar between the Chinchaga and Hay River sites. In general, the standard error associated with each heritability estimate was quite high, even exceeding the heritability of the trait for DR at Hay River and for DIB at Chinchaga and Red Earth. In all other cases, the relative value of standard error was approximately one third to one half of the respective heritability. However, it does appear that standard error was somewhat lower when there were more observations for a trait and site. For example, the standard error for the heritability of DR was 0.23, 0.17 and 0.11 with 195, 230 and 279 observations for Chinchaga, Red Earth and Hay River, respectively.

**Table 3.16 – Narrow sense heritability ($h^2$) and its associated ± standard error (inside brackets) by site and trait for drilling resistance (%) using Resistograph, penetration depth (mm) using Pilodyn and diameter inside bark (mm) at breast height using Resistograph for the Region H white spruce Controlled Parentage Program at age 26.**

| Site/Trait | Drilling Resistance (%) | Penetration Depth (mm) | Diameter Inside Bark (mm) at Breast Height |
|---|---|---|---|
| **Chinchaga** | 0.62 (0.23) | 0.35 (0.20) | 0.11 (0.17) |
| **Hay River** | 0.11 (0.12) | 0.27 (0.15) | 0.42 (0.17) |
| **Red Earth Creek** | 0.31 (0.17) | - | 0.09 (0.14) |

### 3.7 – Genetic Correlations Between Drilling Resistance, Penetration Depth and Diameter Inside Bark at Breast Height by Site

Overall, the individual-level genetic correlations, which were calculated using Pearson's correlation method using BVs for each respective trait and site, were all significant and varied between 0.27 to 0.71 (Table 3.17, Figure 3.9A-C. The correlation between DR and DIB was similar between the Chinchaga and Red Earth sites, whereas Hay River showed a somewhat stronger correlation (Figure 3.9A). The correlation between PD and DIB for Chinchaga and Hay River was positive and moderate-strong for both sites, in contrast to the relationships found for DR and DIB; however, both correlations indicate a relationship where an increase in DIB reflects a decrease in WD. The significant and moderate negative correlation between DR and PD was similar to that found throughout this chapter, both in direction and strength.

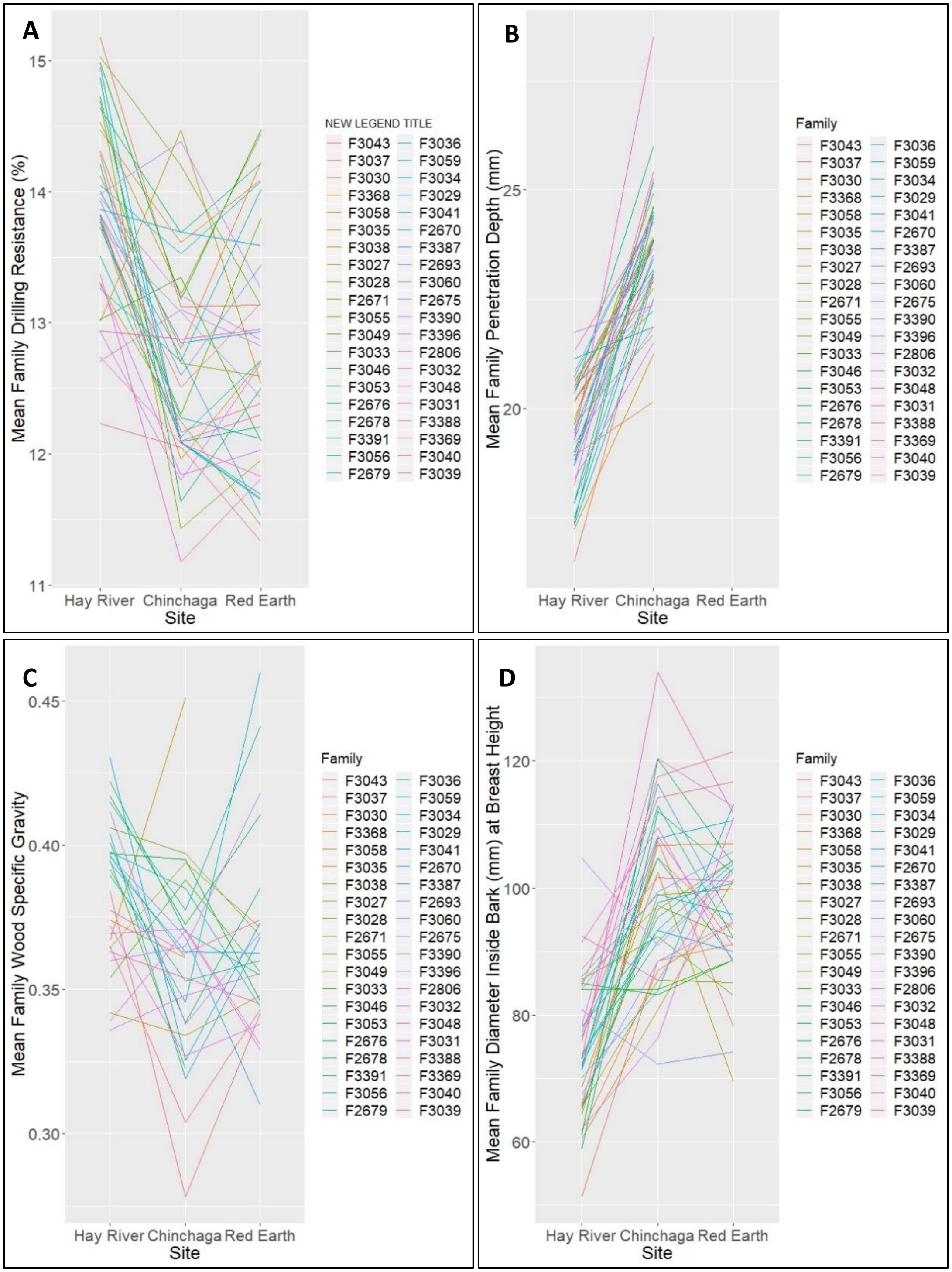

**Figure 3.8: Family ranking for drilling resistance (%) using Resistograph (A), penetration depth (mm) using Pilodyn (B), wood specific gravity using water displacement (C) and diameter inside bark (mm) at breast height using Resistograph (D) for the Region H Controlled Parentage Program at age 26. In general, most families display no or small rank changes by site (i.e. little gene-environment interaction), though there are some families with disparate performance between sites. For example, F3038 ranks highly for DR at Chinchaga but poorly at Hay River and Red Earth. Families are ordered from lowest to highest breeding value for height at age 18, starting on the left and proceeding downwards, in the legend of each plot.**

Family-level genetic correlations (Table 3.18, Figure 3.10) were somewhat different to those found above. It should be noted that the family-level genetic correlations included analyses with the breeding value for height at 25 years, which were provided by the GoA. In general, the relationship between WD traits (i.e. DR and PD) and growth traits (DIB and Height) were found to be weak and not significant (Figure 3.10A, B, C, E F). The only exception was the correlation between PD and DIB, which was positive, significant and moderate in strength (Figure 3.10D). In general, the BVs for height were the most variable and possessed the greatest range, followed by DIB. The BVs of DR and PD were very low and occupied a vary narrow range (Table 3.19, Figure 3.11). In general, the BVs for DR, PD and DIB showed no clear relationship with the BVs for height at age 25. Specifically, the range of the BVs for height was large and there was a clear trend where the high, medium and low BV category families possessed positive, near zero and negative BVs, respectively. Additionally, there was greater variation between the high and low families (i.e. medium BV families occurred over a very narrow ranged compared to either high or low BV families). In contrast, the mean BVs for DR, PD and DIB across the three BV categories were near zero, and the dispersion of BVs was similar between BV categories (Figure 3.11). In summary, there are clear differences in the genetic performance between high, medium and low BV families for height at 25 years (as determined by the GoA), but not for DR, PD or DIB at age 26 and no genetic correlation was found between height and DR, PD or DIB in the present study. Part of the discrepancy between the differences in genetic performance for height and DIB may be related to the way BVs were calculated between the two studies. For example, the GoA study compares all selected families to wild bulk check lots collected form the Region H

CPP, while the present study compares improved families directly to each other, which may reduce the apparent differences in performance.

**Table 3.17: Individual-level genetic correlations (r) and its associated standard errors by site, p-value and degrees of freedom by site for drilling resistance (%) using Resistograph, penetration depth (mm) using Pilodyn and diameter inside bark (mm) at breast height using Resistograph for the Region H white spruce Controlled Parentage Program at age 26.**

| Site | Traits Measured[1] | Correlation Coefficient (SE) | p-value (df) |
|---|---|---|---|
| **Chinchaga** | DR ~ DIB | -0.29 (0.49) | < 0.001 (193) |
| **Hay River** | DR ~ DIB | -0.47 (0.37) | < 0.001 (277) |
| **Red Earth Creek** | DR ~ DIB | -0.27 (0.60) | < 0.001 (228) |
| **Chinchaga** | DR ~ PD | -0.48 (0.25) | < 0.001 (193) |
| **Hay River** | DR ~ PD | -0.55 (0.38) | < 0.001 (277) |
| **Chinchaga** | PD ~ DIB | 0.65 (0.38) | < 0.001 (193) |
| **Hay River** | PD ~ DIB | 0.71 (0.17) | < 0.001 (277) |

[1]**DR:** Drilling resistance (%); **PD:** Penetration depth (mm); **DIB:** Diameter inside bark (mm) at breast height; **SE:** Standard error; **df:** Degrees of freedom.

**Table 3.18: Family-level genetic correlations (r) ands its associated p-value and degrees of freedom for drilling resistance (%) using Resistograph, penetration depth (mm) using Pilodyn, wood specific gravity using water displacement and diameter inside bark (mm) at breast height using Resistograph for the Region H white spruce Controlled Parentage Program at age 26. Standard errors were not estimated as a suitable method to estimate this parameter was not found in the literature.**

| Traits Measured[1] | Correlation Coefficient | p-value (df) |
|---|---|---|
| **DR ~ DIB** | -0.08 | 0.61 (38) |
| **DR ~ Ht** | -0.07 | 0.65 (38) |
| **DR ~ PD** | -0.12 | 0.44 (38) |
| **PD ~ DIB** | 0.52 | < 0.001 (38) |
| **PD ~ Ht** | -0.11 | 0.49 (38) |
| **Ht ~ DIB** | -0.11 | 0.50 (38) |

[1]**DR:** Drilling resistance (%); **PD:** Penetration depth (mm); DIB**:** Diameter inside bark (mm) at breast height; Ht**:** Height (at age 25); **df:** Degrees of freedom.

**Table 3.19: Summary of breeding values (%) for Height at 18 years, provided by the Government of Alberta, drilling resistance using Resistograph at 26 years, penetration depth using Pilodyn at 26 years and diameter inside bark at breast height using Resistograph at 26 years for the Region H white spruce Controlled Parentage Program.**

| [1]Trait | Height at 25 Years | | | DR at 26 Years | | | PD at 26 Years | | | DIB at 26 Years | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Stat/BVCat** | High | Medium | Low | High | Medium | Low | High | Medium | Low | High | Medium | Low |
| **Mean** | 11.99 | 0.71 | -10.61 | -0.03 | 0.01 | 0.02 | -0.09 | -0.20 | 0.23 | -0.31 | -0.36 | 0.55 |
| **StDev** | 4.21 | 2.80 | 5.73 | 0.39 | 0.27 | 0.28 | 0.71 | 0.56 | 0.60 | 4.25 | 4.29 | 4.35 |
| **Min** | 3.47 | -2.81 | -21.66 | -0.71 | -0.44 | -0.47 | -1.11 | -1.14 | -0.98 | -6.84 | -4.74 | -5.41 |
| **Max** | 18.85 | 5.35 | -1.68 | 0.64 | 0.49 | 0.45 | 1.26 | 0.59 | 1.06 | 6.50 | 8.53 | 7.66 |

[1] **Stat:** Statistic; **BVCat:** Breeding value category for height at age 18; **DR:** Drilling resistance; **PD:** Penetration Depth; **DIB:** Diameter inside bark at breast height; **StDev:** Standard deviation; **Min:** Minimum; **Max:** Maximum.

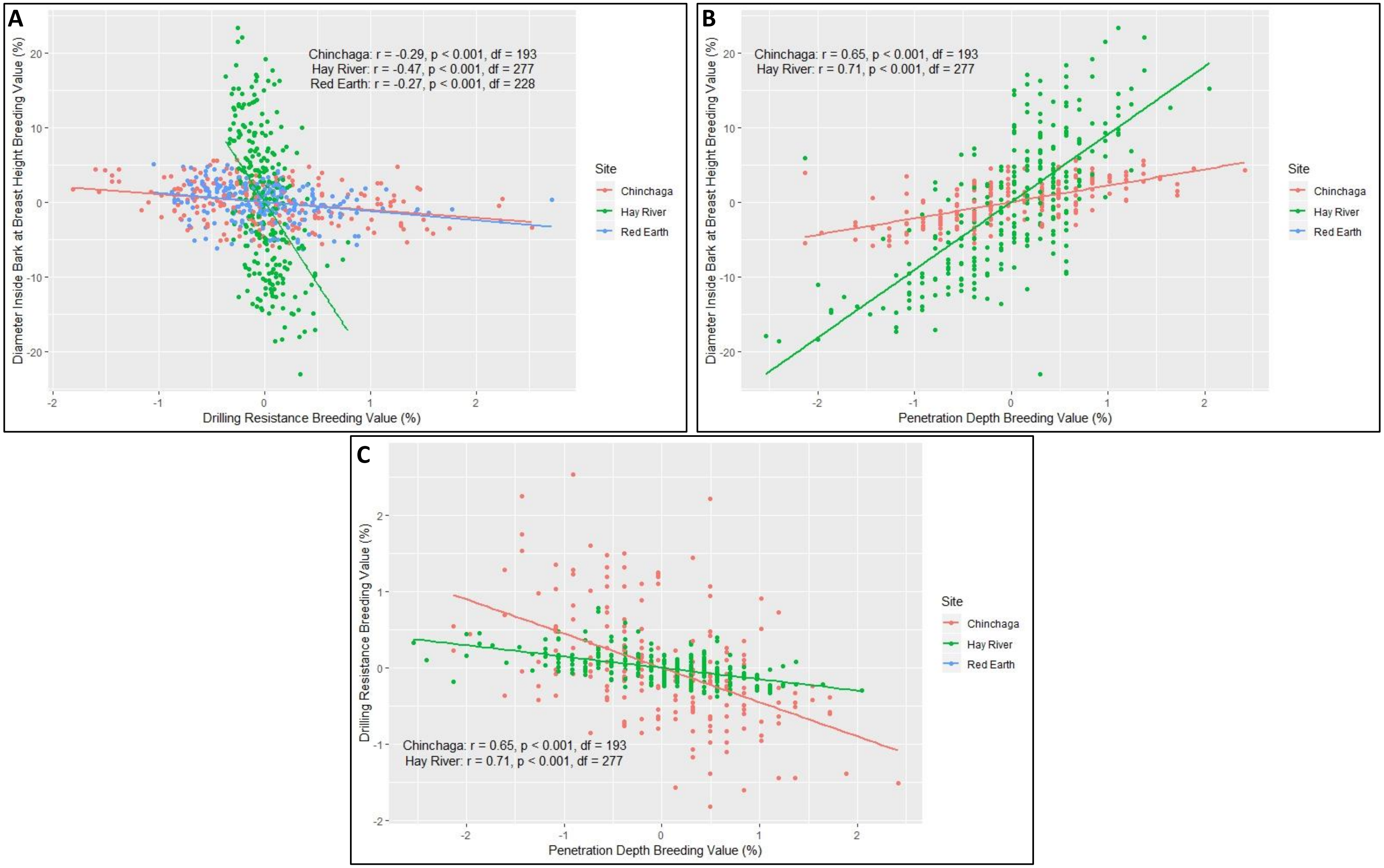

**Figure 3.9: Individual-level genetic correlations ($r_g$) between drilling resistance and diameter inside bark at breast height (A), penetration depth and diameter inside bark at breast height (B) and drilling resistance and penetration depth (C) using breeding values (%) calculated for each respective trait and site at age 26 for the Region H white spruce CPP. Drilling resistance and diameter inside bark at breast height were measured using a Resistograph device, while penetration depth was measured using a Pilodyn. Sites are coded by colour: red for Chinchaga, green for Hay River and blue for Red Earth.**

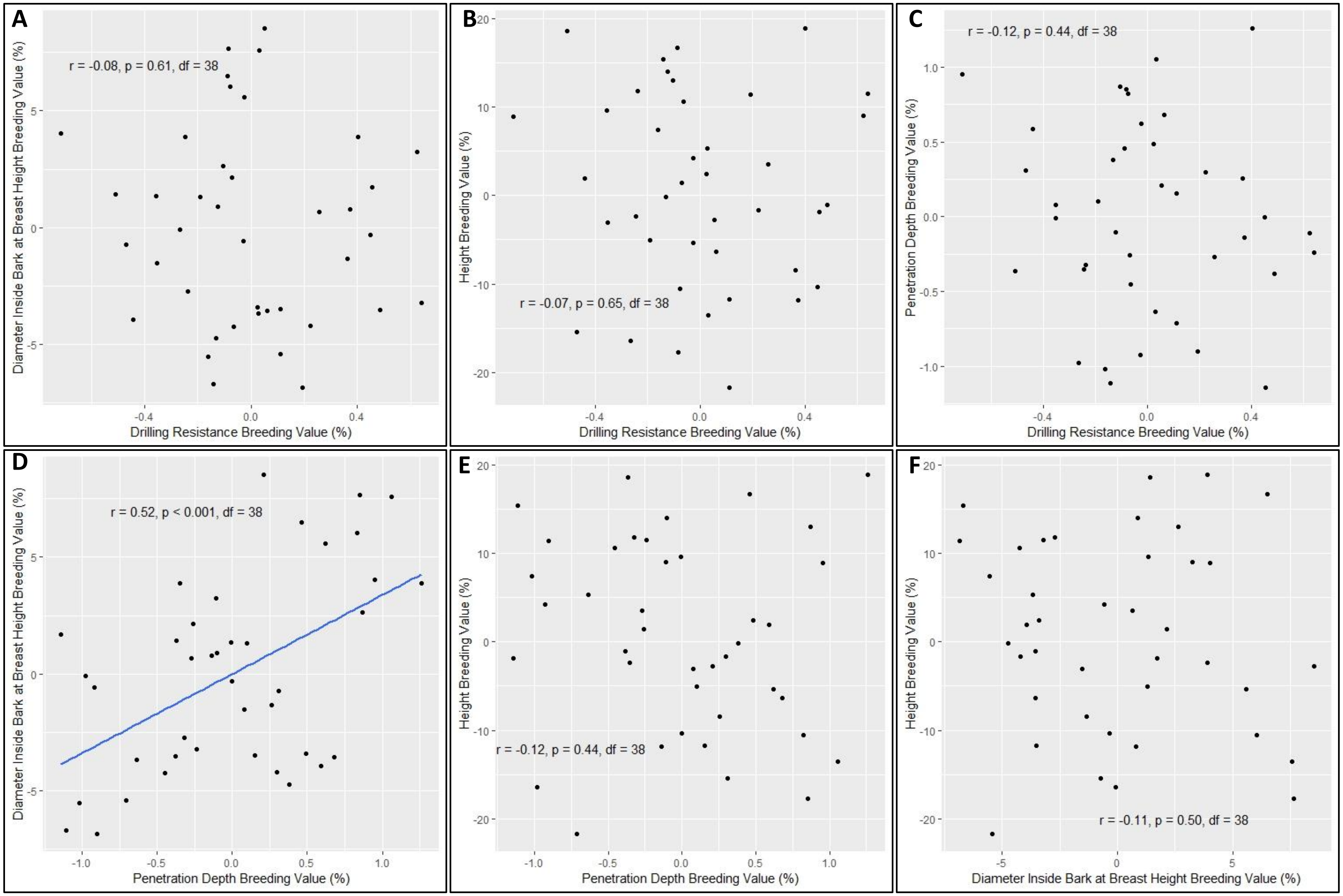

**Figure 3.10: Family-level genetic correlations ($r_g$) using breeding values between drilling resistance (DR) and diameter inside bark at breast height (DIB) (A), DR and height (B), penetration depth (PD) and DR (C), PD and DIB (D), PD and height (E) and DIB and height (F) for the Region H white spruce Controlled Parentage Program. Breeding values for DR, PD and DIB were calculated from data collected at age 26 while breeding values for height were provided by the Government of Alberta and were calculated from data collected at age 25. All breeding values are aggregated values from the Chinchaga, Hay River and Red Earth Creek progeny test sites.**

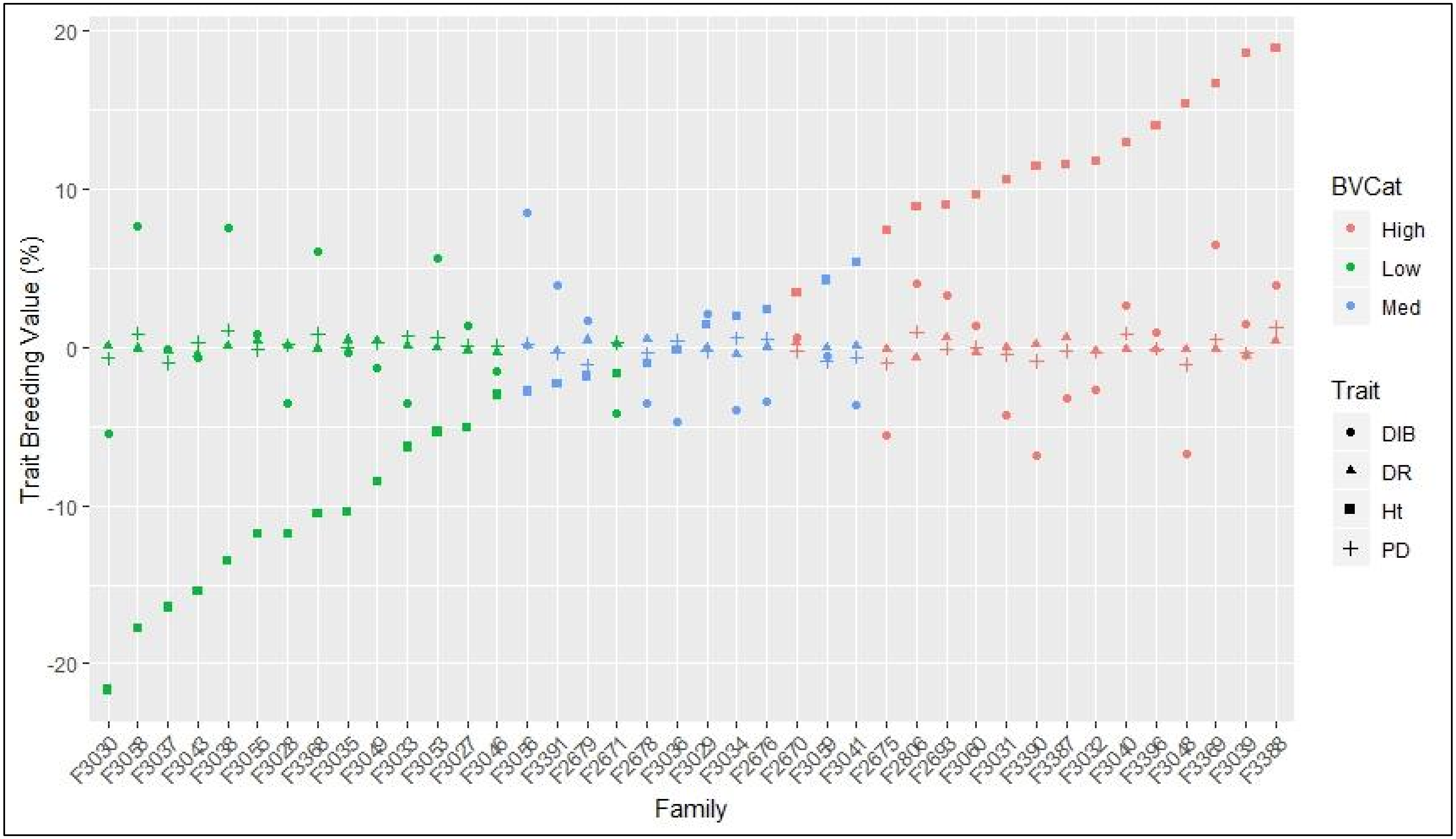

**Figure 3.11: Family breeding values across three test sites (%) for height (calculated from data collected at age 25 provided by the Government of Alberta) and drilling resistance, penetration depth and diameter inside bark at breast height calculated from data collected at age 26. Families are sorted lowest-to-highest starting on the left by their breeding value for height at 25 years, which is the primary selection criteria used in Alberta’s tree improvement programs. Each trait (e.g. Ht, DIB) is coded by shape while colour codes the breeding value category for height at 18 years (Figure 2.1) that were used to select families for assessment in the present study. It should be noted that there were some rank changes, as indicated by the overlapping of colours representing the high (orange), medium (blue) and low (green) breeding value categories.**

**DIB: Diameter inside bark at breast height; DR: Drilling resistance; Ht: Height; PD: Penetration depth**

# Chapter 4: Discussion

## 4.1 – Resistograph and Pilodyn Measurements

Overall, the correlation between the paired (i.e. north and east aspects) DR measurements was weaker than expected (r = 0.66, Figure 3.2A). There are several possible explanations for this discrepancy. The most obvious explanation is that differences exist in WD throughout the stem of a tree (Plate 1.1), including on different aspects (i.e. north *versus* east). Compression wood, for example, forms on the underside of leaning conifers and possesses structural and functional differences to that of 'normal' wood not formed under stress (Du and Yamamoto 2007). Some structural differences in compression wood include thicker cell walls, increased proportion of lignin, decreased cellulose content and rounded tracheids that result in intercellular spaces between fibres, all of which contribute to correcting the stem position (Du and Yamamoto 2007). Prevailing winds may cause the formation of compression wood on the leeward side, leading to elliptical stems (Barnett *et al.,* 2014). Much of Alberta experiences prevailing westerly winds (GoA 2003), which may cause the formation of compression wood on the east aspect of conifers. Compression wood is of higher density compared to normal wood (Harris 1977) or wood formed on the opposite aspect of compression wood (Diaz-Vaz *et al.,* 2009). Additionally, the difference in structure between normal stem wood and knot wood is assumed to cause some inconsistencies in Resistograph measurements (Plate 4.1); therefore, it is advised to drill through clear wood, avoiding defects including knots, depressions or other visible defects (Fundova *et al.,* 2018). However, young spruce trees tend to possess many branches

(Plate 4.2), so it is altogether impossible to completely avoid drilling through knots and it may not be possible to detect knots hidden within the stem of older trees at the time of measurement. Additionally, knots develop at an angle from where the branch enters the stem, proceeding towards the pith (Plate 4.1). Because of this knot angle, it may be difficult to judge the path of knots through the stem. Together, these factors may provide some explanation of the difference between the mean values of the DR from the north *versus* east aspects observed in the present study.

A second factor explaining the difference in DR taken from the north and east aspects is measurement errors introduced through the Resistograph method itself. Ukrainetz and O’Neill (2010) found that drill bit flexion, air temperature and moisture content all had a significant effect on DR measurements taken using Resistograph. All Resistograph measurements in the present study were taken under similar weather conditions (hot and dry) over one or two consecutive days; therefore, this factor is unlikely to have introduced noticeable measurement error. Moisture content was not measured, so it is possible this may have caused a small amount of measurement error; however, it is unlikely that the moisture content was extremely different within a single tree, but it is very likely that moisture content could vary somewhat over an entire test site and certainly between sites. Additionally, it would not be possible to control for moisture content in standing trees, other than sampling within a compact time frame and consistent weather conditions, as in the present study. The most likely factor to introduce error is bit flexion, which occurs if the operator cannot hold the device steady (Ukrainetz and O’Neill 2010). All efforts were made to hold the device (weight = 3.9 kg [Rinntech Date Unknown] tightly to the tree (Plate 4.3), to minimize movement and a single

**Plate 4.1: Examples of small (A) and large (B) knot formations (outlined in black) in the stems of two boreal conifer trees. Knots are variable both in size and angle. Knots occur diagonally downwards from where the branch meets the stem, proceeding towards the pith of the tree. The structure of knots is obviously different from that of ‘normal’ wood (e.g. presence of compression wood, grain orientation) and will affect Resistograph measurements if knots cannot be avoided. Avoiding knots is sometimes difficult as it is not possible to tell exactly where they will occur within the stem.**

**Plate 4.2: An example of the typical branching habit of a young (~17 years) white spruce tree. Although sampling between branches using Resistograph and Pilodyn is simple, predicting where knots will occur within the stem is impossible due to differences in branch size, branching angle and branch density.**

operator conducted all measurements; however, it is obviously not possible to avoid some movement, thereby introducing this type of error. In short, all efforts were made to minimize extraneous measurement error introduced through using the Resistograph device.

Bouffier *et al.,* (2008) found a correlation of 0.79 between two Resistograph measurements taken from the same tree in maritime pine (*Pinus pinaster* Ait.), which was slightly stronger than the correlation found in the present study (r = 0.66, Figure 3.2A); however, their sampling methodology called for observations to be taken from within ~5 cm of one another on the same aspect, whereas observations were taken from the north and east aspects in the present study. Pines generally have a more spaced-out and regular branching habit, making it somewhat easier to sample normal stem wood than is possible in young Sw (Plate 4.4). The close proximity of the two samples and different species tested by Bouffier *et al.,* (2008) likely explain the slightly higher correlation obtained compared to the present study.

**Plate 4.3: Jesse Shirton holding the Resistograph device in the typical fashion used for sampling in the present study. The end of the drill is held tightly against the tree stem and pressure is applied by leaning gently towards the tree to increase stability. The bottom handle may also be used to increase stability while sampling.**

**Plate 4.4: An example of the branching habit typical of lodgepole pine in Alberta (age estimated at 15-20 years). The much more predictable and wider spacing between branches simplifies sampling with Resistograph and Pilodyn. This may increase the quality of drilling resistance measurements in pine relative to white spruce.**

Although significant differences (df = 703, $p < 0.001$, Table 3.2) were found between DR measurements for the north *versus* east aspects, it is unlikely that these differences are biologically relevant. The relative difference between the mean DR for the north and east aspects (13.0% and 13.3%, respectively) was 2.3%. The fact that significant differences exist between the two aspects is likely a function of the large sample size, the higher power of paired t-tests (Kim and Seo 2013) and the relatively low levels of variation ($CoV_{North} = 0.14$, $CoV_{East} = 0.14$, data not shown – see Figure 3.1A) (Kadam and Bhalerao 2010). In conclusion, the correlation in DR between the north and east aspect appear to be reasonable and representative of the relationship in WD between wood occurring on different aspects of a single Sw tree.

Differences between the paired PD measurements, which were taken on the same trees and in the same manner as the DR measurements, were not as large (r = 0.81, Figure 3.2B) as found with the DR measurements, and were not significant (df = 473, p = 0.124, Table 3.2). Compared to Resistograph, data collected using Pilodyn appears to be less sensitive (Isik and Li 2003; Fundova *et al.,* 2018) and contains no other useful information (e.g. ring width, tree age, changes in growth rate over time); however, Pilodyn is easier to use and data processing is much quicker. The age of the wood being sampled is likely to play a role in the relative reduced variability between the paired PD measurements compared to DR. Previous studies have shown that the relative variation in WD is higher in juvenile wood compared to mature wood (Corriveau *et al.,* 1987; Koubaa *et al.,* 2000). Corriveau *et al.,* (1987) estimated that Sw will begin to transition from juvenile wood to mature wood at approximately 13 years of age, while Mvolo *et al.,* (2015) estimated a transition age range of 11-27 years at breast height, depending on the modeling method used. Mvolo *et al.,* (2015) have provided a specific height (e.g. at breast height – 1.3 m) for this transition as juvenile wood is more accurately called crown-influenced wood. This definition better reflects the gradual transition in wood characteristics which are partially attributed to whether that wood is being produced under the direct influence of a live crown and how a single tree possesses wood of different physiological ‘ages’ (i.e. juvenile wood and mature wood) throughout the stem (Yang *et al.,* 1994). The GoA recognizes this gradual transition between these two somewhat indistinct states in their wood quality determination procedures (ATISC 2000), which takes measurements of WSG and fibre length from distinct age ranges: 0-20 (earlywood), 21-50 (transition wood) and 50+ (mature wood) years. Fundova *et al.,* (2018) made a similar distinction in their study. Measurements taken using Pilodyn are likely to have sampled primarily older, less variable, outer wood (Fundova *et al.,* 2018). Due to their age, the wood of the trees sampled in the present study were likely to be composed primarily of juvenile wood; however, the outermost wood may have been transitioning to mature wood where the PD measurements occur. Together, these factors may explain the higher observed correlation between the paired PD measurements compared to the paired DR measurements, as the properties of mature wood are less variable than those of juvenile wood (Corriveau 1987; Mvolo *et al.,* 2015).

The correlation between DR and PD measurements taken from the same aspect of a tree were only moderate (Figure 3.2C and D), despite being taken concurrently and near one another. A moderate negative correlation was expected because although the measurements were taken near each other, the Pilodyn measurements sample a much smaller proportion of the stem (max 40 mm, typically 15-25 mm in the present study) than does Resistograph (max 50 cm, bark-to-pith measurements used in the present study). Therefore, Pilodyn measurements were likely to have sampled primarily less variable mature wood (Corriveau 1987; Mvolo *et al.,* 2015), while Resistograph measurements would have included (and aggregated) data from mature wood, juvenile wood and transition wood, which would be expected to relatively increase variability; however, this was not the case. Despite this clear disadvantage, the variability associated with Resistograph measurements was equal to, or oftentimes lower than, the variability associated with Pilodyn measurements (Figures 3.1, Tables 3.5-3.10). Interestingly, the strength of the phenotypic correlation between DR and PD remained relatively constant at all levels of comparison, including between DR and PD measurements taken from the same aspect (r = -0.58 and -0.51 for the north and east aspects, respectively – Figure 3.2C and D), or at the individual-level (r = -0.61, Figure 3.6A) and family-levels (r = -0.53, Figure 3.7A) using mean DR and PD measurements. These results support the conclusion that at the phenotypic level, DR and PD have a stable and predictable relationship within the present study. Previous work assessing correlations between DR and PD measurements were not found in the literature.

## 4.2 – Trait Variation by Site, Breeding Value Category for Height at 18 Years and Family

Overall, DIB was a much more variable trait than WD in the present study. The CoV for DIB was consistently two to three times higher than that for any of the WD traits measured and had a greater relative range (e.g. the spread between min/max DIB was relatively larger than the spread between min/max DR, PD or WSG - Tables 3.5-3.10, Figures 3.3-3.5). This result was not surprising, given the higher heritability of WD compared to radial growth rate found in the literature (Merrill and Mohn 1985; Cornelius 1994; Zobel and Jett 1995; Beaulieu *et al.,* 2006; Hong *et al.,* 2015; Fundova *et al.,* 2018) and the present study (Table 3.15). The higher heritability of WD indicates that environment plays a relatively small role in determining the WD phenotype of any one individual tree; rather, genetics play a large role in determining WD, which tends to be well-conserved within a family and has a relatively narrow range within the entire population. Even distant provenances in Quebec (Corriveau 1987; Duchesne and Zhang 2003) have WD ranges similar to the present study.

Variation was found to be greatest between sites (Table 3.5, Figures 3.3A-D) and significant differences were found for all traits between sites (Table 3.2). Specifically, the means for all traits did not differ significantly between Chinchaga and Red Earth, but Hay River was significantly different from both Chinchaga and Red Earth for all traits (Table 3.2). Hay River possessed trees with the lowest diameter (~25% smaller than Chinchaga or Red Earth) but with slightly higher WD (~7% higher than Chinchaga or Red Earth). The magnitude of this trade-off is similar to what has been documented in the literature for various silvicultural treatments, including site preparation (Clark and Edwards 1999), fertilization (Nyakuengama *et al.,* 2002), thinning (Peltola *et al.,* 2007), spacing (Yang 2002), as well as TI (Pike and Montgomery 2017).

Hay River is the furthest north site, being $1.5^0$ and $2.7^0$ further north than Chinchaga and Red Earth, respectively (Figure 2.1). Because of this, the climate differs somewhat between sites. Specifically, Hay River has lower precipitation, higher drought stress and a shorter growing season than either Chinchaga or Hay River, which are very similar to each other (Table 2.1, Figure 2.1). Overall, all three sites appear to experience similar temperature regimes, though Hay River is slightly colder than Chinchaga and Red Earth (Gray and Hamann 2015). Additionally, there is the possibility for other factors to affect site productivity, such as soil type and fertility. Unfortunately, site ecology was not well-documented in the establishment reports for the Region H Sw CPP (AAF 1994a; AAF 1994b; AAF 1994c). Corriveau (1987) did show considerable variation in radial growth rate in many Sw populations in Quebec. The CoV for ring widths (analogous to DIB), as calculated from Corriveau’s (1987) data, were 0.35 and 0.14 for juvenile wood and mature wood, respectively, while the CoV for juvenile wood WSG and mature wood WSG were calculated as 0.14 and 0.12, respectively, which were similar to the

CoV for DIB and WSG observed in the present study which ranged from 0.25-0.29 and 0.09-0.11, respectively. Overall, the site effect appears to have a relatively large impact on radial growth rate in Sw. In turn, decreases in radial growth rate (i.e. DIB) are reflected as increased WD, though the relative change in WD is smaller compared to the change in DIB. Specifically, trees at Hay River were, on average, approximately 25% smaller than trees present at Chinchaga and Hay River, but their WSG was approximately 7% greater.

Compared to site effects, the effects of BV category for height at age 18 on WD traits and DIB were much smaller. While the BV categories assigned in the present study were used for selection purposes (i.e. targeting high, medium and low BV families), this categorical variable is very useful for examining the general effects of high and low BVs for height on WD. One interesting observation is that the performance for height within the medium category showed little variability compared to either the high or low categories (Table 2.2). There was no significant difference found between the three BV categories for PD, and the medium category overlapped with both the high and low category for both DR and DIB. Significant differences between the BV categories also existed for WSG, but the result was quite different. Specifically, the low category overlapped with both the high and medium categories, but the high and medium categories were different from each other (Table 3.3, 3.6, Figure 3.4). This may be the result of random chance and the lower number of observations for WSG (i.e. a Type I error). As with site, the relative variation for WD traits was lower by a factor of two to three compared to DIB. The relatively smaller genetic effect is not surprising, given the generally higher heritability of WD, and associated indirect measures, compared to diameter growth rate (Merrill and Mohn 1985; Cornelius 1994; Zobel and Jett 1995; Beaulieu *et al.,* 2006; Hong *et al.,* 2015; Fundova *et* *al.,* 2018) and the relatively narrow range associated with each respective WD traits observed in the present study.

When the genetic effect was fully examined by testing for significant differences between families, rather than by the broader BV categories, the trends are quite different and much more variable. Although there is still an over-arching trend where as DIB increases WD decreases, there were no significant differences detected between families for PD, WSG or DIB, but significant differences do exist between families for DR (Tables 3.7-3.10, Figures 3.5A-D). This further corroborates the observation that Resistograph is a more sensitive device for detecting differences in WD compared to Pilodyn (Isik and Li 2003; Fundova *et al.,* 2018). Overall, all four traits were more variable at the family level, explaining the lack of significant differences compared to BV category. Because the number of observations/family was much lower than the number of observations/BV category (or site), the power of statistical tests to detect differences between groups is greatly reduced because there is relatively higher uncertainty when estimating treatment (i.e. family) means, and their associated confidence intervals are inflated. This can be confirmed by comparing the CoV for the four traits by family and by BV category in Tables 3.6-3.10, which are relatively greater by family compared to BV category. Interestingly, the relative level of variation for all traits is lower for high BV families compared to low BV families. This is valuable because it reinforces that families with high-performance for a specific trait are also consistent performers for that trait, which is important from a manufacturing standpoint.

## 4.3 – Phenotypic Correlation Strength

Rinntech (Year Unknown) claims that there is a strong positive correlation ($r^2 > 0.90$) between WD and DR for the Series 6 Resistograph device. However, the nature of this relationship is not further elaborated on in the sales literature. For example, there is no reference to specific literature to support this claim, nor is there information regarding species tested, if the relationship is for gymnosperms or angiosperms, if it is based on several individual observations or if it is for aggregated data. However, this information is contained in other documents authored by Frank Rinn (and others), the founder of Rinntech. The high correlation stated in the brochure appears to be based on aggregated mean averages from several different tree species (Rinn *et al.,* 1996; Rinn 2012). The observed phenotypic correlation between individual- and family-level DR and WSG measurements in the present study however, was much lower than advertised by Rinntech (Date Unknown).

Individual-level phenotypic correlations between DR and WSG were 0.56 in the present study (Table 3.11, Figure 3.6). Isik and Li (2003) found phenotypic correlations of 0.29-0.65, depending on site, for WD and DR in loblolly pine while Fundova *et al.,* (2018) found phenotypic correlations of 0.41-0.67 between WD and DR, depending on the treatment of the profile and the age of the wood (i.e. juvenile wood, intermediate wood and mature wood) in Scots pine. In general, Fundova *et al.,* (2018) found that the strength of the correlation increased when Resistograph profiles had the bark removed and were detrended (i.e. the trend of increasing DR with drilling depth was adjusted). A similar conclusion was reached in the present study during a preliminary investigation into this phenomenon (see Appendix 2). Additionally, Fundova *et al.,* (2018) found that the correlation was slightly stronger in transition wood and mature wood compared to earlywood, which is unsurprising given the more stable properties associated with mature wood (Corriveau 1987; Cown *et al.,* 1996; Mvolo *et al.,* 2015; Fundova *et al.,* 2018). Bouffier *et al.,* (2008) found a phenotypic correlation of 0.64 and 0.69 at ages of 30 and 12, respectively, in maritime pine. Their study differed from the previous two in that only the first 5 cm of the profile was utilized and correlated with the WD measured from the first 5 cm of a core, which may account for the relatively higher correlations. Gwaze and Stevenson (2008) found an individual-level phenotypic correlation of 0.48 between DR and WD in shortleaf pine (*Pinus echinate* Mill.). Overall, a similar phenotypic correlation strength between DR and WSG was observed in this study (r = 0.56, Table 3.11, Figure 3.6B) as shown in the above four examples.

The family-level phenotypic correlation between DR and WSG was essentially identical to the individual-level correlation in the present study (r = 0.54 and 0.56, respectively, Figures 3.7A and 3.8A, Table 3.11 and 3.12). This result is contrary to what is published in the literature, which showed that phenotypic correlations were stronger at the family-level. Specifically, Isik and Li (2003), Gwaze and Stevenson (2008) and Bouffier *et al.,* (2008) found family-level phenotypic correlations between DR and WD of 0.92, 0.69 and 0.96, respectively. The relatively lower family-level phenotypic correlation between DR and WSG found in the present study is most likely a result of using far fewer observations for WSG (n = 192) compared to the three above studies, each of which had a 1:1 ratio of DR to WD (using either WSG or X-ray densitometry) measurements. In the present study, there were only a few samples available for a family in some cases (e.g. F2693 had only two WSG observations), which would not produce consistent or representative results of family mean WSG. While more observations would have been desirable, working in a research program led by another organization (i.e. GoA) requires some sacrifices to meet their requirements and stipulations. Additionally, many observations were removed due to a number of trees being difficult to identify to the family level at the Chinchaga and Hay River test sites (Appendix 1). Given time constraints and the potential for identification errors, substituting several hundred (~250) trees unexpectedly in the field was not considered feasible at the time of sampling. The set of progeny trials assessed in the present study are still actively growing and there was a need to prevent harm to trees as it may affect future growth, and therefore, future results. Overall, the three above studies show that family-level data are generally more reliable than are individual-level data when sampling using Resistograph. The results of this study, which are contrary to the above, appears to be the exception, rather than the rule. Increasing the number of cores used for correlation analysis would be expected to increase the strength of the family-level phenotypic correlation observed between DR and WSG.

The observed phenotypic correlations for PD and WSG (Figures 3.6C and 3.7C, Tables 3.11 and 3.12) in the present study were similar to those of past studies (McConochie *et al.,* 1997; Greaves *et al.,* 2015; Fundova *et al.,* 2018). Interestingly, none of the above studies explicitly state if the phenotypic correlations were for individual measurements or for family means, though they appear to be for individual measurements, given the number of observations. McConochie *et al.,* (1997) found a phenotypic correlation of -0.68 between WSG and PD in shining gum (*Eucalyptus nitens* H Deane & Maiden), while Greaves *et al.,* (2015) found a phenotypic correlation of -0.59 in the same species. Fundova *et al.,* (2018) found a phenotypic correlation of 0.44 in Scots pine (using inverse PD, reversing the direction of correlation compared to most other studies). Overall, correlations between PD and DIB obtained in the present study appear to be similar to that of previous work.

Additionally, all of the above also applies to the predictive relationship between DR or PD and WSG with only a single caveat. Because a multiple linear regression analysis was used to model this relationship, the strength of the relationship is stronger than was observed for a simple Pearson's correlation (Tables 3.11-3.14). The explanation for this is quite simple: it was found in the present study that there was a weak to moderate correlation between DR (positive correlation) or PD (negative correlation) and DIB. Because there is a negative correlation between WD and radial growth in Sw, this results in the multiple linear regression model having superior power compared to a model with a single term when using DIB as a covariate in the model.

### 4.4 – Trait Heritabilities

The narrow sense heritability of each of the measured traits (DR, PD, DIB) were within the typical ranges found in the literature (Merrill and Mohn 1985; Cornelius 1994; Beaulieu *et al.,* 2006; Kiss and Yeh 2011). Fundova *et al.,* (2018) found the heritability of DR to range between 0.29-0.44, depending on how profiles were processed (e.g. raw *versus* detrended) while the heritability for PD was 0.32, with or without removing the bark from the tree, in Scots pine. Isik and Li (2003) found the heritability of DR to be 0.85 in loblolly pine, while Bouffier *et al.,* (2008) found the heritability of DR in maritime pine to be 0.32 and 0.43 at two different test sites in maritime pine. Chen *et al.,* (2015) found the heritability of PD was 0.34 in Norway spruce (*Picea* *abies* [L.] H. Karst), while Aguiar *et al.,* (2003) found the heritability of PD was very low at 0.024-0.100 in maritime pine. Isik and Li (2003), Chen *et al.,* (2015) and Aguiar *et al.,* (2003) also found the heritability of diameter to be 0.55, 0.18-0.24 and 0.049-0.056 in their respective studies. Overall, the heritabilities of the traits assessed in the present study compare favourably (Table 3.15) with those in the literature, and are, in general, close to what should be expected according to the literature (Cornelius 1994); however, considerable variation exists, not only within the present study, but in others (Cornelius 1994), as well. For example, the estimated heritability of 0.11 and 0.42 for DR and DIB at Hay River, respectively, difference from what was expected and from what was observed at Chinchaga or Red Earth (Table 3.16). This is likely the result of differences in between and within family variation for the respective traits between these sites and the observed differences in the level of genetic expression for each trait at each site (Figure 3.9A). (Isik and Li 2003). It is possible that this may be the result of a lack of site maintenance (two of three sites were very remote, particularly Hay River), differences in climate among sites (the climate at Hay River differed from Chinchaga and Red Earth – Chapter 2 Section 2.1.2) or differences in abiotic factors, such as soil fertility, which are undocumented in the test establishment reports (AAF 1994a; AAF 1994b; AAF 1994c). An additional observation is that in most of the above studies, the absolute and relative standard errors associated with each heritability estimate were lower than in the present study (Table 3.16). The explanation for this is likely due to the larger sample sizes utilized in the above studies have increased statistical power relative to the present study, which directly influences estimates of standard error (McDonald 2014). Many observations/site and /family should be taken to maximize statistical power. The work of Isik and Li (2003), Bouffier *et al.,* (2008) and Fundova *et* *al.,* (2018) indicate that several hundred (~700+) observations/site are required. Increasing the number of observations/family to approximately 30 is also likely to provide robust results, as this should produce a near-normal distribution for any particular trait for a family. In any case, the high variability of heritability for all traits between sites, studies and species reinforces that heritability is really a 'snapshot' of that population at that time and place and is dependent on several factors, including data quality, site conditions, site maintenance, tree age and the nature of the trait in question.

## 4.5 – Genetic Correlation Strength

Overall, the strength of the various genetic correlations was somewhat surprising, as were the associated estimates of standard error. In general, the correlation between DR and DIB at the individual-level was low ($r_g$ = -0.29 to -0.47), though it was significant for each site; however, the associated standard errors were very large (+/- 0.37-0.60). Additionally, the relationships were somewhat different, depending on site (i.e. the regression slope was different – Figure 3.9A). This result is in agreement with Isik and Li (2003), Lenz *et al.,* (2013) and Desponts *et al.,* (2017) who found genetic correlations between WD (or an indirect measure of WD) and diameter of -0.47, -0.41 and -0.43 in loblolly pine, white spruce and black spruce, respectively. However, once the data were analyzed at the family-level, the strength of the correlation was much smaller ($r_g$ = -0.08, Table 3.18, Figure 3.10A) and the relationship was not significant. This result is contrary to the results found by other researchers and the cause of this discrepancy is unknown. Proposed differences for this discrepancy may include differences in analysis techniques, the way family data were aggregated (i.e. only by site *versus* by an entire program) and differences in types of measurements (i.e. inside *versus* outside bark diameter measurements).

The genetic correlation between PD and DIB was found to be much stronger than any of the other genetic correlations, both at the individual-level ($r_g$ = 0.65-0.71 - Table 3.17, Figure 3.9B) and the family-level ($r_g$ = 0.52 – Table 3.18, Figure 3.10D). It is unclear why this specific correlation was found to be much stronger than the rest, especially when considering the relatively similar results for DR and PD throughout the present study. This may be in part be a result of the relatively less sensitive nature of Pilodyn compared to Resistograph (Fundova *et al.,* 2018), and the fact that Pilodyn measurements only sample a small portion (max 40 mm penetration depth) of the stem. The results obtained in the present study were however, similar to those of previous research. Lee (2001) and Lee and Connolly (2010) found genetic correlations between PD and diameter at breast height of -0.66 and -0.60, respectively, in Sitka spruce (*Picea sitchensis* (Bong.) Carr.).

The genetic correlation between height and diameter is unique. Where the other genetic correlations in the present study, in general, are in agreement with the published literature, height and diameter are not; however, the relationship between height and diameter in trees appears to be highly variable. For example, Kroon *et al.,* (2013) and Yeh and Heaman (1982) showed genetic correlations of -0.62 and 0.81 in Scots pine and Douglas-fir, respectively. Additionally, the genetic correlation between height and diameter at age 25 for the Region H Sw CPP was 0.91 (March 2019 email communication with A Benowicz – GoA). All of these results are vastly different from what was observed in the present study (r = -0.11). It is hypothesized that part of this discrepancy was due to differences in analysis and the way diameter was measured (i.e. inside bark diameter in the present study, generally outside bark diameter in the literature). Additionally, diameter in conifers is a plastic trait that is greatly influenced by environment (Clark and Edwards 1999; Yang 2002; Nyakuengama *et al.,* 2002; Renninger *et al.,* 2006; Peltola *et al.,* 2007; Grover *et al.,* 2014), which has the potential to greatly modify the relationship between height and diameter. Cornelius' (1994) review of the heritability of various traits in conifers suggests that diameter growth is less heritable than height growth.

It is worth noting the differences between the way data was gathered and analyzed in the present study compared to the GoA's process and how this is hypothesized to affect the above genetic correlations. The first major difference is that the GoA has assessed and measured each living tree in the progeny trials. The number of observations is in the thousands for each site, which would substantially increase the precision of their estimates of heritability and BVs. Additionally, the data for all sites are aggregated during genetic analysis (see Chapter 2 Section 2.2.1) which would increase the power of the analysis (i.e. by sample size and associated degrees of freedom) (March 2019 email communication with A Benowicz – GoA) compared to the present study, where the mean BV for each trait was calculated across all three sites after genetic analysis. Lastly, the GoA analysis included all 55 families, as well as the six bulk wild check lots (i.e. control lots) to which all families were compared (March 2019 email communication with A Benowicz – GoA). In the present study, the 40 selected families were compared relative to each other, despite capturing the range in variability for height as identified by the BVs calculated by the GoA. The GoA analysis makes comparisons of improved trees to a wild, unimproved control, whereas the analysis in the present study compares improved trees to improved trees. The crux of this is that it is assumed (although not necessarily true) that improved families will be superior performers to wild trees, and when compared to wild trees, will have elevated BVs. This assumption is violated when comparing BVs between only improved trees because BVs are a relative measure of performance within the population (i.e. an improved family that looks good compared to wild trees may seem average when compared to other improved families). Therefore, comparisons/correlations between BVs calculated in the present study and by the GoA should by no means be considered entirely equivalent; rather, comparisons to traits measured and analyzed within the present study are valid.

One last consideration in regard to the strength of the genetic correlations are the high standard errors associated with each correlation (Table 3.17). In the present study, standard errors ranged from 0.25-2 times the value of their respective genetic correlations (Table 3.16). Such a result is concerning and reinforces that the estimation of genetic parameters can be imprecise (Rweyongeza 2016). Additionally, the results of the present study demonstrate the importance of selecting a sufficiently large sample size, rigorous experimental design and collecting high-quality, accurate data. The genetic correlation standard errors were also inflated compared to their respective phenotypic correlation standard errors (Table 3.15), which were relatively small. There exist two probable explanations for this result: firstly, estimates for phenotypic correlations had sites aggregated, whereas the genetic correlations were separated by site (due to heritability being site- and time-specific), meaning the sample size (and degrees of freedom) were much greater for the phenotypic analyses. Secondly, estimates of standard error for genetic correlations integrate both the heritabily of a trait, as well as the standard error associated with that heritability estimate (Koots and Gibson 1996). Because the standard errors for each of the heritability estimates were relatively large (Table 3.16), this likely inflated the estimated standard error for the respective genetic correaltions.

### 4.6 – Effects of Increased Radial Growth Rate on Wood Quality

Despite the small observed effect of radial growth rate on WD observed in this study, there is still the potential for overall wood quality to decrease as a result of TI. This is a result of the definition of wood quality given in Chapter 1 Section 1.3, which was defined both by wood physical characteristics, such as WD, microfibril angle, diameter, the presence of knots or abnormal wood (Jozsa and Middleton 1994) and the effect of those characteristics on the value-recovery chain (Zhang 2003). Although the wood quality is not expected to diminish substantially due to a mild decrease in WD associated with increased radial growth, other factors may affect wood quality, both positively and negatively. Such factors may include changes in the juvenile wood:mature wood ratio, earlywood:latewood ratio or taper.

Due to increased radial growth rates, the average diameter of harvested trees will, in general, be larger than their unimproved counterparts. This has the potential to increase wood quality by creating the opportunity to mill larger lumber from improved trees, which can increase the value-recovery chain through increased product value (Random Lengths 2012), as well as through increases to the lumber recover factor (Steele 1984). Additionally, lumber milled from larger diameter logs may achieve higher grading, and therefore, substantially increase the value of the forest resource (Moore *et al.,* 2012). Specifically, lumber milled from areas adjacent to the pith (i.e. from juvenile wood) has a substantially decreased modulus of rupture, modulus of elasticity and increased knot frequency and area compared to lumber cut from the outer wood (i.e. from mature wood) and is much more prone to drying distortions and possible culling (Cown *et al.,* 1996; Moore *et al.,* 2012); however, the distribution and proportion of juvenile wood may be substantially different in improved trees and should be studied.

Many of the issues plaguing lumber quality appear to be related to the presence of juvenile wood (Cown *et al.,* 1996; Moore *et al.,* 2012). Currently, the juvenile wood proportion of Sw in Alberta is likely to be in the range of 15-50% as found by Mvolo *et al.,* (2015) in Ontario. Although the trees used in their study were from a research plantation, the juvenile wood:mature wood ratio was calculated at breast height using samples from 30 trees, from distinct social classes (dominant, codominant and suppressed), from different thinning treatments (control, low, medium and heavy thinning treatments), using several different types of models and were felled at age 79 (Mvolo *et al.,* 2015), which is similar to the rotation age in Alberta (80-100 years [Rweyongeza 2013]); therefore, their estimates of the juvenile wood:mature wood ratio are likely robust and representative of an average Sw stand (i.e. the confidence interval is wide enough to represent a variety of trees and stand conditions). Comparatively, the proportion of juvenile wood in short-rotation (17-25 years) loblolly pine grown in the Southeastern United States may be up to 70% juvenile wood (McKeand *et al.,* 2006). If current rotation lengths of 80-100 years (Rweyongeza 2016) are maintained, the proportion of juvenile wood:mature wood is unlikely to be greatly modified, though the diameter of the juvenile wood core will increase; however, if rotation lengths are decreased, there will undoubtedly be an increase in the proportion of juvenile wood and an associated decrease in WD; however, diameter growth is highly plastic and may be modified through other silvicultural practices including spacing (Yang 2002), fertilization (Nyakuengama *et al.,* 2002), thinning (Peltola *et al.,* 2007), and site preparation (Clark and Edwards 1999). Specifically, using release treatments on suppressed Sw, which are commonly associated with mixedwood stands in Alberta (Lieffers *et al.,* 1996), could result trees with small juvenile wood cores and high proportions of mature wood (Renninger *et al.,* 2006; Grover *et al.,* 2014). However, genetic gain cannot be claimed, and associated increases to the annual allowable cut, are not currently allowed when improved material is planted in mixedwood stands (AAF 2018).

A further important consideration to the potential effects of increased radial growth rates on wood quality is the increase in earlywood:latewood ratio. Even in wild populations, Sw is composed largely of earlywood (up to 90% - Lenz *et al.,* 2013). Due to the decreased WD associated with increased radial growth (Middleton and Munro 2002; Pike and Montgomery 2017), it is reasonable to conclude that the proportion of earlywood is likely to have increased relative to latewood. However, because Sw is already composed primarily of earlywood (Lenz *et al.,* 2013), an incremental increase to this ratio appears unlikely to substantially affect wood quality in regard to product quality and value; however, the changes in the earlywood:latewood ratio associated with increased diameter growth in the present study are unknown. The cores collected in the present study offer an excellent opportunity to perform correlation analyses to examine the relationship between WD and early wood:mature wood ratio, in addition to being able to assess the age of transition from juvenile wood:mature wood.

## 4.7 – Genotype-by-Environment Interaction

There was limited evidence of genotype-by-environment interaction observed in the present study (Figure 3.8). There are two types of genotype-by-environment interaction possible: 1) family rank changes between sites and 2) changes in level of expression (i.e. changes in BVs) between sites (Li *et al.,* 2017). Although some level of interaction was observed in each of the quantitative traits (DR, PD, WSG and DIB), the majority of the observed rank order changes are likely attributed to the following two factors: firstly, WD, measured using any of the methods in the present study, was not highly variable between families and the range of WD was relatively narrow (Figures 3.3-3.5 and Tables 3.5-3.10). The result of these two factors is that even relatively small changes in mean family WD may cause a rank order change between sites; however, large rank order changes were uncommon. Secondly, WSG, which appears to experience the greatest level of genotype-environment interaction, but was found to be non-significant, may be a result of the low number of observations/family/site (0-3 observations/family/site). This small number of observations does not adequately represent the true WSG of each family. There was also some variation in the level of expression of traits between sites. Specifically, the BVs (%) for DIB at Hay River possessed a much greater range (-22.30 to 34.54) compared to either Chinchaga or Red Earth (-6.21 to 8.46 and -8.58 to 7.15, respectively). Breeding values for DR and PD did not differ between sites, with aggregated ranges of -1.44 to 1.97 and -2.25 to 2.15, respectively. Baltunis *et al.,* (2010) and Kien *et al.,* (2010) showed that genotype-by-environment interactions were greatest in growth traits (e.g. diameter, height) and much lower in WD in radiata pine and river red gum (*Eucalyptus camaldulensis* Dehnh.), respectively.

### 4.8 – Critique of Experimental Design and Suggested Improvements

As with any experiment, there are improvements that could be made in hindsight. For the present study, one of the major weaknesses was that a reconnaissance visit to the sites was not undertaken prior to taking measurements. The reason for this was simply practical in nature as the sites were very remote; however, a simple site visit would have allowed for substitutions for those families where trees could not be readily identified, resulting in an increased sample size and statistical power, particularly for WSG, which suffered greatly from a reduced number of observations.

Another simple improvement to the present study would have been to make better use of the experimental design of the progeny trials to take advantage of blocking effects and the associated reduction in environmental variability, which would have increased estimates of trait heritability. The totally random tree selection method resulted in several cases where there were multiple (2 or more) representatives of a family occurring within a single row-plot (i.e. within a single replicate). Within the GoA's experiment, the row-plot is the experimental unit, hence individual trees within a row-plot cannot be considered independent observations. Although replicate was used as a random effect while modeling genetic effects, the replicate effect was quite small. Limiting the number of representatives to two trees within a single row-plot and taking observations from a greater number of replicates would have increased the amount of variation attributed to the replication effect, ultimately resulting in higher, more precise, estimates of heritability; however, this would not have been possible for all families due to the uneven survival throughout the progeny trials, but could have been improved, regardless. A spatial analysis using an x-y grid overlaid onto the trial design may yield increased statistical power but would require significant effort to implement but is planned for the future.

The last simple improvement to the present study is related to equipment and sample handling, specifically regarding extracting increment cores. Because cores are a physical sample, ensuring sample integrity is more complicated than with Resistograph or Pilodyn measurements. One issue was that the increment borer used was not extracting high-quality cores. The instrument should have been tested prior to going out into the field, yet it was not. It was assumed that because the instrument was new that it would work correctly; however, this was not true and the result was that most cores were only partially usable (the first half), and others were essentially unusable. Additionally, the labeling on several samples was worn off throughout handling and appeared to degrade in the freezer. A label more resistant to wear should have been used to ensure positive identification and prevent the loss of some (~15) samples.

The family-level correlation between DR and WSG was found to be weak compared to other studies. As previously noted in Section 4.3, each of the other studies performing similar analyses had a 1:1 ratio between DR and WSG or X-ray densitometry measurements, which was much greater than what was used and possible in the present study. Extracting more cores and increasing the number of WSG observations/family would have likely corrected this; however, as the present study was performed within GoA progeny trials, the number of cores that could be extracted was limited due to concerns over affecting test results over the course of the trial’s life.

## 4.9 – Conclusions, Recommendations and Future Directions

### 4.9.1 – Conclusions

Measuring WD in standing trees accurately and precisely is a challenging task. Not only is there the potential to damage the trees, resulting in a possible decrease in future performance and ultimately affecting long-term results of progeny tests, ensuring that the observations are representative of the population is difficult. Measuring WD is much more labour intensive than measuring either height or diameter, which are by no means easy tasks in and of themselves; however, given the requirement in FGRMS (AAF 2016a) to consider the effects of selection on any traits which are correlated with the selection trait (i.e. height and WD), an efficient method to assess WD is a necessity, as is an efficient sampling strategy.

Both Resistograph and Pilodyn have proven to be suitable tools for rapidly assessing WD in not only the present study, but several previous studies. Compared to Pilodyn, Resistograph provides high-resolution data that can tease apart differences in WD between families more effectively. Additionally, Resistograph allows for sampling of the entire stem profile, rather than being limited to the outermost wood, as is Pilodyn. The importance of this is simple: the entirety of the stem is used to manufacture most products, therefore understanding how WD varies throughout the stem is important to understanding how this affects end-use product quality and value.

However, it is important to understand the limitations of both Resistograph and Pilodyn. Both methods ultimately return indirect, relative measures of WD. While this can and does work for selection within a program, calibrating the methods to return estimates of actual WD is also important. Specifically, Resistograph is sensitive to operator error, moisture content and temperature. This is problematic because assessing the thousands of trees planted in each progeny trial is extremely time consuming and would take place over several days to weeks. While it is reasonable to expect weather to remain stable over one or two days, sampling over additional days runs the risk of dealing with changes in weather, and therefore, changes in DR. Calibrating Resistograph measurements with WSG or X-ray densitometry measurements, which are standardized, would alleviate this issue. However, relationships between DR and WSG were weak at the individual-level in the present study ($r^2 = 0.38$, Table 3.13) and in the literature (Isik and Li 2003, Fundova *et al.,* 2018). The literature showed that relationships between DR and WSG improve significantly at the family-level but require at least several hundred observations/program and many observations/family to show strong relationships (Isik and Li 2003, Fundova *et al.,* 2018). Therefore, it is suggested that WD assessment using destructive methods be delayed at least until the end of a progeny test's useful life (~40 years). Otherwise, using Resistograph or Pilodyn to evaluate relative WD within a site or program is an acceptable substitute for the purposes of early assessment and selection, but measurements should be conducted under similar conditions and within a compact time frame. A sample size of approximately 300/site appears to return results with adequate precision for highly heritable traits (e.g. WD), whereas less heritable traits (e.g. height, diameter) require several hundred to a few thousand observations/site to obtain heritability estimates with relatively low associate standard error.

Similar to previous studies, the narrow sense heritability of DR and PD was found to be generally higher than that of diameter growth rate; however, Hay River was a notable exception to this ‘rule.’ The reason for this discrepancy is not entirely known. It is hypothesized that this may be partly due to a relatively higher level of variation between families for DR and lower level of variation between families for DIB relative to the Chinchaga and Red Earth sites, both of which were significantly more productive sites. It was noted during profile processing that Resistograph profiles taken from Hay River were generally not as well delineated as those from either Chinchaga or Red Earth. This is likely a result of the effective resolution of the Resistograph device, which cannot detect differences in ring boundaries when the rings are closely spaced together, as they would be in the generally smaller trees present at the Hay River site. Therefore, Resistograph may not be as appropriate for measuring WD in extremely slow growing trees. A minimum diameter at breast height of 2.5 cm was used for Resistograph and Pilodyn sampling in the present study. Delineation of ring boundaries was poor in the resulting profiles of such small trees. Further work should be done to determine the minimum effective resolution of Resistograph.

Generally, Resistograph was able to show significant differences between the WD of selected families at the phenotypic-level, while Pilodyn could not (Table 3.4); however, while significant differences in DR between families using Resistograph did exist, the differences were, in general, minimal (~4.5% decrease in DR when comparing average performance of high to low BV categories for height at age 18). Additionally, the range of Sw WSG observed in the present study was similar to that of previous studies in wild populations, both in terms of range (0.231-0.480 in the present study [Table 3.5], 0.26-0.52 in the literature [Wang *et al.,* 1982; Micko *et* *al.,* 1982; Corriveau 1987]) and variation (CoV = 0.09-0.11 in the present study [Table 3.5], CoV 0.14-0.35 in the literature [Corriveau 1987]). Upon genetic analysis, it was quite clear that BVs for WD, using either DR or PD, occurred over a very narrow range and had an extremely weak and non-significant correlation with the BVs for DIB or height (Table 3.18, Figure 3.11). Additionally, the genetic correlation between DIB and height was found to be very weak ($r_{g=}$, which was unexpected. In contrast, the genetic correlation between diameter at breast height and tree height was strong ($r_g$ ~ 0.9 – data not shown) when calculated from data taken at age 25 provided by the GoA. It is hypothesized that this was due to differences in analysis, the number of observations taken, and the fact that only 40 of 55 families and none of the bulk wild check lots were assessed (i.e. GoA data compared improved trees to wild trees, while the present study provides comparisons between improved trees) in the present study. In conclusion, PD was moderately heritable while DR was moderately to highly heritable. Due to the relatively high heritability of these traits and their relatively low levels of variation, differences in BVs for DR and PD between families were minimal (i.e. BVs for DR and PD were nearly equal for fast-, slow-growing families). It does not appear that WD is being indirectly selected against by selecting families with superior height and diameter growth rates in the Region H Sw CPP at this time; rather the minimal decreases in WD associated with superior height and diameter growth are likely a manifestation of an increase in the earlywood:latewood ratio. Evaluating wood anatomy alongside WD would provide valuable insights into this relationship. Decreases to overall wood quality in the Region H Sw CPP are unlikely to be of concern at this time, therefore, opportunity exists to select for volume growth in this program without negatively affecting WD. This will assist in maintaining wood and end-use product quality in the face of increasingly intensive management of Alberta’s forest resource.

### 4.9.2 – Recommendations

Resistograph is, overall, a superior method (i.e. more sensitive to differences in WD) to Pilodyn for assessing WD in standing trees; however, Pilodyn is easier to use consistently, more cost-effective, faster and a much less laborious with regards to data processing and cleaning. Either method is suitable for assessing WD in Alberta’s TI programs. The method chosen should be tailored to the level of information desired by the proponent (e.g. approximate ring width, variation in wood structure over time, density throughout profile), time available for sampling/data processing, tree age (i.e. Pilodyn samples a decreasing proportion of the wood as diameter increases), as well as access to the instruments.

Wood density data is available for each of the parents incorporated into Alberta’s TI programs; however, WD data of natural stands is required to make meaningful comparisons between improved and wild trees. Ongoing, extensive sampling of natural WD, perhaps incorporated into operational logging, similar to scaling, should be implemented by forest companies. Additionally, the WD of stands regenerated using various silvicultural treatments, most notably site preparation, which may be more productive than naturally regenerated stands (therefore, possessing lower average WD and larger juvenile cores), should be assessed. Extensive assessment of WD in these stands will establish the natural range of WD occurring throughout a forest companies' Forest Management Agreement area, facilitating comparisons with improved families.

While decreases in WD associated with increased productivity do not appear to be a concern in the present study, this may not be true at different ages or for different programs. Additionally, the Region H Sw CPP is currently a first-generation program and while all selections may have been made from phenotypically-superior (i.e. tall) parents, they are, essentially, wild trees. Relationships between WD and growth rate will require assessment in subsequent generations to ensure that continual selection for improved volume growth (via selection for superior height) does not result in selection against WD, and therefore, decreased wood and product quality.

### 4.9.3 – Future Directions

Although only the Region H Sw CPP was analyzed in the present study, WD was also assessed in the Region D1 and I white spruce CPPs. These programs are older and younger than the Region H program, respectively. This additional data will allow for a meaningful comparison between assessing WD using Resistograph for early and late selections within a program. Analysis of the data from these programs will be conducted in a manner similar to the present study in the near-future.

Many cores were extracted from the Region D1 and H Sw CPPs. It is possible to evaluate the earlywood:latewood proportions in cores, juvenile wood:mature wood transition, as well as the cell wall and lumen areas of tracheids using specialized software called WinDENDRO and

WinCELL. This will allow for WD to be related to the anatomy of the wood and to evaluate what drives decreases in WD as radial growth rate increases.

As stated above, extensive assessment of WD in natural stands on a forest companies Forest Management Agreement area should be considered prudent. A meaningful comparison between the WD of wild and improved Sw (or any other species) will not be possible without this supporting data. This work should also include assessment of WD in stands regenerated using other silvicultural practices (e.g. site preparation). While constructing such a dataset would require considerable time, incorporating this monitoring into operational logging programs (i.e. collecting wood cookies during harvesting) would be an efficient way to sample WD across a companies Forest Management Agreement area and from a variety of stands.

Relationships between WD and growth rate for advanced generations of improved stock are currently unknown and must be assessed. Most of Alberta’s TI programs are currently in their first generation, though a few programs are moving into advanced generations. Assessing advanced generation programs will not yet happen for many years but forest companies and the GoA should prepare to do this work in the future.

Resistograph clearly is a powerful tool that can be implemented into TI programs for sampling WD, especially where taking physical wood samples is either impossible or undesirable (i.e. young progeny trials); however, the method is not without caveats. Specifically, assessing genetic traits using quantitative data requires high-quality data that are both accurate and precise so as to not otherwise confound interpretations or reduce estimates of genetic parameters (e.g. heritability, BVs). An in-depth assessment of methods for compensating for the trend of increasing DR with increasing drilling depth is planned to be carried out shortly.

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## Appendix 1: Summary of Removed Trees Due to Identification Concerns or Substitutions

This appendix lists the trees that were removed from the present study either because misidentification of trees was deemed to be likely or because there was an in-field substitution due to mortality since the last set of measurements performed by the GoA or other factors that made the tree unsuitable for assessment (e.g. too small in diameter, major defects). Because this project relies on accurate family-level data, misidentification of trees has the potential to severely bias the data, so no chances were taken in this regard.

**Table A1.1: Trees removed from study due to risk of misidentification or due to substitution from Chinchaga, Hay River and Red Earth Creek of the Region H Controlled Parentage Program.**

| Site | Tier | Row | Tree | Family | Note |
|---|---|---|---|---|---|
| **Hay River** | 5 | 28 | 3 | 3059 | Could not ID |
| **Hay River** | 1 | 8 | 5 | 3035 | Subbed Tree 1 |
| **Hay River** | 3 | 62 | 5 | 3053 | Subbed Tree 1 |
| **Hay River** | 2 | 28 | 3 | 3030 | Subbed Tree 5 |
| **Hay River** | 7 | 4 | 2 | 3055 | Subbed Tree 4 |
| **Hay River** | 3 | 49 | 2 | 3037 | Subbed Tree 3 |
| **Red Earth** | 7 | 2 | 2 | 3043 | Could not ID |
| **Red Earth** | 7 | 3 | 1 | 3058 | Could not ID |
| **Red Earth** | 7 | 4 | 2 | 3049 | Could not ID |
| **Red Earth** | 7 | 4 | 3 | 3049 | Could not ID |
| **Red Earth** | 7 | 8 | 1 | 3039 | Could not ID |
| **Red Earth** | 7 | 8 | 2 | 3039 | Could not ID |
| **Red Earth** | 7 | 9 | 1 | 3396 | Could not ID |
| **Red Earth** | 7 | 10 | 1 | 3027 | Could not ID |
| **Red Earth** | 7 | 16 | 1 | 3034 | Could not ID |
| **Red Earth** | 7 | 16 | 2 | 3034 | Could not ID |
| **Red Earth** | 7 | 16 | 3 | 3034 | Could not ID |
| **Red Earth** | 7 | 16 | 4 | 3034 | Could not ID |
| **Red Earth** | 7 | 19 | 2 | 3046 | Could not ID |
| **Red Earth** | 7 | 20 | 1 | 3043 | Could not ID |
| **Red Earth** | 7 | 22 | 1 | 2676 | Could not ID |
| **Red Earth** | 7 | 22 | 2 | 2676 | Could not ID |

| | | | | | |
|---|---|---|---|---|---|
| **Red Earth** | 7 | 22 | 3 | 2676 | Could not ID |
| **Red Earth** | 7 | 25 | 3 | 3032 | Could not ID |
| **Red Earth** | 7 | 26 | 1 | 2678 | Could not ID |
| **Red Earth** | 7 | 26 | 2 | 2678 | Could not ID |
| **Red Earth** | 7 | 30 | 2 | 3055 | Could not ID |
| **Red Earth** | 7 | 31 | 2 | 2679 | Could not ID |
| **Red Earth** | 7 | 31 | 3 | 2679 | Could not ID |
| **Red Earth** | 7 | 32 | 2 | 3053 | Could not ID |
| **Red Earth** | 7 | 32 | 4 | 3053 | Could not ID |
| **Red Earth** | 7 | 33 | 1 | 3058 | Could not ID |
| **Red Earth** | 7 | 33 | 3 | 3058 | Could not ID |
| **Red Earth** | 7 | 35 | 4 | 3033 | Could not ID |
| **Red Earth** | 8 | 1 | 2 | 3388 | Could not ID |
| **Red Earth** | 8 | 1 | 3 | 3388 | Could not ID |
| **Red Earth** | 8 | 1 | 4 | 3388 | Could not ID |
| **Red Earth** | 8 | 2 | 1 | 3029 | Could not ID |
| **Red Earth** | 8 | 2 | 2 | 3029 | Could not ID |
| **Red Earth** | 8 | 9 | 2 | 3391 | Could not ID |
| **Red Earth** | 8 | 9 | 3 | 3391 | Could not ID |
| **Red Earth** | 8 | 11 | 4 | 2806 | Could not ID |
| **Red Earth** | 8 | 13 | 1 | 3032 | Could not ID |
| **Red Earth** | 8 | 13 | 3 | 3032 | Could not ID |
| **Red Earth** | 8 | 16 | 2 | 3046 | Could not ID |
| **Red Earth** | 8 | 16 | 3 | 3046 | Could not ID |
| **Red Earth** | 8 | 17 | 2 | 3027 | Could not ID |
| **Red Earth** | 8 | 21 | 1 | 3056 | Could not ID |
| **Red Earth** | 8 | 21 | 4 | 3056 | Could not ID |
| **Red Earth** | 8 | 23 | 2 | 3049 | Could not ID |
| **Red Earth** | 8 | 24 | 4 | 3030 | Could not ID |
| **Red Earth** | 8 | 26 | 1 | 2693 | Could not ID |
| **Red Earth** | 8 | 26 | 3 | 2693 | Could not ID |
| **Red Earth** | 8 | 30 | 3 | 3040 | Could not ID |
| **Red Earth** | 8 | 32 | 3 | 3048 | Could not ID |
| **Red Earth** | 8 | 34 | 1 | 3035 | Could not ID |
| **Red Earth** | 8 | 34 | 3 | 3035 | Could not ID |
| **Red Earth** | 8 | 34 | 4 | 3035 | Could not ID |
| **Red Earth** | 8 | 35 | 1 | 3033 | Could not ID |
| **Red Earth** | 8 | 36 | 2 | 3031 | Could not ID |
| **Red Earth** | 8 | 37 | 2 | 3369 | Could not ID |
| **Red Earth** | 8 | 37 | 3 | 3369 | Could not ID |
| **Red Earth** | 8 | 39 | 2 | 2671 | Could not ID |
| **Red Earth** | 8 | 39 | 3 | 2671 | Could not ID |

| | | | | | |
|---|---|---|---|---|---|
| **Red Earth** | 8 | 40 | 3 | 3038 | Could not ID |
| **Red Earth** | 8 | 40 | 4 | 3038 | Could not ID |
| **Red Earth** | 8 | 42 | 2 | 3387 | Could not ID |
| **Red Earth** | 8 | 43 | 4 | 3368 | Could not ID |
| **Red Earth** | 8 | 45 | 1 | 2675 | Could not ID |
| **Red Earth** | 8 | 45 | 2 | 2675 | Could not ID |
| **Red Earth** | 8 | 45 | 3 | 2675 | Could not ID |
| **Red Earth** | 8 | 47 | 2 | 2670 | Could not ID |
| **Red Earth** | 8 | 47 | 3 | 2670 | Could not ID |
| **Red Earth** | 8 | 52 | 1 | 3037 | Could not ID |
| **Red Earth** | 8 | 52 | 3 | 3037 | Could not ID |
| **Red Earth** | 8 | 53 | 1 | 3036 | Could not ID |
| **Red Earth** | 8 | 55 | 1 | 3059 | Could not ID |
| **Red Earth** | 8 | 56 | 2 | 3060 | Could not ID |
| **Red Earth** | 8 | 56 | 3 | 3060 | Could not ID |
| **Red Earth** | 5 | 37 | 2 | 3396 | Subbed Tree 3 |
| **Red Earth** | 6 | 24 | 1 | 2676 | Subbed Tree 4 |
| **Red Earth** | 6 | 27 | 1 | 3032 | Subbed Tree 2 |
| **Red Earth** | 6 | 46 | 3 | 3040 | Subbed Tree 4 |
| **Red Earth** | 3 | 46 | 2 | 3027 | Subbed Tree 4 |
| **Red Earth** | 4 | 39 | 4 | 3033 | Subbed Tree 3 |
| **Chinchaga** | 1 | 28 | 1 | 3058 | Could not ID |
| **Chinchaga** | 1 | 28 | 2 | 3058 | Could not ID |
| **Chinchaga** | 1 | 29 | 2 | 3031 | Could not ID |
| **Chinchaga** | 1 | 29 | 3 | 3031 | Could not ID |
| **Chinchaga** | 1 | 31 | 1 | 3046 | Could not ID |
| **Chinchaga** | 1 | 31 | 3 | 3046 | Could not ID |
| **Chinchaga** | 1 | 36 | 1 | 2675 | Could not ID |
| **Chinchaga** | 1 | 37 | 4 | 3043 | Could not ID |
| **Chinchaga** | 1 | 44 | 2 | 2679 | Could not ID |
| **Chinchaga** | 1 | 46 | 2 | 2806 | Could not ID |
| **Chinchaga** | 1 | 46 | 3 | 2806 | Could not ID |
| **Chinchaga** | 1 | 46 | 5 | 2806 | Could not ID |
| **Chinchaga** | 2 | 5 | 4 | 3032 | Could not ID |
| **Chinchaga** | 2 | 6 | 1 | 3038 | Could not ID |
| **Chinchaga** | 2 | 6 | 3 | 3038 | Could not ID |
| **Chinchaga** | 2 | 6 | 5 | 3038 | Could not ID |
| **Chinchaga** | 2 | 7 | 1 | 2678 | Could not ID |
| **Chinchaga** | 2 | 7 | 3 | 2678 | Could not ID |
| **Chinchaga** | 2 | 8 | 3 | 3028 | Could not ID |
| **Chinchaga** | 2 | 8 | 5 | 3028 | Could not ID |
| **Chinchaga** | 2 | 9 | 2 | 3388 | Could not ID |

| | | | | | |
|---|---|---|---|---|---|
| **Chinchaga** | 2 | 10 | 3 | 3027 | Could not ID |
| **Chinchaga** | 2 | 11 | 4 | 3391 | Could not ID |
| **Chinchaga** | 2 | 11 | 5 | 3391 | Could not ID |
| **Chinchaga** | 2 | 13 | 4 | 3048 | Could not ID |
| **Chinchaga** | 2 | 14 | 3 | 3396 | Could not ID |
| **Chinchaga** | 2 | 15 | 5 | 3387 | Could not ID |
| **Chinchaga** | 2 | 21 | 2 | 3056 | Could not ID |
| **Chinchaga** | 2 | 21 | 5 | 3056 | Could not ID |
| **Chinchaga** | 2 | 23 | 1 | 3030 | Could not ID |
| **Chinchaga** | 2 | 23 | 3 | 3030 | Could not ID |
| **Chinchaga** | 2 | 24 | 4 | 3036 | Could not ID |
| **Chinchaga** | 2 | 25 | 1 | 3029 | Could not ID |
| **Chinchaga** | 2 | 25 | 2 | 3029 | Could not ID |
| **Chinchaga** | 2 | 28 | 2 | 3059 | Could not ID |
| **Chinchaga** | 2 | 28 | 4 | 3059 | Could not ID |
| **Chinchaga** | 2 | 33 | 3 | 3033 | Could not ID |
| **Chinchaga** | 2 | 39 | 1 | 3034 | Could not ID |
| **Chinchaga** | 2 | 40 | 1 | 3055 | Could not ID |
| **Chinchaga** | 2 | 40 | 3 | 3055 | Could not ID |
| **Chinchaga** | 2 | 45 | 4 | 2693 | Subbed Tree 5 |
| **Chinchaga** | 3 | 1 | 2 | 2670 | Could not ID |
| **Chinchaga** | 3 | 1 | 3 | 2670 | Could not ID |
| **Chinchaga** | 3 | 1 | 4 | 2670 | Could not ID |
| **Chinchaga** | 3 | 1 | 5 | 2670 | Could not ID |
| **Chinchaga** | 3 | 3 | 1 | 3037 | Could not ID |
| **Chinchaga** | 3 | 3 | 4 | 3037 | Could not ID |
| **Chinchaga** | 3 | 3 | 5 | 3037 | Could not ID |
| **Chinchaga** | 3 | 4 | 4 | 3040 | Could not ID |
| **Chinchaga** | 3 | 4 | 5 | 3040 | Could not ID |
| **Chinchaga** | 3 | 6 | 5 | 2675 | Could not ID |
| **Chinchaga** | 3 | 7 | 5 | 3058 | Could not ID |
| **Chinchaga** | 3 | 9 | 1 | 3046 | Could not ID |
| **Chinchaga** | 3 | 9 | 2 | 3046 | Could not ID |
| **Chinchaga** | 3 | 10 | 2 | 3031 | Could not ID |
| **Chinchaga** | 3 | 10 | 3 | 3031 | Could not ID |
| **Chinchaga** | 3 | 12 | 2 | 3390 | Could not ID |
| **Chinchaga** | 3 | 12 | 3 | 3390 | Could not ID |
| **Chinchaga** | 3 | 12 | 4 | 3390 | Could not ID |
| **Chinchaga** | 3 | 14 | 1 | 3043 | Could not ID |
| **Chinchaga** | 3 | 14 | 2 | 3043 | Could not ID |
| **Chinchaga** | 3 | 15 | 1 | 3053 | Could not ID |
| **Chinchaga** | 3 | 15 | 2 | 3053 | Could not ID |

| | | | | | |
|---|---|---|---|---|---|
| **Chinchaga** | 3 | 17 | 1 | 3035 | Could not ID |
| **Chinchaga** | 3 | 17 | 3 | 3035 | Could not ID |
| **Chinchaga** | 3 | 17 | 4 | 3035 | Could not ID |
| **Chinchaga** | 3 | 18 | 3 | 3369 | Could not ID |
| **Chinchaga** | 3 | 27 | 2 | 2693 | Could not ID |
| **Chinchaga** | 3 | 27 | 3 | 2693 | Could not ID |
| **Chinchaga** | 3 | 29 | 1 | 2679 | Could not ID |
| **Chinchaga** | 3 | 29 | 2 | 2679 | Could not ID |
| **Chinchaga** | 3 | 29 | 4 | 2679 | Could not ID |
| **Chinchaga** | 3 | 34 | 3 | 3048 | Could not ID |
| **Chinchaga** | 3 | 36 | 1 | 3368 | Could not ID |
| **Chinchaga** | 3 | 36 | 2 | 3368 | Could not ID |
| **Chinchaga** | 3 | 36 | 3 | 3368 | Could not ID |
| **Chinchaga** | 3 | 39 | 3 | 3034 | Could not ID |
| **Chinchaga** | 3 | 40 | 1 | 3033 | Could not ID |
| **Chinchaga** | 4 | 2 | 5 | 2693 | Missing tree, no sub |
| **Chinchaga** | 4 | 13 | 5 | 3031 | Missing tree, no sub |
| **Chinchaga** | 4 | 14 | 4 | 2675 | Could not ID |
| **Chinchaga** | 4 | 14 | 5 | 2675 | Could not ID |
| **Chinchaga** | 4 | 17 | 1 | 3058 | Missing Tree, no sub |
| **Chinchaga** | 4 | 22 | 2 | 2676 | Could not ID |
| **Chinchaga** | 4 | 23 | 4 | 3039 | Could not ID |
| **Chinchaga** | 4 | 23 | 5 | 3039 | Could not ID |
| **Chinchaga** | 4 | 25 | 2 | 3038 | Could not ID |
| **Chinchaga** | 4 | 25 | 3 | 3038 | Could not ID |
| **Chinchaga** | 4 | 26 | 1 | 2678 | Could not ID |
| **Chinchaga** | 4 | 26 | 3 | 2678 | Could not ID |
| **Chinchaga** | 4 | 29 | 2 | 3032 | Could not ID |
| **Chinchaga** | 4 | 29 | 5 | 3032 | Could not ID |
| **Chinchaga** | 4 | 30 | 1 | 3027 | Could not ID |
| **Chinchaga** | 4 | 33 | 3 | 2670 | Could not ID |
| **Chinchaga** | 4 | 33 | 5 | 2670 | Could not ID |
| **Chinchaga** | 4 | 34 | 1 | 3030 | Could not ID |
| **Chinchaga** | 4 | 34 | 3 | 3030 | Could not ID |
| **Chinchaga** | 4 | 34 | 4 | 3030 | Could not ID |
| **Chinchaga** | 4 | 35 | 5 | 3388 | Could not ID |
| **Chinchaga** | 4 | 37 | 2 | 3396 | Could not ID |
| **Chinchaga** | 4 | 45 | 1 | 3036 | Could not ID |
| **Chinchaga** | 4 | 45 | 4 | 3036 | Could not ID |
| **Chinchaga** | 4 | 46 | 4 | 3041 | Could not ID |
| **Chinchaga** | 7 | 8 | 2 | 2676 | Subbed Tree 3 |
| **Chinchaga** | 4 | 9 | 3 | 3369 | Subbed Tree 4 |

| | | | | | |
|---|---|---|---|---|---|
| **Chinchaga** | 4 | 13 | 2 | 3031 | Subbed Tree 4 |
| **Chinchaga** | 4 | 17 | 4 | 3058 | Subbed Tree 3 |
| **Chinchaga** | 5 | 35 | 2 | 2671 | Subbed Tree 3 |
| **Chinchaga** | 6 | 3 | 5 | 3030 | Subbed Tree 1 |

## Appendix 2: Assessing Inherent Biases in Resistograph Profiles

### Introduction

As noted in the main body of this study, there are clear signals that there is an inherent bias present in Resistograph measurements. This observation is corroborated by Oliveira *et al*. (2017) and Fundova *et al.,* (2018). A significant amount of effort is invested into obtaining measurements from progeny trials; thus, researchers should process profiles in a way that provides the highest quality data and removes, or otherwise compensates for, inherent measurement bias. The suspected culprit of this bias is friction on the drill bit shaft which increases with drilling depth (Fundova *et al*., 2018).

Three potential methods for ameliorating this bias were encountered in the literature. Fundova *et al.,* (2018) applied a linear regression model specific to each individual profile that detrended this bias. Although this appears to be solid in theory, two concerns should be noted. Firstly, if each individual data point within a profile, of which there are thousands, every single data point will then be an estimate with its own confidence interval. Essentially, one would be basing an estimated average DR for a profile on an estimated DR for thousands of individual data points, each with all the caveats associated with regression analyses. Secondly, the method used by Fundova *et al.,* (2018) seems extremely time consuming.

Oliveira *et al.,* (2017) suggest only drilling half of the diameter of a tree (i.e. from bark-to-pith). There does not appear to be a specific downfall associated with this method, other than one may want to take multiple measurements on an individual tree in order to adequately sample

WD throughout the stem. Although there may still be some bias present, it appears to be reduced relative to the whole profile (Figure A3.1). For profiles collected in the present study, visual assessment supports the conclusion that measurement bias appears to be much greater after drilling through the pith. The cause of this discrepancy is not clear and will not be investigated here. Bouffier *et al.,* (2008) utilized the first 5 cm of each profile. The strength of this method would appear to be a reduction in the measurement bias associated with drilling depth; however, only a small portion of the stem is sampled. This method is probably best used where one is only interested in the properties of the outer wood (i.e. mature wood).

## Methodology

For this preliminary investigation 30 random profiles taken from the north aspect were selected among the thee test sites. Only the north aspect was tested because there did not appear to be any difference in measurement bias associated with aspect on visual assessment. Each profile was processed into four different profile types and DR was calculated to test for differences. The first profile type was simply a raw profile with no processing, the second profile was complete, except for having the bark removed, the third type was the first half of the profile (bark-to-pith) and the last type was the second half of the profile (pith-to-bark). It was hypothesized that raw profiles would have the lowest mean DR, followed by the bark-to-pith section, followed by the whole profile with bark removed, and finally, the pith-to-bark section. Differences between profile types were conducted using ANOVA at a significance level of $\alpha = 0.05$.

## Results and Discussion

Summary statistics were calculated for each profile type (Table A3.1). Overall, the average DR matches the hypothesis. Additionally, the standard error and coefficient of variation were lowest for the bark-to-pith profile type (0.25 and 0.11, respectively). The ANOVA revealed that there were significant differences between the mean DR of the different profile types ($F(3,116) = 26.86$, $p < 0.001$). For the purposes of this preliminary analysis, more detailed analyses between groups were not investigated. However, the results reaffirm that the bark-to-pith profiles types are relatively less variable than any of the other profiles types. Additionally, the second profile half (i.e. from pith-to-bark) showed an elevated DR compared to the first half (i.e. bark-to-pith) without exception. This reduction in variability indicates a relative increase in data quality. The importance of this result is simply that for the purposes of genetic analysis, removing any source of extraneous variation is favorable to increasing estimates of narrow sense heritability by removing error that would otherwise become part of the denominator in the equation used to calculate narrow sense heritability (Redei 2008); hence, estimates of BVs will be relatively increased and more accurate and precise. A more intensive investigation of this phenomenon is planned for the future.

**Table A2.1: Summary statistics for the four different profile types used to assess for inherent measurement biases in the Resistograph method.**

| Stat/Profile Type[1] | Raw | Whole – Bark Removed | Half – Bark-to-Pith | Half – Pith-to-Bark |
|---|---|---|---|---|
| **N** | 30 | 30 | 30 | 30 |
| **Mean** | 11.55 | 14.10 | 12.59 | 15.61 |
| **SE** | 0.35 | 0.32 | 0.25 | 0.43 |
| **StDev** | 1.90 | 1.74 | 1.37 | 2.37 |
| **CoV** | 0.16 | 0.12 | 0.11 | 0.15 |
| **Min** | 8.1 | 11.0 | 10.1 | 11.6 |
| **Max** | 15.8 | 18.3 | 16.6 | 22.4 |
| **Skewness** | -0.11 | 0.33 | 0.72 | 0.56 |
| **Kurtosis** | -0.50 | -0.13 | 1.22 | 1.03 |

[1] **Stat:** Statistic; **SE:** Standard error; **Stdev:** Standard deviation; **CoV:** Coefficient of variation

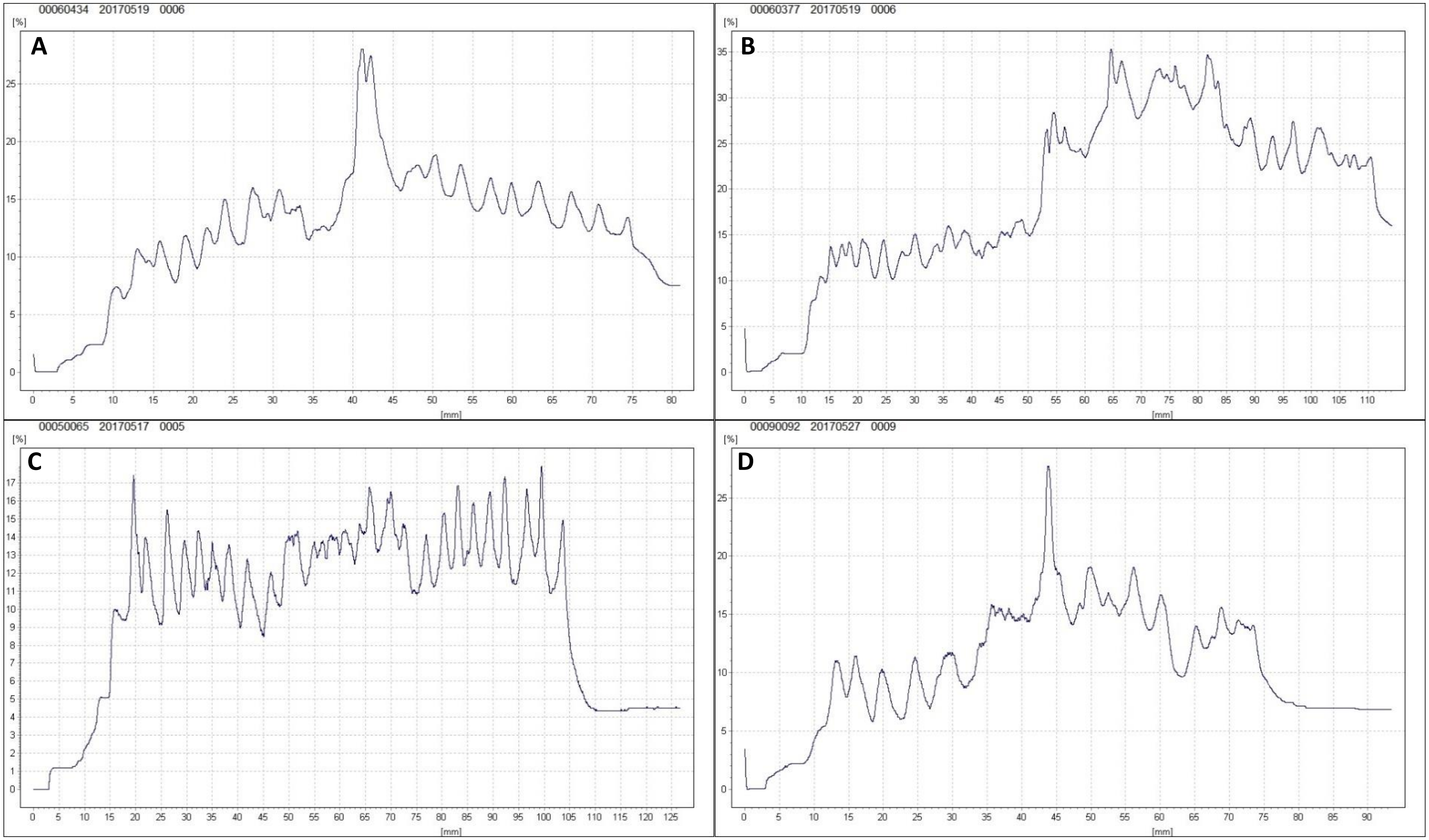

**Figure A2.1: Four examples of Resistograph profiles collected from across the three progeny test sites and with various diameters in the Region H white spruce Controlled Parentage Program displaying measurement bias associated with drilling depth. Each example (A-D) is taken from a different tree and there is at least one example from each of the three test sites. Drilling resistance (%) is displayed on the y-axis and drilling depth (mm) on the x-axis. The apparent bias becomes much more obvious after the midway point (i.e. pith) in each profile.**

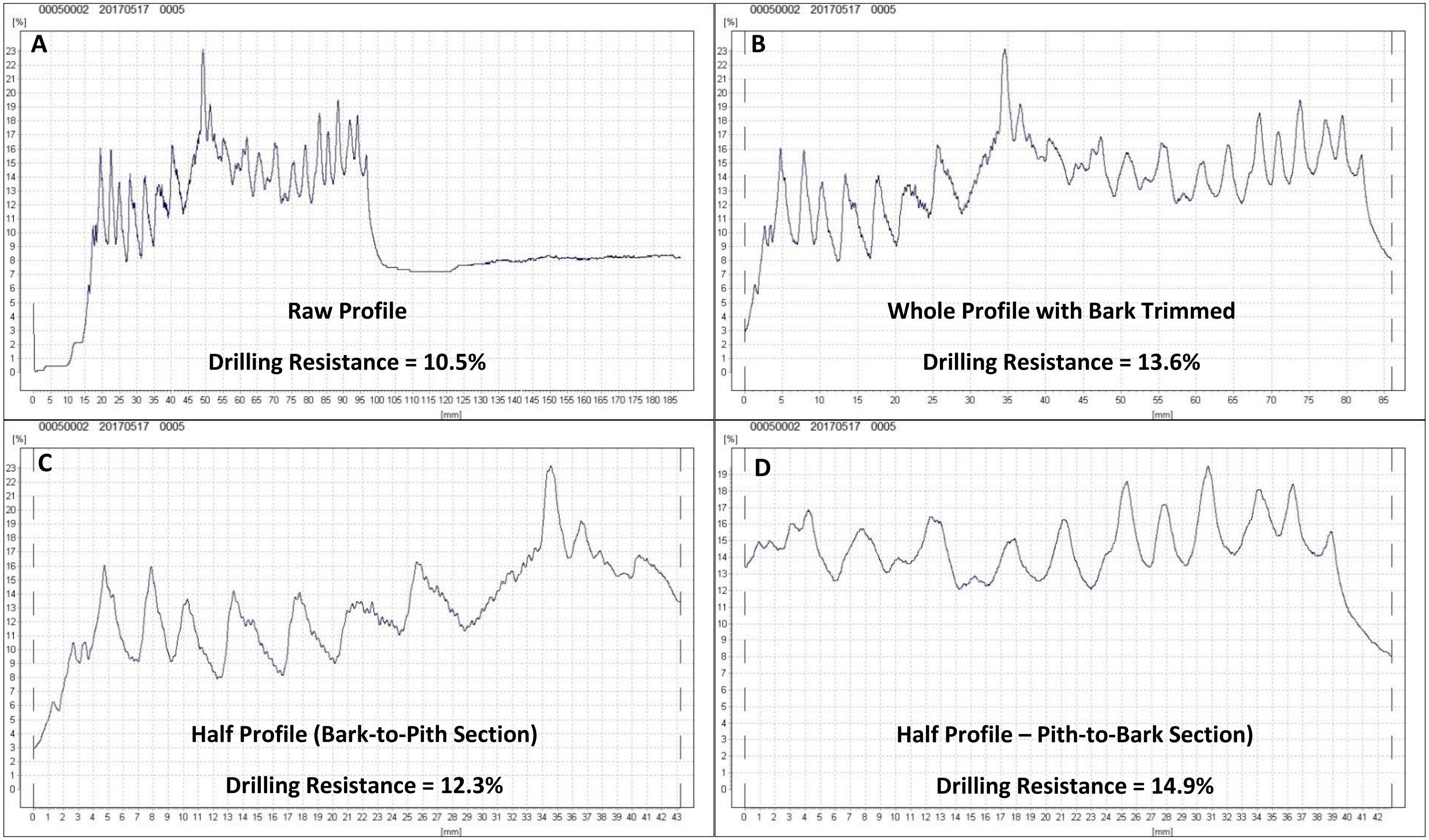

**Figure A2.2: Examples of the four different types of profiles for which drilling resistance (%) was calculated for preliminary analysis of inherent Resistograph measurement bias. Each example was created from the same raw profile (A). The other three profiles types are the whole profile with bark removed (B), the bark-to-pith section (C – the type of profile used in the main body of the present study) and the pith-to-bark section (D). Drilling resistance is displayed on the y-axis and drilling depth (mm) on the x-axis.**

## Appendix 3: Summary of Outlier Treatment and Removal

The purpose of this appendix is to document removed DR, PD and WSG outliers and the reason for their removal as described in Chapter 2 Section 2.4.2. A list of removed data may be found in Tables A3.1 and A3.2. The purpose of this process was not to remove outliers which may have been true outliers for that trait within the population, as the family selection method used in this study was likely to produce some outliers due to the inherent bias of selecting families that represented the extremes in growth performance; rather, this process was intended to remove trees where differences between the paired DR and PD measurements were large or where WSG measurements fell well outside of the range of Sw density established in the literature. The assumption was that there should be a relatively strong correlation between the paired DR and PD measurements of each tree and large differences between the measurements were caused either by measurement error or non-normal wood (e.g. knots or compression wood). This correlation was established in this study (Table 3.8) and was corroborated by the work of (Bouffier *et al.,* 2008). No outliers were removed based on DIB measurements because it was assumed that the risk of measurement error resulting in an outlier was very small. Indeed, the distribution of DIB is platykurtic and contains very few outliers (Tables 3.2 and 3.3).

**Table A3.1: Summary of removed data based on differences between paired drilling resistance (%) using Resistograph and penetration depth (mm) using Pilodyn for the Region H white spruce Controlled Parentage Program.**

| Site | Rep | Tier | Row | Tree | Family | Reason |
|---|---|---|---|---|---|---|
| **Chinchaga** | Re3 | Ti4 | R13 | Tr4 | 3031 | Moderate measurement deviation and Res/Pil[1] disagreement |
| **Chinchaga** | Re3 | Ti4 | R2 | Tr2 | 2693 | Moderate measurement deviation and Res/Pil disagreement |
| **Chinchaga** | Re3 | Ti4 | R9 | Tr5 | 3369 | Moderate measurement deviation and Res/Pil disagreement |
| **Chinchaga** | Re3 | Ti5 | R35 | Tr3 | 2671 | Moderate measurement deviation and Res/Pil disagreement |
| **Chinchaga** | Re4 | Ti6 | R11 | Tr5 | 3033 | High Pil measurement deviation |
| **Chinchaga** | Re4 | Ti6 | R37 | Tr4 | 3053 | High Res measurement deviation |
| **Chinchaga** | Re4 | Ti7 | R13 | Tr1 | 3060 | High Pil measurement deviation |
| **Chinchaga** | Re5 | Ti8 | R22 | Tr1 | 3032 | High Res measurement deviation |
| **Chinchaga** | Re5 | Ti8 | R27 | Tr3 | 3041 | Moderate measurement deviation and Res/Pil disagreement |
| **Chinchaga** | Re5 | Ti8 | R42 | Tr1 | 3055 | Moderate measurement deviation and Res/Pil disagreement |
| **Chinchaga** | Re6 | Ti9 | R28 | Tr4 | 3368 | High Pil measurement deviation |
| **Chinchaga** | Re6 | Ti9 | R31 | Tr4 | 3028 | Moderate measurement deviation and Res/Pil disagreement |
| **Chinchaga** | Re6 | Ti9 | R44 | Tr3 | 3040 | High Res measurement deviation |
| **Chinchaga** | Re7 | Ti10 | R26 | Tr5 | 3046 | High Res measurement deviation |
| **Chinchaga** | Re7 | Ti11 | R13 | Tr3 | 3033 | High Res measurement deviation |
| **Chinchaga** | Re7 | Ti11 | R31 | Tr2 | 3391 | High Res measurement deviation |
| **Hay River** | Re1 | Ti1 | R26 | Tr4 | 3368 | Moderate measurement deviation and Res/Pil disagreement |
| **Hay River** | Re1 | Ti1 | R37 | Tr4 | 3048 | High Res measurement deviation |
| **Hay River** | Re1 | Ti1 | R38 | Tr1 | 3029 | High Res measurement deviation |
| **Hay River** | Re1 | Ti1 | R60 | Tr1 | 3391 | High Res measurement deviation |
| **Hay River** | Re1 | Ti1 | R8 | Tr1 | 3035 | High Res measurement deviation |
| **Hay River** | Re2 | Ti2 | R30 | Tr3 | 3041 | High Res measurement deviation |
| **Hay River** | Re2 | Ti2 | R34 | Tr1 | 3037 | High Res measurement deviation |
| **Hay River** | Re2 | Ti2 | R46 | Tr3 | 3055 | Moderate measurement deviation and Res/Pil disagreement |
| **Hay River** | Re2 | Ti2 | R54 | Tr1 | 3035 | High Res measurement deviation |
| **Hay River** | Re2 | Ti2 | R57 | Tr1 | 3369 | High Pil measurement deviation |
| **Hay River** | Re2 | Ti2 | R65 | Tr1 | 3031 | High Pil measurement deviation |
| **Hay River** | Re3 | Ti3 | R19 | Tr3 | 3041 | High Res measurement deviation |
| **Hay River** | Re3 | Ti3 | R24 | Tr4 | 3387 | High Res measurement deviation |

| | | | | | | |
|---|---|---|---|---|---|---|
| **Hay River** | Re3 | Ti3 | R25 | Tr1 | 3368 | High Res measurement deviation |
| **Hay River** | Re3 | Ti3 | R45 | Tr5 | 3038 | High Pil measurement deviation |
| **Hay River** | Re3 | Ti3 | R47 | Tr5 | 3060 | High Pil measurement deviation |
| **Hay River** | Re4 | Ti4 | R22 | Tr3 | 2670 | High Res measurement deviation |
| **Hay River** | Re4 | Ti4 | R29 | Tr1 | 3038 | High Res measurement deviation |
| **Hay River** | Re4 | Ti4 | R51 | Tr1 | 3368 | High Res measurement deviation |
| **Hay River** | Re4 | Ti4 | R62 | Tr5 | 3049 | Moderate measurement deviation and Res/Pil disagreement |
| **Hay River** | Re5 | Ti4 | R4 | Tr2 | 3369 | High Pil measurement deviation |
| **Hay River** | Re5 | Ti5 | R13 | Tr5 | 3387 | High Res measurement deviation |
| **Hay River** | Re5 | Ti5 | R19 | Tr5 | 3055 | High Res measurement deviation |
| **Hay River** | Re5 | Ti5 | R22 | Tr1 | 3056 | High Res measurement deviation |
| **Hay River** | Re5 | Ti5 | R25 | Tr2 | 3037 | High Res measurement deviation |
| **Hay River** | Re5 | Ti5 | R34 | Tr5 | 3027 | High Res measurement deviation |
| **Hay River** | Re5 | Ti5 | R40 | Tr4 | 2676 | High Pil measurement deviation |
| **Hay River** | Re5 | Ti5 | R43 | Tr5 | 3032 | High Pil measurement deviation |
| **Hay River** | Re6 | Ti5 | R60 | Tr1 | 3046 | Moderate measurement deviation and Res/Pil disagreement |
| **Hay River** | Re6 | Ti6 | R62 | Tr1 | 2693 | High Res measurement deviation |
| **Hay River** | Re6 | Ti6 | R62 | Tr5 | 2693 | High Pil measurement deviation |
| **Hay River** | Re7 | Ti6 | R1 | Tr3 | 2693 | High Pil measurement deviation |
| **Hay River** | Re7 | Ti6 | R10 | Tr2 | 3043 | High Res measurement deviation |
| **Hay River** | Re7 | Ti6 | R13 | Tr4 | 3035 | High Pil measurement deviation |
| **Hay River** | Re7 | Ti6 | R22 | Tr4 | 3058 | High Res measurement deviation |
| **Hay River** | Re7 | Ti7 | R37 | Tr4 | 3391 | High Res measurement deviation |
| **Red Earth** | Re1 | Ti1 | R23 | Tr3 | 3048 | High Res measurement deviation |
| **Red Earth** | Re1 | Ti1 | R39 | Tr1 | 3388 | High Res measurement deviation |
| **Red Earth** | Re1 | Ti2 | R9 | Tr2 | 3036 | High Res measurement deviation |
| **Red Earth** | Re2 | Ti3 | R42 | Tr2 | 3040 | High Res measurement deviation |
| **Red Earth** | Re3 | Ti4 | R32 | Tr2 | 3035 | High Res measurement deviation |
| **Red Earth** | Re4 | Ti4 | R50 | Tr2 | 3048 | High Res measurement deviation |
| **Red Earth** | Re4 | Ti4 | R51 | Tr3 | 3368 | High Res measurement deviation |
| **Red Earth** | Re4 | Ti5 | R14 | Tr3 | 3059 | High Res measurement deviation |
| **Red Earth** | Re4 | Ti5 | R15 | Tr2 | 3041 | High Res measurement deviation |
| **Red Earth** | Re5 | Ti5 | R8 | Tr4 | 3030 | High Res measurement deviation |
| **Red Earth** | Re5 | Ti6 | R20 | Tr3 | 3059 | High Res measurement deviation |

[1] **Res:** Resistograph; **Pil:** Pilodyn

**Table A3.2: Summary of removed data based on wood specific gravity for the Region H Controlled Parentage Program.**

| Site | Rep | Tier | Row | Tree | Family | Reason |
|---|---|---|---|---|---|---|
| **Chinchaga** | Re4 | Ti6 | R42 | Tr1 | 3043 | Calculated density over 10% out of published ranges |
| **Red Earth** | Re6 | Ti6 | R54 | Tr3 | 3387 | Calculated density over 10% out of published ranges |
| **Hay River** | Re2 | Ti2 | R59 | Tr3 | 3053 | Calculated density over 10% out of published ranges |
| **Red Earth** | Re6 | Ti7 | R56 | Tr3 | 2806 | Calculated density over 10% out of published ranges |
| **Hay River** | Re2 | Ti1 | R63 | Tr5 | 3058 | removed from main data set |
| **Hay River** | Re1 | Ti1 | R40 | Tr2 | 3036 | removed from main data set |
| **Chinchaga** | Re3 | Ti4 | R13 | Tr4 | 3031 | removed from main data set |
| **Chinchaga** | Re7 | Ti11 | R31 | Tr2 | 3391 | removed from main data set |
| **Hay River** | Re1 | Ti1 | R37 | Tr4 | 3048 | removed from main data set |
| **Hay River** | Re1 | Ti1 | R8 | Tr1 | 3035 | removed from main data set |
| **Hay River** | Re2 | Ti2 | R46 | Tr3 | 3055 | removed from main data set |
| **Hay River** | Re3 | Ti3 | R25 | Tr1 | 3368 | removed from main data set |
| **Hay River** | Re5 | Ti5 | R43 | Tr5 | 3032 | removed from main data set |
| **Hay River** | Re6 | Ti5 | R60 | Tr1 | 3046 | removed from main data set |
| **Hay River** | Re6 | Ti6 | R62 | Tr1 | 2693 | removed from main data set |
| **Hay River** | Re7 | Ti6 | R1 | Tr3 | 2693 | removed from main data set |
| **Red Earth** | Re4 | Ti5 | R37 | Tr3 | 3396 | removed from main data set |
| **Red Earth** | Re5 | Ti6 | R20 | Tr3 | 3059 | removed from main data set |
| **Hay River** | Re4 | Ti4 | R23 | Tr4 | 3039 | removed from main data set |