FAMILY BY ENVIRONMENT INTERACTIONS FOR 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 and slash pine. We examined genotype (family) by environmental interactions (G x E) through age five years using a factorial experiment consisting of silvicultural treatment intensity, planting density and full-sib families Five years after planting, both loblolly and slash pine demonstrated significant interactions among several factors: G by site ($p < 0.028$ and $p < 0.016$ respectively) and G by silvicultural treatment intensity ($p < 0.055$ and $p < 0.059$ for basal area and standing stem volume). G by silvicultural treatment interactions were positive, large and of the scale-type effe. . Changes in slash pine family rankings between sites were partly explained by a combination of fusiform rust infection [*Cronartium quercum* (Berk.) Miyabe ex Shirai f. sp. *fusiforme*] and wind damage from the 2004 hurricane season.

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. When a combination of elite genetic materials are combined with site-specific silvicultural treatments, mean annual increments of up to 20 m^3/a/ per year have been documented (Allen and others 2005). However, as resource managers begin to deploy selected full-sib families or clones (Bridgwater and others 2005), there is a greater likelihood that genotype by environmental (G x E) interactions will occur, especially under conditions of increased silvicultural intensity (McKeand and others 2006).

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 x E would not be of major consequence for the majority of genotypes being deployed under traditional silvicultural systems (McKeand and others 2006) and tree improvement programs have historically assessed G x E interactions for determining the need for site specific breeding efforts (McKeand and others 1997). While few studies have documented G x E interactions among silvicultural treatments, available evidence suggests that when G x E does occur in these situations, it is caused by relatively few genotypes in the population that were highly sensitive to environmental variation (Zas and others 2004). It appears that G x 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 overall objectives of this study were to investigate and quantify the magnitude and nature of G x E in full-sib families of loblolly and slash pine. This was accomplished using a series of replicated factorial experiments and family block plantings established in FL and GA that manipulated gradients in planting density, understory competition, and soil nutrient availability.

METHODS

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 installations in southeast GA and northeast FL that were designed to examine interactions of full-sib loblolly and slash pine families with several environmental factors, including study location, nutrient manipulation treatments, and planting density (Roth and others 2002). The topography is nearly flat, with less than a 1 percent 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). All study sites share a subtropical and humid climate with long hot wet summers and mild dry winters and long-term (1931–2000) precipitation has averaged 1384 mm/ year (NOAA, 2002).

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 by 2 by 7 (silviculture by planting density by 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. Silvicultural and planting density treatments are at the whole-plot level and genetic entries are at the sub-plot level

Treatment Descriptions

Each installation was double bedded at 2.75 m spacing and treated in the late summer/early fall of 1999 with pre-plant herbicides with the goal of removing all woody competition and reducing initial levels of herbaceous vegetation. Following planting, competing vegetation was controlled for two years using directed herbicide applications. The intensive plots were fertilized with 660 kg/ha of 10-10-10 plus micronutrients at the time of planting, which was followed by

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Citation for proceedings: Stanturf, John A., ed. 2010. Proceedings of the 14th biennial southern silvicultural research conference. Gen. Tech. Rep. SRS-121. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southern Research Station. 614 p.

annual applications of macro- and micronutrient fertilizers. Contrasting planting densities of 1 334 trees/ha and 2 990 trees/ha were created by varying the spacing within beds. Genetic were represented by first generation full-sib genetic entries: 1) elite families for growth, and 2) a poor grower.

Inventory, Yield and Biomass Estimates

Diameter at breast height (d.b.h.) was measured at age five on all measurement trees. In addition, total height (HT) was measured on a 20 percent sub-sample with the remaining heights predicted from measured d.b.h., using site and treatment specific relationships. 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) which accounts for variation due to mortality. Individual tree stem volume was calculated as the sum of the volume of a cylinder from the base of the tree to 1.37 m in height and the volume of a cone from 1.37 m to the top of the tree. Individual surviving trees per plot were summed and scaled to yield total standing stem volume (VOL; m^3/ha). Aboveground biomass (AGB) equations were developed using a dataset consisting of treatment specific data from this experiment along with supplemental data from several previous regional studies of similar age and treatment history.

Analysis

All analyses were performed using PROC MIXED (Littel and others 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 (equation 1):

$$\begin{aligned} Y_{ijklmn} = {} & \mu + S_i + b(s)_{ij} + C_k + D_l + CD_{kl} + \\ & F_m + CF_{km} + DF_{lm} + CDF_{klm} + SC_{ik} \\ & + SD_{il} + CD_{ikl} + SF_{im} + SCF_{ikm} \\ & + SDF_{ilm} + SCDF_{iklm} + b(s)C_{ijk} \\ & + b(s)D_{ijl} + b(s)CD_{ijkl} + b(s)F_{ijm} \\ & + b(s)CF_{ijkm} + b(s)DF_{ijlm} + b(s) \\ & CDF_{ijklm} + b(s)S_{ij} + b(s)SC_{ijk} + \\ & b(s)SD_{ijl} + b(s)CD_{ijkl} + b(s)SF_{ijm} + \\ & b(s)SCF_{ijkm} + b(s)SDF_{ijlm} + w_{ijklmn} \end{aligned} \qquad (1)$$

where Y_{ijklmn} is the response variable (BA, VOL, or AGB) of the *n*th plot of the *m*th family of the *l*th planting density of the *k*th silvicultural intensity of the *j*th block of the *i*th site (i = 1,2; j = 1,2, …, 4; k = 1,2; l = 1,2; m = 1,2,…, 6 for slash and 7 for loblolly pine; and n = 1); μ is the overall mean; S_i is the fixed effect of the *i*th site; $b(s)_{ij}$ is the random interaction effect of the *j*th block within the *i*th site; C_k is the fixed effect of the *k*th silvicultural intensity; D_l is the fixed effect of the *l*th planting density F_m is the fixed effect of the *m*th family and w_{ijklmn} is the random error. Blocks were nested within sites, 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). Where multiple non-planned comparisons were made, a Bonferroni's adjusted significance level was used.

RESULTS

Strong and significant G x E in BA, VOL, and AGB were apparent in this experiment for both species. The strength of the experimental design enabled the detection of two types of unit-area production interactions: genotype by site and genotype by silviculture (tables 1 and 2.). There were no significant three-way interactions involving genotype, site and silviculture. Despite the high statistical power to detect interactions, there was no evidence through age five years for genotype by density interactions of any kind.

Genotype by Site Interactions

At age five there were significant interactions for BA, VOL, and AGB (p = 0.0271, p = 0.0224, p = 0.0388) (table 1). For slash pine, G x E between sites was more significant than those for loblolly by age five (p = 0.0127, p = 0.0157, p = 0.0158) (table 2). 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 (fig. 1).

Genotype by Silviculture Interactions

G x E as influenced by silviculture was significant in loblolly pine for VOL (p = 0.0019) (table 1). The significance of the interaction for loblolly pine in BA (p = 0.0541) and AGB (p = 0.0502) at age five was not as strong as for volume. In contrast, elite families of slash pine were not as responsive to silviculture as loblolly pine and, similarly the performance among slash pine families was more stable when grown under contrasting silvicultural regimes. In slash pine, G x E (as driven by silviculture) was not significant until age five and then only for VOL (p = 0.0126); BA was weakly significant at p = 0.0589 (table 2).

As with genotype by site 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 five showed that loblolly family L4 was most responsive to increasing silvicultural intensity (75 percent increase), while family L5 was one of the least responsive families (55 percent increase) (fig. 2a). Family L5 also exhibited the least difference in volume growth across contrasting sites (13 percent difference). All other families were intermediate in their response. For slash pine, families S2 and S6 were the most responsive in VOL at age five to increasing intensity of silvicultural treatment intensity (63 percent increase), with all other families exhibiting a lower response (combined 55 percent increase) (fig. 2b).

Effects of Disease and Hurricanes

Plot level, incidence of fusiform rust and wind damage at age five was examined in an attempt to partially explain genotype by site interactions. Despite the fact that all families in the study were selected to have some level of fusiform

Table 1—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 5 years *

Source of variation	Basal area†			Stem volume‡			Aboveground biomass§		
	Num. df	*Den. df*	*p-value*	*Num. df*	*Den. df*	*p-value*	*Num. df*	*Den. df*	*p-value*
Age 5									
Culture (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 x 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 x F	6	136	0.0541	6	136	**0.0019**	6	142	0.0502
D x F	6	136	0.1022	6	136	0.1149	6	142	0.4576
C x D x F	6	136	0.8249	6	136	0.6683	6	142	0.5154
Site (S)	1	6	**0.0021**	1	6	**0.0028**	1	6	**0.0032**
S x C	1	6	**0.0056**	1	6	**0.0038**	1	6	**0.0005**
S x D	1	6	0.1092	1	6	0.1314	1	6	0.0708
S x C x D	1	6	0.4445	1	6	0.2368	1	142	**0.0007**
S x F	6	136	**0.0271**	6	136	**0.0224**	6	142	**0.0388**
S x C x F	6	136	0.3847	6	136	0.2075	6	142	0.5364
S x D x F	5	136	0.4779	5	136	0.5922	5	142	0.4878
S x C x D x F	5	136	0.6594	5	136	0.5897	5	142	0.4361

Note: * 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. † Basal area is expressed in $m^2 \cdot ha^{-1}$. ‡ Stem volume is expressed in $m^3 \cdot ha^{-1}$ 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 if the tree. § Aboveground biomass is expressed in $Mg \cdot ha^{-1}$. P-values significant at the 95% level of confidence are shown in bold type.

Table 2—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 5 years *

Source of Variation	Basal area†			Stem volume‡			Aboveground biomass§		
	Num. df	*Den. df*	*p-value*	*Num. df*	*Den. df*	*p-value*	*Num. df*	*Den. df*	*p-value*
Age 5									
Culture (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 x 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 x F	5	116	0.0589	5	116	**0.0126**	5	116	0.4432
D x F	5	116	0.2837	5	116	0.1763	5	116	0.1259
C x D x F	5	116	0.4665	5	116	0.5684	5	116	0.7740
Site (S)	1	6	**0.0024**	1	6	**0.0037**	1	6	0.0937
S x C	1	6	0.1441	1	6	0.1880	1	6	0.1037
S x D	1	12	**0.0439**	1	12	**0.0197**	1	12	**0.0369**
S x C x D	1	12	0.2945	1	12	0.2869	1	12	0.3651
S x F	5	116	**0.0127**	5	116	**0.0157**	5	116	**0.0158**
S x C x F	5	116	0.0510	5	116	0.0790	5	116	0.2363
S x D x F	5	116	0.7333	5	116	0.5427	5	116	0.4500
S x C x D x F	5	116	0.9229	5	116	0.8777	5	116	0.9953

Note: * 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. † Basal area is expressed in m2·ha-1. ‡ Stem volume is expressed in m3·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 if the tree. § Aboveground biomass is expressed in Mg·ha-1. P-values significant at the 95% level of confidence are shown in bold type.

rust resistance, there were significant rank changes among slash pine families in fusiform occurrence between sites at age five (p = 0.0189). Similar results have been previously documented in slash pine (Schmidt and Allen 1998). Of the six slash pine families in the experiment, three (S4, S5, and S6) demonstrated a GxE in fusiform rust incidence, with the Waldo, FL location having the highest incidence (fig. 3a). The other three families had a similar but low overall incidence of fusiform rust between sites. 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 site. Damage from these storms was minimal at the Perry, FL site and barely evident at either of the two loblolly sites. There was significant G x E for wind damage in slash pine between sites (p < 0.0001) (fig. 3b). Trees at the two slash pine sites may have toppled due to indirect effects of weak root systems, combined with a relatively large leaf area, or stems may have broken due to fusiform rust galls located on tree stems.

DISCUSSION

This experiment provided the opportunity to quantify the combined effects of silvicultural treatments and genetic improvement on unit-area production in full-sib loblolly and slash pine families. The G x E observed in this study occurred at the two-way level: genotype by site and genotype by silviculture. Genotype by density interactions were not significant. The variety of interactions evident in this study was not surprising given the range of contrasting elite genotypes, silvicultural treatments and study sites

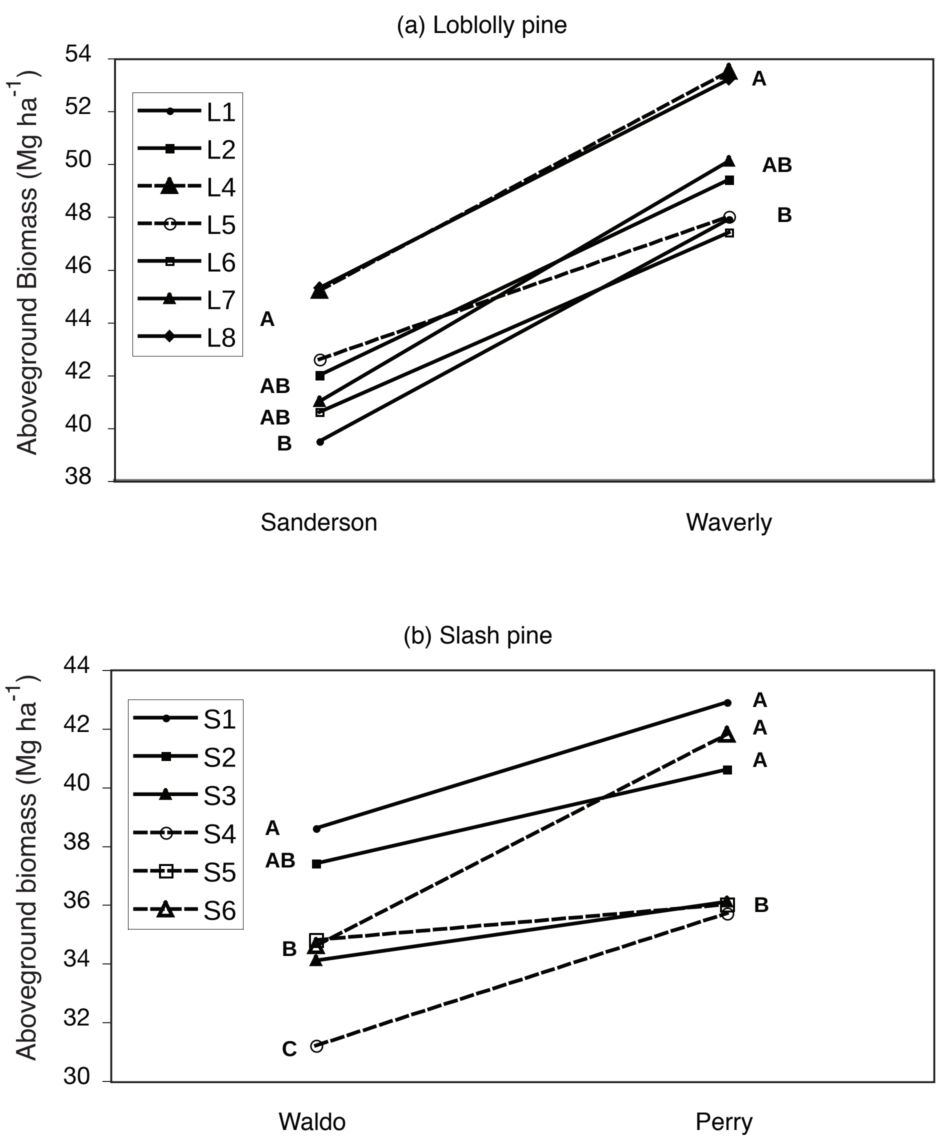


Figure 1—Standing crop biomass (metric tons per hectare) at age five demonstrating a genotype x location interaction for (a) loblolly pine (p=0.0388) and (b) slash pine (p=0.0158). Data points within sites with the same letter are not significantly different at the 90% level of confidence using Bonferroni's Least Significant Difference (LSD).

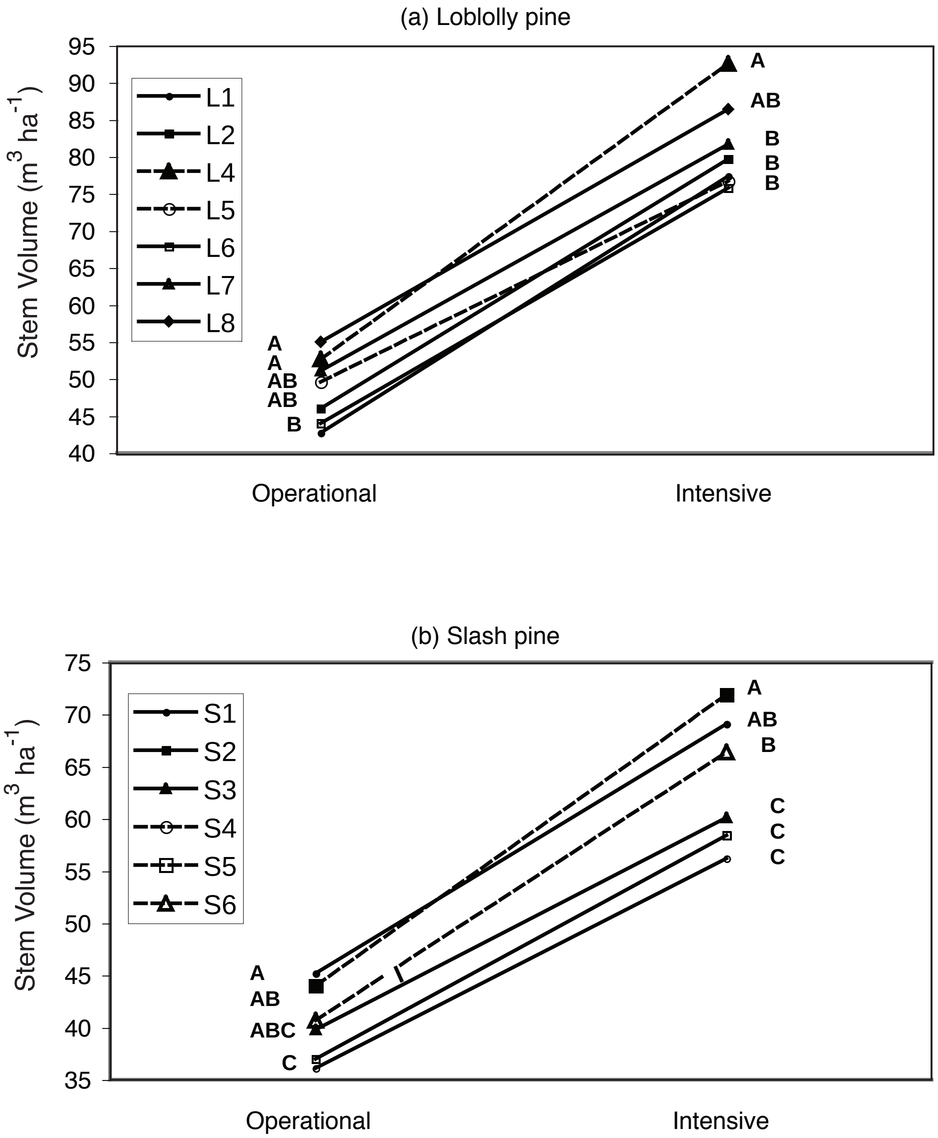


Figure 2—Standing volume (m3·ha-1) at age five demonstrating a genotype x silviculture interaction for (a) loblolly pine (p=0.0019) and (b) slash pine (p=0.0126). Data points within species and cultures having the same letter are not significantly different at the 90% level of confidence using Bonferroni's Least Significant Difference (LSD).

established. When combined with the high statistical power associated with a complex experimental design, we had the ability to detect significant differences in the responses of the elite genotypes across soils, climates and silvicultural treatments that had not previously been observed for plantations of loblolly and slash pine.

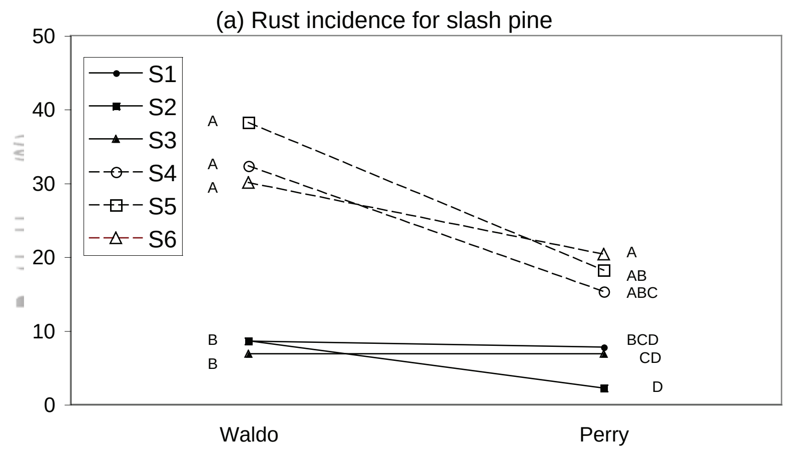
Genotype by Silviculture

McKeand and others (2006) suggest that GxE issues in Southern forestry will not become important unless silviculture or propagule type changes significantly from those currently in use. Therefore, it was somewhat surprising that the genotype by site interactions were more significant and consistent than the genotype by silviculture interactions, especially given the extremes in silvicultural intensity. However, the magnitude of increase in productivity with increasing silviculture likely overpowered the statistical significance of this interaction as certain families tended to show greater response than others. One example was loblolly family L4 which is widely deployed in the Southeastern United States and 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 have been previously demonstrated in loblolly pine (McKeand and others 1997a). It follows that this variation in GxE between sites and silvicultural treatments could potentially be exploited if the relatively few 'responding' genotypes are identified and deployed on the proper sites in combination with site-specific silvicultural treatments.

Genotype by Site

The strongly significant genotype by site 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. Soil conditions, such as the ability to supply moisture and nutrients, may be partly responsible for the GxE observed in this experiment, as has been suggested by other researchers (Fox 2000). Certain soils with high clay content, such as the Ultisols at Waverly, GA, have a relatively high water holding capacity and when combined with favorable nutrient availability, could potentially supply water and nutrients for a longer duration than the sandy Spodosols at Sanderson, FL. Growth response to nutrition has been shown to vary by family, especially for loblolly pine (Li and others1991, 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 and others 1991, Wu and others 2004). For example, Samuelson (2000) found variation among loblolly pine families in fine root production under low N treatments, but not under high N levels. Examination of foliar nutrition at age five on the current experiment was not able to explain the G x E observed in production at age five (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, particularly where there



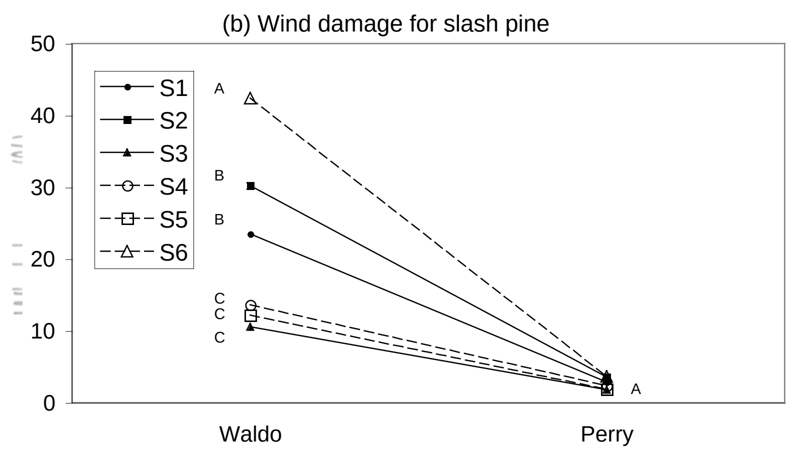


Figure 3—(a) Percent incidence of fusiform rust per plot at age five demonstrating a genotype x location interaction for slash pine (p=0.0189). Trees were considered infected if galls were noted on the branches or the main stem. (b) Percent incidence of wind damage per plot at age five, also demonstrating a significant genotype x location interaction for slash pine (p<0.0001). Trees were considered to be impacted by wind if they were leaning by more than 22 degrees 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).

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 x E across sites for slash pine but not for loblolly pine. This does not totally explain the G x E in production as only two of the three families responsible for the G x E in rust occurrence (S4 and S6) corresponded to the GxE between sites in AGB at age five. In other words, two of the three families with a proportionally greater occurrence of rust at Waldo, FL also exhibited a lower than expected amount of AGB at age five at that same site. It is somewhat surprising that fusiform rust incidence did not explain the genotype x site interactions in loblolly pine given that the performance of resistant families of this species are the most unpredictable across sites (McKeand and others 2003).

Since all test sites were located within USDA Plant Hardiness Zone 8b, adaptation problems across sites should not be expected in this experiment (Schmidtling 2001, Lambeth and others 2005). One anomaly is the single slash pine family (S5), which had a greater incidence of fusiform rust occurrence at Waldo, FL (fig. 3a), 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. 3b). In contrast, family S6 had the highest incidence of weather damage at the Waldo, FL site (42.4 percent), in combination with a fairly high occurrence of fusiform rust (30.1 percent). While there were large-scale effects of wind damage, there were no changes in rank among the slash pine families (fig. 3b). Occurrence of pitch canker, insect damage, and forking was examined, but did not explain the G x E observed in this study.

CONCLUSIONS

The significant genotype by 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. It follows that the best genotypes should be identified and deployed on the most suitable sites in combination with site- and genotype-specific silvicultural treatments. However, genotype deployment and silvicultural treatment decisions must also take into account localized pest and climactic conditions which may unexpectedly alter genotype performance.

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