

GENETIC IMPROVEMENT OF FIBER LENGTH AND COARSENESS BASED ON PAPER PRODUCT PERFORMANCE AND MATERIAL VARIABILITY – A REVIEW

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SUMMARY

Improvement of specific gravity through tree breeding was an early choice made in the mid 20th century due to its ease of measurement and impact on pulp yield and lumber strength and stiffness. This was often the first, and in many cases, the only wood quality trait selected for. However, from a product standpoint, increased specific gravity has shown to lower many paper strength and stiffness properties and has been assumed to be directly attributable to increased fiber coarseness. As a result, it is currently not clear which fiber trait would best benefit a tree improvement program for paper products. This review found coarseness to be perhaps more important to paper strength and stiffness whereas tracheid length showed better promise from a breeding point of view due to its independence from specific gravity. However, both traits possessed strong heritability and influence on product performance and thus both would be beneficial to breed for depending on organizational goals and end product mix. The objective of this paper is to review and prioritize coarseness and tracheid length from both an end use and raw material perspective. To aid in prioritization, the variation, correlation, and heritability of both traits were reviewed along with significant genetic and phenotypic correlations. Variation trends within and between families as well as within a tree were reviewed.

Key words: Coarseness, family, combining ability, genotype, heritability, phenotype, tracheid length, variation.

INTRODUCTION

Improvement of specific gravity has been implemented by tree improvement programs with the goal of improving pulp yield, lumber strength, and stiffness (Talbert *et al.* 1983; Ridoutt *et al.* 1998; Apiolaza & Garrick 2001). However, the majority of programs have limited their focus to easily measurable phenotypic traits such as volume, straightness,

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form, height, disease resistance, and spiral grain (Farmer & Wilcox 1965; Maynard 1976; White *et al.* 1993; Simpson & Tosh 1997; Simpson 1997; Ridoutt *et al.* 1998; Cumbie *et al.* 2001; Land *et al.* 2001). Conversely, while research on tracheid morphology has been voluminous, few programs have integrated other internal qualities such as tracheid length, cell wall thickness, coarseness, or pulp yield (Valente *et al.* 1992; Dean 1995; Pereira *et al.* 1995). Through personal communication with industry, inclusion of these internal characteristics, including microfibril angle, is becoming essential.

With increased interest in internal quality, it is important to decide which traits should be improved, especially if the population has already been selected for higher density. Coarseness and tracheid length are two traits very important to pulp and paper; however, coarseness and tracheid length have not been implemented in most tree improvement programs, due to the cost and time of measurement. Since coarseness is defined as the weight per unit length of fiber, it can be deduced that increased specific gravity may not be desired, assuming coarseness and specific gravity are highly related. Veal *et al.* (1987) demonstrated that a 15% increase in coarseness occurred in conjunction with a 10% increase in specific gravity.

Perhaps a long ignored paradox is the mixed effect of coarseness on paper yield and strength. Although increased coarseness will increase pulp yield, due to higher density (Gladstone *et al.* 1970), the same increase in coarseness will lower most strength properties. As a result, one needs to account for the full variation in cost and profit, attributable to yield and coarseness change, from the manufacturing process to sale of the product. For example, for kraft pulp, an increase of coarseness by 4% increased pulp yield by 2%, but decreased strength by 4% (Hakanen & Hartler 1995). Other studies show increased density to decrease burst and tensile strength while increasing tear strength and pulp yield (Kleppe 1970; Farrington 1980; Kibblewhite 1984; Duffy & Kibblewhite 1989). Perhaps, the often-overlooked effect of coarseness on strength, by tree breeders, may be due to their fear that decades of density improvement would now be labeled counterproductive; instead, admission of this evidence may compel tree breeders to find an acceptable solution. One solution might be that one could maintain a higher density raw material for increased pulp yield, whilst not falling below some limiting strength factor as established by paper standards or internal quality control. But regardless of this predicament, one needs to first determine if any correlations between density and coarseness exist and, if so, what proportion of phenotypic covariance is commonly attributable to genetic variation *versus* environment.

For tree improvement tracheid length is a contender to coarseness due to its significant impact on product performance. But to the knowledge of Whiteman *et al.* (1996), neither tracheid length nor coarseness has been bred for despite potential genetic gain. A comparison of the two would thus be useful.

For paper strength or yield improvement, a trait may appear optimal for improvement, but have little opportunity for genetic gain. Conversely, a trait may encompass high variation and heritability, but have limited impact on paper strength or yield. Thus, both factors, raw material and final product, need to be considered. For the paper product, different fiber traits can have contrasting influence on product quality when compared to solid wood products. For example, a low microfibril angle is perhaps the

most beneficial trait to accompany high specific gravity for solid wood products. However, for paper, microfibril angle has limited value on most properties, with the exception of stretch, which increases linearly with increasing microfibril angle (Watson & Dadswell 1964; French *et al.* 2000; Wimmer *et al.* 2002). Instead, the variation in fiber dimensions and alignment are two factors to influence sheet properties and are dictated by the headbox during manufacturing (Olson 2002).

After leaving the headbox, the sheet is later pressed to reduce voids and increase contact surface area between fibers, which is essential for hydrogen bonding. Increased fiber length and decreased coarseness at this stage will help to promote fiber flexibility and collapsibility needed for better bonding (Paavilainen 1993). For example, an increase in coarseness has been shown to have a negative impact on tensile index, apparent density, burst ratio, and breaking length but had a positive impact on tear (Barefoot *et al.* 1964; Kibblewhite *et al.* 1999). Thus, one may want to consider which strength properties are most important for a given product mix.

Page and colleagues were pioneers in tensile strength modeling of paper products. Two critical variables included in their equations were length and coarseness. They showed that coarseness was an order of magnitude higher than tracheid length in predicting tensile strength (Page 1969; Seth 1995; Seth & Page 1996). This was corroborated by Broderick *et al.* (1996) who attributed the tensile strength increase to better fiber flexibility, a trait associated with decreased coarseness. On the other hand, increased tracheid length is better for burst strength (Hosseiny & Anderson 1999). Overall, coarseness appeared to surpass tracheid length for most strength properties, but in almost every case, tracheid length was still important.

The objectives of this paper are to review the importance of tracheid length and coarseness on product strength. Furthermore, the magnitude of heritability, genetic correlation, and source of variation, are reviewed so that the reader may surmise which trait is most beneficial for tree improvement.

Morphology effect on product performance

Several works found coarseness to be more influential than tracheid length for some paper properties (Page 1969; Seth & Page 1996). When wet web tensile strength was divided by tracheid length, a strong linear correlation to fiber coarseness emerged (Seth 1995). After further examination, the square of coarseness was found to best predict tensile strength, after inclusion of tracheid length, thus supporting that coarseness was an order of magnitude greater than tracheid length in the strength relationship (Seth 1995).

Coarseness and tracheid length were both deemed important in high yield pulp when chemical treatment was used over mechanical pulping (Broderick *et al.* 1996). Although realistically, there is no explanation supporting how tracheid length may directly influence pulp yield and is, perhaps, due to some covariance between tracheid length and another trait. Tracheid length appeared as important as coarseness to tear and tensile strength until 3 mm in length was approached (Broderick *et al.* 1996). Increased fiber

length and decreased coarseness promoted better bonding between fibers within the sheet. For eucalyptus (*Eucalyptus globulus*), tensile, tear, bending, freeness, and pulp yield was positively correlated to fiber length (O'Neill 1999; Wimmer *et al.* 2002).

At the refining stage, increased beating resulted in better fiber flexibility and compressive strength (Seth 1986). Meanwhile, the original fiber length was of minor influence due to fiber length reduction during refining. However, fiber length reduction depends on the type of mechanical treatment one imposes during refining (Seo *et al.* 2002). Since fiber length may be reduced during refining, it is important to consider if refining should be included in the experimental design.

Variation in tracheid length and coarseness

Geography

An understanding of how a raw material varies is one factor that determines if a trait can feasibly be improved. Provenance variation and differences are usually the first step in determining what gains are possible.

Provenance testing of tracheid length and coarseness has been performed to determine the ranking of potential seed source. Latitude and longitude differences are sometimes the best indicators of genetic superiority. For example, Zobel *et al.* (1960) found tracheid length to gradually increase from north to south for loblolly pine (*Pinus taeda*). For radiata pine (*Pinus radiata*), the correlation between latitude and tracheid length was moderate with an $r^2 = 0.587$ (Harris 1965). East to west differences in tracheid length was insignificant for mature Pino rojo (*Pinus tecunumanii*) (Piedra & Zobel 1986).

No literature could be found describing the relation between geography and fiber coarseness. However, because fiber coarseness is defined as weight per unit length, then it is possible that tracheid length and specific gravity trends influence coarseness. Specific gravity has shown to increase from north to south and west to east for loblolly pine (Zobel *et al.* 1960; Zobel & Jett 1995), whereas cell wall thickness was dependent on provenance location (Miranda & Pereira 2002). Coarseness was shown to be dependent on cell wall thickness (Nyakuengama *et al.* 2003). For slash pine (*Pinus elliottii*), specific gravity increased southward from South Carolina, to Georgia, to Florida, U.S.A. (Clark & Saucier 1991). In Mississippi (U.S.A), isograms were developed showing distinct increases in specific gravity in gradients from north to south for loblolly and shortleaf pine (*Pinus echinata*) (Mitchell 1964). Megraw suggested an increase in specific gravity, with decreasing latitude, maybe due to prolonged growing period, which tends to have a higher ratio of latewood to earlywood production (Megraw 1985).

The physiological needs of a tree can vary with geography and may require specific fiber morphology. For instance, in gymnosperms, the density within a stem may be correlated to water flow rate since lumen or vessel diameter controls flow rates and determines density (Roderick & Berry 2001). This theory may partially explain why the density of loblolly pine increased from north to south (Zobel *et al.* 1960; Mitchell 1964; Clark & Saucier 1991; Miranda & Pereira 2002). However, Dean and Long (1986) countered the flow theory with strong empirical evidence that stem formation is a function of stress distribution within the tree, as per cantilever beam loading theory. Their

data supports that a tree has an adjustment in taper along the stem so as to maintain a uniform stress during cantilever loading. Furthermore, extending this theory, it may be possible that in high wind load areas, increased density has evolved to resist higher loads. This may explain why some investigators witnessed higher density in southern pines from the coastal region than the piedmont, where latitude did not vary (Clark & Saucier 1989; Szymanski & Tauer 1991).

Altitude is another geographic variable shown to influence tracheid formation. Within Norway spruce (*Picea abies*), tracheids from trees higher in altitude reached maturity earlier in the year resulting in shorter tracheid length (Gindl *et al.* 2001).

Within and between families

The variation in phenotypic traits, between trees or within families, is useful when estimating how much total genetic gain may be possible. Should phenotypic variation be low, then strong heritabilities will not yield enough predicted gain to justify improvement. If, on the other hand, phenotypic variation is high, then one needs to further partition the genotype and environmental variation and consider if the heritability is strong enough to reach acceptable gains. For pino rojo, the phenotypic coefficient of variation (COV) for tracheid length ranged from 10 to 16% depending on site (Piedra & Zobel 1986). Eucalyptus (*Eucalyptus grandis*) exhibited a lower COV of 5 to 8% for tracheid length (Raymond *et al.* 1998; Kibblewhite *et al.* 1999). For radiata pine, larger variations within families occurred for tracheid length. For example, only 5 out of 30 families significantly differed from a set of control trees, at the $\alpha = 0.06$ level, as a result of the high variation (Cown *et al.* 1992). It may therefore be concluded that variation in tracheid length is dependent on species. This variation should be accounted for in estimating predicted gain. Alternatively, additional value could potentially be achieved in the log yard by categorizing species and/or species groups by their mean going into the pulp mill. Such mean categorization would also reduce variation going into the mill resulting in improved process control.

For coarseness, a COV of 7 to 9% was observed for whole radiata pine trees and clones respectively (Evans *et al.* 1997; Kibblewhite & Evans 2001) but can be as high as 20% under different environments (Nyakuengama *et al.* 1997). However, the 20% COV should be considered with caution since the variance estimate included rings of different ages. For Douglas-fir (*Pseudotsuga menziesii*) clones, large variation in late-wood percent enabled the detection of significant differences in coarseness (Chantre *et al.* 2002). In eucalyptus, 30% of the variation in vessel diameter and frequency was accounted for genetically (Leal *et al.* 2003). Vessel size and frequency may be an important parameter influencing coarseness since hardwoods are more diverse in cell types.

Morphological variations from pith to bark are, quite often, more pronounced than vertically for many species (Evans *et al.* 1997; Koubaa *et al.* 1998; Raymond *et al.* 1998). For scots pine (*Pinus sylvestris*), the COV for tracheid length was 7% at both ring 4 and 24 (Hannrup *et al.* 2001). Among 10 poplar hybrid clones (*Populus* sp.), the COV was 3% (Koubaa *et al.* 1998). However, the mean of each poplar clone was

estimated from two to four trees and then COVs determined which would underestimate tree-to-tree variation.

Within a tree

Measurement of fiber morphology from increment cores may not be useful if the data do not estimate whole tree values accurately. Additionally, one assumes that each family does not significantly differ in slope when traits at breast height are plotted against whole tree values. Therefore, height patterns of variation are important in understanding how useful heritability studies may be when using increment cores.

For coarseness, the relationship between breast height and whole tree estimates were greater than $r = 0.90$ for eleven radiata pine clones. Even more noteworthy, tracheid wall thickness histograms from whole trees and increment cores were coincident, exhibiting similar mean and variance. For eucalyptus, the correlation between increment core and whole tree coarseness was lower, at around $r = 0.7$, and was between 0.7 to 0.87 for tracheid length (Muneri & Raymond 2001). As a result, to estimate a stand to an accuracy of $\pm 5\%$ using increment cores, 8 to 13 trees were needed to estimate mean tracheid length whereas, for coarseness, 11 to 21 trees were needed. Since environments may differ from site to site, lower r -square values should be assumed when determining sample size.

From pith to bark, fiber length was shown to increase for pino rojo, radiata pine, loblolly pine, eastern cottonwood (*Populus deltoides*), and Douglas-fir (Zobel *et al.* 1960; Boyce & Kaeiser 1961; Dadswell *et al.* 1961; Koch 1972; Piedra & Zobel 1986; Goyal *et al.* 1999). As mentioned earlier, pith to bark trends were usually more pronounced than height trends; i.e., the radial position usually accounted for a higher proportion of the variation in tracheid length than the vertical position. Nevertheless, the age to demarcation from juvenile to mature wood is considered to be nearly equal to slightly decreasing, with increasing height, forming a cylinder up the tree (Zobel & Van Buijtenen 1989; Tasissa & Burkhart 1998). Consequently, the proportion of juvenile to mature wood increases vertically in a tree stem, unless newer juvenile wood classification standards are considered (Burdon *et al.* 2004).

Heritability, additive, and non-additive variance

The additive or non-additive nature of a trait directly influences the experimental design needed and the financial cost to implement the design since it is easier and less expensive to select for general combining ability (Zobel & Talbert 1984). The additive nature of a trait changes with age; therefore, a representative contrast of ages should be sampled for tracheid length and coarseness heritability studies.

For radiata pine, coarseness had a strong additive component for the first seven years of growth with year 7 possessing the highest proportion of variance attributable to additive genetic variance (Nyakuengama *et al.* 1997). No non-additive variance component or specific combining ability (SCA) was found in this study. Environmental variance was high in the first years of growth but decreased after crown closure, suggesting that selection efficiency increased after crown closure. Additive variances or general combining ability (GCA), where no particular allele is dominant, were also shown to increase over time for density, fiber radial, and fiber tangential diameter, all of which

influenced coarseness (Nyakuengama *et al.* 2000). Significant additive variance was also shown for tracheid length in scots pine while SCA was negligible (Hannrup & Ekberg 1998). Age 11 was the optimal age for selection of scots pine, the point when environmental variance was lowest while additive variance was highest. Similarly, for maritime pine (*Pinus pinaster*), both tracheid length and coarseness exhibited significant additive effects with no significant SCA effects (Pot *et al.* 2002). For loblolly pine, heritability estimates for tracheid length increased to age 4, stayed constant until age 6 and then decreased throughout the mature wood zone (Loo *et al.* 1984). As a result, year 5 or 6 appeared to be optimal to estimate GCA and hence heritability for both tracheid length and coarseness for radiata and loblolly pine.

For radiata pine, the narrow sense heritability of coarseness was 0.67 to 0.92 (Shelbourne *et al.* 1997; Nyakuengama *et al.* 1999). However, the high heritability of 0.92 was probably an overestimation since they only measured four families within a diallel. For eucalyptus, the heritability of coarseness was 0.15 with a percentage gain of 3.3% above the mean coarseness (Raymond *et al.* 1998). The narrow sense heritability of coarseness for maritime pine was slightly higher at 0.374 with a confidence interval of ± 0.13 (Pot *et al.* 2002). For interior spruce (*Picea glauca*), the heritability for double wall thickness ranged between 0.24 to 0.38 depending on site (Ivkovich *et al.* 2002). One can conclude that species has an effect on heritability even though large differences may also be attributable to environment.

Tracheid length also exhibited strong heritability within several species. The narrow sense heritability of loblolly pine tracheid length was 0.97 (Matziris & Zobel 1973). Another study partitioned the latewood from earlywood for two different sites. The latewood tracheid length was found to have 0.85 to 0.97 heritability while the earlywood was under genetic control between 0.54 to 0.77 (Nicholls *et al.* 1964). For radiata pine, the narrow sense heritability of tracheid length was 0.28 (Nicholls *et al.* 1964). However, the investigators used only the last-formed latewood cells within a ring for analysis. Later work revealed that last-formed latewood cells did not adequately predict mean tracheid length for a whole latewood ring (Smith 1967), so heritability in Nicholls *et al.* (1964) may have been higher than estimated. Dadswell *et al.* (1961) found strong gross heritabilities for tracheid length in radiata pine. For scots pine, the narrow sense heritability was 0.31 to 0.48 (Hannrup & Ekberg 1998; Hannrup *et al.* 2000). For eucalyptus, a similar narrow sense heritability of 0.36 was found (Raymond *et al.* 1998). Finally, interior spruce exhibited heritabilities for tracheid length between 0.30 to 0.59 depending on site (Ivkovich *et al.* 2002).

In summary, reported estimates for heritability varied greatly for tracheid length and coarseness. The estimates for genetic parameters for hard-to-measure traits, like coarseness, are usually sampled from a small sample of families, from a few trees, on a single site, and often from a single ring. So, in many instances, the reliability of the estimate is more variable and less reliable. Since many programs own material genetically improved for specific gravity, the next question to ask is what are the interrelationships between tracheid length or coarseness and specific gravity? Such information could be the deciding factor on which trait is more important for selection.

Phenotypic and genotypic trait correlations

Many articles report phenotypic correlations, between traits such as coarseness and tracheid length, without regard for whether the correlation is due to genetics or environment. Such conclusions could mislead the paper scientist involved in material improvement through genetics. A strong genetic relationship suggests that tree breeding may yield value, whereas a strong environmental component may require silvicultural support.

Density has been the primary focus of quality improvement. It has been found that latewood tracheid length did not genetically correlate with latewood density (Goggans 1964). The same conclusion was drawn by Matziris and Zobel (1973), who observed only a slight genetic correlation ($r_g = -0.18$) between density and tracheid length. For maritime pine, the genetic correlation between density and tracheid length was also insignificant (Pot *et al.* 2002). Selection for density would thus not be expected to alter tracheid length.

For coarseness, a surprisingly weak genetic correlation to density occurred in radiata pine (Shelbourne *et al.* 1997; Nyakuengama *et al.* 1999). Given that coarseness is measured on a weight per unit length of fiber basis, one would expect significant correlations. Conversely, for maritime pine, Pot *et al.* (2002) observed a strong relationship between density and coarseness. Interestingly, they noted the low genetic correlation observed by Nyakuengama *et al.* (1999) and attributed the lower correlation to the method by which Nyakuengama estimated coarseness. The higher correlation was substantiated for loblolly pine, in which density accounted for 94% of coarseness for 30 trees (Veal *et al.* 1987). However, this was not observed in radiata pine clones, in which fiber coarseness did not relate to chip basic density (Kibblewhite & Uprichard 1996). As a result of inconsistent behavior, specific studies, for less researched species, are advised to determine the extent of density to coarseness relationship. But perhaps even more important, a study investigating the relationship between coarseness and density by tracheid length interaction is needed. Such a correlation would make coarseness manipulation possible by selection for specific gravity and tracheid length. Such possibility was implied by Kibblewhite and Uprichard (1996), who found weighted fiber length and fiber wall area to be moderately correlated with coarseness. Such a relationship would justify breeding for tracheid length and density, with coarseness acting as a covariate.

Genetic and economic value

Normally, geneticists improve one trait at a time; as a result, when additional traits are selected for improvement, a lower selection intensity on already improved traits are probable to occur. As a result, it makes it difficult to maintain genetic gain. To complicate matters, as time passes, what was once considered an optimal trait may turn into a less desirable trait. Take the earlier example, companies have long increased specific gravity for improved pulp yield without recognizing the reduction in paper strength. A different approach would be to partition the raw material variation going into the mill by categorizing stems by family, age, location within the tree, and species. If coarseness

and tracheid length were indexed for each family, then a resulting specification sheet on modeled properties (e.g., strength, stiffness, opacity, etc.) could be developed. The lowest cost raw material, to meet minimum property requirements, could then be fed to the digester, but perhaps of higher benefit, the variation of the raw material going into the mill would be tightly reduced (Kärenlampi & Hamari 1997; Chatre *et al.* 2002).

Alternatively, at the tree breeding level, it would be wise to consider linear combinations of several traits as opposed to improving one trait at a time. For the example above, instead of improving specific gravity to increase mean pulp yield, one could develop equations relating many variables to pulp yield like specific gravity, coarseness, cellulose, lignin, and extractives content. Then the families with the highest predicted pulp yield, as a function of these variables, would be selected.

By use of multiple linear regression, tracheid length, density, and wood brightness was equally influential on pulping costs while coarseness was five times less influential on pulping costs (Chambers & Borralho 1999). However, these results demonstrate little correlation between density and coarseness. For species of higher density to coarseness covariance, this ranking may change considerably. For example, King *et al.* (1998) found a strong genetic correlation between coarseness and density for western hemlock (*Tsuga heterophylla*). Strong family effects were present for density, fiber length, and coarseness.

When volume and density were compared for eucalyptus, density was much more influential on cost reduction than increasing volume (Borralho *et al.* 1993). The use of all three traits to predict pulping costs optimized genetic gain in breeding objectives. For radiata pine, density had an economic weight of 1.5 compared to the weight of 1 for volume (Apiolaza & Garrick 2001). However, costs associated with the planting, transporting, and growing of trees were not considered in these studies (Borralho *et al.* 1993; Apiolaza & Garrick 2001). When these additional costs were considered, density still had higher genetic gain. For loblolly pine, wood density had a breeding index over eight times greater than volume in reducing pulp costs when the costs to establish, manage, harvest, and transport trees were accounted for (Lowe *et al.* 1999). For eucalyptus kraft pulp, the density was slightly more influential on pulp costs than volume by a ratio of 1.125 when harvesting and transport costs were considered (Greaves *et al.* 1997). But in all the studies, using a combination of variables to predict cost yielded greater gain than when only one trait was selected.

CONCLUSIONS

To date, most tree improvement efforts have been on specific gravity and little on coarseness and tracheid length. Coarseness and tracheid length were both important for product strength and both were highly heritable within the raw material. From a theoretical modeling standpoint, coarseness appeared to be of a second order to tracheid length in predicting tensile strength. Tracheid length did not correlate genetically with specific gravity, while coarseness showed a weak genetic correlation for radiata pine, but a very strong correlation for maritime pine. As a result, it seems clear that if one starts

from a population already improved for specific gravity, it would further improve the value to select for tracheid length; while it is less clear whether gain can be achieved by selection for coarseness.

When considering coarseness for a tree improvement program, one needs to investigate the interaction of specific gravity and tracheid length and its genetic correlation to coarseness. Perhaps one could infer coarseness given the family mean tracheid length and density. If this is possible, then tracheid length may be the better trait to improve, for a population already improved for specific gravity. More research is needed to understand how, and if, specific gravity and tracheid length predict coarseness. Perhaps building a cell model as a function of tracheid length and specific gravity would provide some insight on coarseness variability.

The lateral movement of seed source for loblolly pine negligibly influenced tracheid length while movement of seed resulted in increased tracheid length from north to south. No trends were established for coarseness. Given density and tracheid length both increased from north to south, it was unclear how coarseness might respond, since that depends on the magnitude of increase for specific gravity and tracheid length.

Radiata, scots, and maritime pines showed a strong additive component of genetic variation for coarseness and tracheid length. No non-additive variance components were found to exist for either coarseness or tracheid length for any species studied. Still, the presence or absence of non-additive variance components may be species specific. As a result, further research, for less known species, is advised before assuming a dominant additive component of genetic variation.

ACKNOWLEDGEMENTS

This study was funded by the USDA National Research Initiative Competitive Grants Program Agreement No. 2001-35103-10908. This paper (No. 03-40-1178) is published with the approval of the Director of the Louisiana Agricultural Experiment Station.

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