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Genotype × environment interactions in selected loblolly and slash pine plantations in the Southeastern United States

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Abstract

Few studies have quantified the combined effects of silvicultural treatments and genetic improvement on unit area production of full-sib family blocks of loblolly (*Pinus taeda* L.) and slash pine (*P. elliottii* Engelm. var. *elliotttii*). Efficient operational deployment of genetic materials requires an understanding of possible site and silvicultural treatment interactions to maximize yield potential. We examined genotype (family) by environmental interactions (G × E) through age 5 years using a factorial experiment consisting of silvicultural treatment intensity (operational versus intensive), planting density (1334 versus 2990 trees ha^{-1}) and families (seven elite full-sib loblolly and six elite full-sib slash pine families). In January of 2000, randomized complete block, split-plot experiments were installed at two locations for each species in southeast Georgia and northeast Florida. Five years after planting, both loblolly and slash pine demonstrated significant interactions among several factors: genotype × location ($p < 0.028$ and $p < 0.016$, respectively), genotype × silvicultural treatment intensity ($p < 0.055$ and $p < 0.059$), and silvicultural treatment intensity × density ($p < 0.002$ and $p < 0.001$) for basal area (BA) and standing stem volume (VOL). Genotype × silvicultural treatment interactions were positive, with the best overall performing families responding the greatest to intensive treatment. There were changes in slash pine family rankings between locations, which were partly explained by reductions in growth associated with a combination of fusiform rust infection [*Cronartium quercum* (Berk.) Miyabe ex Shirai f. sp. *fusiforme*] and wind damage from the 2004 hurricane season. No three-way interactions, which included family, were evident and all genetic sources were stable across the contrasting planting densities. At age 5, loblolly pine outperformed slash pine ($p < 0.0001$), especially under the intensive silvicultural intensity. While loblolly performance was similar whether deployed in mixtures or pure family blocks, slash pine tended to be more productive in intimate mixtures than when grown in pure family blocks ($p = 0.0754$ for aboveground biomass).

Keywords: *Pinus taeda*; *Pinus elliottii*; Aboveground biomass; Fertilization; Nutrition; Weed control; Density; Genotype; Family; G × E; Genotype × environ-environment; Genotype × silviculture; Genotype × location

1. Introduction

Considerable gains in the productivity of loblolly (*Pinus taeda* L.) and slash pine (*Pinus elliottii* Englm. var. *elliottii*) plantations in the Southeastern United States have been achieved over the past 30 years. Demonstrated increases in unit area production have been realized through silvicultural inputs of fertilization, competition control, and density management. These treatments are aimed at relieving site resource limitations and focusing growth on crop trees (Colbert et al., 1990; Jokela et al., 2000; Borders and Bailey, 2001; Martin and Jokela, 2004). Growth responses to intensive silvicultural practices range from 2- to 3.5-fold at age 15 for loblolly pine in the Southeastern USA (Jokela et al., 2004). Additionally, tree breeding programs have increased volume production by 10–30% over unimproved sources (Li and McKeand, 1989; McKeand et al., 2003a). When a combination of elite genetic materials are combined with site-specific silvicultural treatments, mean annual increments of up to 20 m^3 ha^{-1} $year^{-1}$ have been documented (Allen et al., 2005). However, as resource managers begin to deploy selected full-sib families or clones (Bridgwater et al., 2005), there is a greater likelihood that genotype × environmental (G × E) interactions will occur, especially under conditions of increased silvicultural intensity (McKeand et al., 2006). These interactions may be manifest as rank changes among genotypes when grown

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under different environments/treatment conditions, or as ''scale effects'' in which the absolute differences among genotypes change with environment.

Research studies aimed at quantifying the combined effects of silvicultural treatments and genetic improvement on unit area production in loblolly and slash pine are rare. Earlier studies indicate that G × E would not be of major consequence for the majority of genotypes being deployed under traditional silvicultural systems (McKeand et al., 2006). For example, no G × E was found for total standing volume at age 12 in a loblolly pine genotype × vegetation control study in Georgia, USA (Martin and Shiver, 2002), and none was found at age 4 for five open-pollinated loblolly pine families grown under two spacings in South Carolina, USA (McCrady and Jokela, 1996). Likewise, an analysis of whole tree biomass of 5-year-old loblolly pine from two seed sources did not demonstrate G × E using a factorial genotype × fertilization experiment in North Carolina, USA (Retzlaff et al., 2001).

Tree improvement programs have historically assessed G × E interactions for determining the need for site-specific breeding efforts (McKeand et al., 1997b). Generally, in these investigations, a large number of genotypes are tested across a range of sites. Environmental variance in these breeding programs is due to localized climatic, edaphic and disease conditions, rather than to specific silvicultural treatments that manipulate site resources. Few studies have documented G × E interactions among silvicultural treatments, but available evidence suggests that when G × E did occur in these situations, it was caused by a limited number of genotypes in the population that were highly sensitive to environmental variation (Zas et al., 2004). For example, Duzan and Williams (1988) found modest rank changes in family performance across a variety of sites in the Southeastern USA, while Yeiser et al. (2001) showed instability in volume production at ages 5 and 10 among loblolly pine families from some, but not all, seed zones in the Western Gulf region of the USA. Similarly, a large G × E was documented for growth traits in loblolly pine families from Florida sources when moved northward one USDA Plant Hardiness Zone (Atwood et al., 2002; Sierra-Lucero et al., 2002); yet, none was observed for other provenances (McKeand et al., 1990; Sierra-Lucero et al., 2002). It appears that G × E may become significant only under extremes in seed source movement and/or site productivity and that relatively few genotypes from the population contribute to this response.

The intensity of genetic selection and silvicultural treatments is expected to increase in the future as resource managers move seed sources long distances in an effort to increase yields (Lambeth et al., 2005). Likewise, the probability of G × E becoming significant in the future is real and site/genotype specific silvicultural prescriptions may be needed to maximize volume and value production (Allen et al., 2005). It follows that resource managers will benefit from an understanding of how elite genotypes respond across naturally occurring and man-made environmental gradients (i.e., fertilization, spacing and associated vegetation control), as well as how soil physical, chemical and biological processes affect productivity (Fox, 2000).

The overall objectives of this study were to investigate and quantify the magnitude and nature of G × E in full-sib families of loblolly and slash pine. This was accomplished by using a series of replicated factorial experiments and family block plantings established in Florida and Georgia that manipulated gradients in planting density, understory competition and soil nutrient availability.

2. Methods

2.1. Study description

In January of 2000, the Forest Biology Research Cooperative (http://fbrc.ifas.ufl.edu), located at the University of Florida, established a series of field research installations that were designed to examine the interactions of full-sib loblolly and slash pine families with several environmental factors, such as: location, silvicultural treatment intensity, and planting density (Roth et al., 2002). This trial series, referred to as Pine Productivity INteractions on Experimental Sites (PPINES), is the only one of its kind where the combined effects of species, genotype, silviculture and planting density can be examined singly or in combination across a range of site conditions in the Southeastern USA. Large family block plots, combined with contrasting treatments provide a unique opportunity to examine G × E using stand level variables (i.e., basal area, stem volume, and aboveground biomass).

Four study locations were included in this trial series representing two distinctly contrasting soil types (Table 1). The topography is nearly flat, with less than a 1% slope. Soil series for the four sites were—Sanderson, FL: Leon (sandy, siliceous, thermic Aeric Alaquods); Waverly, GA: Bladen (mixed, semiactive, thermic Typic Albaquults); Perry, FL: Leon (sandy, siliceous, thermic Aeric Alaquods); Waldo, FL: Newnan (sandy, siliceous, hyperthermic Ultic Haplohumods). Trials were installed on sites that held recently harvested southern pine plantations. Associated woody vegetation common to all sites included sawtooth palmetto [*Serenoa repens* (B.) Small.], wax myrtle (*Myrica ceriferea* L.), runner oak (*Quercus pumila* Walt.), blueberries (*Vaccinium* spp.), gallberry [*Ilex glabra* (L.) Gray], and St. John's-wort [*Hypericum fasciculatum* (Lam.)]. Herbaceous plants in the understory commonly included bluestem grasses (*Andropogon* spp.), panic grasses (*Panicum* spp.), sedges (*Carex* spp. and *Cyperus* spp.), and dogfennel [*Eupatorium capillifolium* (Lam.) Small.]. All study locations share a subtropical and humid climate with long hot wet

Table 1
Characteristics of the PPINES[a] experimental locations

Site location	Species	Latitude (°)	Longitude (°)	Soil order	Elevation (m)
Sanderson, FL	Loblolly	29.28	−82.33	Spodosol	45
Waverly, GA	Loblolly	31.13	−81.75	Ultisol	10
Perry, FL	Slash	30.17	−83.73	Spodosol	15
Waldo, FL	Slash	29.80	−82.21	Spodosol	50

[a]PPINES: pine productivity interactions on experimental sites. All locations were planted in January of 2000.

summers and mild dry winters. Long-term (1931–2000) precipitation has averaged 1384 mm year^{-1} (NOAA, 2002).

2.2. Experimental design

The PPINES series is composed of two installations each of loblolly pine and slash pine. Within each installation, the experimental design is a 2 × 2 × 8 (silviculture × planting density × genetic entry) factorial which is planted in a randomized complete block, split-plot design. Each site has four complete blocks consisting of four silviculture-density whole plots. At the whole-plot level, the two contrasting silvicultural treatments are operational versus intensive, while the two planting density treatments are 1334 trees ha^{-1} versus 2990 trees ha^{-1}. Within each of these whole-plot treatment combinations, there are eight sub-plots representing the genetic entries. Throughout the paper, genetic entries are alpha numerically coded using the prefix letter L for loblolly and S for slash pine. Each installation has 13 312 trees, on 128 plots, which are distributed on approximately 10 ha of experimental area.

2.3. Treatment descriptions

Prior to planting, each installation was double bedded on separate passes following a 2.75 m spacing pattern. In the late summer/early fall of 1999, all installations were treated with pre-plant herbicides consisting of Arsenal® (imazapyr) at 1.02 ℓ ha^{-1} and Garlon (triclopyr) at 7.02 ℓ ha^{-1} with the goal of removing all woody competition and reducing initial levels of herbaceous vegetation. The objective was to provide a site with resources suitable for optimum growth while minimizing the variation within individual study sites. The operational silviculture treatment represented a typical regime utilized by forest industry throughout the Southeastern USA at the time. After receiving a common site preparation treatment, the operationally treated plots received a single banded, or broadcast application of 280 kg ha^{-1} diammonium phosphate at the time of planting.

The contrasting intensive treatment was mainly driven by early vegetation control and annual fertilization. On these plots, competing vegetation was controlled for 2 years following planting using directed applications of Arsenal® (imazapyr) at 0.28 ℓ ha^{-1} (limited to loblolly pine installations) and Oust® (sulfometuron methyl) at 0.14 ℓ ha^{-1} on all installations. For the follow-up treatments ground cover was kept below a 30% threshold through age 3. By age 5, the tree crowns had closed canopy and the herbaceous component was limited due to light availability. The intensive plots were fertilized with 660 kg ha^{-1} of 10-10-10 plus micronutrients at the time of planting, which was followed by annual applications of macro- and micronutrient fertilizers using prescriptions based on foliar analyses. The total amounts of nutrients applied on each installation through age 5 are presented in Table 2.

The second treatment factor at the whole-plot level is contrasting planting density: 1334 trees ha^{-1} planted at a spacing of 2.75 m × 2.75 m, and 2990 trees ha^{-1} planted at a spacing of 1.22 m × 2.75 m. The 2990 trees ha^{-1} sub-plots of each genetic entry are arranged in eight beds of 16 planting positions each, for a total of 128 trees per gross treatment plot. A two-tree border around the perimeter results in a 48-tree interior measurement plot of 0.016 ha. The 1334 trees ha^{-1} sub-plots of each genetic entry are arranged in 8 beds of 10 planting positions each, for a total of 80 trees per gross plot. A single tree buffer around the perimeter results in a 48-tree interior measurement plot of 0.036 ha. Despite an ongoing drought at the time of establishment, survival was over 95% in all treatments at the end of the first growing season.

Table 2
Cumulative elemental nutrient application rates for the PPINES intensive silvicultural treatments[a] through five growing seasons (kg ha^{-1})

Site location	N	P	K	Mg	Ca	S	B	Zn	Mn	Fe	Cu
Sanderson, FL	369	128	121	45	45	35	0.9	2.7	2.2	14.7	3.9
Waverly, GA	369	128	121	45	45	35	0.9	2.7	2.2	14.7	3.9
Perry, FL	373	112	115	56	45	139	1.1	3.0	3.0	15.5	5.2
Waldo, FL	370	124	124	63	56	33	1.7	2.5	6.1	6.1	4.4

[a]Operational silviculture treatments all received 45 kg ha^{-1} N and 50 kg ha^{-1} of P in the form of diammonium phosphate at the time of planting only.

At the sub-plot level, genetic entries consist of first generation elite full-sib families. On loblolly sites there are seven entries of full-sib families, including a previously identified poor grower, and an intimate mixture of the top six full-sib families. The entries are similar for the slash pine sites, with the exception of one less full-sib family to make room for the loblolly mixture in addition to a slash mixture. This allows for a direct comparison of species performance across spacing and silvicultural treatments on these two slash pine locations.

All genetic entries in the study were selected from sources exhibiting moderate to excellent resistance to fusiform rust [*Cronartium quercum* (Berk.) Miyabe ex Shirai f. sp. *fusiforme*] based upon *a priori* knowledge from breeding programs. This was done in order to reduce the confounding effects of disease incidence. Seedlings were grown in 66 ml cell^{-1} Ray Leach 'Cone-tainer'™ cells (Stuewe and Sons, Inc., Corvallis, OR). Each site was hand planted over a 2-day period in January 2000.

2.4. Inventory, yield and biomass estimates

Annual measurements of DBH were made at ages 2, 3, and 5 years on all trees in the measurement plots. Total height (HT) was measured on every tree at ages 2 and 3, but was limited to a representative 20% sub-sample at age 5. Individual tree HT at age 5 was determined from site and treatment specific HT versus DBH relationships developed from this sub-sample. Abiotic and biotic tree damage was assessed at the time of measurement. Basal area (BA) was calculated on a per family plot basis (m^2 ha^{-1}), which accounts for variation due to mortality. Since the trees were relatively small at these ages, we used a simple index of individual tree stem volume: the sum of a cylinder from the tree base to breast height (BH = 1.37 m) and of a cone from BH to the top if the tree. Individual surviving trees per plot were summed to yield total standing stem volume per plot (VOL) and are expressed in m^3 ha^{-1}.

Aboveground biomass equations were developed using a treatment specific dataset from this experiment along with supplemental data from previous regional studies of similar age and treatment history (see Table A1 in Appendix A). Biomass harvests on PPINES were conducted at age 2 and 5 and covered the full range of locations and silvicultural treatments. Due to resource limitations, we chose to develop allometric equations that were common to the full-sib families represented in the study. This was done in order to increase the power to detect differences between species, locations, densities and silvicultural intensities. Two families were harvested within each species at age 2. At age 5, due to further resource limitations, the harvest was restricted to two locations of loblolly pine and limited to a subset of silvicultural treatments and families. Trees selected for each harvest originated from border rows. These border rows were buffering the effects of genotype only since there were additional buffers separating the density and silvicultural intensity treatments. The age 2 harvest consisted of 47 loblolly pine (families L2 and L4) and 60 slash pine (S1 and S6) trees, which were harvested across each of the four-culture/density whole plots on two sites from each species. The age 5 harvest consisted of 54 loblolly pine trees from the 2290 trees ha^{-1} planting density over both contrasting silvicultural intensities at Sanderson, FL and the intensive cultural treatment at Waverly, GA.

Within each harvest year, sample trees free of damage and disease, were selected at random from across the diameter distribution representative of each treatment and site. Prior to harvest, an inventory was completed on each sample tree consisting of HT, DBH, diameter at ground line, and crown width at the widest point parallel to, and perpendicular to the planting bed. Sample trees were felled at ground line using a hand saw, placed on a tarp and separated into four aboveground components: foliage, branches, stem and dead branches. The total fresh weight of each component was measured separately in the field. The fraction of bark to stem components was estimated from 6 cm disks of wood, cut from the base of each of three equally spaced stem segments along the full length of the stem. Bark was separated from each disk and the fresh weight of each was determined in the field. Tissue samples were transported from the field and dried to a constant weight at 70 °C.

Logarithmically transformed linear allometric equations were developed using a combination of the biomass harvests and the regional data set according to the base model (Eq. (1)) (Crow, 1988):

$$\ln(Y_i) = \ln(\beta_0)_{i0} + \beta_1 \ln X_{i1} + \ln(\varepsilon_i) \qquad (1)$$

where ln is the natural logarithm, Y_i the dry weight of the unit area aboveground biomass (AGB) of the ith sample tree expressed in kg $tree^{-1}$, $(\beta_0)_{i0}$ the mean of the ith sample tree within each species, X_{i1} the product of the combined variables of DBH squared times HT for the ith sample tree expressed in dm^3, and ε_i is the random error associated with estimating the weight of the aboveground biomass of the ith sample tree. The need for separate groups of equations by species, location, silviculture, and density was examined utilizing PROC MIXED (Littel et al., 1996) in SAS. These were evaluated by beginning with a pooled dataset and systematically decomposing the general model by entering treatment variables and their interactions. At each step slopes and intercepts of the resulting equations were evaluated through covariance analysis. The large sample size in the pooled regional dataset ($n = 432$ harvest trees) yielded tests with many degrees of freedom, thereby increasing the power to detect differences in parameters between treatments. Variables were included in the development of the model if they were significant at $\alpha = 0.05$. However, there were some instances where various combinations of treatments in the PPINES trial resulted in individual trees of much larger size than those from the regional dataset. Therefore, results could not be extrapolated for those individual treatment combinations. As a result, only the variable of species was included in the allometric relationships (see Table A2 in Appendix A). Probability plots of the residuals indicated that the normality assumption was satisfied and plots of residuals versus predicted values showed no obvious pattern, suggesting that the assumptions of independence and equal variance were met. Corrections for bias in the transformation of logarithmic units to arithmetic units, was done using Eq. (2) (Baskerville, 1972):

$$\hat{Y} = e^{\hat{\mu} + \hat{\sigma}^2/2} \qquad (2)$$

where $\hat{Y}$ is the estimated aboveground biomass in arithmetic units of the skewed Y distribution at X from Eq. (1). AGB was calculated for each plot and is expressed in Mg ha^{-1} of dry matter.

2.5. Analysis

All analyses were performed using PROC MIXED (Littel et al., 1996) in SAS. To test for differences in stand level attributes among treatments, separate analyses of variance (ANOVA) were performed for loblolly and slash pine using a mixed linear model for data pooled across two sites within each species (Eq. (3)):

$$\begin{aligned} Y_{ijklmn} = {} & \mu + S_i + b(s)_{ij} + C_k + D_l + CD_{kl} + F_m + CF_{km} \\ & + DF_{lm} + CDF_{klm} + SC_{ik} + SD_{il} + CD_{ikl} + SF_{im} \\ & + SCF_{ikm} + SDF_{ilm} + SCDF_{iklm} + b(s)C_{ijk} \\ & + b(s)D_{ijl} + b(s)CD_{ijkl} + b(s)F_{ijm} + b(s)CF_{ijkm} \\ & + b(s)DF_{ijlm} + b(s)CDF_{ijklm} + b(s)S_{ij} + b(s)SC_{ijk} \\ & + b(s)SD_{ijl} + b(s)CD_{ijkl} + b(s)SF_{ijm} + b(s)SCF_{ijkm} \\ & + b(s)SDF_{ijlm} + w_{ijklmn} \end{aligned} \qquad (3)$$

where Y_{ijklmn} is the response variable (BA, VOL, or AGB) of the nth plot of the mth family of the lth planting density of the kth silvicultural intensity of the jth block of the ith site ($i = 1, 2$; $j = 1, 2, \ldots, 4$; $k = 1, 2$; $l = 1, 2$; $m = 1, 2, \ldots, 6$ for slash and 7 for loblolly pine; $n = 1$); μ the overall mean; S_i the fixed effect of the ith location; $b(s)_{ij}$ the random interaction effect of the jth block within the ith location; C_k the fixed effect of the kth

Table 3
Summary of statistical significance (prob. > *F*) and associated degrees of freedom from ANOVA to test loblolly pine basal area, stem volume and aboveground biomass at age 2, 3 and 5 years[a]

Source of variation	Basal area[b]			Stem volume[c]			Aboveground biomass[d]		
	Numerator d.f.	Denominator d.f.	*p*-Value	Numerator d.f.	Denominator d.f.	*p*-Value	Numerator d.f.	Denominator d.f.	*p*-Value
Age 2									
Silviculture (*C*)	1	76	**<0.0001**	1	76	**<0.0001**	1	76	**<0.0001**
Density (*D*)	1	6	**<0.0001**	1	6	**<0.0001**	1	6	**<0.0001**
$C \times D$	1	72	**<0.0001**	1	72	**<0.0001**	1	72	**<0.0001**
Family (*F*)	6	76	**<0.0001**	6	76	**<0.0001**	6	76	**<0.0001**
$C \times F$	6	76	0.3689	6	76	0.2596	6	76	0.4582
$D \times F$	6	72	0.1361	6	72	0.1015	6	72	0.1785
$C \times D \times F$	6	72	0.4031	6	72	0.3705	6	72	0.3433
Location (*S*)	1	6	**0.0263**	1	6	**0.0219**	1	6	**0.0276**
$S \times C$	1	76	**<0.0001**	1	76	**<0.0001**	1	76	**0.0002**
$S \times D$	1	6	0.1887	1	6	0.1672	1	6	0.1537
$S \times C \times D$	1	72	**0.0097**	1	72	**0.0094**	1	72	**0.0055**
$S \times F$	6	76	**0.0474**	6	76	**0.0390**	6	76	**0.0440**
$S \times C \times F$	6	76	0.8238	6	76	0.7674	6	76	0.8742
$S \times D \times F$	5	72	0.7599	5	72	0.7067	5	72	0.5411
$S \times C \times D \times F$	5	72	0.2597	5	72	0.2553	5	72	0.2679
Age 3									
Silviculture (*C*)	1	6	**<0.0001**	1	6	**<0.0001**	1	6	**<0.0001**
Density (*D*)	1	6	**<0.0001**	1	6	**<0.0001**	1	6	**<0.0001**
$C \times D$	1	72	**<0.0001**	1	6	**0.0024**	1	72	**<0.0001**
Family (*F*)	6	70	**<0.0001**	6	70	**<0.0001**	6	70	**<0.0001**
$C \times F$	6	70	0.0701	6	70	**0.0421**	6	70	0.1081
$D \times F$	6	72	0.5611	6	66	0.6152	6	72	0.8293
$C \times D \times F$	6	72	0.4365	6	66	0.3392	6	72	0.3136
Location (*S*)	1	6	**0.0023**	1	6	**0.0042**	1	6	**0.0061**
$S \times C$	1	6	0.1132	1	6	0.2190	1	6	**0.0290**
$S \times D$	1	6	0.1526	1	6	0.1837	1	6	0.1664
$S \times C \times D$	1	72	0.0715	1	6	0.2083	1	72	**0.0178**
$S \times F$	6	70	0.0550	6	70	0.1195	6	70	0.1899
$S \times C \times F$	6	70	0.7820	6	70	0.7901	6	70	0.9084
$S \times D \times F$	5	72	0.8857	5	66	0.9280	5	72	0.6851
$S \times C \times D \times F$	5	72	0.4151	5	66	0.3647	5	72	0.4449
Age 5									
Silviculture (*C*)	1	6	**<0.0001**	1	6	**<0.0001**	1	6	**<0.0001**
Density (*D*)	1	6	**<0.0001**	1	6	**<0.0001**	1	6	**<0.0001**
$C \times D$	1	6	**0.0014**	1	6	**0.0011**	1	142	**<0.0001**
Family (*F*)	6	136	**<0.0001**	6	136	**<0.0001**	6	142	**<0.0001**
$C \times F$	6	136	0.0541	6	136	**0.0019**	6	142	0.0502
$D \times F$	6	136	0.1022	6	136	0.1149	6	142	0.4576
$C \times D \times F$	6	136	0.8249	6	136	0.6683	6	142	0.5154
Location (*S*)	1	6	**0.0021**	1	6	**0.0028**	1	6	**0.0032**
$S \times C$	1	6	**0.0056**	1	6	**0.0038**	1	6	**0.0005**
$S \times D$	1	6	0.1092	1	6	0.1314	1	6	0.0708
$S \times C \times D$	1	6	0.4445	1	6	0.2368	1	142	**0.0007**
$S \times F$	6	136	**0.0271**	6	136	**0.0224**	6	142	**0.0388**
$S \times C \times F$	6	136	0.3847	6	136	0.2075	6	142	0.5364
$S \times D \times F$	5	136	0.4779	5	136	0.5922	5	142	0.4878
$S \times C \times D \times F$	5	136	0.6594	5	136	0.5897	5	142	0.4361

p-Values significant at the 95% level of confidence are shown in bold type.
[a] Different models were constructed for each variable within each age with varying random effects in the variance terms; hence the need for different numerator and denominator degrees of freedom in the mixed model (see Table 7).
[b] Basal area is expressed in $m^2\ ha^{-1}$.
[c] Stem volume is expressed in $m^3\ ha^{-1}$ and is calculated as the sum of per tree measurements of the volume of a cylinder to 1.37 m and the volume of a cone from 1.37 m to the top of the tree.
[d] Aboveground biomass is expressed in metric tonnes per hectare and was calculated using individual tree allometric equations per Appendix A.

Table 4
Summary of statistical significance (prob. > *F*) and associated degrees of freedom from ANOVA to test slash pine basal area, stem volume and aboveground biomass at age 2, 3 and 5 years[a]

Source of variation	Basal area[b]			Stem volume[c]			Aboveground biomass[d]		
	Numerator d.f.	Denominator d.f.	*p*-Value	Numerator d.f.	Denominator d.f.	*p*-Value	Numerator d.f.	Denominator d.f.	*p*-Value
Age 2									
Silviculture (*C*)	1	18	**0.0002**	1	18	**0.0004**	1	18	**0.0018**
Density (*D*)	1	18	<**0.0001**	1	18	<**0.0001**	1	18	<**0.0001**
$C \times D$	1	18	0.0659	1	18	0.0760	1	18	0.1300
Family (*F*)	5	119	<**0.0001**	5	119	<**0.0001**	5	119	<**0.0001**
$C \times F$	5	119	0.4326	5	119	0.4252	5	119	0.6137
$D \times F$	5	119	0.1267	5	119	0.1027	5	119	0.3591
$C \times D \times F$	5	119	0.8362	5	119	0.8065	5	119	0.8731
Location (*S*)	1	6	0.9236	1	6	0.9826	1	6	0.7859
$S \times C$	1	18	0.7668	1	18	0.8279	1	18	0.8956
$S \times D$	1	18	0.2432	1	18	0.2885	1	18	0.4431
$S \times C \times D$	1	18	0.7714	1	18	0.8336	1	18	0.8855
$S \times F$	5	119	0.1953	5	119	0.1890	5	119	0.1649
$S \times C \times F$	5	119	0.9212	5	119	0.9251	5	119	0.8537
$S \times D \times F$	5	119	0.7424	5	119	0.7318	5	119	0.6487
$S \times C \times D \times F$	5	119	0.9946	5	119	0.9951	5	119	0.9982
Age 3									
Silviculture (*C*)	1	18	<**0.0001**	1	18	<**0.0001**	1	18	<**0.0001**
Density (*D*)	1	18	<**0.0001**	1	18	<**0.0001**	1	18	<**0.0001**
$C \times D$	1	18	**0.0003**	1	18	**0.0007**	1	18	**0.0037**
Family (*F*)	5	119	<**0.0001**	5	119	<**0.0001**	5	119	<**0.0001**
$C \times F$	5	119	0.1182	5	119	0.0797	5	119	0.4432
$D \times F$	5	119	0.0641	5	119	0.0559	5	119	0.1259
$C \times D \times F$	5	119	0.6940	5	119	0.6627	5	119	0.7740
Location (*S*)	1	6	**0.0257**	1	6	**0.0410**	1	6	0.0937
$S \times C$	1	18	**0.0121**	1	18	**0.0240**	1	18	0.1037
$S \times D$	1	18	**0.0118**	1	18	**0.0159**	1	18	**0.0369**
$S \times C \times D$	1	18	0.1990	1	18	0.2184	1	18	0.3651
$S \times F$	5	119	**0.0039**	5	119	**0.0046**	5	119	**0.0158**
$S \times C \times F$	5	119	0.0549	5	119	0.0608	5	119	0.2363
$S \times D \times F$	5	119	0.4222	5	119	0.4083	5	119	0.4500
$S \times C \times D \times F$	5	119	0.9283	5	119	0.9148	5	119	0.9953
Age 5									
Silviculture (*C*)	1	6	<**0.0001**	1	6	<**0.0001**	1	6	<**0.0001**
Density (*D*)	1	12	<**0.0001**	1	12	<**0.0001**	1	12	<**0.0001**
$C \times D$	1	12	**0.0007**	1	12	**0.0002**	1	12	**0.0037**
Family (*F*)	5	116	<**0.0001**	5	116	<**0.0001**	5	116	<**0.0001**
$C \times F$	5	116	0.0589	5	116	**0.0126**	5	116	0.4432
$D \times F$	5	116	0.2837	5	116	0.1763	5	116	0.1259
$C \times D \times F$	5	116	0.4665	5	116	0.5684	5	116	0.7740
Location (*S*)	1	6	**0.0024**	1	6	**0.0037**	1	6	0.0937
$S \times C$	1	6	0.1441	1	6	0.1880	1	6	0.1037
$S \times D$	1	12	**0.0439**	1	12	**0.0197**	1	12	**0.0369**
$S \times C \times D$	1	12	0.2945	1	12	0.2869	1	12	0.3651
$S \times F$	5	116	**0.0127**	5	116	**0.0157**	5	116	**0.0158**
$S \times C \times F$	5	116	0.0510	5	116	0.0790	5	116	0.2363
$S \times D \times F$	5	116	0.7333	5	116	0.5427	5	116	0.4500
$S \times C \times D \times F$	5	116	0.9229	5	116	0.8777	5	116	0.9953

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

[a] Different models were constructed for each variable within each age with varying random effects in the variance terms; hence the need for different numerator and denominator degrees of freedom in the mixed model (see Table 7).

[b] Basal area is expressed in $m^2\ ha^{-1}$.

[c] Stem volume is expressed in $m^3\ ha^{-1}$ and is calculated as the sum of per tree measurements of the volume of a cylinder to 1.37 m and the volume of a cone from 1.37 m to the top of the tree.

[d] Aboveground biomass is expressed in metric tonnes per hectare and was calculated using individual tree allometric equations per Appendix A.

silvicultural intensity; D_l the fixed effect of the lth planting density; F_m the fixed effect of the mth family and w_{ijklmn} is the random error. Blocks were nested within locations, while the factors of silviculture (C), planting density (D), and genotype (F) were crossed. All terms containing $b(s)_{ij}$ 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 $b(s)CD_{ijkl}$, which was never pooled as it is used as the error term to test the main effects of S_i, C_k and D_l. Individual variance components were pooled when the probability of a greater F statistic was 0.25 or larger. As noted by Bancroft and Han (1983), the significance level for the F-test is much higher than conventional levels of 0.01 or 0.05 and is a conservative measure of the relative efficiency of pooling the sources of variation.

Since the analysis of each variable has a differing model construct, the variance components for each model are presented in a separate table subsequent to the traditional ANOVA tables in Section 3. Assumptions of equal variance between the two planting density treatments were violated for all variables examined. This was due to heterogeneity in the covariance structure associated with planting density; there was greater variation within the 2290 trees ha^{-1} treatment. To account for this heterogeneous variance, the residual was grouped by the fixed effect of density (Bozivich et al., 1956). Where significant effects were found, least squares means were generated between levels of the factors of interest. Where multiple non-planned comparisons were made, a Bonferroni's adjusted significance level was used. Single degree of freedom contrasts were performed to test for differences between species (mixed loblolly versus mixed slash pine plots) and also method of deployment (mixed versus pure plots).

3. Results

Strong and significant G × E in BA, VOL, and AGB was apparent in this experiment for both species. The strength of the experimental design enabled the detection of three types of unit area production interactions: genotype × site, genotype × silviculture, and silviculture × density (Tables 3–5). There were no significant three-way interactions involving genotype, site and silviculture. Some combinations of treatments interacted as early as age 2 and all increased in significance with time. Despite the high statistical power to detect interactions, there was no evidence for genotype × density interactions of any kind, despite the extremes in planting density combined with the contrasting silvicultural treatments and locations.

Table 5
Variance components and associated statistical significance (prob. > |Z|) for individual model results in Tables 4 and 5

Source of variation[a]	Slash pine			Loblolly pine		
	Basal area[b]	Stem volume[c]	Aboveground biomass[d]	Basal area[b]	Stem volume[c]	Aboveground biomass[d]
Age 2						
Location (block)	0.0928	0.0965	0.0967	0.1129	0.1205	0.1442
$S \times D$ (block)				0.1177	0.1164	0.1192
$S \times C \times D$ (block)	0.0268	0.0245	0.0311			
$S \times C \times F$ (block)				0.0647	0.0609	0.0364
Residual at 2990 tph	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
Residual at 1334 tph	<0.0001	<0.0001	<0.0001	0.0090	0.0103	0.0415
Age 3						
Location (block)	0.0915	0.0908	0.1037	0.2663	0.2733	0.2539
$S \times C$ (block)				0.1119	0.1691	0.1380
$S \times D$ (block)				0.1024	0.1654	0.0978
$S \times C \times D$ (block)	0.0153	0.0131	0.0197		0.2337	
$S \times C \times F$ (block)				0.2404	0.1763	0.2309
Residual at 2990 tph	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
Residual at 1334 tph	<0.0001	<0.0001	<0.0001	0.0026	0.0038	0.0143
Age 5						
Location (block)	0.3690	0.3663	0.3769	0.1579	0.1594	0.1661
$S \times C$ (block)	0.1667	0.1468	0.2149	0.1374	0.1356	0.1026
$S \times D$ (block)				0.1707	0.1746	0.0992
$S \times C \times D$ (block)	0.0736	0.0688	0.1142	0.2415	0.2037	
Residual at 2990 tph	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
Residual at 1334 tph	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001

Random variance components and their interactions were pooled when the p-value was greater than 0.25 and are either left blank or not shown in this table.

[a] Sources of variation are location (S), planting density (D), silvicultural intensity (C), and family (F). Due to heterogeneity in the covariance structure with respect to the fixed effect of planting density and greater variation within the 2290 trees ha^{-1} (tph) treatment, the residual was grouped according to the planting density treatment.

[b] Basal area is expressed in m^2 ha^{-1}.

[c] Stem volume is expressed in m^3 ha^{-1} and is calculated as the sum of per tree measurements of the volume of a cylinder to 1.37 m and the volume of a cone from 1.37 m to the top of the tree.

[d] Aboveground biomass is expressed in metric tonnes per hectare and was calculated using individual tree allometric equations per Appendix A.

3.1. Genotype × site interactions

At age 2 there were strong and significant interactions between sites and loblolly pine families for BA, VOL and AGB ($p = 0.0474$, 0.0390, and 0.0440, respectively); by age 5 the significance of these interactions had increased ($p = 0.0271$, 0.0224, and 0.0388) (Table 3). For slash pine, G × E between sites was not evident at age 2 but became significant for BA, VOL and AGB by age 3 ($p = 0.0039$, 0.0046, and 0.0158, respectively) and gained in significance over those for loblolly by age 5 ($p = 0.0127$, 0.0157, and 0.0158) (Table 4). The varying performance of families across sites was largely due to scale effects, with certain families performing better or worse than their peers when grown together on contrasting sites. For example, at age 5, the difference between sites in AGB for loblolly pine family L5 was 13% (versus a 19% average for all other families) (Fig. 1a). In terms of absolute production, family L4 was the top performer across both sites. Similar effects were observed for slash pine families between sites. Generally, these can be split into three groups based on their performance. The first group (S4 and S6) was the most sensitive across locations, and despite varying yields, both families had similar slopes representing the degree of performance across locations (Fig. 1b). The second group had intermediate sensitivities despite a wide range of yields in AGB (S1, S2, and S3). Family S5 had similar levels of AGB at both locations which resulted in a rank change (Fig. 1b).

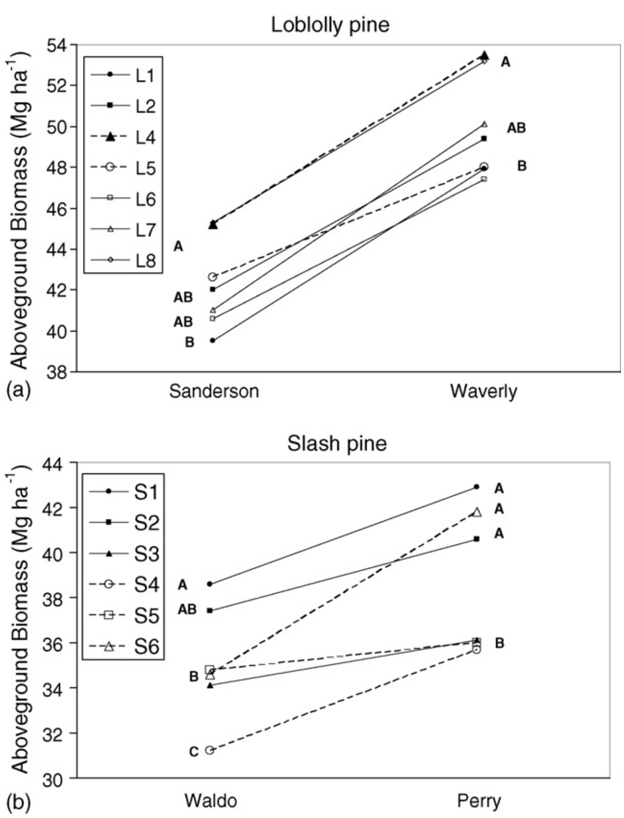

Fig. 1. Standing crop biomass (metric tonnes per hectare) at age 5 demonstrating a genotype × location interaction for (a) loblolly pine ($p = 0.0388$) and (b) slash pine ($p = 0.0158$). Data points within sites with the same letter are not significantly different at the 90% level of confidence using Bonferroni's least significant difference (LSD).

3.2. Genotype × silviculture interactions

G × E as influenced by silviculture was not as strong as the interaction of families between locations. Significant G × E became apparent by age 3 among the loblolly pine families for VOL ($p = 0.0421$) (Table 3) and grew stronger with time ($p = 0.0019$ at age 5). The significance of the interaction for loblolly pine in BA ($p = 0.0541$) and AGB ($p = 0.0502$) at age 5 was not as strong as was for volume. In contrast, elite families of slash pine were not as responsive to silviculture as was loblolly pine. Similarly, the performance among slash pine families was more stable when grown under contrasting silvicultural regimes. In slash pine, G × E (as driven by silviculture) was not significant until age 5 and then only for VOL ($p = 0.0126$); BA was weakly significant at $p = 0.0589$ (Table 4).

As with genotype × location interactions, the instability of family performance across contrasting silvicultural treatments was mainly the result of scale effects, where certain families either outperformed or underperformed their peers with increasing intensity of silvicultural treatment. Examination of least squares means for VOL at age 5 showed that loblolly family L4 was most responsive to increasing silvicultural intensity (75% increase), while family L5 was one of the least responsive families (55% increase) (Fig. 2a). Family L5 was also the family that exhibited the least difference in volume growth across contrasting locations (13% difference). All other families were intermediate in their response. For slash pine, families S2 and S6 were the most responsive in VOL at age 5 to increasing intensity of silvicultural treatment (63% increase), with all other families exhibiting a lower response (combined 55% increase) (Fig. 2b).

3.3. Silviculture × planting density interactions

Interactive effects of culture and density for loblolly pine were highly significant ($p < 0.0001$) for all growth metrics at age 2, and continued through age 5. Similar effects were noted for slash pine, but they did not become significant until age 3 ($p < 0.005$). In all cases, the interactions were due to larger responses to increasing silvicultural intensities under conditions of increasing density. For example, on the slash pine sites, the intensive silvicultural treatment increased AGB by 5.7 Mg ha^{-1} at 1334 trees ha^{-1} versus 12 Mg ha^{-1} at 2990 trees ha^{-1} (Fig. 3c). However, there was one case where this two-way interaction at age 5 for loblolly AGB was dependent on location (three-way interaction, $p = 0.0007$). In this case (Sanderson, FL), the 2990 trees ha^{-1} operational treatment produced a much lower than expected response in AGB than that at the Waverly site (Fig. 3a and b). All other combinations of silviculture and density between sites had similar responses for AGB at age 5.

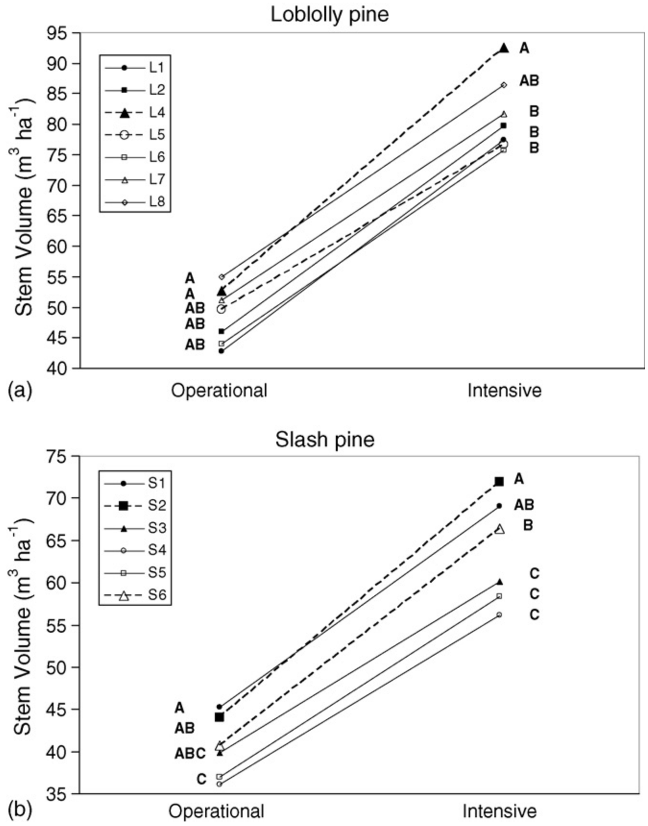

Fig. 2. Standing volume ($m^3\ ha^{-1}$) at age 5 demonstrating a genotype × silviculture interaction for (a) loblolly pine ($p = 0.0019$) and (b) slash pine ($p = 0.0126$). Data points within species and cultures having the same letter are not significantly different at the 90% level of confidence using Bonferroni's least significant difference (LSD).

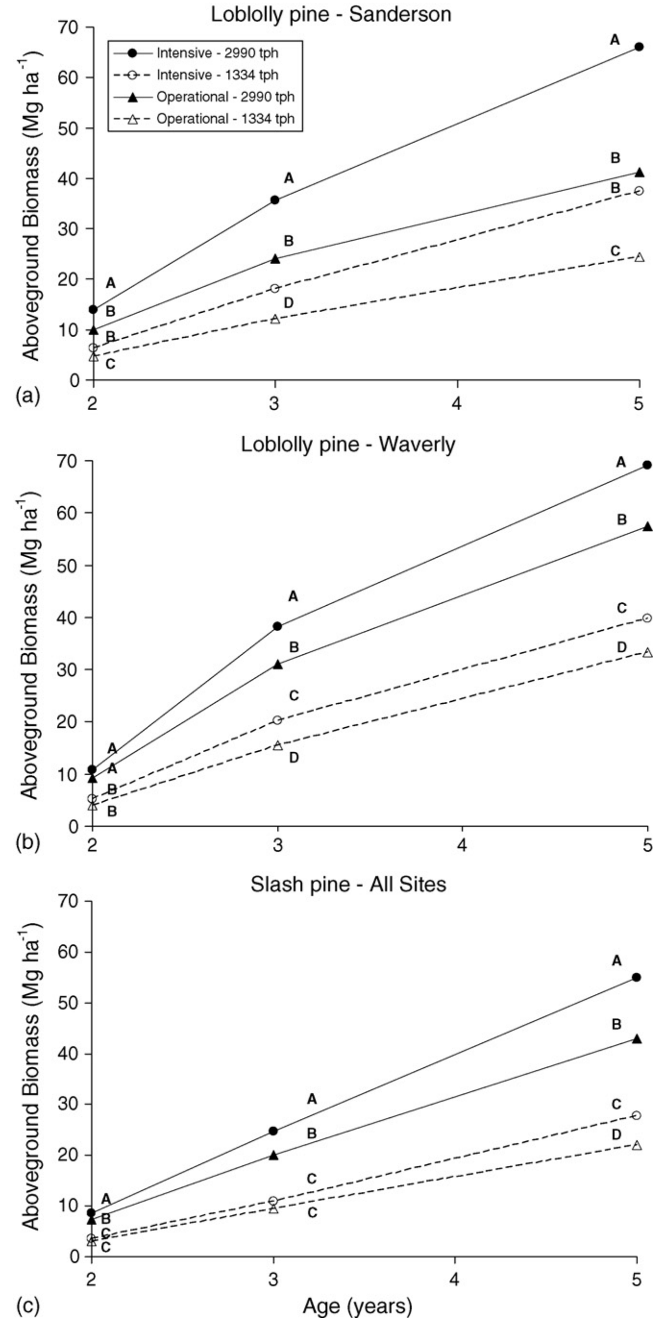

Fig. 3. Aboveground biomass accretion by cultural treatment for loblolly pine at the (a) Sanderson, FL location, (b) Waverly, GA location, and (c) across both locations with slash pine. Loblolly pine is expressed by location for ease of presentation due to a three-way, location × silviculture × density interaction. There was no three-way interaction for slash pine. Data points within ages on each graph having the same letter are not significantly different at the 90% level of confidence using Bonferroni's least significant difference (LSD).

3.4. Location × planting density interactions

There were significant location × planting density interactions for all variables at ages 3 and 5 for slash pine ($p < 0.05$) (Table 4) but not for loblolly pine (Table 3). In general, mortality was greatest in slash pine, with the majority occurring between ages 3 and 5. Despite similar survival between the two slash pine locations (Table 6), the Perry, FL location had greater VOL at age 5 than the Waldo, FL location at the 2990 trees ha^{-1} planting density ($p < 0.0197$).

3.5. Species and deployment interactions

There were strong and significant species × silviculture interactions ($p < 0.0001$) for all variables. Loblolly pine was more responsive in aboveground biomass than slash pine on the two locations where a direct comparison was possible (Fig. 4). Top performing full-sib loblolly pine families expressed similar yields at age 5 whether grown in intimate mixtures or pure blocks. However, slash pine tended to have greater BA, VOL, and AGB on a unit area basis when grown in mixtures, as compared to pure plots of the same full-sib families (Table 7).

3.6. Effects of disease and hurricanes

Plot level incidence of fusiform rust and wind damage at age 5 was examined in an attempt to partially explain genotype × location interactions. Despite the fact that all families in the study were selected to have some level of fusiform rust resistance, based on *a priori* knowledge, there were significant rank changes among slash pine families in fusiform rust

Table 6
Summary of mensurational characteristics by species, silvicultural treatment[a] and planting density[b] at age 2, 3 and 5 years ($n = 56$ plots for loblolly and $n = 48$ plots for slash pine when averaged across sites and families)

Age and planting density	Silvicultural treatments[a]					
	Operational			Intensive		
	DBH (cm)	Height (m)	tph[b]	DBH (cm)	Height (m)	tph[b]
Loblolly pine						
Age 2						
1334 tph[b]	2.8 (0.06)	2.68 (0.04)	1328 (1)	3.5 (0.07)	2.88 (0.04)	1329 (0)
2990 tph[b]	2.7 (0.06)	2.76 (0.04)	2990 (1)	3.3 (0.07)	2.97 (0.04)	2990 (0)
Age 3						
1334 tph[b]	6.5 (0.12)	4.24 (0.06)	1324 (3)	8.5 (0.10)	4.66 (0.05)	1328 (0)
2990 tph[b]	5.7 (0.12)	4.27 (0.07)	2984 (2)	7.3 (0.07)	4.67 (0.05)	2984 (3)
Age 5						
1334 tph[b]	11.0 (0.21)	7.10 (0.08)	1232 (9)	13.9 (0.10)	7.73 (0.05)	1227 (8)
2990 tph[b]	8.6 (0.18)	6.78 (0.10)	2769 (21)	11.1 (0.10)	7.77 (0.05)	2742 (20)
Slash pine						
Age 2						
1334 tph[b]	2.4 (0.07)	2.00 (0.03)	1325 (2)	2.7 (0.07)	2.04 (0.03)	1324 (2)
2990 tph[b]	2.6 (0.06)	2.10 (0.02)	2985 (3)	2.9 (0.05)	2.10 (0.02)	2982 (4)
Age 3						
1334 tph[b]	5.5 (0.12)	3.14 (0.05)	1309 (6)	6.2 (0.14)	3.24 (0.05)	1317 (4)
2990 tph[b]	5.1 (0.09)	3.32 (0.04)	2973 (8)	6.1 (0.12)	3.43 (0.04)	2973 (6)
Age 5						
1334 tph[b]	10.5 (0.17)	6.22 (0.06)	1072 (45)	13.1 (0.10)	6.50 (0.03)	1107 (23)
2990 tph[b]	8.7 (0.11)	6.31 (0.04)	2690 (35)	10.9 (0.14)	6.81 (0.04)	2608 (36)

Values in parentheses are one standard error of the mean.
[a] The operational treatment represents silviculture best practices in the Southeast at the end of the 20th century, receiving a common site preparation treatment and single banded application of 280 kg ha^{-1} diammonium phosphate at the time of planting. The contrasting intensive treatment is driven mainly by early complete vegetation control and annual fertilization.
[b] Planting density and subsequent density are expressed as the number of trees ha^{-1} (tph).

occurrence between locations at age 5 ($p = 0.0189$). Similar results have been previously documented in slash pine by Schmidt and Allen (1998). Of the six slash pine families in the experiment, three (S4, S5, and S6) demonstrated G × E in fusiform rust incidence, with the Waldo, FL location having the highest incidence levels (Fig. 5a). The other three families had a similar, but low overall incidence of fusiform rust between locations. Loblolly pine families generally had low incidence of fusiform rust and no significant interactions were found.

In the summer of 2004 two hurricanes, Frances and Jeanne, passed in close proximity to the Waldo, FL location. While damage was not extensive, there were a substantial proportion of trees toppled or leaning at varying degrees throughout the study area. Damage from these storms was minimal at the Perry, FL location and barely evident at either of the two loblolly pine locations. There was significant G × E for wind

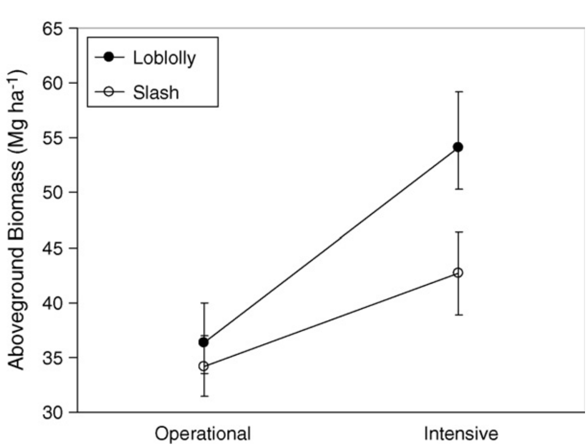

Fig. 4. Standing crop biomass (metric tonnes per hectare) at age 5 demonstrating a species × silviculture interaction for loblolly and slash pine ($p < 0.0001$). Mixed family plots across two locations and two levels of silvicultural intensity were compared. *Y* error bars represent plus or minus one standard error of the mean.

Table 7
Age 5 contrasts between slash pine families grown in mixtures vs. grown in pure plots

Variable	Deployment[a]		
	Mixed	Pure	*p*-Value
Basal area[b]	17.2	16.7	0.1016
Stem volume[c]	54.1	52.5	0.1089
Aboveground biomass[d]	38.4	37.4	0.0754

[a] Intimate mixtures of all top performing slash pine full-sib families (S1, S2, S4, S5 and S6) were contrasted with the average of the same full-sib families grown in pure blocks across two locations (Waldo and Perry), two planting densities, and two silvicultural intensities.
[b] Basal area is expressed in m^2 ha^{-1}.
[c] Stem volume is expressed in m^3 ha^{-1} and is calculated as the sum of per tree measurements of the volume of a cylinder to 1.37 m and the volume of a cone from 1.37 m to the top of the tree.
[d] Aboveground biomass is expressed in metric tonnes per hectare and was calculated using individual tree allometric equations per Appendix A.

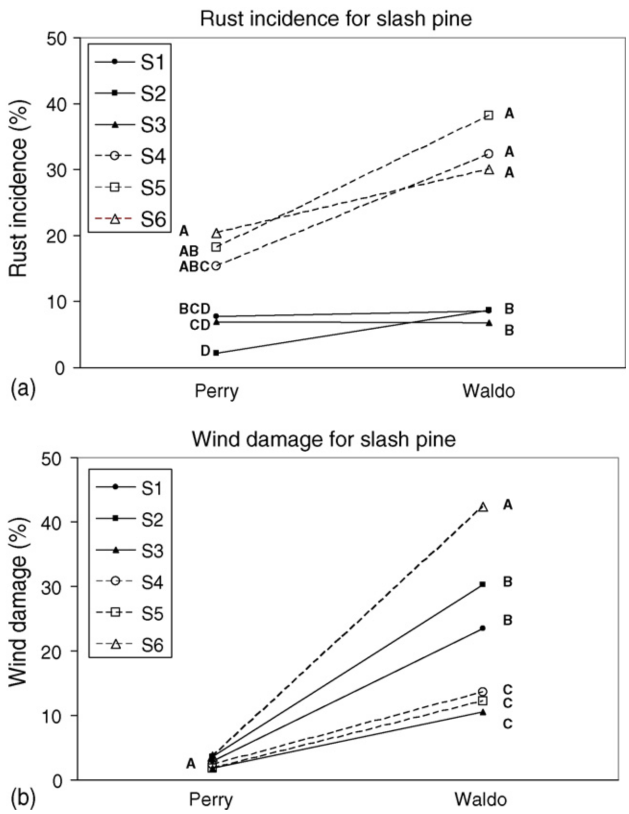

Fig. 5. (a) Percent incidence of fusiform rust per plot at age 5 demonstrating a genotype × location interaction for slash pine ($p = 0.0189$). Trees were considered infected if galls were noted on the branches or the main stem. (b) Percent incidence of wind damage per plot at age 5, also demonstrating a significant genotype × location interaction for slash pine ($p < 0.0001$). Trees were considered to be impacted by wind if they were leaning by more than 22° from vertical or had a broken top. Data points within sites with the same letter are not significantly different at the 90% level of confidence using Bonferroni's least significant difference (LSD).

damage in slash pine between locations ($p < 0.0001$) (Fig. 5b). Trees on the slash pine locations may have toppled due to indirect effects of weak root systems in combination with relatively large canopies. Diseased trees may have broken due to fusiform rust galls located on tree stems.

4. Discussion

This experiment provided the opportunity to quantify the combined effects of silvicultural treatments and genetic improvement on unit area production in selected full-sib loblolly and slash pine families. The G × E observed in this study occurred at the two-way level: genotype × location and genotype × silviculture. While genotype × density interactions were not significant, as found by McCrady and Jokela (1996), there were significant silviculture × planting density interactions for unit area production, which occurred independent of mortality. The variety of interactions evident in this study was not surprising given the range of contrasting elite genotypes, silvicultural treatments and study locations established. When combined with the high statistical power associated with the complex experimental design, we had the ability to detect significant differences in the responses of these elite genotypes to various environmental conditions in plantations of loblolly and slash pine in the Southeastern USA.

4.1. Genotype × silviculture

McKeand et al. (2006) suggest that G × E issues in southern forestry will not be of importance unless silviculture or propagule type changes significantly from those currently in use. Therefore, it was somewhat surprising that the genotype × location interactions were more significant and consistent than the genotype × silviculture interactions. This is even more striking given the extremes in the silvicultural intensity employed in this study. However, the magnitude increase in productivity with increasing silviculture likely overpowered the statistical significance of this interaction, as certain families tended to show a greater response than others. One example was loblolly family L4 which is widely deployed operationally across the Southeastern USA. Its plasticity with regard to intensive management demonstrates responsiveness considerably greater than its peers. While not of the same magnitude, the same is true for select families of slash pine in this experiment (S2 and S6). This effect of similar relative differences in yield, yet larger absolute differences with increasing silvicultural intensity has been previously demonstrated in loblolly pine (McKeand et al., 1997a). It follows that this variation in G × E across locations and silvicultural treatments could potentially be exploited if the relatively few 'responding' genotypes were to be identified and deployed on the proper sites in combination with appropriate site-specific silvicultural treatments.

4.2. Genotype × location

The strongly significant genotype × location interaction, even after accounting for the extremes in silvicultural treatments, is an indication that variation in soils, climate, edaphic variables, and pests (even across relatively short distances) are important regardless of the level of silvicultural intensity. As other researchers have suggested, soil conditions that regulate the ability to supply moisture and nutrients (Fox, 2000), may be partly responsible for the G × E observed in this experiment. Growth response to nutrition has been shown to vary by family, especially for loblolly pine (Li et al., 1991b; Samuelson, 2000). There is also evidence that carbon allocation to above- and belowground tissues is sensitive to soil fertility and varies with provenance and family (Crawford et al., 1991; Wu et al., 2004). For example, Samuelson (2000) found variation among loblolly pine families in fine root production under low nitrogen (N) treatments, but not under high N levels. Examination of foliar nutrition at age 5 on the current experiment did not explain the G × E observed in production at age 5 (unpublished data).

Genetic variability within a population allows for the potential to buffer against the effects of disease and weather, and is an important aspect of family stability. This becomes critical in areas where there are extremes in localized climatic conditions and/or pathogen populations. In the current study, through examination of damage codes made at the time of inventory, we were able to partially explain the G × E across locations for slash pine, but not for loblolly pine. In slash pine, the occurrence of fusiform rust and hurricane damage influenced the genotype × location interaction. Two of the three families responsible for the age 5 G × E in rust occurrence (S4 and S6) (Fig. 5a) corresponded to the G × E between locations in AGB (Fig. 1b). It was somewhat surprising that fusiform rust incidence did not explain the genotype × location interactions in loblolly pine given that the performance of resistant families of this species are the most unpredictable across sites (McKeand et al., 2003b).

Since all test locations were located within USDA Plant Hardiness Zone 8b, adaptation problems across sites should not be expected in this experiment (Schmidtling, 2001; Lambeth et al., 2005). One anomaly is the single family (S5), which had a greater incidence of fusiform rust occurrence at Waldo, FL (Fig. 5a), yet similar biomass production when compared across locations (Fig. 1b). The explanation for this anomaly may lie with its relative stability to the severe winds of 2004 (Fig. 5b). In contrast, family S6 had the highest incidence of weather damage at the Waldo, FL location (42.4%), in combination with a fairly high occurrence of fusiform rust (30.1%). While there were large-scale effects from wind damage, there were no changes in rank among the slash pine families (Fig. 5b). Occurrence of pitch canker, insect damage, and forking was examined, but did not explain the G × E observed in this study.

The significant genotype × location interactions as demonstrated in this study, with limited genotypes and locations, serves to emphasize the importance of carefully considering deployment and management of elite genotypes in the future. In some cases, existing expert local knowledge of site conditions, including those not foreseen such as catastrophic insect, disease or climatological variation, may provide critically important information needed to make successful deployment decisions. For locations with extreme site conditions or unknown climate variability, it may be desirable to emphasize pest resistance over growth when selecting genotypes to deploy, which could minimize the risk of unexpected growth performance.

4.3. Culture × density

Interactions between silvicultural treatments and stand density are well known to occur and have been described using several conceptual models that link silviculture with ecology (Long et al., 2004). We noted significant silviculture × density interactions, with the greatest response in production occurring under conditions of intensive silviculture and high initial planting density (Fig. 3). This interactive effect is due to better and earlier site resource capture at higher planting densities. Treatments planted at 2990 trees ha^{-1} closed canopy a minimum of 2 years earlier than the lower densities. The low-density plots were not able to take full advantage of the extra resources made available through the intensive silvicultural treatment, which was applied to both planting densities. The location × silviculture × density interaction noted for loblolly AGB is likely a function of differences in the inherent productivity of the two contrasting locations examined in combination with the relatively high nutrient demands of loblolly pine (Jokela et al., 2000). Inherent productivity differences between locations are demonstrated using a surrogate of average tree height at age 5 (averaged across families and densities) on the operational treatments (6.64 m at Sanderson, FL versus 7.65 m at Waverly, GA). The nutrient poor, sandy soil at Sanderson, FL is clearly unable to supply the nutrients demanded for maximum growth in the absence of nutrient additions. This effect has been well documented by Adegbidi et al. (2005). Nutrient limitations are exacerbated when tree density, and resulting unit area AGB, is dramatically increased to levels approaching 2990 trees ha^{-1} (Burkes et al., 2003). Resource managers will need to be aware that plantations in the Southeastern USA growing on nutrient poor sites at higher densities will be in critical need of nutrient amendments much earlier in their rotations than previously thought. As seen in other experiments, where limiting site resources were ameliorated through combinations of competing vegetation control and nutrient applications, loblolly pine productivity was close to it is predicted biological maximum, regardless of the inherent site quality (Jokela et al., 2004; Sayer et al., 2004).

4.4. Species and deployment interactions

It is curious that loblolly performance was similar regardless of deployment in mixtures or pure plots, while slash pine performed better when grown in mixtures. It has been documented in other ecosystems that contrasting species can exploit different resource strata and therefore have greater yields when grown together on the same site. Perhaps the families chosen for the slash pine installations are truly an example of this. A more likely explanation is that there may be differential pest or environmental stress between the mixed and pure plots.

5. Conclusions

The significant genotype × location interactions that were found in this study, despite limited genotypes and locations, serves to emphasize the importance of carefully considering deployment strategies of improved genotypes of loblolly and slash pine in the Southeastern United States. As resource managers make decisions about where to deploy this elite genetic material, they also will need to know how these genotypes will respond to intensive silvicultural treatments in association with localized pest and climatic conditions. For example, as silvicultural treatments become more effective at ameliorating limiting site resources, the efficiency of nutrient uptake and utilization among genotypes will likely play a larger role in their differentiation of performance (Li et al., 1991a). Variation in crown structure could also lead to significant G × E (McCrady and Jokela, 1996).

This issue is certain to increase in importance as advances in clonal forestry occur (McKeand et al., 2003a; Bouvet et al., 2005). In certain cases where intensive silviculture and advanced breeding strategies are combined, it may become necessary to develop site-specific silvicultural treatments for particular genotypes or to modify breeding strategies in order to capture the full advantage of the G × E interaction.

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Appendix A

Description of biomass harvest data to develop allometric and parameter estimates and standard errors of the estimate aboveground biomass are shown in Tables A1 and A2, respectively.

Table A1
Description of biomass harvest data to develop allometric the allometric equations displayed in Table A2

Silvicultural intensity[a]	Planting density (tph)[b]	Age[c]	Year[d]	Sample size (trees)	Reference
Loblolly					
Intensive	495	2	2003	24	FBRC (2004)
Intensive	540	2	2001	17	This article
Intensive	608	4	1999	8	Adegbidi et al. (2002)
Intensive	625	4	1986	27	Colbert et al. (1990)
Intensive	1200	2	2001	18	This article
Intensive	1200	5	2004	72	This article
Operational	495	2	2003	24	FBRC (2004)
Operational	540	2	2001	16	This article
Operational	608	3	2000	24	Adegbidi et al. (2002)
Operational	608	4	1999	24	Adegbidi et al. (2002)
Operational	625	4	1986	6	Colbert et al. (1990)
Operational	1200	2	2001	18	This article
Operational	1200	5	2004	36	This article
Slash					
Intensive	495	2	2003	12	FBRC (2004)
Intensive	540	2	2001	14	This article
Intensive	625	4	1986	27	Colbert et al. (1990)
Intensive	1200	2	2001	14	This article
Operational	495	2	2003	12	FBRC (2004)
Operational	540	2	2001	16	This article
Operational	625	4	1986	7	Colbert et al. (1990)
Operational	1200	2	2001	16	This article

[a] Silvicultural intensity is a generalized grouping of cultural treatments found in the individual studies that closely approximates that found in the current PPINES investigation: the operational treatment represents silviculture best practices in the Southeast at the end of the 20th century, receiving a common site preparation treatment and single banded application of 280 kg ha^{-1} diammonium phosphate at the time of planting. The contrasting intensive treatment is driven mainly by early complete vegetation control and annual fertilization.
[b] Planting density is expressed as the number of trees ha^{-1} (tph).
[c] Age is the age in years of the trees at time of the biomass harvest.
[d] Year is year of the biomass harvest.

Table A2
Parameter estimates and standard errors of the estimate for aboveground biomass (kg $tree^{-1}$) equations developed for loblolly and slash pine

Species	β_0			β_1		
	Estimate	S.E.	*p*-Value	Estimate	S.E.	*p*-Value
Loblolly	0.63065	0.02679	<0.0001	0.53480	0.00774	<0.0001
Slash	0.56723	0.02678	<0.0001	0.53480	0.00774	<0.0001

Data used to develop equations were generated from regional trials in FL and GA, 2–5 years in age. (Regression model: $\ln Y = \beta_0 + \beta_1 \ln X$, where ln = natural logarithm, Y = aboveground total dry weight (kg $tree^{-1}$), β_0 and β_1 = regression coefficients (intercept and slope, respectively), $X = DBH^2\,HT$ in dm^3. Overall model $R^2 = 0.929$, RMSE = 0.26574, $n = 432$.)

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