Canadian Journal of Forest Research

Wood density and growth in clonally propagated aspen

Journal:	<i>Canadian Journal of Forest Research</i>
Manuscript ID	cjfr-2018-0297.R1
Manuscript Type:	Article
Date Submitted by the Author:	22-Oct-2018
Complete List of Authors:	Brouard, Jean; Isabella Point Forestry Ltd.,
Keyword:	Aspen, correlation, growth, density, P. tremuloides
Is the invited manuscript for consideration in a Special Issue? :	Not applicable (regular submission)

SCHOLARONE™
Manuscripts

Wood density and growth in clonally propagated aspen

Jean S. Brouard

Isabella Point Forestry Ltd.
331 Roland Road
Saltspring Island
BC V8K 1V1 Canada
johnbro@saltspring.com

corresponding author:
J.S. Brouard
johnbro@saltspring.com
Tel: (250) 653-2335

Abstract

Do fast growing trees produce lower density wood? In order to determine the relationship between growth rate and wood density in plantation-grown aspen, 199 trees in 20 clones were sampled from a 15 year-old clonal trial. This study found no evidence that fast-grown trees produce less dense wood.

Phenotypic and genetic correlations between height, diameter, volume and biomass were all high and significant. Wood density was not correlated with height or volume but there were small and significant ($p \leq 0.05$) positive phenotypic correlations with stem diameter. Genetic correlations between breast height wood density and all three growth measures (height, DBH, and volume) were not significantly different from zero. This suggests that selection for growth will not influence wood density nor vice versa.

This paper discusses some possible reasons for the contradictions in the literature about the relationship between growth rate and wood density in aspen. The anatomy of juvenile or core wood is different from that of mature wood, and the relationship between density and growth rate also differs. The changing relative proportion of juvenile core wood with tree size may explain many of the apparent contradictions.

Keywords: Wood density; aspen; phenotypic & genetic correlations; growth rate.

1. Introduction

Aspen (*Populus tremuloides* Michx.) is an important constituent of Canada's 270 million hectares of boreal forests (Natural Resources Canada 2017). In northwestern Alberta, aspen wood is used for production of pulp as well as oriented strand board, and represents an annual provincial harvest of approximately six million cubic metres (Government of Alberta 2017). Aspen wood waste has long been used for heat and power cogeneration in Alberta wood processing industries. Woody biomass also has the potential to be used as a renewable energy source for public power generation (Stener and Westin 2017) or for conversion to liquid biofuels (Mansfield et al. 2012).

Although aspen is one of the fastest growing tree species in Alberta, all of the harvest comes from natural forests, and there is no history of aspen plantations. In order to assess the costs and benefits of aspen plantation silviculture it is essential to gain an understanding of potential biomass yields. Density can be used to convert volume to dry matter biomass for use in bioenergy planning or carbon balance calculations.

Basic density is defined as oven-dry weight divided by green (or saturated) volume. The average basic density for aspen in Canada has been reported as 370 kg/m³ (Kennedy 1965). In Alberta, Saskatchewan and Manitoba, Singh (1984) reported basic density averaging 424 kg/m³ with an individual tree range of 360 to 497 kg/m³. Considerably higher basic density has been reported for aspen bark (450 kg/m³) compared to wood (380 kg/m³) in the western United States (Wengert et al. 1985). Branches and twigs tend to have a higher proportion of bark than mature stems, and branch wood is usually denser than stem wood (Hytonen et al. 2018).

Wood density provides an indication of the proportion of solid matter. Because cell cavities are filled with water in live trees, basic density is usually negatively correlated with moisture content. Wood density influences strength and stiffness in solid wood products, but it is also an important indicator of fibre yield per unit volume of wood in the pulping process. In oriented strand board (OSB) production, wood density affects the

ease of chipping, the bonding of resins and the compressibility of the wood flakes and chip mat. Lower density wood is thus preferred in the OSB manufacturing process (Woodson 1976, Wegner et al. 2010).

Wood properties such as density, strength or pulp yield result from the combination of three factors:

- i. macroscopic morphology – presence, extent and distribution of different types of wood tissue, e.g. reaction wood, heartwood, knots, wound wood, growth rings;
- ii. anatomy – types of cells and biometry, and their proportion;
- iii. chemical composition – cell wall components and extraneous materials (Pereira et al. 2003).

Wood formed close to the pith, either in young and small trees, or in the crowns of larger and older ones, is termed juvenile or core wood. Wood formed close to the bark at the periphery of the stem and away from the influence of a live crown is called mature or outer wood (Cobas et al. 2013). In diffuse-porous species, juvenile wood usually has shorter and thinner-walled fibres and larger fibril angle in the fibre cell wall; it may also have a higher frequency of smaller diameter vessels, and lower basic density (Bendtsen and Senft 1986). Juvenile wood sometimes presents elevated levels of tension wood composed of gelatinous fibres (Isebrands 1969). However, the presence of tension wood may be erratic, with no obvious age trends (Bendtsen and Senft 1986). Juvenile wood in poplars (including aspen) is dimensionally unstable, and has undesirable pulping properties. In short-rotation biomass plantations, trees are harvested at a young age and may have 100% juvenile or core wood (Balatinecz and Kretschmann 2001). In larger and older (mature) trees, the proportion of juvenile wood can vary between 10 and 20% depending on age at harvest and age of transition from juvenile to mature properties.

Wood density can vary between populations (Einspahr et al. 1965) and between individual trees within populations. Variation has also been observed within individual stems from pith to bark at a particular height, at various heights in the stem, and with

tree age (Yanchuk et al. 1983, Kärki 2001, Hytönen et al. 2018). Juvenile (or core) wood formed in proximity to the live crown tends to be of lower density than mature (or outer) wood laid down in the lower portions of the main stem of larger and older trees.

Aspen is classified as a diffuse-porous species because there is no abrupt transition from early (spring) to late (summer) wood. It is so named in contrast to ring-porous species, where large diameter vessels in early wood form a clear ring (Panshin and de Zeeuw 1970). In diffuse-porous species, water-conducting vessels are evenly scattered in a matrix of libriform fibres which provide strength and stiffness. Bimodal distributions of vessel diameters have been reported in some environments for aspen, suggesting that it can sometimes tend towards a semi-ring porous pattern (Schreiber et al. 2015). The relative proportions of vessels and fibres, together with their diameter, length, and cell wall thickness, are the primary determinants of wood density.

The relationship between growth rate and wood density is complex. There have been contradictory reports of genetic and phenotypic correlations in aspen and other *Populus* species. Some studies report negative phenotypic or genetic correlations in juvenile *Populus* (Kennedy 1968, Beaudoin et al. 1992, Olson et al. 1985, Stener 1998), others report positive correlations (Valentine 1962), some report both positive and negative correlations in different clones (Einspahr et al. 1965, Brown and Valentine 1963), and a large number of studies report that wood density is largely uncorrelated to growth rate in *Populus* in particular, and diffuse-porous hardwoods in general (Johnson 1942, Taylor and Wooten 1972, Einspahr and Winton 1976, Hillis and Brown 1978, Yanchuk 1982, Ilstedt and Gullberg 1993, Zhang 1995, DeBell et al. 2002, Zhang et al. 2003, Miranda and Pereira 2015).

Micko et al. (1984) found no (phenotypic) correlation between diameter and oven-dry wood density in aspen in western Canada. Yanchuk et al. (1984) studied 15 putative aspen clones in two natural stands and suggested a weak positive phenotypic correlation between rate of growth and wood density, but weak negative phenotypic correlations on the basis of four-year sections through 11 mm-diameter increment

cores. The calculation of genetic correlations between adjacent four-year sections suggested stronger negative correlations (overall non-significant correlation -0.479) but because of the lack of replication among clones, and the confounding of genetic and environmental effects their inferences are only applicable to the two stands sampled. Schreiber et al. (2011) reported a negative correlation between height and branch wood density for hybrid poplars ($r = -0.82$, $P < 0.02$) and no correlation in aspen. Kennedy (1968) suggested that the weight of evidence was for a negative correlation between growth rate and wood density, but that the trend may not be strong or of much practical importance.

Zobel and van Buijtenen (1989) reviewed the literature concerning density and growth rate and concluded that for diffuse-porous hardwoods these two traits are mainly uncorrelated. They suggested that the error of comparing wide-ringed, low specific gravity wood of young trees with narrow-ringed, high specific gravity wood of older trees has been repeated many times, and the relationships found were erroneously interpreted as the effect of growth rate rather than juvenile wood.

The current study was initiated to evaluate the heritability and correlations between height, diameter, volume, density and biomass for trees of known genotype, grown under uniform conditions and harvested at mid-rotation. The purpose was to determine if selection for volume might engender a negative correlated response in wood density.

2.1 Test materials

The test materials for this study consisted of 88 clones of 15-year-old plantation-grown aspen (*Populus tremuloides* Michx.) from clonal trial G812C at the Weyerhaeuser-Western Boreal Aspen Corporation Tree Improvement Centre in Drayton Valley, Alberta (Lat. 53.39°N, Long. 114.95°W).

The experiment used an incomplete block alpha design Williams and Matheson (1994) with five replicates, four-tree row plots with 90 treatments (88 clones and 2 seedlots).

The 90 treatments were arranged in nine alpha blocks with ten treatments per block. In the event of insufficient ramets per clone, filler trees were used. There was one surround row on the perimeter of the trial. The soil was a moderately well-drained loam with clay-loam to sandy loam texture. The site was an abandoned pasture with a grass and legume forage mixture and patches of aspen, willow and balsam poplar. Prior to planting, the site was sprayed with glyphosate, disked, and then sub-soiled. Competing vegetation was controlled with 60 x 60 cm Arbortech brush mats, and annual spraying with glyphosate for the first five years.

The test clones were phenotypically superior 'plus tree' selections from wild clones in northwestern Alberta (See Table S1 for source information). The planting stock was produced using excised juvenile sucker shoots taken from mature roots from the selected wild trees. The propagation method was adapted from that of Zufa (1971) and is described more fully by Gylander et al. (2012). Roots for propagation were collected in May 1999 and juvenile sucker cuttings were rooted and grown on a two-year cycle at the Weyerhaeuser Tree Improvement Centre in Drayton Valley, Alberta, Lat. 53.39°N, Long. 114.95°W, and the Woodmere forest nursery at Fairview, Alberta, Lat. 56.06°N, Long. 118.37°W. The planting stock was lifted in January 2001 and the trees were field planted in June 2001. The trees were planted at 2.5 m x 2.5 m spacing or 1,600 stems/ha.

2.2 Sampling for stem analysis and wood properties

A sample of 20 clones was chosen to cover the range in size observed in the trial. Samples were restricted to clones with at least 10 surviving ramets at age 15 years. A total of 200 sample trees were felled for stem analysis, and 5 cm thick breast height disks were taken. All clones were initially represented by 10 ramets, however one ramet of Clone 3113 was later excluded from volumetric calculations due to top breakage. A second ramet of the same clone was excluded from wood property determinations due to canker and decay at breast height, which made the disk unusable.

2.3 Stem analysis

Diameter was measured standing, and the breast height position (1.3 m) marked on the stem. The sample trees were then felled, and measured on the ground. Diameter was measured outside bark at two meter intervals along the stem. The trees were harvested in October 2016 (end of season) and the samples were taken at the same time. Breast height disks were cut, labelled, placed in plastic food storage bags, and frozen.

Total stem volume was calculated by summing over two-meter lengths. The volume of each 2 m length was calculated by multiplying the average sectional area of the two ends by the segment length. The terminal segment was assumed to be conical with a volume of $\frac{1}{12} \times \pi \times D^2 \times L$, where D = basal diameter and L = terminal segment length (Philip, 1983, p64).

Breast height form factor for each tree was calculated as the ratio of measured individual tree volume to $\pi/4 \times (DBH)^2 \times H$. The average breast height form factor was calculated for application in an individual tree volume equation of the form:

$$(1) \quad VOL = FF \times \pi/4 \times (DBH)^2 \times H \text{ (Philip, 1983, p33)}$$

Where:

VOL = individual tree volume (including bark) in cubic decimeters,

FF = breast-height form factor,

DBH = over-bark diameter at breast height in decimeters,

H = total tree height in decimeters.

2.4 Wood density determination

Samples were stored in a household freezer at approximately -15°C overwinter at the Weyerhaeuser Tree Improvement Center in Drayton Valley, Alberta. The samples were shipped by courier in the spring to the FP Innovations forest products laboratory in

Vancouver, British Columbia. Processing was done in BC. Prior to density determination, the bark was removed from all samples, all wood disks were cut in half through the pith, and one half was replaced in the bag for future testing. Twenty halves were cut into quarters through the pith for consistency testing. Test samples consisted of half-disks for small-diameter disks, and quarter-disks for large samples.

The testing followed Test Method B of Standard D2395-07a of the American Society for Testing and Materials (2014). The specimens were weighed to obtain green weight, and then submerged in water to obtain green volume by displacement. The specimens were then oven dried at 103°C for 48 hours.

The basic density and moisture content were calculated as follows:

$$\text{Basic (dry) density, kg/m}^3 = \text{oven dry weight, kg} / \text{green volume, m}^3$$

$$\text{Moisture content \%} = (\text{green weight} - \text{dry weight}) / \text{dry weight}$$

2.5 Statistical analyses

All statistical analyses were performed using SAS 9.4 software (SAS Institute Inc. 2017).

The following linear model was used:

$$(2) \quad y_{ij} = \mu + c_i + \varepsilon_{ij} \quad (\text{Becker, 1984, p27})$$

where:

y_{ij} = observation on ramet j in clone i ,

ε_{ij} = residual error associated with the j_{th} ramet of the i_{th} clone, $NID(0, \sigma_e^2)$.

The SAS MIXED procedure was used for estimation of best-linear unbiased predictor (BLUP) clone means, as well as variances and standard errors. With clones specified as random effects, the MIXED procedure provided estimates and standard errors for clonal and residual variances through the COVTEST option. The variance components and standard errors were also used in calculation of coefficients of variation and their

standard errors. Genetic, environmental and phenotypic variances were derived from the clonal, residual and total variance estimates.

The CORR procedure was used for calculation of simple statistics as well as calculation of phenotypic (individual tree) and genetic (BLUP clone mean) correlations. Broad-sense or clonal heritability was calculated as:

$$(3) \quad H^2 = \sigma^2_G / \sigma^2_P \text{ (White et al. 2007, p124)}$$

where:

σ^2_G = total genetic variation represented by σ^2_{Clone} , and

σ^2_P = total phenotypic variance estimated by $\sigma^2_{\text{Clone}} + \sigma^2_{\text{Error}}$.

The standard error for σ^2_P was calculated as:

$$(4) \quad SE\sigma^2_P = [SE_{\text{Clone}}^2 + SE_{\text{Error}}^2]^{1/2} \text{ (Yates, 1953, p198)}$$

The standard error for H^2 was calculated using the method for error estimation in variance ratios as follows:

$$(5) \quad SE(H^2) = H^2 \times [(SE_{\text{Clone}}/\sigma^2_G)^2 + (SE\sigma^2_P/\sigma^2_P)^2]^{1/2} \text{ (Yates, 1953, p198)}$$

3. Results and discussion

3.1 Simple statistics

The trial had 1238 surviving ramets at age 15 years. The simple statistics, coefficients of variation and trait correlations were calculated for the whole trial, for height, DBH and volume, with no selection or subsampling. However, density could only be measured on a limited number of trees. The 200 samples were selected from 20 clones which had at least 10 surviving ramets. The means and variances for the whole trial and for the 200 tree sample were similar for the growth traits.

The sampled trees averaged 12.2 m for height, 13.5 cm for DBH and 72.1 dm³ for individual tree volume (Table 1). The volume growth rate is similar to that reported for hybrid aspen plantations in Sweden (Rytter & Stener 2005) and in Latvia (Zeps et al. 2016). This is consistent with culmination of mean annual increment around age 30 years.

Phenotypic coefficients of variation (CV_P) for these three traits were 17%, 24% and 53%, respectively; however the genetic variation (CV_G) was lower for all three traits, at 12%, 19% and 42%, respectively (Table 3). There was considerable variation in volume, with the largest tree 26 times larger than the smallest. The clone mean values for the same three traits reduced this variation, but there was still a four-fold difference between the largest and smallest clone for mean volume. Breast height form factor averaged 0.390 with a CV_P of 18% (Table 2). The extreme values 0.234 and 0.643 represent broken-topped or forked trees. The genetic variability was much smaller (CV_G = 5%), suggesting that clones produce trees of the same shape. Moisture content averaged 98%, and there was considerable tree-to-tree variation (CV_P = 29%). Trees damaged by stem canker had broken bark, and were considerably drier than average (as low as 20% moisture content). There was very little genetic variation in moisture content, with clone mean values ranging from 92% to 104%, and very small genetic variation (CV_G = 6%). Wood basic density varied between 308 and 515 kg/m³, with a mean of 402 kg/m³ and a CV_P of 10%. Clone mean values ranged between 368 and 425 kg/m³ with very little genetic variation (CV_G = 4%).

3.2 Repeatability of moisture content and density measurements

Twenty of the wood disk samples were subjected to duplicate moisture content and basic density determination. The correlations between the paired samples were 0.57 and 0.62 for moisture content and density, respectively. While these correlations were both strong and highly significant, the corresponding repeatabilities were 33% and 39%, suggesting that there was considerable variation within breast-height disks. This large variability may have been caused in part by the presence of stem cankers. Branch stubs

and pockets of tension wood in many of the sample disks likely also contributed to the heterogeneity and low repeatability. Branch stubs and stem cankers were observed in some sample disks, and the presence of tension wood was inferred from the asymmetric position of the pith in others.

3.3 Genetic and phenotypic correlations between density and growth traits

Genetic and phenotypic correlations are presented in Table 4. Height, DBH and volume were strongly correlated, with phenotypic correlations of 0.76 to 0.91, while the genetic correlations were even higher: 0.90 to 0.99. Density was not correlated to height or volume, but there was a weak ($r = 0.14$) and significant ($p < 0.05$) positive phenotypic correlation with DBH. The genetic correlations between density and height, DBH or volume were not significantly different from zero. The positive phenotypic correlation between DBH and density at breast height may indicate that the trees are transitioning to mature wood characteristics, with larger diameter trees transitioning earlier.

3.4 Correlations between density and growth for ramets within clones

There was considerable variation between ramets within clones in the relation of density to growth rate. Correlations and their significance are summarized in Table 5. Of the 60 correlations, 37 were positive and 23 were negative. There appears to be no clear relationship between breast height density and height, with half showing positive and half showing negative correlations. Correlations between density and DBH were mostly positive but only four were significant.

3.5 Biomass

Individual tree biomass values were calculated by multiplying individual tree volume by individual tree density. The phenotypic and genetic statistics are summarized in Tables 1, 2 and 3. Volume and biomass had very similar levels of phenotypic and genetic variation, suggesting that volume explains most of the observed variation in biomass. The greater influence of volume in driving biomass yields was also observed in hybrid

poplar clones by Pliura et al. (2007). Genetic (r_G) and phenotypic (r_P) correlations (Table 4) between biomass and volume are both very strong and significant ($r_G = 0.99$ and $r_P = 0.98$ respectively), but those between biomass and density are weaker ($r_G = 0.08$ and $r_P = 0.19$) and the genetic correlation is not significantly different from zero.

3.6 Effects of latitudinal transfer

The test site was at latitude 53.4°N and the tested clones originated between 53.2°N and 57.0°N. This means that most of the materials have been transferred southwards by up to 3.6 degrees of latitude. The effect of latitude of origin on volume, density and biomass is illustrated in Figure S1. Clones from north of latitude 56.5°N have half the productivity of the southern ones. Genetic and phenotypic correlations of volume, biomass and density with latitude of clone origin are presented in Table 6. While growth rate is influenced by latitude of origin, wood density is not. Similar results are reported for *Populus balsamifera* by Ivkovich (1996) who detected significant differences in growth between northern and southern sources but no differences in density. Likewise, Viherä-Aarnio and Velling (2017) found no consistent differences in wood density with latitude of origin in silver birch. Hart et al. 2013 measured wood density in 7-year old aspens originating in Finland (*P. tremula*), China (*P. davidiana*) and Canada (*P. tremuloides*). In that study, the regression of density on latitude of origin was not significant. However, since the three species were each represented by a single source, any inferences concerning the relationship of density with latitude of origin have limited generality.

Biomass and volume show a similar relationship to latitude of clone origin. When traits are collinear, partial correlations can be used to measure the strength of the linear relationship while adjusting for the effect of other variables. This was done here to tease out the effects of volume and density, which were multiplied to generate biomass. Partial correlations are presented in Table 7. When both volume and density are accounted for, there is no linear relationship between latitude and biomass. When volume is accounted for, there is still no significant correlation. However, when density is accounted for there is a significant negative correlation between biomass and latitude.

This again demonstrates the stronger influence of volume over density in biomass determination.

3.7 Broad-sense heritability

Height, DBH and volume had heritabilities of 0.50, 0.64 and 0.62, respectively, suggesting strong genetic control of growth. Biomass had a heritability of 0.59 ± 0.24 (Table 8). Form factor and wood moisture content have very low heritability, suggesting weak, if any, genetic control. Basic density had low heritability ($H^2 = 0.20 \pm 0.094$). This value is similar to that reported by Ilsted and Gullberg (1993) for 26-year-old hybrid aspen, but lower than those reported for younger trees by Stener (1998) and Rytter and Stener (2003). The latter studies also report negative phenotypic and genetic correlations between density and growth in young hybrid aspen trees.

3.8 Growth rate and wood density

All of the trees in this study were of the same age. Despite the relatively uniform growing conditions there were large differences in individual tree volume; however there was relatively little variability in wood density, as evidenced by the low coefficient of genetic variation. Similar patterns were reported for hybrid poplar by Pliura et al. 2006. Wood density appeared to be uncorrelated with volume growth rate, as has been reported elsewhere for similar-aged aspens (Zeps and Zarina, 2016).

3.9 Practical implications for genetic selection

Both OSB producers and pulp manufacturers are focused primarily on accessible wood supply. So volume is the most important single trait. The important finding here is that selection on volume will generate bigger gains, firstly because of the high heritability, and secondly because of the larger coefficient of variation. Density has a much lower coefficient of variation, and low heritability. Density and growth traits are essentially uncorrelated, so selection for growth will not substantially impact density one way or the other.

The economics of selection for density are complex. In pulp production, higher density means greater yield of pulp per cubic metre of wood, but denser wood is harder on the

chipping blades. Furthermore higher density is associated with thicker cell walls and changes in coarseness making the fibres less conformable. High density chips have poorer liquor penetration. High density waste wood makes better hog fuel for cogeneration. So there are pluses and minuses associated with high and low density wood at different stages of the pulping process. In most cases the overwhelming consideration is volume with a smaller value attached to uniformity. Similar arguments apply to oriented strand board production, where high or low density has positive or negative effects at different points in the manufacturing cycle.

4. Conclusion

In this study the genetic and phenotypic variation in volume ($CV_G = 42\%$ and $CV_P = 53\%$) was considerably larger than that for wood density ($CV_G = 4\%$ and $CV_P = 10\%$). Volume also had higher heritability ($H^2 = 0.62 \pm 0.25$) compared to that for density ($H^2 = 0.20 \pm 0.09$), and genetic correlations between density and growth traits were negligible. Considerable gains in biomass productivity are likely achievable through selection on volume alone. In plantation grown aspen trees measured at mid-rotation, there is no evidence that faster growth causes a reduction in wood density.

Acknowledgements

The author is grateful to Weyerhaeuser Company Limited, Pembina Region, for funding this project. Thanks are extended to: Dave Swindlehurst who obtained the necessary funding; Bonnie Baker who conducted trial measurements and wood sample collection; and Paul Symons of FP Innovations, Vancouver BC who did the wood density determinations. The Western Boreal Aspen Corporation provided access to growth data and materials from clonal trial G812 series.

Draft

5. References

- American Society for Testing and Materials. 2014. D2395-07a, 2014. Standard test methods for specific gravity of wood and wood-based materials, Test Method B.
- Balatinecz, J.J. and Kretschmann, D.E. 2001. Properties and utilization of poplar wood. In Poplar Culture in North America. Part A. Chapter 9. Edited by Dickmann, D.I., Isebrands, J.G., Eckenwalder, J.E. and Richardson, J. NRC Research Press, National Research Council of Canada, Ottawa, ON K1A 0R6, Canada. pp 277-291.
- Beaudoin, M., Hernández, R.E., Koubaa, A., and Poliquin, J. 1992. Interclonal, intraclonal and within-tree variation in wood density of poplar hybrid clones. Wood and Fiber Science, 24(2): 147-153.
- Becker, W.A. 1984. Manual of quantitative genetics. Washington State Univ. Pullman, WA. 186 pp.
- Bendtsen, B.A. and Senft, J. 1986. Mechanical and anatomical properties in individual growth rings of plantation-grown eastern cottonwood and loblolly pine. Wood and Fiber Science, 18(1):23-38.
- Brown, I.R. and Valentine, F.A. 1963. Natural variation in specific gravity and fibre length in *Populus tremuloides* clones. Proc. Northeast. For. Tree Imp. Conf., 10:25-41.
- Cobas, A.C., Area, M.C. and Monteoliva, S. 2013. Transición de madera juvenile a madura en un clon de *Populus deltoides* implantado en Buenos Aires Argentina. Maderas. Ciencia y tecnología, 15(2):223-234.
- DeBell, D.S., Singleton, R., Harrington, C.A. and Gartner, B.L. 2002. Wood density and fiber length in young *Populus* stems: Relation to clone, age, growth rate and pruning. Wood and Fiber Science, 34(4):529-539.
- Einspahr, D.W. and Winton, L.L. 1976. Genetics of quaking aspen. USDA For. Serv. Res. Pap. WO-25. 23p.

- Einspahr, D.W., Winton, L.L., Benson, M.K. and Van Horn, W. 1965. A study of the genetic improvement of quaking and bigtooth aspen by selection, hybridization and the exploitation of polyploidy. Project 2412. Report Two. Institute of Paper Chemistry, Appleton, Wisconsin.
- Government of Alberta. 2017. Sustainable Forest Management. 2015 Facts and Statistics. Agriculture and Forestry. ISBN 979-1-4601-3520-4.
- Gylander T., Hamann, A., Brouard, J.S. and Thomas, B.R. 2012. The potential of aspen clonal forestry in Alberta: breeding regions and estimates of genetic gain from selection. PLoS ONE, 7(8) art. no. e44303. 11p.
- Hart, J.F., de Araujo, F., Thomas, B.R. and Mansfield, S.D. 2013. Wood quality and growth characterization across intra- and inter-specific hybrid aspen clones. Forests, 4:786-807.
- Hillis, W.E. and Brown, A.C. 1978. Eucalyptus for wood production. CSIRO Griffin Press Ltd. Adelaide.
- Hytönen, J., Beuker, E., and Viherä-Aarnio, A. 2018. Clonal variation in basic density, moisture content and heating value of wood, bark and branches in hybrid aspen. Silva Fennica, 52(2) article id:9938 15p.
- Ilsted B. and Gullberg, U. 1993. Genetic variation in a 26-year old hybrid aspen trial in southern Sweden. Scand J For Res, 8:185-192.
- Isebrands, J.G. 1969. Cellular variation within the wood of eastern cottonwood. Retrospective Theses and Dissertations. 3747. <http://lib.dr.iastate.edu/rtd/3747>
- Ivkovich, M. 1996. Genetic variation of wood properties in balsam poplar (*Populus balsamifera* L.). Silvae Genetica, 45:119-124.
- Johnson, L.P.V. 1942. Studies on the relation of growth rate to wood quality in *Populus* hybrids. Canadian Journal of Research, 20c(1):28-40.

- Kärki, T. 2001. Variation of wood density and shrinkage in European aspen (*Populus tremula*). Holz als Roh- und Werkstoff, 59:79-84.
- Kennedy, E.I. 1965. Strength and related properties of woods grown in Canada. Department of Forestry Publication No. 1104. Canada Forest Products Research Branch, Ottawa, Canada.
- Kennedy, R.W. 1968. Strength and related properties of woods grown in Canada. Department of Forestry Publication No. 1104. Canada Forest Products Research Branch, Ottawa, Canada.
- Mansfield, S.D., Kang, K.Y., and Chapple, C. 2012. Designed for deconstruction-poplar trees altered in cell wall lignification improve the efficacy of bioethanol production. New Phytol., 194: 91–101.
- Micko, M.M., Wang, E.I.C., and Bains, B.S. 1984. Wood properties of prairie provinces and N.W.T.; statistical analysis. University of Alberta. ENFOR Project P-255, CSS Contract 01SG.KH-505-3-0035.
- Miranda, I. and Pereira, H. 2015. Variation of wood and bark density and production in coppiced *Eucalyptus globulus* trees in a second rotation. iForest (early view) e1-e6. Online 2015-09-08.
- Natural Resources Canada. 2017. www.nrcan.gc.ca/forests/boreal/13071. Modified 2017-06-06.
- Olson, J.R., Jourdain, C.R., and Rousseau, R.J. 1985. Selection for cellulose content, specific gravity, and volume in young *Populus deltoides* clones. Can. J. For. Res., 15: 393-396.
- Panshin, A.J. and de Zeeuw, C. 1970. Textbook of wood technology. Third Edition. McGraw-Hill, New York, USA.
- Pereira, H, Graca, J. and Rodrigues, J.C. 2003. Wood chemistry in relation to wood quality. p 53-83. In: Barnett, J.R. and G. Jeronimidis. Eds. Wood quality and its biological basis. Oxford, Boca Raton, FL: Blackwell, CRC Press.

- Philip, M.S. 1983. Measuring trees and forests. U. of Dar-es-Salaam. 338 pp.
- Pliura, A., Zhang, S.Y., Bousquet, J. and Mackay, J. 2006. Age trends in genotypic variation of wood density and its intra-ring components in young poplar hybrid crosses. *Ann. For. Sci.*, 63: 673-685.
- Pliura, A., Zhang, S.Y., MacKay, J. and Bousquet, J. 2007. Genotypic variation in wood density and growth traits of poplar hybrids at four clonal trials. *Forest Ecology and Management*, 238: 92-106.
- Rytter, L. and Stener L.-G. 2003. Clonal variation and nutrient content in woody biomass of hybrid aspen (*Populus tremula* L. x *P. tremuloides* Michx.). *Silva Fennica*, 37(3): 313-324.
- Rytter, L. and Stener L.-G. 2005. Productivity and thinning effects in hybrid aspen (*Populus tremula* L. x *P. tremuloides* Michx.) stands in southern Sweden. *Forestry*, 78(3): 285-295.
- SAS Institute Inc. 2017. SAS/STAT® 14.3 User's Guide. Cary, NC: SAS Institute Inc. SAS/STAT® 14.3 User's Guide.
- Schreiber, S.G., Hacke, U.G., Hamann, A. and Thomas, B.R. 2011. Genetic variation of hydraulic and wood anatomical traits in hybrid poplar and trembling aspen. *New Phytologist*, 190: 150-160.
- Schreiber, S.G., Hacke, U.G. and Hamann, A. 2015. Variation of xylem vessel diameters across a climate gradient: insight from a reciprocal transplant experiment with a widespread boreal tree. *Functional Ecology*, 29: 1392–1401.
- Singh, T. 1984. Variation in the oven-dry wood density of ten prairie tree species. *Forestry Chronicle*, 60(4): 217-221.
- Stener, L.-G. 1998. Analys av fiberegenskaper för kloner av hybridasp. Arbetsrapport Nr 387. SkogForsk, Uppsala, Sweden.

- Stener, L.-G. and Westin, J. 2017. Early growth and phenology of hybrid aspen and poplar in clonal field tests in Scandinavia. *Silva Fennica*, 51(3) article id:5656. 22p.
- Taylor, F.W. and Wooten, T.E. 1972. Wood property variation of Mississippi delta hardwoods. *Wood and Fiber*, 5(1):2-13.
- Valentine, F.A. 1962. Natural variation in specific gravity in *Populus tremuloides* in northern New York. *Proc. Northeast. For. Tree Imp. Conf.*, 9:17-34.
- Viherä-Aarnio, A. and Velling, P. (2017). Growth, wood density and bark thickness of silver birch originating from the Baltic countries and Finland in two Finnish provenance trials. *Silva Fennica*, 51(4) article id:7731. 18p.
- Wegner, T., Skog, K.E., Ince, P.J. and Michler, C.J. (2010) Uses and desirable properties of wood in the 21st century. *J. For.*, 108:165–17
- Wengert, E.M., Donnelly, D.M., Markstrom, D.C. and Worth, H.E. 1985. Wood utilization. In: *Aspen: Ecology and Management in the Western United States*. Debye, N.V. and Winokur R.P., eds. USDA Forest Service, General Technical Report RM-119. Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO: 169–180.
- White, T.L., Adams, W.T., and Neale, D.B. 2007. *Forest Genetics*. CABI publishing. 682 pp.
- Woodson, G.E. 1976. Properties of medium-density fiberboard related to hardwood specific gravity. 10th Washington State University Particleboard Symposium, Pullman, WA. 175-192.
- Yanchuk, A.D. 1982. Clonal variation of wood density and fibre length of trembling aspen (*Populus tremuloides* Michx.) in north-central Alberta. MSc Thesis. University of Alberta. 85 p.
- Yanchuk, A.D., Dancik, B.P. and Micko, M.M. 1983. Intraclonal variation in wood density of trembling aspen in Alberta. *Wood and Fiber Science*, 15(4):387-394.

- Yanchuk, A.D., Dancik, B.P. and Micko, M.M. 1984. Variation and heritability of wood density and fibre length of trembling aspen in Alberta, Canada. *Silvae Genetica*, 33(1):11-16.
- Yates, F. 1953. Sampling methods for censuses and surveys. London. C. Griffin Co. Ltd. 401p.
- Zeps, M. and Zarina, I. 2016. Hybrid aspen clone wood mechanical properties. *Agronomy Research*, 14(S1):1147-1152.
- Zeps, M., Gailis, A., Smilga, J., Miežite, O., Sisenis L. and Zarina, I. 2016. Productivity and quality of hybrid aspen at the age of 18 years. *Research for Rural Development*, 2:55-61.
- Zhang, S.Y. 1995. Effect of growth rate on wood specific gravity and selected mechanical properties in individual species from distinct wood categories. *Wood Science and Technology*, 29: 451-465.
- Zhang, S.Y., Yu, Q, Chauret, G. and Koubaa, A. 2003. Selection for both growth and wood properties in hybrid poplar clones. *For. Sci.*, 49(6):1-8.
- Zobel, B.J. and van Buijtenen, J. 1989. Wood variation: its causes and control. Springer -Verlag, Berlin. 418p.
- Zufa, L. 1971. A rapid method for vegetative propagation of aspens and their hybrids. *Forestry Chronicle*, 47(1):36-39.

Table 1. Simple phenotypic and genetic growth statistics, for whole trial versus sampled trees

		phenotypic					
	Variable	# ramets	Mean	S _P	Min.	Max.	Max/Min
Whole Trial	Height	1238	12.3	1.928	7.0	18.7	2.7
	DBH	1238	13.7	2.901	5.4	22.3	4.1
	Volume	1238	76.5	39.792	6.5	251.1	38.9
Density samples	Height	199	12.2	2.032	7.2	17.5	2.4
	DBH	199	13.5	3.247	6.4	21.3	3.4
	Volume	199	72.1	38.121	8.9	231.6	25.9
		genetic (based on BLUP clone means)					
	Variable	# clones	Mean ^a	S _G	Min. ^a	Max. ^a	Max/Min
Whole Trial	Height	88	12.3	1.202	9.8	15.1	1.5
	DBH	88	13.7	2.122	9.3	18.6	2.0
	Volume	88	76.5	27.906	31.6	151.8	4.8
Density samples	Height	20	12.2	1.434	9.7	14.4	1.5
	DBH	20	13.5	2.588	9.7	18.2	1.9
	Volume	20	72.1	29.928	32.9	124.9	3.8

Height = total height, m; DBH = diameter at breast height measured outside bark, cm; Volume = total main stem volume with bark, dm³

^a BLUP Mean, Minimum and Maximum values were calculated as deviations with a mean of zero. Here they have been adjusted through the addition of the appropriate phenotypic mean for clarity of interpretation.

Note: Clone 3113 had only nine surviving ramets. Hence only 199 sample trees.

Table 2. Simple phenotypic and genetic statistics for sample trees

phenotypic						
Variable	# ramets	Mean	S _P	Min.	Max.	Max/Min
FF	199	0.390	0.070	0.234	0.643	2.7
MC	198	97.9	27.984	20.3	176.4	8.7
Density	198	402	38.807	308	515	1.7
Biomass	198	29.1	15.389	3.0	84.4	28.0
genetic (based on BLUP clone means)						
Variable	# clones	Mean ^a	S _G	Min. ^a	Max. ^a	Max/Min
FF	20	0.390	0.021	0.363	0.419	1.2
MC	20	97.9	5.840	91.8	103.6	1.1
Density	20	402	17.321	368	425	1.2
Biomass	20	29.1	11.789	12.7	49.7	3.9

FF= breast height form factor; MC = wood moisture content, %; Density = basic density of wood, no bark, kg/m³; Biomass = volume x (density/1000), kg; S_P = (V_P)^{1/2}, where V_P = phenotypic variance from mixed model ANOVA; S_G = (V_C)^{1/2}, where V_C = clonal variance from mixed model ANOVA; ^a BLUP Mean, Minimum and Maximum values were calculated as deviations with a mean of zero. Here they have been adjusted through the addition of the appropriate phenotypic mean for clarity of interpretation.

Note: Clone 3113 lost one density sample due to decay

Draft

Table 3. Coefficients of variation (standard errors)

Variable	CV _G		CV _e		CV _P	
Height	12%	(4.6%)	12%	(2.4%)	17%	(4.2%)
DBH	19%	(8.0%)	15%	(3.8%)	24%	(7.9%)
Volume	42%	(26.2%)	33%	(17.7%)	53%	(30.2%)
Form Factor	5%	(3.7%)	17%	(3.5%)	18%	(3.8%)
Moisture Content	6%	(6.6%)	28%	(3.5%)	29%	(8.8%)
Density	4%	(2.0%)	9%	(1.2%)	10%	(1.5%)
Biomass	41%	(25.7%)	34%	(18.3%)	53%	(30.1%)

CV_G = Genetic coefficient of variation

CV_e = Environmental coefficient of variation

CV_P = Phenotypic coefficient of variation

Draft

Draft

Table 4. Genetic and phenotypic correlations

Genetic correlations above the diagonal, phenotypic below

Prob > | r | under H0: Rho=0

	Height	DBH	Volume	Biomass	Density
Height		0.90	0.92	0.91	-0.07
		<.0001	<.0001	<.0001	0.7675
DBH	0.76		0.99	0.98	0.01
	<.0001		<.0001	<.0001	0.9538
Volume	0.85	0.91		0.99	-0.03
	<.0001	<.0001		<.0001	0.9070
Biomass	0.82	0.92	0.98		0.08
	<.0001	<.0001	<.0001		0.7406
Density	-0.06	0.14	0.02	0.19	
	0.3752	0.0487	0.7768	0.0086	

N = 198 trees for phenotypic correlations
n = 20 clones for genetic correlations

Table 5. Correlations between density and growth traits, for ramets within clones

Clone	No. ramets	Height	DBH	Volume
1065	10	-0.70 *	-0.11	-0.22
1104	10	0.14	0.33	0.31
1109	10	0.63	0.76 *	0.84 **
3044	10	-0.06	0.70 *	0.54
3085	10	-0.57	-0.44	-0.60
3099	10	0.23	0.53	0.18
3100	10	0.62	0.72 *	0.68 *
3104	10	0.68 *	0.45	0.61
3109	10	-0.19	0.00	-0.37
3113	8	0.23	0.41	0.39
3114	10	0.26	0.61	0.50
3124	10	-0.67 *	-0.07	-0.33
8003	10	-0.21	0.60	0.41
8005	10	-0.20	0.14	0.09
8021	10	-0.44	-0.23	-0.43
8024	10	-0.34	0.13	-0.29
8025	10	-0.03	0.38	-0.15
8031	10	0.16	0.64 *	0.48
8035	10	0.21	0.46	0.19
8037	10	0.00	-0.60	-0.27
All clones	198	-0.06	0.14 *	0.02

significant correlations: * = $p < 0.05$, ** = $p < 0.01$

Table 6. Correlations with latitude of clone origin

Pearson Correlation Coefficients

Prob > |r| under H0: Rho=0

Latitude °N:	Volume	Biomass	Density
Genetic	-0.41	-0.42	-0.07
correlation	0.0717	0.0666	0.7536
Phenotypic	-0.34	-0.34	-0.04
correlation	<.0001	<.0001	0.6126

N = 198 trees for phenotypic correlations

n = 20 clones for genetic correlations

Draft

Table 7. Partial correlations Biomass with Latitude

Pearson Partial Correlation Coefficients
Prob > |r| under H0: Rho=0

Latitude °N:	Biomass	
	0.02	Volume and density
	0.7613	partialled out
	-0.02	Volume
	0.8039	partialled out
	-0.34	Density
	<.0001	partialled out

N = 198 trees

Draft

Table 8. Broad sense heritabilities

Variable	Heritability	(S.E.)
Height	0.50	(0.20)
DBH	0.64	(0.26)
Volume	0.62	(0.25)
Form factor	0.09	(0.06)
Moisture content	0.04	(0.05)
Density	0.20	(0.09)
Biomass	0.59	(0.24)

Draft