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Growth and wood properties of genetically improved loblolly pine: propagation type comparison and genetic parameters

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Abstract: The use of clonal varieties in forestry offers great potential to improve growth traits (quantity) and wood properties (quality) of loblolly pine (*Pinus taeda* L.). Loblolly pine trees established via somatic embryogenesis (clones), full-sib zygotic crosses, and half-sib zygotic open-pollinated families were sampled to identify variation in growth and wood properties among and within clonal lines and zygotic controls. Increment cores 5 mm in diameter were collected at age 4 from a total of 2615 trees. Growth properties (diameter at 1.4 m and total tree height) and wood properties (whole-core density, latewood and earlywood density, and latewood percent) were measured for each tree sampled in the study. Overall, growth properties were better for full-sib seedling than for clonal lines, whereas wood density was higher for clonal lines than full-sib and open-pollinated seedlings. However, there were clonal lines with better growth and higher wood density. Clonal repeatability of both growth and wood properties across sampled sites and genetic correlations between growth and wood traits were determined, with higher repeatability observed for wood traits compared with growth traits. Significant genetic correlations were observed for tree height and wood properties, whereas weak correlations were observed for diameter and wood properties.

Résumé : L'utilisation de variétés clonales en foresterie présente un fort potentiel pour améliorer les traits de croissance (quantité) et de propriétés du bois (qualité) du pin à encens (*Pinus taeda* L.). Des pins à encens issus de l'embryogenèse somatique (clones), de croisements de descendances biparentales et de descendances uniparentales allofécondées ont été échantillonnés pour identifier la variation dans la croissance et les propriétés du bois dans et entre les lignées clonales et les témoins zygotiques. Des carottes de 5 mm de diamètre ont été prélevées à l'âge de 4 ans sur un total de 2615 arbres. Les propriétés de la croissance (diamètre à 1,4 m et la hauteur totale de l'arbre) ainsi que les propriétés du bois (densité globale de la carotte, densité du bois initial et du bois final et pourcentage de bois final) ont été mesurées pour chacun des arbres échantillonnés dans l'étude. Dans l'ensemble, les propriétés de la croissance étaient meilleures chez les semis issus de descendances biparentales que chez lignées clonales alors que la densité du bois étaient plus élevée chez les variétés clonales que chez les semis issus de descendances biparentales ou uniparentales allofécondées. Cependant, certaines lignées clonales avaient une meilleure croissance et une plus grande densité du bois. La reproductibilité clonale des propriétés de la croissance et du bois parmi les stations ainsi que les corrélations génétiques entre les traits de croissance et de propriétés du bois ont été déterminées; la reproductibilité des traits de propriétés du bois était meilleure que celle des traits de croissance. Des corrélations génétiques significatives ont été observées entre la hauteur des arbres et les propriétés du bois alors que de faibles corrélations ont été observées entre le diamètre et les propriétés du bois. [Traduit par la Rédaction]

Introduction

Genetic improvement programs for loblolly pine (*Pinus taeda* L.) began in the 1950s in the United States (US) with the aim of producing abundant high-quality seedlings to support planting activities in the southern US (Fox et al. 2007). Today the main objective of breeding programs is to increase productivity (McKeand et al. 2003) to meet increasing wood demand. Over the last three decades, the productivity of southern pine plantations has increased dramatically owing to the use of genetically improved seedlings in combination with intensive silviculture treatments. The use of genetically improved seedlings with suitable silviculture management can now yield a mean annual increment up to 9–12 $m^3 \cdot ha^{-1} \cdot year^{-1}$ over a 25-year rotation compared with 2–6 $m^3 \cdot ha^{-1} \cdot year^{-1}$ for the same rotation in the past (Aspinwall et al. 2012; Fox et al. 2007). Research suggests that combining the best silviculture operations with the best genetic material can increase mean annual increment up to 21 $m^3 \cdot ha^{-1} \cdot year^{-1}$ (Aspinwall et al. 2012; McKeand et al. 2003).

Second-generation seed orchards supply 54% of the loblolly pine and slash pine seedlings deployed in the southern US (McKeand et al. 2003). Genetically improved open-pollinated loblolly pine planting stock has provided significant gains in productivity (7%–12% for the first generation and 13%–21% for the second generation compared with unimproved check lots) over two completed breeding cycles (Li et al. 1999). The ongoing third generation of breeding has a predicted gain of 35% in productivity (McKeand et al. 2003).

Clonal or varietal forestry is expected to play a crucial role in meeting future timber demands by improving productivity (Fox et al. 2007). Presently, about 10% of loblolly pine plantations are

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being established with seedlings from specific crosses or clonal propagules (McKeaned et al. 2012). A clonal forestry system, compared with recurrent selection for general combining ability, can capture gain from both the additive and nonadditive portions of genetic variation, resulting in higher realized genetic gain (Baltunis et al. 2009; Baltunis and Brawner 2010). Recent advancements in technology have allowed the mass propagation of elite clones with predicted productivity increases up to 50% (Bettinger et al. 2009; McKeand et al. 2003; Isik et al. 2005). Somatic embryogenesis is one way to mass produce clonal seedlings and is based on initiation and development of somatic embryos (SE) from immature zygotic embryos in an artificial environment (Gleed et al. 1995; Klimaszewska et al. 2007). The improved growth, rust resistance, and stem quality of clonal seedlings, compared with open-pollinated planting stock, should increase pulp yield and sawlog recovery at harvest and therefore greatly increase the value of a stand (Bettinger et al. 2009; Sorensson 2006). Clonal propagation of high-value forest trees through somatic embryogenesis also has the potential to improve raw material uniformity and quality (Pullman et al. 2003*a*).

Microfibril angle (MFA) and wood density are strong indicators of wood quality as they affect the yield and quality of fibrous and solid wood products (Zobel and van Buijtenen 1989; Megraw et al. 1999). More recently, the rotation age of loblolly pine plantations has drastically decreased primarily through the use of genetically superior trees and intensive management causing trees to reach merchantable size at younger ages (Allen et al. 2005). Because of this trend, the future timber supply will likely be from young plantations that have a high proportion of juvenile wood with low density and high MFA, which results in low stiffness, poor dimensional stability, and low pulp yield. Recently, tree breeders have started to consider wood quality traits in their breeding programs by using inexpensive measurement tools (Isik and Li 2003).

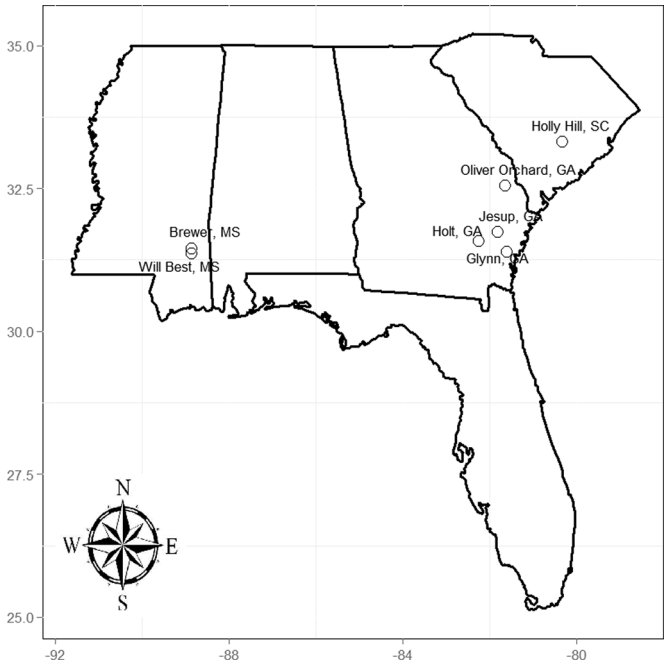
Developments in clonal forestry, especially somatic embryogenesis technology, will allow the mass production of genetically superior loblolly pine seedlings from a single seed (McCall and Isik 2003). Currently, tissue-cultured clonal seedlings are expensive (35 to 45 cents per seedling) compared with second-generation open-pollinated seedlings (5 cents per seedling) (South 2013). The increased investment in clonal planting should be justified through gains in timber yield, disease resistance, improvements in wood quality traits, and uniformity of the stand. Studies are being established to examine the short- and long-term benefits of clonal forestry compared with traditional or genetically improved seedlings. Given that more pine plantations are going to be established with clonal loblolly pine seedlings, it is imperative to compare the growth and wood properties of clonally propagated loblolly pine with full-sib and open-pollinated seedlings. The objective of this study was to compare the growth and wood density of three types of loblolly pine planting stock: (*i*) full-sib zygotic seedlings (FS), (*ii*) half-sib zygotic seedlings (OP), and (*iii*) somatic embryo seedlings (SE). In addition, the repeatability of clonal lines for both wood density and growth characteristics and the genetic correlations between growth and wood properties were explored.

Materials and methods

Data

Growth and wood trait data collected from eight sites located in Georgia, South Carolina, and Mississippi were utilized for this study (Fig. 1). The sites were selected to cover a range of soil drainage class and soil groups (Table 1). Seedlings from the three propagation types (FS, OP, and SE) (Pullman et al. 2003*b*) were used in this study to compare their performance for growth and wood characteristics. At each site, an alpha-lattice incomplete-block design (a resolvable incomplete block design; see Williams et al. 2002) was used with eight replicates and 10–22 incomplete blocks within each replication. Overall, this study used clonal lines from

Fig. 1. Map showing the sites sampled for this study.



16 SE families and seedlings from 12 FS families and two commonly used OP families. At the time of planting, the seedlings of SE, FS, and OP families were not visibly different in terms of height, branching, and needle distribution (Paul Belonger, Plum Creek, Inc., personal communication). A single-tree plot (one ramet per clone per replication) was used for clonal lines and four trees planted as a noncontiguous plot were used for full-sib and half-sib seedlings.

A subsample of families was selected to compare the growth and wood properties of each propagation type. Table 2 provides information for families sampled at each location and the number of trees sampled by propagation type. The subsample of trees included 10 distinct somatic clonal lines from each of three unrelated full-sib families (families L, N, and Q from four sites and families J, O, and Q from the remaining four sites). The clonal lines were chosen to represent the range in height growth performance for the family. To expand the potential range in variability, an additional two to three families with two lines per family were also sampled from each site (families K and O from four sites and families K, L, and N from the other four sites). Eight ramets were sampled from each line within each family at each site, yielding 272 and 288 trees per site, respectively, from sites where five (families K, L, N, O, and Q) and six (families J, K, L, N, O, and Q) families were sampled. In addition to these trees, 12 zygotic FS trees from three families from which SE lines are sampled were included (families L, N, and Q from four sites and families J, O, and Q from the other four sites), yielding 36 trees per site. A line from two to three commercially utilized OP families (families 07056, 22063, and 23001 from four sites and families 07056 and 10005 from the remaining four sites) was also sampled to examine variability under conditions of lesser genetic control.

Trees were sampled after the completion of their fourth growing season to measure their growth (diameter at breast height (DBH) and total tree height (THT)) and wood quality traits. Increment cores, 5 mm in diameter, were bored bark-to-bark through the pith from all sampled trees. The target height for collecting cores was between 0.6 to 0.9 m to ensure that all growth rings were included, and care was taken to avoid any branch whorls. Immediately after removal from the tree, the increment cores were frozen to maintain their green condition and shipped to the

Table 1. Location of the sampled sites along with CRIFF (Cooperative Research in Forest Fertilization) forest soil group and drainage class.

Site	Latitude	Longitude	CRIFF* soil group	Drainage class
Brewer, MS	31.3619	−88.8561	E	Well drained
Glynn Co., GA	31.3875	−81.6167	B	Poor / very poorly drained
Holly Hill, SC	33.3125	−80.3342	E	Moderately well drained
Holt, GA	31.5781	−82.2606	E	Moderately well drained
Jesup, GA	31.7334	−81.8187	B	Somewhat poorly / moderately well drained
Oliver Orchard, GA	32.5394	−81.6383	B	Somewhat poorly drained
Will Best 1, MS†	31.4421	−88.8568	A	Poorly drained
Will Best 2, MS†	31.4421	−88.8568	A	Poorly drained

*Refer to Jokela and Long (2000) for more information.
†Two sites were established at Will Best, MS.

Table 2. Family information and number of trees sampled by propagation type for each site.

	Site							
	Brewer, MS	Glynn Co., GA	Holly Hill, SC	Holt, GA	Jesup, GA	Oliver Orchard, GA	Will Best 1, MS	Will Best 2, MS
Full-sib								
Families sampled	L, N, Q	L, N, Q	J, O, Q	J, O, Q	L, N, Q	J, O, Q	L, N, Q	J, O, Q
No. of trees	33	35	34	35	34	36	35	36
Open-pollinated								
Families sampled	07056, 22063, 23001	07056, 22063, 23001	07056, 10005	07056, 10005	07056, 22063, 23001	07056, 10005	07056, 22063, 23001	07056, 10005
No. of trees	34	35	24	24	34	24	35	23
Somatic embryogenesis								
Families sampled	K, L, N, O, Q	K, L, N, O, Q	J, K, L, N, O, Q	J, K, L, N, O, Q	K, L, N, O, Q	07056, 10005	K, L, N, O, Q	07056, 10005
No. of trees	258	253	260	274	249	289	250	271

USDA Forest Service Southern Research Station in Athens, Georgia, for further processing. In the lab, the cores were divided into two radii at the pith and dried to a moisture content of 10% (50 °C for 24 h). One of the radii was glued to a core holder, and 1.6 mm thick radial strips were cut using a twin-blade saw. The radial strips were not extracted given that the trees were young (4 years old) and had sapwood only with very low extractive content. Typically, heartwood formation in loblolly pine begins between 20 and 30 years of age (Paul 1930). The radial strips were analyzed using a Quintek Measurement System™ scanning X-ray densitometer at a resolution of 0.06 mm to determine radial growth, earlywood and latewood width for each ring, and density of earlywood and latewood of each annual ring. Density values were determined on the basis of green volume and oven-dried mass; a threshold value of 480 kg·m^{-3} was used to distinguish between earlywood and latewood specific gravity. Based on previous research, we have found this to be an excellent threshold value for demarcating earlywood from latewood in loblolly pine (Antony et al. 2012*a*) owing to the abrupt earlywood–latewood transition within individual annual rings for this species (Fig. 2). The inflexion point method provides an alternative for identifying the earlywood–latewood transition within a ring, and although it may result in the identification of a slightly different transition point (Koubaa et al. 2002), it would have little impact on the genetic parameters examined in this study.

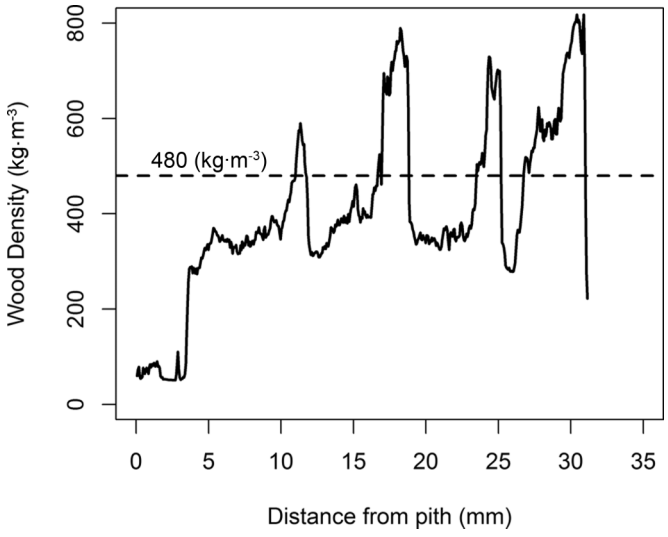
A ring basal area weighted-average whole-core ring density (WCD), earlywood density (EWD), latewood density (LWD), and latewood percentage (LWP) were obtained for each core sampled. The weight used to compute the whole-core average was a ratio of individual ring basal area to the corresponding whole-core basal area, assuming that each ring was a circle.

Statistical analysis

Propagation type difference

A separate analysis of variance (ANOVA) was performed on each trait of interest, here DBH, THT, WCD, EWD, LWD, and LWP. A linear mixed-effect model was used to test the effect of propagation type on each trait of interest. Site, propagation type, and their interaction were considered as fixed effects in the model. The effect of replication at each site and incomplete block within each replication within site were considered as random in the model. Also, the effect of families nested within a propagation type and the lines nested within families from the somatic embryogenesis-derived clones (SE type) were assumed as random in the model. First, we allowed the family and line effect and also the residual variance to have unique estimates for each site by allowing for a

Fig. 2. Intra-ring variation in wood density from pith to bark for a loblolly pine sample with four rings showing the abrupt transition from earlywood to latewood within a ring. Reference line shows the threshold (480 kg·m^{-3}) used to demarcate earlywood from latewood.



diagonal variance–covariance matrix (with dimension equal to the number of sites (8 × 8 matrix in this study) for each random effect). The full model is presented as

$$\boldsymbol{y} = \mathbf{X}\boldsymbol{\beta} + \mathbf{Z}\boldsymbol{b} + \boldsymbol{e} \quad (1)$$

where $\boldsymbol{y}$ is a vector of phenotypic observations; $\mathbf{X}$ and $\mathbf{Z}$ are incidence matrices relating $\boldsymbol{y}$ to effects in $\boldsymbol{\beta}$ and $\boldsymbol{b}$, respectively, where $\boldsymbol{\beta}$ is a vector of fixed effects (here population mean, site, propagation type, and the interaction of site and propagation type effects) and $\boldsymbol{b}$ is the vector of random effects and includes effects representing replications nested within site, incomplete block effect nested within replication within site, family effect nested within propagation type, and clonal line effect nested within family within propagation type SE; $\boldsymbol{b}$ can be represented using a diagonal variance–covariance matrix as

$$\boldsymbol{b} \sim N(0,\ \mathbf{D} \otimes \mathbf{I}_n), \text{ where } \mathbf{D} = \begin{bmatrix} \sigma^2_{\mathrm{r}} & & & \\ & \sigma^2_{\mathrm{b}} & \mathbf{0} & \\ & \mathbf{0} & \sigma^2_{\mathrm{f},h} & \\ & & & \sigma^2_{\mathrm{l},h} \end{bmatrix} \quad (2)$$

where $\mathbf{I}_n$ is an identity matrix, where n is the total number of observations; σ^2_{r} is the random effect variance of replications nested within site; σ^2_{b} is the random effect variance of incomplete block effect nested within replication within site; $\sigma^2_{\mathrm{f},h}$ is the random effect variance of family effect nested within propagation type of site h; $\sigma^2_{\mathrm{l},h}$ is the random effect variance of clonal line effect nested within family within propagation type SE of site h; $\boldsymbol{e}$ is the vector of residuals $e \sim N(0, \sigma^2_{\mathrm{e},h} \otimes \mathbf{I}_n)$, where $\sigma^2_{\mathrm{e},h}$ is residual variance estimate of site h, here $h = 1, 2, \ldots, 8$; and $\otimes$ represents the Kronecker matrix product. The residuals are assumed to be identical and independently normally distributed.

Further, reduced models were fitted by assuming a common variance estimate for family, line, and residual effect for all sites in the study. A series of likelihood ratio tests (LRTs) were conducted between the full model with separate variance estimates by site and reduced models having a common variance estimate for all the sites for family, line, and residual effects. Akaike information criterion (AIC) was also used to compare different nested models (Table 3). Based on the LRTs, the model with common variance estimates for all the sites for family, line, and separate residual variance for each site was favored for each trait of interest, represented as

$$\boldsymbol{b} \sim N(0, \mathbf{D} \otimes \mathbf{I}_n), \text{ where } \mathbf{D} = \begin{bmatrix} \sigma^2_{\mathrm{r}} & & & \\ & \sigma^2_{\mathrm{b}} & \mathbf{0} & \\ & \mathbf{0} & \sigma^2_{\mathrm{f}} & \\ & & & \sigma^2_{\mathrm{l}} \end{bmatrix} \quad (3)$$

and

$$\boldsymbol{e} \sim N\left(0, \sigma^2_{\mathrm{e},h} \otimes \mathbf{I}_n\right)$$

where σ^2_{f} and σ^2_{l} are common for the sites in the study.

Clonal repeatability for site h was estimated for each trait using variance estimates from eq. 1 and represents individual-tree broad-sense heritability assuming that the selected clonal lines represents a random sample from the whole population and no bias was present from any extraneous effect from the clonal propagation, as follows:

Table 3. Akaike information criterion (AIC) from full model with unique family, line within type SE, and residual variance components for each site and reduced models having common variance across sites for each of these random effects.

Property	Full model	RM1	RM2	RM3
DBH	5105.5*	5067.7	4979.0	5078.5
THT	1568.6	1524.2	1441.9	1631.7
WCD	19445.8	19436.6	19231.3	19587.6
LWD	19322.8	19254.9	19151.4	19233.1
EWD	17672.9	17646.7	17467.2	17783.7
LWP	11894.1	11874.9	11691.3	12035.7

Note: DBH, diameter at 1.4 m; THT, total tree height; WCD, whole-core density; LWD, latewood density; EWD, earlywood density; LWP, latewood percent; RM1, reduced model with common family variance estimate for all sites; RM2, reduced model with common family and line within type SE variance estimate for all sites; RM3, reduced model with common family, line within type, and residual variance estimate for all sites.

*Model with smaller AIC is better.

Table 4. *P* values from the analysis of variance for diameter at 1.4 m (DBH), total tree height (THT), whole-core density (WCD), latewood density (LWD), earlywood density (EWD), and latewood percent (LWP).

Trait	Type	Site	Type × Site
DBH	<0.001	<0.001	0.035
THT	0.002	<0.001	0.245
WCD	<0.001	<0.001	0.395
LWD	<0.001	<0.001	0.082
EWD	<0.001	<0.001	0.305
LWP	0.004	<0.001	0.201

$$\hat{H}^2_h = \frac{\hat{\sigma}^2_{\mathrm{l}}}{\hat{\sigma}^2_{\mathrm{l}} + \hat{\sigma}^2_{\mathrm{e},h}} \quad (4)$$

where $\hat{\sigma}^2_{\mathrm{l}}$ is the genetic variance among clonal lines, $\hat{\sigma}^2_{\mathrm{e},h}$ is the residual variance site h, and the summation $\hat{\sigma}^2_{\mathrm{l}} + \hat{\sigma}^2_{\mathrm{e},h}$ gives estimated phenotypic variance. Approximate standard error for clonal repeatability was estimated using the Taylor series expansion method (Gilmour et al. 2005). As the number of families sampled in this study was too low for an accurate estimate of family heritability, these values are not reported here.

Trait–trait genetic correlation

The genetic correlation between growth traits (here DBH and THT) and wood traits (here WCD, EWD, LWD, and LWP) for clonal lines within families (data from type SE seedlings was used) was estimated using pooled data from all sites by estimating genetic variance and covariance between phenotypic measurements. A bivariate mixed-effect model was used to estimate the variance parameters with two traits at a time (for e.g., DBH–WCD, DBH–EWD, etc.) for a total of eight combinations (two growth traits × four wood traits). The model used was

$$\boldsymbol{y} = \mathbf{X}\boldsymbol{\beta} + \mathbf{Z}_1\boldsymbol{b} + \mathbf{Z}_2\boldsymbol{g} + \boldsymbol{e} \quad (5)$$

where $\boldsymbol{y}$ is a vector of phenotypic observations; $\mathbf{X}$, $\mathbf{Z}_1$, and $\mathbf{Z}_2$ are incidence matrices relating $\boldsymbol{y}$ to effects in $\boldsymbol{\beta}$, $\boldsymbol{b}$, and $\boldsymbol{g}$, respectively; $\boldsymbol{\beta}$ is a vector of fixed effect (here mean trait, site effect by trait); $\boldsymbol{b}$ is the vector of random replication, incomplete block effect nested within replication and family effect represented using a diagonal variance–covariance matrix as

Table 5. Estimated least square means (standard error in parentheses) of diameter at 1.4 m (DBH), total tree height (THT), whole-core density (WCD), latewood density (LWD), earlywood density (EWD), and latewood percent (LWP) by propagation type for each site in the study.

Site	Propagation type	DBH (cm)	THT (m)	WCD (kg·m^{-3})	LWD (kg·m^{-3})	EWD (kg·m^{-3})	LWP
Brewer, MS	FS	10.5 (0.4)	6.22 (0.19)	407.3 (4.8)	599.5 (6.4)	336.7 (3.0)	26.2 (1.1)
	OP	9.3 (0.5)	5.73 (0.21)	398.9 (5.0)	603.6 (7.2)	330.8 (3.1)	24.3 (1.1)
	SE	9.5 (0.3)	6.00 (0.16)	423.3 (3.9)	612.6 (5.6)	343.8 (2.4)	29.0 (0.8)
Glynn Co., GA	FS	11.6 (0.4)	7.44 (0.18)	434.6 (6.6)	621.4 (6.9)	352.4 (4.5)	29.8 (1.4)
	OP	10.8 (0.4)	6.74 (0.21)	414.7 (6.8)	605.6 (7.7)	351.8 (4.6)	24.4 (1.4)
	SE	10.3 (0.3)	7.03 (0.16)	446.0 (4.2)	628.6 (5.7)	362.3 (2.7)	31.4 (0.8)
Holly Hill, SC	FS	12.7 (0.4)	7.37 (0.20)	376.7 (4.4)	577.0 (6.1)	326.9 (3.1)	19.6 (0.9)
	OP	12.2 (0.6)	7.34 (0.24)	371.3 (5.4)	583.1 (7.4)	328.2 (3.7)	17.5 (1.0)
	SE	11.4 (0.3)	7.18 (0.16)	389.9 (3.8)	590.2 (5.5)	339.1 (2.4)	19.9 (0.7)
Holt, GA	FS	10.2 (0.4)	7.45 (0.22)	397.0 (4.5)	634.1 (6.6)	334.4 (3.0)	20.9 (1.0)
	OP	10.5 (0.5)	7.51 (0.26)	384.2 (5.5)	616.7 (8.1)	332.7 (3.6)	18.5 (1.2)
	SE	9.4 (0.3)	7.16 (0.16)	404.6 (3.8)	634.8 (5.6)	342.8 (2.4)	20.9 (0.7)
Jesup, GA	FS	10.4 (0.4)	6.29 (0.21)	453.7 (7.1)	628.5 (7.2)	360.2 (4.8)	34.3 (1.6)
	OP	10.0 (0.5)	5.82 (0.23)	435.0 (7.4)	620.0 (8.0)	350.7 (5.0)	31.4 (1.6)
	SE	9.3 (0.3)	6.16 (0.16)	462.8 (4.3)	639.8 (5.7)	361.8 (2.8)	35.9 (0.9)
Oliver Orchard, GA	FS	13.0 (0.4)	8.15 (0.19)	398.0 (5.2)	585.2 (6.6)	338.9 (3.5)	23.7 (1.1)
	OP	12.3 (0.5)	7.76 (0.24)	397.2 (6.4)	586.4 (8.1)	340.6 (4.3)	23.4 (1.4)
	SE	11.5 (0.3)	7.80 (0.16)	406.2 (3.9)	598.5 (5.6)	343.7 (2.5)	24.0 (0.8)
Will Best 1, MS	FS	9.5 (0.4)	6.06 (0.18)	408.7 (4.9)	619.1 (6.8)	339.7 (3.1)	23.9 (1.0)
	OP	9.2 (0.4)	5.79 (0.20)	398.4 (5.1)	619.6 (7.6)	331.2 (3.2)	22.7 (1.0)
	SE	9.1 (0.3)	5.99 (0.16)	416.1 (3.9)	627.0 (5.7)	341.3 (2.4)	25.8 (0.7)
Will Best 2, MS	FS	12.9 (0.4)	7.90 (0.24)	393.6 (4.6)	624.4 (6.5)	332.8 (3.1)	20.9 (0.9)
	OP	12.9 (0.5)	7.89 (0.29)	384.6 (5.7)	620.3 (8.1)	327.1 (3.8)	20.1 (1.2)
	SE	12.0 (0.3)	7.67 (0.17)	400.2 (3.8)	633.4 (5.6)	336.6 (2.4)	21.2 (0.7)

Note: FS, full-sib; OP, open-pollinated; SE, somatic embryogenesis.

Table 6. Estimated means for the main effect of propagation type and sites from the analysis of variance for diameter at 1.4 m (DBH), total tree height (THT), whole-core density (WCD), latewood density (LWD), earlywood density (EWD), and latewood percent (LWP).

	DBH (cm)	THT (m)	WCD (kg·m^{-3})	LWD (kg·m^{-3})	EWD (kg·m^{-3})	LWP
Type						
FS	11.4a	7.1a	408.7a	611.1a	340.2a	24.9ac
OP	10.9ab	6.8ab	398.0a	606.9ab	336.7a	22.8a
SE	10.3b	6.9b	418.6b	620.6b	346.4b	26.0c
Site						
Brewer, MS	9.8a	6.0a	409.8a	605.2a	337.1a	26.5a
Glynn Co., GA	10.9b	7.1b	431.8b	618.5b	355.5b	28.5b
Holly Hill, SC	12.1c	7.3c	379.3c	583.4c	331.4c	19.0c
Holt, GA	10.0a	7.4c	395.2d	628.5d	336.7a	20.1d
Jesup, GA	9.9a	6.1d	450.5e	629.4d	357.5b	33.9e
Oliver Orchard, GA	12.3c	7.9e	400.5d	590.0e	341.1a	23.7f
Will Best 1, MS	9.2d	5.9a	407.7f	621.9b	337.4a	24.1f
Will Best 2, MS	12.6e	7.8e	392.8g	626.0d	332.2c	20.7d

Note: FS, full-sib; OP, open-pollinated; SE, somatic embryogenesis. Values followed by the same letters within columns are not significantly different at the level of significance of 0.05.

$$(6)\qquad \boldsymbol{b} \sim N(0, \mathbf{D} \otimes \mathbf{I}_n), \text{ where } \mathbf{D} = \begin{bmatrix} \sigma^2_{r_1} & 0 & & & \\ 0 & \sigma^2_{r_2} & & \mathbf{0} & \\ & & \sigma^2_{b_1} & 0 & \\ & & 0 & \sigma^2_{b_2} & \\ & \mathbf{0} & & & \sigma^2_{f_1} \quad 0 \\ & & & & 0 \quad \sigma^2_{f_2} \end{bmatrix}$$

where $\mathbf{I}_n$ is an identity matrix; $\sigma^2_{r_1}$ and $\sigma^2_{r_2}$ are the replication variances for two traits; $\sigma^2_{b_1}$ and $\sigma^2_{b_2}$ are the incomplete block variance components for two traits; $\sigma^2_{f_1}$ and $\sigma^2_{f_2}$ are family effect variance components from two traits; $\boldsymbol{g}$ is the vector of random effect of clonal lines,

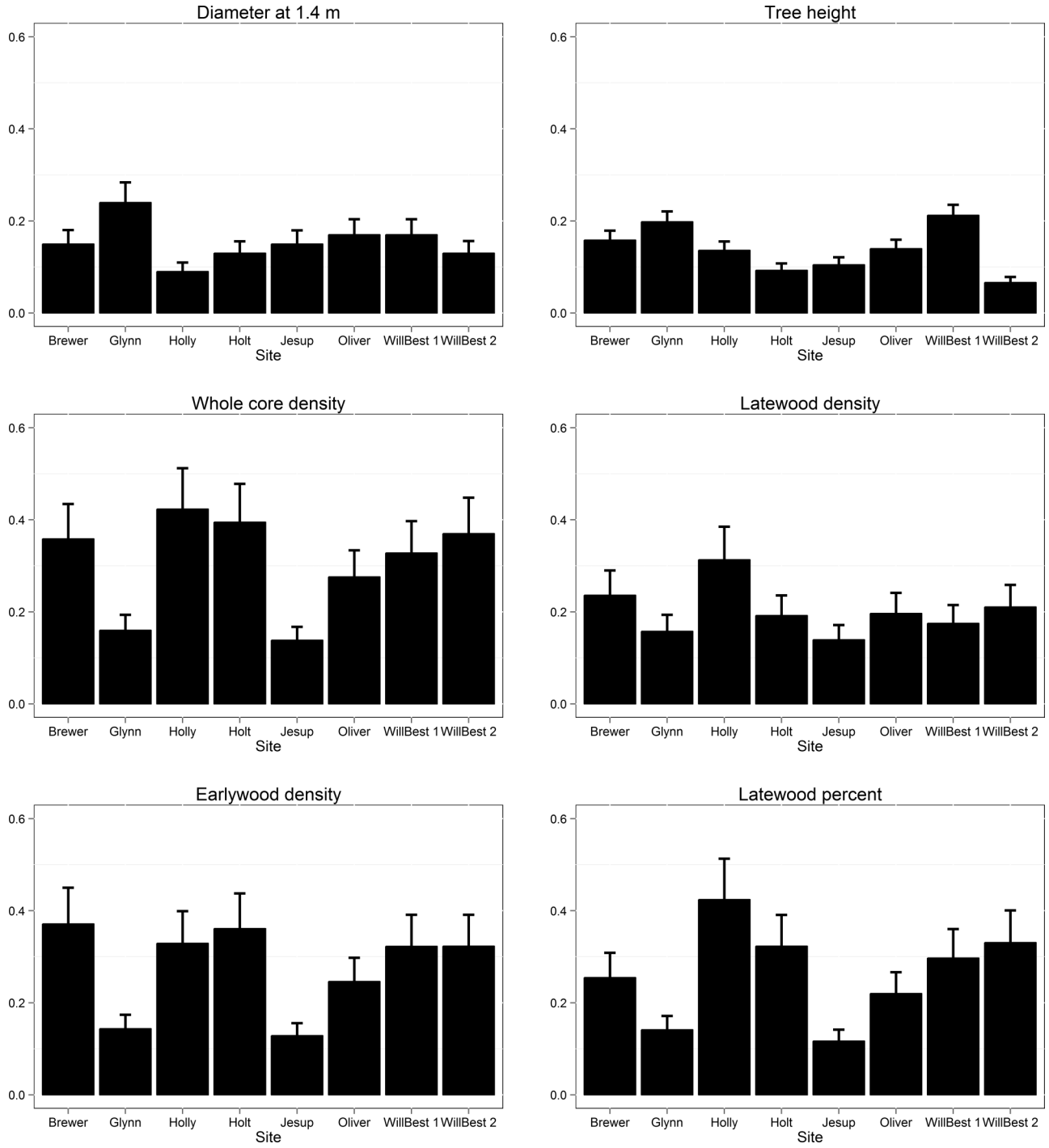
$$(7)\qquad \boldsymbol{g} \sim N(0, \mathbf{G} \otimes \mathbf{A}_l), \text{ where } \mathbf{G} = \begin{bmatrix} \sigma^2_{l_1} & \sigma^2_{l_1 l_2} \\ \sigma^2_{l_1 l_2} & \sigma^2_{l_2} \end{bmatrix}$$

where $\mathbf{A}_l$ is the numeric relationship matrix for clonal lines; $\sigma^2_{l_1}$, $\sigma^2_{l_2}$, and $\sigma^2_{l_1 l_2}$ are the genetic variances for growth and wood traits and the genetic covariance among traits of clones, respectively; $\boldsymbol{e}$ is the vector of residuals,

$$(8)\qquad \boldsymbol{e} \sim N(0, \mathbf{R} \otimes \mathbf{I}_n), \text{ where } \mathbf{R} = \begin{bmatrix} \sigma^2_{e_1} & 0 \\ 0 & \sigma^2_{e_2} \end{bmatrix}$$

where $\sigma^2_{e_1}$ and $\sigma^2_{e_2}$ are residual variances of growth and wood traits, respectively; and $\mathbf{I}_n$ is an identity matrix. The residuals are assumed

Fig. 3. Clonal repeatability (individual-tree) estimate for each trait in the study by site. Error bar indicates ±1 standard error.



to be identically and independently normally distributed. Here, we are not interested in the correlation of residuals between traits.

The genetic correlation between traits for each site was estimated as

$$\hat{r}_1 = \frac{\hat{\sigma}_{l_1 l_2}}{\hat{\sigma}_{l_1}\hat{\sigma}_{l_2}} \quad (9)$$

All analyses were conducted using asreml-r, an implementation of ASReml (Gilmour et al. 2005) for the R statistical software system (R Development Core Team 2008).

Results

Propagation type difference

The ANOVA results for each trait are presented in Table 4. Estimated least square means from the model for propagation type within each site are presented in Table 5. The main effect of site and propagation type was significantly different for both growth and wood traits (at the 0.05 level of significance). Results from the multiple mean comparisons among main effect factors (propagation type and site) are presented in Table 6. A significant interaction between propagation type and site was observed for DBH only. Overall, the DBH of FS seedlings was greater than that of SE

seedlings (Tables 5 and 6). Though DBH of OP seedlings was not significantly different from FS and SE seedlings (Table 6), it was slightly better than SE seedlings at most of the sites (Table 5). Similarly, FS seedlings performed better in THT growth than the SE seedlings (Table 6). Though not statistically significant, THT was observed to be better for FS and SE seedlings than for OP seedlings. Unlike growth traits, WCD was consistently higher for SE seedlings compared with FS (6–15 kg·m^{-3} lower) and OP (8–31 kg·m^{-3} lower) seedlings (Tables 5 and 6). The trend of SE seedlings having higher wood density than OP and FS seedlings was consistently observed in LWD (Table 5) and EWD (Table 5) across sites. Latewood proportion for SE seedlings was higher than the FS and OP seedlings (Table 5), but the only significant difference was observed between SE and OP seedlings (Table 6). Significant differences between sites were observed for both growth and wood properties (Table 6).

Clonal repeatability

The clonal repeatability estimates for both growth and wood traits at each site are presented in Fig. 3. On average, the repeatability was greater for wood traits (WCD, 0.31; LWD, 0.20; EWD, 0.28; LWP, 0.26) than for growth traits (DBH, 0.15; THT, 0.14). An inverse trend is evident between clonal repeatability estimates of growth and wood traits among sites. Sites having higher repeatability estimates for growth traits tend to have lower repeatability estimates for wood traits. For example, Holly Hill has a clonal repeatability estimate of 0.12 for DBH, but the repeatability estimate for WCD is 0.42, whereas for Glynn, repeatability estimates for DBH and WCD were 0.30 and 0.16, respectively (Fig. 3).

Trait–trait genetic correlation

The genetic correlations between DBH and THT with wood traits for clones within family were estimated from the pooled site data and are presented in Table 7. Genetic correlations of DBH with WCD, LWD, EWD, and LWP were not significant. Similarly, the correlation between THT with EWD was not significant. However, higher genetic correlations were observed for THT with WCD, LWD, and LWP and were all significant.

Table 7. Pooled site clonal genetic correlation and standard error (SE) of diameter at 1.4 m (DBH) and total tree height (THT) with wood traits whole-core density (WCD), latewood density (LWD), earlywood density (EWD), and latewood percent (LWP).

Traits	Correlation	SE
DBH–WCD	–0.07	0.15
DBH–LWD	0.01	0.16
DBH–EWD	–0.17	0.15
DBH–LWP	0.08	0.15
THT–WCD	0.33	0.14
THT–LWD	0.33	0.15
THT–EWD	0.11	0.15
THT–LWP	0.42	0.13

Note: Genetic correlations of THT with WCD, LWD, and LWP were significant at the level of significance of 0.05.

Discussion

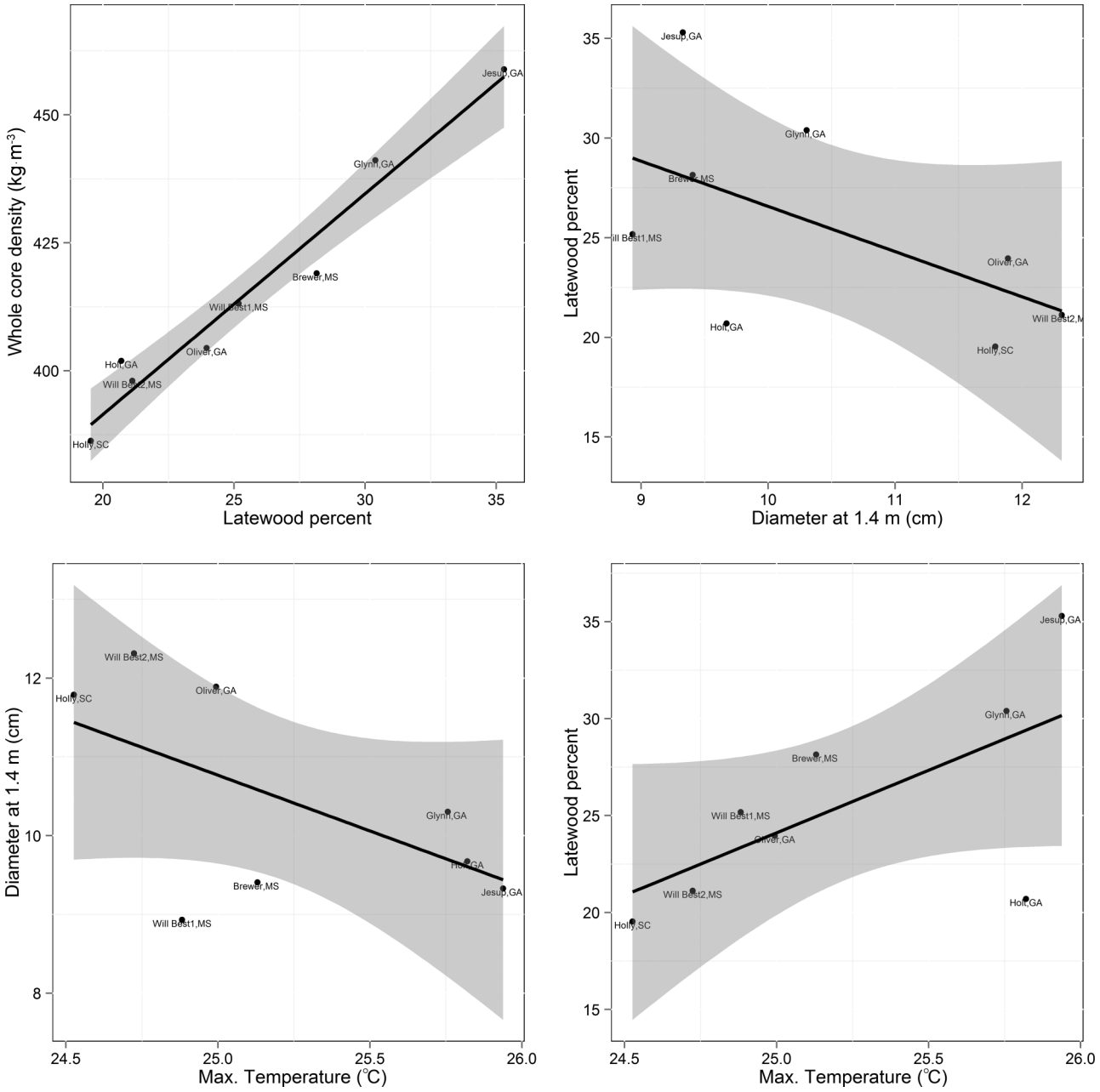
This study compared the early performance of clonal seedlings with full-sib seedlings and open-pollinated check lots. We found that full-sib seedlings consistently outperformed clonal propagules in terms of growth (on average, FS seedlings were 1 cm bigger in DBH, 0.23 m in THT) after their fourth growing season. Similar early growth performance was observed in loblolly pine (Baltunis et al. 2007), with seedlings from a full-sib family 0.10 m taller than rooted cuttings after their second growing year. A similar result was observed by Cown and Sorensson (2008), who reported a 10% decrease in DBH for clonally propagated radiata pine (*Pinus radiata* D. Don.) based on difference studies conducted in New Zealand. They attributed the decrease in growth to the "aged" clone effect as the clones are produced by cuttings from old trees, old mother plants in stoolbeds, or old tissue culture. However, all of the clonal lines used in this study were produced from immature embryos and should not exhibit an "aged" clone effect.

Studies that have compared wood density of rooted cuttings with that of full-sib seedlings in radiata pine (Cown et al. 1989) and loblolly pine (Cumbie 2002) reported no difference in wood density. In this study, overall wood density and latewood proportion were higher for clonal seedlings compared with open-pollinated seedlings, with maximum increases of 7% for LWP and 31 kg·m^{-3} for WCD. A marginal increase was also observed in wood properties for clonal seedlings compared with full-sib seedlings. Interestingly, SE seedlings grew less overall (both DBH and THT) but had higher wood density, and thus, whether or not a propagation type effect exists needs to be studied further.

Differences in growth and wood properties were observed for trees growing on sites in different physiographic regions and were consistent with regional studies based on loblolly pine (Jordan et al. 2006; Antony et al. 2010). Clark and Daniels (2002) attributed differences in ring specific gravity to the proportion of latewood, which is primarily determined by climate. Similar trends have been observed in open-pollinated radiata pine planted across New Zealand, where Apiolaza (2012) reported an increasing trend in wood density with an increase in mean annual temperature. Similar relationships between climate and wood density have been observed in Norway spruce (*Picea abies* (L.) Karst.) (Franceschini et al. 2013) and Scots pine (*Pinus sylvestris* L.) (Kilpeläinen et al. 2005). We explored relationships among mean observed WCD and LWP from each site and mean annual precipitation (mm) and maximum and minimum temperature (°C) using data obtained from the PRISM Climate Group, Oregon State University (http://prism.oregonstate.edu [accessed on 3 January 2013]) using latitude and longitude information (Fig. 4). A positive relationship was observed between WCD and LWP, and a negative trend was observed between DBH and LWP, which is consistent with early fast growth resulting in greater production of low density juvenile wood (Antony et al. 2011). Relating the DBH and LWP to climatic data, we observed a negative trend in DBH and a positive trend in LWP with mean maximum annual temperature, while no relationship was observed with mean annual precipitation and mean annual minimum temperature. In addition to genetics, climatic conditions play an important role in driving the expression of growth and wood traits across sites.

We observed that the clonal repeatability of the wood density traits was higher than that of the growth traits. Higher heritability for wood density compared with growth traits has been reported for both loblolly pine (Zobel and Jett 1995; Belonger 1998; Cumbie 2002; Baltunis et al. 2007) and radiata pine (Cown and Sorensson 2008). Baltunis et al. (2007) reported repeatability estimates of 0.2 to 0.4 (vary by site) for height of loblolly pine clones measured at age 2. Compared with Baltunis et al. (2007), we have observed lower clonal repeatability estimates, which might be due to the sampling strategy adopted in this study and the number of clonal lines sampled per family. Still, the repeatability estimates of wood properties are higher and indicate consistency of performance of clonal lines for wood properties across sites. Even though wood density has been reported to show good correlation with wood mechanical properties, studies in many pine species have reported that MFA is likely more important in determining wood stiffness in juvenile wood (Walker and Butterfield 1995; Cown et al. 1999; Megraw et al. 1999). This warrants measuring other wood quality traits such as MFA or acoustic velocity in future clonal selection programs to determine stiffness of trees in addition to wood density and growth traits.

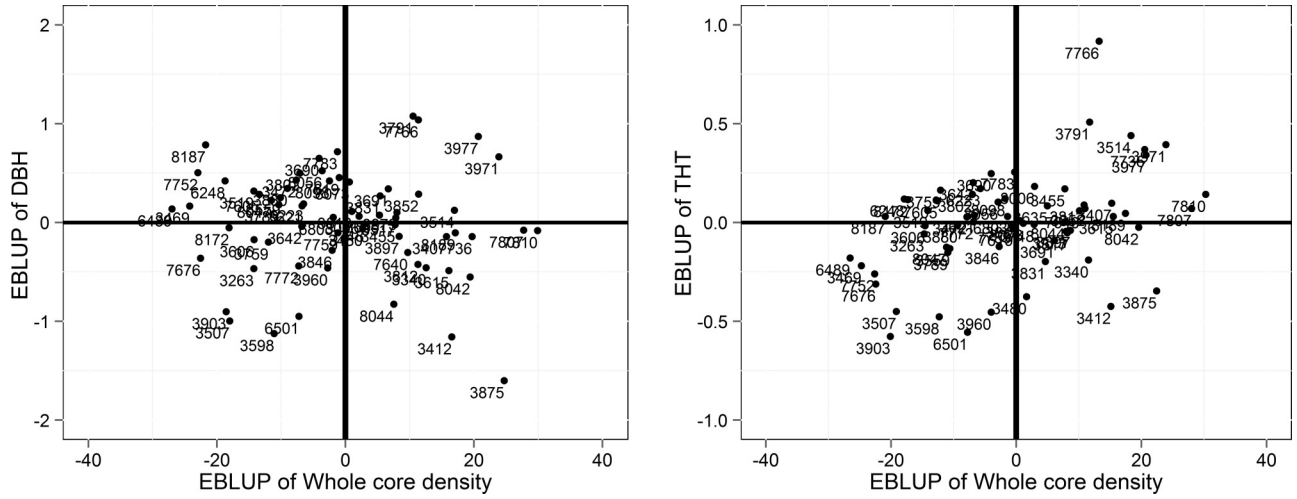
Fig. 4. Plots showing linear relation between average whole-core density and latewood percent, latewood percent and diameter at 1.4 m, diameter at 1.4 m and maximum average temperature, and latewood percent and maximum average temperature. Line represents linear regression, and shaded area indicates 95% confidence interval.



Selecting parents simultaneously for both growth characteristics and wood properties poses considerable challenge as the genetic correlations are relatively poor. Generally, adverse genetic correlations have been reported between growth and wood properties (Loo et al. 1984; Williams and Megraw 1994; Cumbie 2002; Hannrup et al. 2004; Li et al. 2007), indicating that selecting parents for growth probably will be to the detriment of wood quality and vice versa. A genetic correlation of −0.4 has been observed between DBH and wood density for many conifer species including loblolly pine (Gapare et al. 2009). We observed a weak genetic correlation for DBH with wood traits but a higher and positive genetic correlation for THT with wood properties. This might be due to the positive effect of stem slenderness (ratio of THT with DBH) on wood properties that has been reported for radiata pine (Watt and Zoric 2010) and loblolly pine (Antony et al. 2012*b*). Further, we have explored the empirical best linear unbiased predictors (EBLUPs) of clonal lines estimated from the fitted bivariate models (Fig. 5) to identify clonal lines that are "correlation breakers," i.e., to see if any clones showed simultaneous improvement in growth and wood density (two negatively correlated traits). It is evident that many of the clonal lines showed better WCD than the growth traits. Also, there are clonal lines that showed better performance in terms of DBH and THT growth and higher WCD.

Currently, forests of the southern US support the majority of the nation's fiber production, with 60% of all timber in the US being produced from this region (Smith et al. 2009). The pine plantation area in the southeastern US is expected to increase from the current 19% of total land area to 24%–26% by 2060 mainly due to emerging bioenergy markets (Wear and Greis 2011). Clonal forestry is expected to play an important role in meeting growing

Fig. 5. Empirical best linear unbiased predictions (EBLUPs) of diameter at 1.4 m (DBH) and total tree height (THT) with EBLUPs of whole-core density from the bivariate models (clonal line random effects ***g*** from eq. 5). Clonal lines in the upper right quartile are "correlation breakers".



wood demand. Based on this study, there is potential for selecting clonal lines that perform better for growth and wood quality characteristics.

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