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Effects of management intensity, genetics and planting density on wood stiffness in a plantation of juvenile loblolly pine in the southeastern USA

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Abstract

In a 6-year-old plantation of *Pinus taeda* in Northeast Florida, the affects on juvenile corewood stiffness of genotype, planting density and silviculture as well as their interactions, and some potential mechanisms for these effects were investigated. The stress wave method was used to determine the dynamic modulus of elasticity (V^2) of the juvenile corewood in 4091 standing trees of seven full-sib families grown at two planting densities (1334 trees ha^{-1} versus 2990 trees ha^{-1}) with two levels of silvicultural intensity (operational versus intensive). Planting density significantly influenced V^2 ($p < 0.0001$) across all families and silvicultural intensities. At 2990 trees ha^{-1}, V^2 averaged 7.11 and 5.44 km^2 s^{-2} for 1334 trees ha^{-1}. Family and silvicultural intensity interacted significantly for V^2 ($p = 0.0003$) with values ranging from 5.03 to 7.48 km^2 s^{-2}. Under intensive silviculture, one family (L1) exhibited a large decrease in V^2. In contrast, another family (L4) with a high overall V^2 rank was not very sensitive to silvicultural treatment intensity. This lack of response under intensive silviculture occurred despite the fact that family L4 demonstrated the greatest increase in growth. Across all treatments, the ratio of height to diameter at breast height (HT:DBH) was strongly related to V^2 with more slender trees being the stiffest. After adjusting for this ratio, only the main effects of initial planting density and genotype were significant. Thus, HT:DBH correlated with variation in V^2 caused by silvicultural intensity. In a subset of trees within three selected families, variation in latewood percentage (LWP) did not correlate with variation in V^2 as predicted. Analysis of the treatments on LWP, showed a significant three-way interaction between genotype, planting density, and silvicultural intensity. Surprisingly, the LWP of a single family (L4) responded differently to silvicultural treatment under contrasting planting densities. Findings from this study indicate that considerable opportunity exists to improve corewood stiffness in juvenile loblolly pine plantations through the deployment of selected genotypes in combination with appropriate initial planting density and silvicultural intensity.

Keywords: Modulus of elasticity; Latewood percentage; Genotype × environment; Height to diameter ratio; *Pinus taeda*

1. Introduction

Over the past several decades in the southeastern USA, intensively managed plantations of genetically improved loblolly pine have demonstrated dramatically increased wood production compared with previous plantations (Allen et al., 2005). Trees from these rapidly growing plantations reach a merchantable size at a younger age than previous rotations and may have lower wood quality. This reduced wood quality is partially due to greater proportions of lower quality corewood, which is produced during the juvenile growth phase (Zobel and Sprague, 1998). Solidwood products made from this corewood are lower in quality than those made from the outerwood produced during the mature phase of growth (Dadswell, 1958; Kretschmann and Bendtsen, 1992; Larson et al., 2001). The main reason for this lower quality is that juvenile corewood has a significantly lower wood stiffness or modulus of elasticity. Modulus of elasticity (MOE), the ratio of applied stress to the change in shape of an elastic body, is a measure of the resistance of a material to deformation. Because a higher MOE in the longitudinal direction translates to greater stiffness and load bearing making it more desirable as a building product, MOE is one of the most important wood properties (Lindström et al., 2005).

In hardwoods and softwoods, most of the variation in MOE is explained by variation in microfibril angle (MFA) and wood

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density (Evans and Ilic, 2001; Yang and Evans, 2003; Cramer et al., 2005). In softwood species, wood density, juvenile corewood MFA and stiffness are under moderate to strong genetic control (Cornelius, 1994; Kumar et al., 2002; Myszewski et al., 2004; Dungey et al., 2006). In progeny tests with slash pine in the southeast USA, diameter at breast height and tree volume were not genetically correlated with corewood stiffness, but a weak genetic correlation was observed between increased corewood stiffness and tree height (Li et al., in press).

The amount of growing space between trees can affect wood MOE. Initial planting density strongly influences wood MOE in juvenile stands of *Pinus radiata* when the corewood is forming (Lasserre et al., 2004, 2005). While trees planted closer together tend to have higher juvenile corewood stiffness, the stiffness of the mature outerwood has also shown improvement, as was the case with *Cryptomeria japonica*, *Picea mariana*, and *Taiwania cryptomerioides* (Chuang and Wang, 2001; Zhang et al., 2002; Lasserre et al., 2004; Ishiguri et al., 2005; Lei et al., 2005; Wang et al., 2005). However, no relationship between planting density and MOE was found in mature 40-year-old *Pinus elliottii* (McAlister et al., 1997).

Vegetation control and fertilization have also been shown to affect MOE, although the reported effects for fertilization are quite variable. For example, in a *P. radiata* plantation where understory vegetation was controlled for 2 years, MOE was reduced by 93% (Watt et al., 2005). For a study undertaken across a national site quality gradient in New Zealand, fertilization increased phosphorus levels nearly three-fold, but had no significant influence on juvenile corewood stiffness (Watt et al., 2006). However, in a fertilization study with 12-year-old *Pinus taeda* in the coastal plain of the US, nutrient additions significantly reduced corewood MOE (Clark et al., 2004). Additionally, the proportion of corewood to outerwood was also substantially increased due to the accelerated growth which occurred during the juvenile phase.

Modulus of elasticity is known to vary with certain individual tree characteristics such as diameter at breast height (DBH), total tree height, stem taper, crown attributes, and overall branchiness (Haartveit and Flæte, 2002; Hsu et al., 2003; Lei et al., 2005; Watt et al., 2006). For example, in 50-year-old *P. mariana*, the best predictors of MOE were stem taper followed by crown length, DBH, stand density, and crown width (Lei et al., 2005). In juvenile *Pinus radiata*, stem slenderness was found to explain 60% of the variation in MOE across a wide range of locations and climates (Watt et al., 2006). As competition between individual trees for site resources such as light, water and nutrients increases (particularly when grown at close spacing), individual tree DBH growth slows, the live crown recedes and becomes smaller in relation to the stem volume (Long et al., 2004). It follows that strategies to improve the corewood stiffness of juvenile trees could be developed, which would manipulate these individual tree characteristics which are under the control of genetics and silviculture.

Only a few experiments have examined the combined effects of genetics, planting density and silviculture on juvenile corewood stiffness and MFA. For example, in progeny tests of *P. taeda* evidence was found for a genotype by environment interaction for MFA (Myszewski et al., 2004). This result suggests that the MFA of certain families may not be consistent across environments. On the other hand, in a small genotype by spacing study in *P. radiata*, no interaction between families and planting density for corewood stiffness was observed, despite significantly large contrasts between treatments (Lasserre et al., 2004, 2005). Likewise, no interaction between vegetation control and annual fertilization on corewood stiffness was found in a southeastern USA regional study with 12-year-old *P. taeda* (Clark et al., 2004).

A better understanding of how genetics, planting density, and silviculture interact to influence corewood stiffness is needed. If specific silvicultural treatments improve corewood stiffness, and specific genotypes have stiffer corewood, then such information is valuable to forest managers. Thus, our primary objective was to quantify the effect of genotype, planting density, and silvicultural treatment intensity, alone and in combination, on corewood stiffness in juvenile *P. taeda*. A secondary objective was to examine the relationships between individual tree characteristics such as tree size, form, crown attributes, and wood formation patterns on corewood MOE.

2. Materials and methods

2.1. Experimental site and design

The study site was located in Baker County Florida near the town of Sanderson (latitude 29°28′N and longitude 82°33′W). The topography is nearly flat with a slope of less than 1%. The soil series is Leon (sandy, siliceous, thermic Aeric Alaquods) which formed in thick beds of acid sandy marine sediments and is generally poor in soil nutrition; vegetation responds strongly to nutrient additions on this soil. The climate is humid and subtropical with an average annual temperature ranging from 19 to 21 °C. Long-term annual precipitation, from 1931 to 2000, averaged 1384 mm (NOAA, 2002).

The field experiment was designed as a $2 \times 2 \times 7$ (silvicultural intensity × planting density × genotype) factorial, planted in a randomized complete block, split-plot design. In this analysis, four complete blocks, representing the four silviculture/density whole plots were sampled. At the whole-plot level, the two contrasting silvicultural treatments were operational versus intensive, while the two planting density treatments were 1334 trees ha^{-1} versus 2990 trees ha^{-1}. The wide spacing represented the operational average for the region at the time, while the contrasting narrow spacing was an upper extreme selected in order to hasten the onset of inter-tree competition. Within each of these whole plots, there were seven subplots each containing an elite first-generation, full-sib family. For complete documentation of the design and treatment history, refer to Roth et al. (2007).

At the main plot level, the operational silviculture treatment represented a regime typical of the southeastern US forest industry which included a common chemical site preparation treatment followed by a single application of 280 kg ha^{-1} diammonium phosphate at the time of planting. The contrasting intensive silvicultural treatment also received a chemical site preparation treatment followed by complete vegetation control (first 3 years) and regular fertilization (first 6 years) following establishment. Total elements added to the intensive treatment in kg ha^{-1} were: 217 N, 63 P, 49 K, 18 Mg, 8 Ca, 26 S, 0.4 B, 1 Zn, 0.8 Mn, 13 Fe, and 1.6 Cu.

Planting density at the whole-plot level was achieved by planting: 1334 trees ha^{-1} at a spacing of 2.75 m × 2.75 m, and 2990 trees ha^{-1} at a spacing of 1.22 m × 2.75 m. The 2990 trees ha^{-1} plots were arranged in eight beds of 16 planting positions each for a total of 128 trees per treatment plot. The 1334 trees ha^{-1} plots were arranged in eight beds of 10 planting positions each for a total of 80 trees per gross plot. An interior measurement plot of 48 trees was buffered by a single border on the 1334 trees ha^{-1} spacing and a double tree border on the 2990 trees ha^{-1} planting density.

All seven genetic entries at the subplot level were selected *a priori* to have adequate resistance to fusiform rust [*Cronartium quercum* (Berk.) Miyabe ex Shirai f. sp. *fusiforme*]. Six of the families (L1, L2, L4, L5, L7, and L8) were known to have a 15–30% gain in volume over regional unimproved check lots; whereas, one (L6) was similar in growth to the unimproved check and serves as a comparison. Seedlings were grown in Ray Leach 'Cone-tainer'$^{\text{TM}}$ cells (Stuewe and Sons Inc., Corvallis, OR) consisting of 66 ml cell^{-1} and were planted by hand over a 2-day period in January 2000. Survival following planting was greater than 95%.

2.2. Measurements and sampling strategy

An acoustical method was used to estimate dynamic MOE in the lower 1.5 m of standing trees (Lindström et al., 2002, 2004; Grabianowski et al., 2006). The Director ST-300$^{\text{TM}}$ (Fibre-gen, Christchurch, New Zealand, http://www.fibre-gen.com) (Carter et al., 2005) consists of an acoustic wave transmission pin (TX) and a receiver pin (RX), with an ultrasonic distance measure and alignment light emitting diode (LED). Measurements were made by driving the pins about 2 cm deep into the sapwood of each measurement tree. An accurate distance between the RX and TX pins (~1 m) was measured by ultrasound waves. Acoustic waves which travelled through the wood were generated by a gentle strike on the TX pin and were subsequently received by the RX pin. Time-of-flight of the acoustic wave was determined and the velocity calculated using Eq. (1):

$$V = \frac{l}{t} \tag{1}$$

where V is velocity (km s^{-1}), l the length (km) between probes and t is the time (s) for the wave to travel between probes. Three velocities (V) measured from one position in each tree, usually oriented along the bed, were sampled. Velocities were converted to km s^{-1} and squared (km^2 s^{-2}) to generate V^2. There is a strong relationship between V^2 and MOE (Eq. (2)) (Lindström et al., 2004; Lasserre et al., 2005):

$$\text{MOE} = \rho V^2 \tag{2}$$

where ρ is the green density of wood (kg m^{-3}) and V^2 is the velocity squared (km^2 s^{-2}). The green density of all trees sampled is assumed to be constant; therefore, V^2 represents the dynamic longitudinal MOE (Lindström et al., 2004; Lasserre et al., 2005).

In December 2005, 6 years after planting, an inventory of individual tree DBH, and general condition was made on all trees in the interior measurement plots. In February and March of 2006, within tree V^2 was measured on all trees in the measurement plots that were free of stem galls and forks below 2 m, were not leaning, and were greater than 5 cm in DBH. This sample made up more than 90% of the population (4091 trees) from 112 plots across the 10 ha study site. Additionally, total height (HT) and length of live crown were measured from a random 20% sub-sample of trees from each plot to determine the live crown ratio (crown ratio). In the previous year, crown radii were measured perpendicular and parallel to the bed and averaged to create an index of crown-projected area. The ratio of total height to DBH (HT:DBH) was calculated to serve as a surrogate for stem form or tree slenderness.

Following the analysis of the MOE data, a subset of three contrasting families (L1, L4, and L6) were selected *a priori* to determine their latewood percentage (LWP). Five mm wood cores were sampled at breast height from a sub-sample of 359 trees distributed equally across the diameter distribution. The cores were prepared by drying and sanding on a single face. The widths of the latewood and earlywood regions were detected visually and measured with electronic calipers to the nearest tenth mm along the outermost 20 mm of each core.

2.3. Statistical analyses

Analyses of variance (ANOVA) were performed at the single tree level using PROC MIXED (Littel et al., 1996) in SAS according to

$$\begin{aligned} Y_{jklmn} = {} & \mu + b_j + C_k + D_l + CD_{kl} + F_m + CF_{km} + DF_{lm} \\ & + CDF_{klm} + bC_{jk} + bD_{jl} + bDS_{jkl} + bF_{jm} + bCF_{jkm} \\ & + bDF_{jlm} + bCDF_{jklm} + w_{jklmn} \end{aligned} \tag{3}$$

where Y_{jklmn} is the response variable of V^2 of the nth tree of the mth family of the lth planting density of the kth silvicultural intensity of the jth block ($j = 1, 2, \ldots, 4$; $k = 1, 2$; $l = 1, 2$; $m = 1, 2, \ldots, 7$; $n = 1$); μ the overall mean; b_j the random effect of the jth block; C_k the fixed effect of the kth silvicultural intensity; D_l the fixed effect of the lth planting density; F_m the fixed effect of the mth family; w_{jklmn} is the random error. In order to examine the effects of tree size, and crown structure, these variables were included in the model as covariates when they were significant at alpha = 0.05. All terms containing b_j were considered to be random effects in the model and were pooled as appropriate for each variable tested using the procedure described by Bancroft and Han (1983). The only exception was bCD$_{jkl}$, which was never pooled as it was used as the error term to test the main effects of C_k and D_l. Individual variance components were pooled when the probability of a greater F statistic was 0.25 or larger. A conservative significance level of 0.25 was chosen for the preliminary Z-test in order to pool variance terms and increase the power of F tests for fixed

Table 1
Summary of statistical significance (prob. > F) and associated degrees of freedom (d.f.) from ANOVA for V^2 at age six

Source of variation	d.f. numerator[a]	d.f. denominator[a]	F-value	p-Value[*]	z-Value[b]
Silviculture (C)	1	8.76	22.68	**0.0011**	
Density (D)	1	9.85	90.71	<**0.0001**	
$C \times D$	1	8.76	0.02	0.8991	
Family (F)	6	36.5	10.95	<**0.0001**	
$C \times F$	6	35.7	5.74	**0.0003**	
$D \times F$	6	36.5	0.60	0.7309	
$C \times D \times F$	6	35.7	0.74	0.6225	
Block (B)					*0.2018*
$B \times C \times D$					*0.0469*
$B \times C \times F$					*0.1779*
$B \times D \times F$					*0.0007*
Residual					*<0.0001*

[a] The need for different numerator and denominator degrees of freedom in the mixed model is due to the pooling of the random effects in the variance terms.
[b] Random variance components and their interactions were pooled when prob. > |Z| was 0.25.
[*] p-Values significant at the 95% level of confidence are shown in bold type.

effects according to the procedure outlined by Bancroft and Han (1983). Where significant treatment effects were found, least-square means (LS means) were generated for the factors of interest. When multiple, unplanned comparisons were made, a Bonferroni's adjusted significance level was used.

3. Results

3.1. Main effect of planting density

Analysis of variance showed a significant ($p < 0.0001$) and strong main effect of planting density on V^2 (Table 1). At a planting density of 2990 trees ha^{-1}, V^2 averaged 7.11 km^2 s^{-2} compared to 5.44 km^2 s^{-2} for the 1334 trees ha^{-1} density. This effect was consistent across silvicultural intensities and genotypes because no interactions of significance were detected ($p = 0.8991$ and 0.7309, respectively, for each interaction term). Considerable differences between treatments were observed between silvicultural intensities (ranging from 6.82 to 5.89 km^2 s^{-2}) and genotypes (ranging from 6.65 to 5.58 km^2 s^{-2}). However, because there was a significant genotype × silviculture interaction ($p = 0.0003$), it was necessary to examine these effects in combination.

3.2. Interactions between genotype and silviculture

Full-sib families interacted strongly with silvicultural intensity for V^2 ($p = 0.0003$) (Table 1). This significant interaction was due mainly to a single, highly reactive family (L1). L1 had the highest V^2 when grown under the operational silvicultural treatment (7.38 km^2 s^{-2}); yet, when grown under intensive silviculture, it had one of the lowest V^2 (5.64 km^2 s^{-2}) (Fig. 1). While V^2 decreased in all other families with increased silvicultural intensity, one family (L4) was remarkably similar between silvicultural intensities and ranked highest under intensive silviculture (Fig. 1). Family L4 responded well to increases in silvicultural and had the largest trees in the intensive treatment.

3.3. Adjustment for individual tree size and form

The biological mechanisms underlying the interaction between genotype and silviculture for V^2 could be indirect because faster growing trees have larger crowns that influence MOE or a direct influence of the genotype and silviculture on MOE. At age six, tree crowns were beginning to encroach upon one another at the 1334 trees ha^{-1} density, while canopy closure had effectively taken place a full 2 years earlier for the 2990 trees ha^{-1} density (Roth et al., 2007). As expected, trees grown at 1334 trees ha^{-1} under intensive silviculture treatment were the tallest and had the largest DBH; whereas, trees grown at the 2990 trees ha^{-1} under operational silviculture were the shortest and had the smallest DBH (Table 2).

A strong relationship between HT:DBH and V^2 was previously observed in juvenile *P. radiata* trees (Watt et al., 2006). In this study of *P. taeda*, a similar relationship was also observed between V^2 and HT:DBH. V^2 was higher in more slender trees that had a greater HT:DBH (Fig. 2). To isolate the influence of HT:DBH from the main effects of genotype,

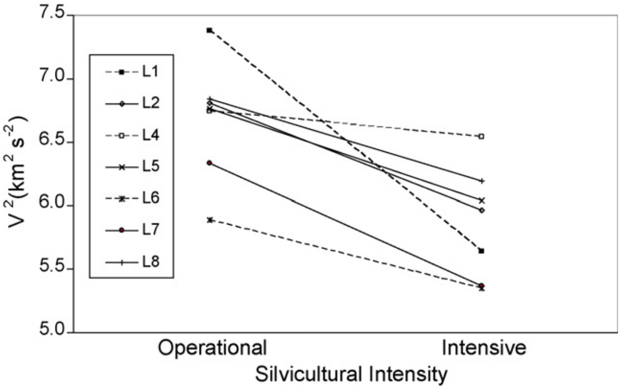

Fig. 1. Effect of silvicultural intensity on family performance for V^2 among seven full-sib loblolly families at age six. The silviculture by family interaction was significant at $p = 0.003$, when no covariates were used. Dotted lines represent families that were subsequently sampled to determine latewood percentage.

Table 2
Raw means for individual tree characteristics by silvicultural intensity and planting density averaged across families at age six

Density (trees ha^{-1})	Silviculture	HT (m)	DBH (cm)	HT:DBH (m m^{-1})	V^2 (km^2 s^{-2})
1334	Intensive	8.97 a	14.6 a	61.4 a	5.03 a
1334	Operational	7.66 b	10.7 b	70.0 b	5.86 b
2990	Intensive	9.14 a	11.4 b	78.6 c	6.71 c
2990	Operational	7.14 c	8.3 c	83.1 d	7.48 d

Note: Values within a column followed by the same letter are not significantly different at alpha = 0.05 using Bonferroni's protected LSD. Significance levels for the planting density by silviculture interaction: HT ($p = 0.0013$), DBH ($p = 0.0156$), HT:DBH ($p = 0.0013$). The interaction between planting density and silviculture for V^2 was not significant ($p = 0.1954$).

planting density, and silviculture; HT:DBH was used as a covariate in the analysis. We also tested other crown characteristics such as width and length as covariates in the analysis; however, only HT:DBH was significantly correlated with variation in V^2 (p-value < 0.0001, Table 3).

After adjustment to a common HT:DBH, the interaction between genotype and silviculture was no longer significant. Only the main effects of planting density and genotype remained significant ($p < 0.0001$). Thus, the silviculture dependent variation in V^2 was correlated with individual tree HT:DBH. After adjustment to a common HT:DBH of 73, V^2 averaged 6.69 $km^2\,s^{-2}$ at 2990 trees ha^{-1}, compared to 6.06 $km^2\,s^{-2}$ at the 1334 trees ha^{-1} planting density. Large differences in V^2 were also apparent among families after the adjustment (Fig. 3). Family L4 remained the stiffest while L6 was the least stiff.

3.4. Latewood percentage does not explain differences in MOE

It is well known that within the same ring, latewood is stiffer than earlywood (Cramer et al., 2005). Consequently, differences in latewood content of the measurement zone are expected to explain any within tree differences in V^2. To test for this possibility, LWP was measured on a subset of three families. The three families included: the fastest grower with the highest V^2 (L4), the most reactive for V^2 averaged across silviculture (L1), and one with a low V^2 (L6). LWP interacted significantly with planting density, silviculture and family ($p < 0.0001$) (Table 4). Family L4 was responsible for this interaction and shifted direction in response to silvicultural intensity between the two planting densities (Fig. 4). When used as a covariate in the model, LWP did not correlate with the V^2 patterns in this subset of families. Thus, differences in corewood V^2 were not explained by differences in LWP.

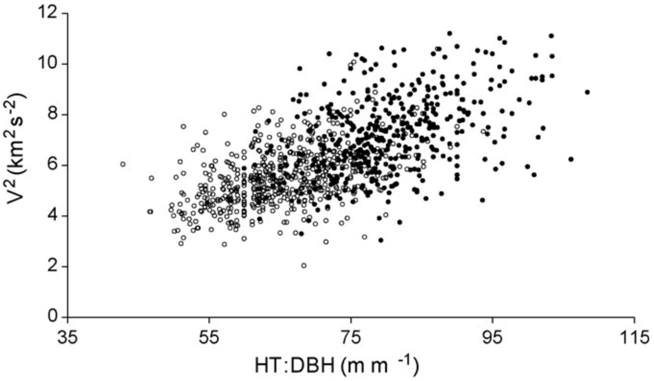

Fig. 2. The relationship between V^2 and HT:DBH as influenced by planting density (open circles represent 1334 trees ha^{-1} and filled circles represent 2990 trees ha^{-1}). Each data point represents an individual tree.

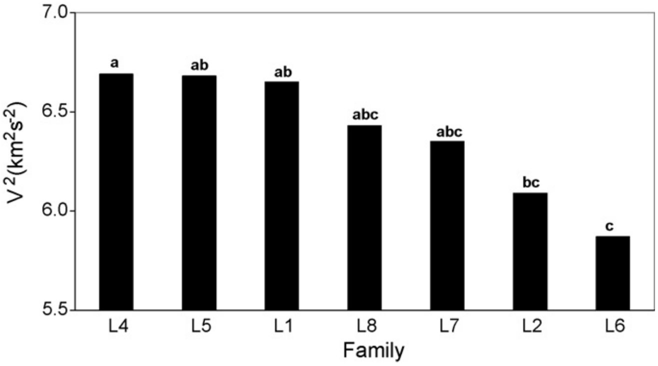

Fig. 3. Family variation in stiffness at age six after adjusting LS means for HT:DBH (to a common ratio of 73 m m^{-1}) ($p < 0.0001$). Bars with same letter are not significantly different at alpha = 0.05 using Bonferroni's adjusted LSD.

Table 3
Summary of statistical significance (prob. > F) and associated degrees of freedom (d.f.) from ANOVA test for V^2 at age six after adjustment with the ratio between HT and DBH

Source of variation	d.f. numerator[a]	d.f. denominator[a]	F-value	p-Value*	z-Value[b]
Silviculture (C)	1	9.3	0.96	0.3520	
Density (D)	1	13.2	11.55	**<0.0047**	
$C \times D$	1	8.8	1.96	0.1954	
Family (F)	6	72.0	5.20	**<0.0002**	
$C \times F$	6	69.4	1.37	0.2379	
$D \times F$	6	69.3	0.70	0.6528	
$C \times D \times F$	6	69.2	0.26	0.9535	
HT:DBH	1	967.0	166.62	**<0.0001**	
Block (B)					*0.2053*
$B \times C \times D$					*0.0989*
$B \times D \times F$					*0.0008*
Residual					*<0.0001*

[a] The need for different numerator and denominator degrees of freedom in the mixed model is due to the pooling of the random effects in the variance terms.

[b] Random variance components and their interactions were pooled when prob. > $|Z|$ as 0.25.

[*] p-Values significant at the 95% level of confidence are shown in bold type.

Table 4
Summary of statistical significance (prob. > F) and associated degrees of freedom from ANOVA to test latewood percentage at age six

Source of variation	d.f. numerator[a]	d.f. denominator[a]	F-value	p-Value	z-Value[b]
Silviculture (C)	1	6.6	6.83	0.0365	
Density (D)	1	10.4	0.00	0.9530	
$C \times D$	1	6.39	6.46	0.0417	
Family (F)	2	10.7	3.03	0.0905	
$C \times F$	2	6.0	0.14	0.8703	
$D \times F$	2	7.7	0.12	0.8863	
$C \times D \times F$	2	333.0	19.01	< .0001	
Block (B)					–
$B \times C \times D$					*0.0896*
$B \times C \times F$					*0.2460*
B x D x F					*0.1003*
Residual					*< 0.0001*

[a] *Note*: No other covariates were significant in explaining the variation in latewood percentage.

[b] Random variance components and their interactions were pooled when prob. > |Z| was 0.25.

4. Discussion

In juvenile pine, the stiffness of corewood is under genetic (Kumar, 2004; Dungey et al., 2006) and environmental control (Lasserre et al., 2004, 2005). The biological mechanisms underlying these genetic and environmental controls of wood stiffness remain largely unknown. Information is also limited as to the extent that stiffness varies by genotype as environmental conditions change. Here we found that the corewood stiffness of juvenile *P. taeda* trees was influenced by the planting density and genotype. In addition, a significant genotype × silvicultural treatment interaction was found, but this interaction was not significant after adjusting for variation in HT:DBH.

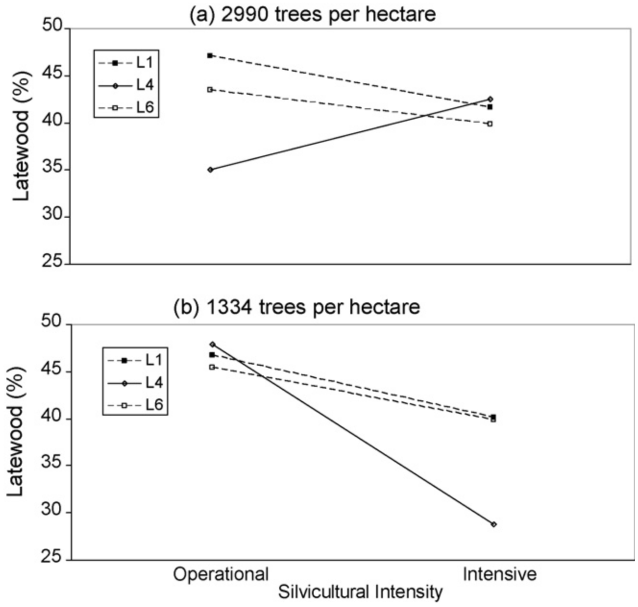

Fig. 4. Effect of silvicultural intensity, planting density and family performance for latewood percentage among three *a priori* selected full-sib loblolly families at age six ($n = 359$). The three-way interaction was significant at ($p < 0.0001$). No adjustments were made for HT:DBH. Note the switch in slope of family L4 between spacings.

Planting density, or tree spacing, is a critical management decision, because of its large effect on overall yield per unit area, stem size and tree form. Within a given age class, trees planted closer together compete with their neighbors for growing space and resources, consequently they tend to have smaller stem diameters than those planted further apart. Consistent with the results reported for *P. radiata* (Lasserre et al., 2004, 2005), we found that more than doubling the planting density from 1334 to 2990 trees ha^{-1} increased V^2 by 31% while decreasing DBH by 28%. In *P. taeda*, tree spacing does not seem to affect the age of transition between juvenile corewood to mature outerwood as judged by wood density profiles, but rather the size and proportion of the corewood in older stems (Clark and Saucier, 1989). Consequently, logs harvested from trees growing at tighter spacings should contain smaller proportions of juvenile corewood that will also have higher MOE.

The strong interaction between genotype and silviculture for stiffness is notable and is of concern to resource managers who may need to develop genotype specific silviculture prescriptions if wood quality is of interest. The fact that the stiffness of family L4 is fairly insensitive to increasing silvicultural intensity is a positive finding. However, the large rank changes in stiffness for family L1 are troubling because stiffness in this family is reduced when grown under higher silvicultural intensities. Genotype and silviculture combinations also influenced the size and stem form of individual trees in this experiment. Lasserre et al. (2005) found a strong influence of DBH on stiffness. In this study, when DBH was used as a covariate, it explained only 0.7% of the variation in corewood stiffness. Watt et al. (2006) showed that HT:DBH, used as a measure of tree form, was highly correlated with stiffness. In the present study, when HT:DBH was used as a covariate in the analysis, both the interaction between genotype and silviculture as well as the main effect of silvicultural intensity, was no longer significant. The ratio between HT and DBH explained 9.6% of the variation in corewood stiffness, about five times more than HT and DBH combined. This confirms the importance of tree form in *P. taeda* as was found for *P. radiata* (Watt et al., 2006). Interestingly, the greater corewood stiffness at the higher planting density can partially be explained by an increase in HT:DBH. Treatment differences were reduced from 1.67 (7.11 km^2 s^{-2} versus 5.44 km^2 s^{-2}) to 0.63 km^2 s^{-2} (6.69 km^2 s^{-2} versus 6.06 km^2 s^{-2}), yet under increased silvicultural intensity this response was dampened as diameter growth responded to a greater extent than tree height. Therefore, the influence of silviculture on corewood stiffness appears related to changes in HT:DBH.

It was encouraging to see, even in this very small number of elite fast growing genotypes, large differences in stiffness because it is a trait known to have modest to high heritability at this age (Kumar et al., 2002; Kumar, 2004; Dungey et al., 2006; Li et al., in press). It was very interesting to see that the family with the fastest growth (L4) also had the highest values of V^2. Generally faster growing and larger trees tend to have larger amounts of corewood with reduced stiffness. This confirms for *P. taeda* that it should be possible to select genotypes with fast growth and high juvenile corewood stiffness, as was found in *P. elliotti* (Li et al., in press).

These results demonstrate how genetics, silviculture and planting density determine individual tree size and form which is related to corewood stiffness. It has been suggested that increases in tree slenderness will induce increases in stiffness to reduce the risk of stem buckling (Watt et al., 2006). Lasserre et al. (2005) proposed that trees growing in dense stands sway less and when they do sway they experience lower stem deflections which in turn leads to greater stiffness. Alternatively, a more cylindrically shaped stem is required to be stiffer than a more conical stem due to physical load bearing constraints (Dean et al., 2002). Interestingly, in *P. elliottii,* Li et al. (in press) detected a significant positive genetic correlation between corewood stiffness and HT, whereas DBH was not genetically correlated with stiffness suggesting that genes and pathways regulating height growth and stiffness share some commonality.

Although differences in juvenile corewood stiffness were reduced following adjustment for HT:DBH, the observation that initial planting density and genotype remain significant factors suggest that environmental and genetic factors modulate corewood stiffness through mechanisms other than tree size and form. We tested the hypothesis that variation in corewood stiffness between genotypes and spacing could be explained by LWP. In this study, however, differences in LWP did not explain corewood variation; rather a three-way interaction between family, planting density and silvicultural intensity was found. This interaction was caused by the unexpected reversal of L4 stiffness at low and high culture in the higher planting density (Fig. 4). While the other families' response to culture and planting density yielded expected results in LWP, the mechanisms underlying this unexpected interaction for family L4 remain unknown.

One possible explanation for the family effect is the genetic control over MFA. It is well known that MFA is under moderate to strong genetic control in corewood in *P. radiata* (Dungey et al., 2006) depending on cambial age. As acoustic velocity is inversely proportional to and highly correlated with MFA (Peter et al., unpublished), we speculate that environmental control of MFA under different spacing may play a significant role since it could be influenced by a combination of genotype, planting density and silvicultural intensities.

5. Conclusions

Planting density, genotype and silvicultural intensity play important roles in determining wood quality in plantations of loblolly pine. In this experiment at age six, silviculture and genotype interacted to influence the stiffness of juvenile corewood. Corewood stiffness of specific families was more reactive than others to silvicultural treatment intensity. In contrast, there was one family that consistently ranked the highest for corewood stiffness across contrasting silvicultural intensities. The ratio between HT and DBH was found to be related to stiffness and is strongly influenced by planting density and silviculture. After adjusting for HT:DBH only the main effects of planting density and genotype were significant. Corewood stiffness is greater when trees are allowed to grow in close proximity to one another which is independent of genotype. A 31% gain in stiffness was achieved by increasing planting density from 1334 to 2990 trees ha^{-1} and independently a 22–25% gain was attributed to genotype at intensive and operational silviculture treatments, respectively. Thus, considerable opportunity exists to manage for improved corewood stiffness in juvenile loblolly pine through the deployment of selected genotypes in combination with appropriate initial planting density and silvicultural intensities.

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References

Allen, H.L., Fox, T.R., Campbell, R.G., 2005. What is ahead for intensive pine plantation silviculture in the south? South J. Appl. Forest. 29, 62–69.

Bancroft, T.A., Han, C.P., 1983. A note on pooling variances. J. Am. Stat. Assoc. 78, 981–983.

Carter, P., Briggs, D., Ross, R.J., Wang, X., 2005. Acoustic testing to enhance western forest values and meet customer wood quality needs. In: Harrington, C.A., Schoenholtz, S.H. (Eds.), Productivity of Western Forests: A Forest Products Focus. General Technical Report PNW-GTR-642. USDA, Forest Service, Pacific Northwest Research Station, Portland, OR, 176, pp. 121–129.

Chuang, S.T., Wang, S.Y., 2001. Evaluation of standing tree quality of Japanese cedar grown with different spacing using stress-wave and ultrasonic-wave methods. J. Wood Sci. 47, 245–253.

Clark, A., Saucier, J.R., 1989. Influence of initial planting density, geographic location, and species on juvenile wood formation in southern pine. For. Prod. J. 39, 42–48.

Clark, A., Borders, B.E., Daniels, R.F., 2004. Impact of vegetation control and annual fertilization on properties of loblolly pine wood at age 12. For. Prod. J. 54, 90–96.

Cornelius, J., 1994. Heritabilities and additive genetic coefficients of variation in forest trees. Can. J. For. Res. 24, 372–379.

Cramer, S., Kretschmann, D., Lakes, R., Schmidt, T., 2005. Earlywood and latewood elastic properties in loblolly pine. Holzforschung 59, 531–538.

Dadswell, H.E., 1958. Wood structure variations occurring during tree growth and their influence on properties. J. Inst. Wood Sci. 1, 11–32.

Dean, T.J., Roberts, S.D., Gilmore, D.W., Maguire, D.A., Long, J.N., O'Hara, K.L., Seymour, R.S., 2002. An evaluation of the uniform stress hypothesis based on stem geometry in selected North American conifers. Trees-Struct. Funct. 16, 559–568.

Dungey, H.S., Matheson, A.C., Kain, D., Evans, R., 2006. Genetics of wood stiffness and its component traits in *Pinus radiata*. Can. J. For. Res. 36, 1165–1178.

Evans, R., Ilic, J., 2001. Rapid prediction of wood stiffness from microfibril, angle and density. For. Prod. J. 51, 53–57.

Grabianowski, M., Manley, B., Walker, J.C.F., 2006. Acoustic measurements on standing trees, logs and green lumber. Wood Sci. Technol. 40, 205–216.

Haartveit, E., Flæte, P., 2002. Mechanical properties of Norway spruce lumber from monocultures and mixed stand-modeling bending stiffness and strength using stand and tree characteristics. In: Nepveu, G. (Ed.), Proceedings of the IUFRO WP S5.01.04 4th Workshop Connection between

Forest Resources and Wood Quality: Modelling Approaches and Simulation Software, Harrison Hot Springs, British Columbia, Canada, September 8–15, p. 2002.

Hsu, L.C.-Y., Chauhan, S.S., King, N., Lindström, H., 2003. Modulus of elasticity of stemwood vs. branchwood in 7-year-old *Pinus radiata* families. New Zeal. J. For. Sci. 33, 35–46.

Ishiguri, F., Kasai, S., Yokota, S., Iizuka, K., Yoshizawa, N., 2005. Wood quality of sugi (*Cryptomeria japonica*) grown at four initial spacings. Iawa J. 26, 375–386.

Kretschmann, D.E., Bendtsen, B.A., 1992. Ultimate tensile-stress and modulus of elasticity of fast-grown plantation loblolly-pine lumber. Wood Fiber Sci. 24, 189–203.

Kumar, S., 2004. Genetic parameter estimates for wood stiffness, strength, internal checking, and resin bleeding for radiata pine. Can. J. For. Res. 34, 2601–2610.

Kumar, S., Jayawickrama, K.J.S., Lee, J., Lausberg, M., 2002. Direct and indirect measures of stiffness and strength show high heritability in a wind-pollinated radiata pine progeny test in New Zealand. Silvae Genet. 51, 256–261.

Larson, P.R., Kretschmann, D.E., Clark, A., III, Isebrands, J.G., 2001. Formation and Properties of Juvenile Wood in Southern Pines: A Synopsis. USDA Forest Service, For. Prod. Lab. Gen. Tech. Rep. 129, 42 pp.

Lasserre, J.P., Mason, E.G., Watt, M.S., 2004. The influence of initial stocking on corewood stiffness in a clonal experiment of 11-year-old *Pinus radiata* [D. Don] New Zeal. J. For. Sci. 49, 18–23.

Lasserre, J.P., Mason, E.G., Watt, M.S., 2005. The effects of genotype and spacing on *Pinus radiata* [D. Don] corewood stiffness in an 11-year old experiment. For. Ecol. Manage. 205, 375–383.

Lei, Y.C., Zhang, S.Y., Jiang, Z., 2005. Models for predicting lumber bending MOR and MOE based on tree and stand characteristics in black spruce. Wood Sci. Technol. 39, 37–47.

Li, X., Huber, D.A., Powell, G.L., White, T.L., Peter, G.F., in press. Breeding for improved growth and juvenile corewood stiffness in slash pine. Can. J. For. Res.

Lindström, H., Harris, P., Nakada, R., 2002. Methods for measuring stiffness of young trees. Holz als Roh-und Werkstoff. 60, 165–174.

Lindström, H., Harris, P., Sorensson, C.T., Evans, R., 2004. Stiffness and wood variation of 3-year old *Pinus radiata* clones. Wood Sci. Technol. 38, 579–597.

Lindström, H., Evans, R., Reale, M., 2005. Implications of selecting tree clones with high modulus of elasticity. New Zeal. J. For. Sci. 35, 50–71.

Littel, R.C., Milliken, G.A., Stroup, W.W., Wolfinger, R.D., 1996. SAS System for Mixed Models. SAS Institute Inc., Cary, NC.

Long, J.N., Dean, T.J., Roberts, S.D., 2004. Linkages between silviculture and ecology: examination of several important conceptual models. For. Ecol. Manage. 200, 249–261.

McAlister, R.H., Clark, A., Saucier, J.R., 1997. Effect of initial spacing on mechanical properties of lumber sawn from unthinned slash pine at age 40. For. Prod. J. 47, 107–109.

Myszewski, J.H., Bridgwater, F.E., Lowe, W.J., Byram, T.D., Megraw, R.A., 2004. Genetic variation in the microfibril angle of loblolly pine from two test sites. South J. Appl. For. 28, 196–204.

NOAA, 2002. State, regional, and national monthly precipitation: area-weighted monthly normals, 1971–2000 (and previous periods). In: Historical Climatography Series 4–2, http://lwf.ncdc.noaa.gov/oa/climate/normals/usnormals.html.

Roth, B.E., Jokela, E.J., Martin, T.A., Huber, D.A., White, T.L., 2007. Genotype × environment interactions in selected loblolly and slash pine plantations in the southeastern United States. For. Ecol. Manage. 238, 175–188.

Wang, S.Y., Chen, J.H., Hsu, K.P., 2005. Effects of planting density on visually graded lumber and mechanical properties of Taiwania. Wood Fiber Sci. 37, 574–581.

Watt, M.S., Downes, G.M., Whitehead, D., Mason, E.G., Richardson, B., Grace, J.C., Moore, J.R., 2005. Wood properties of juvenile *Pinus radiata* growing in the presence and absence of competing understorey vegetation at a dryland site. Trees-Struct. Funct. 19, 580–586.

Watt, M.S., Moore, J.R., Facon, J.P., Downes, G.A., Clinton, P.W., Coker, G., Davis, M.R., Simcock, R., Parfitt, R.L., Dando, J., Mason, E.G., Bown, H.E., 2006. Modelling the influence of stand structural, edaphic and climatic influences on juvenile *Pinus radiata* dynamic modulus of elasticity. For. Ecol. Manage. 229, 136–144.

Yang, J.L., Evans, R., 2003. Prediction of MOE of eucalypt wood from microfibril angle and density. Holz als Roh-und Werkstoff. 61, 449–452.

Zhang, S.Y., Chauret, G., Ren, H.Q.Q., Desjardins, R., 2002. Impact of initial spacing on plantation black spruce lumber grade yield, bending properties, and MSR yield. Wood Fiber Sci. 34, 460–475.

Zobel, B., Sprague, J., 1998. Juvenile Wood of Forest Trees. Springer-Verlag, Berlin, Germany.