

Competition dynamics in pure- versus mixed-family stands of loblolly and slash pine in the southeastern United States

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Abstract: Few studies within the native range of loblolly (*Pinus taeda* L.) and slash pine (*Pinus elliottii* Engelm. var. *elliottii*) have compared yield and stand dynamics in pure-family block versus mixed-family block plantings under a range of silvicultural treatments. Understanding intergenotypic competitive interactions is important for predicting phenotypic performance, defining growth strategies and ideotypes, and deploying the correct mix of families that possess complementary characteristics for enhanced yield and pest resistance. In 2000, replicated experimental trials were installed in the southeastern United States, controlling for genotype (pure- and mixed-family plantings; consisting of seven full-sibling loblolly and six full-sibling slash pine families), planting density (1334 vs. 2990 trees/ha), and levels of silvicultural treatment intensity (operational vs. intensive). We measured four installations of these trials. There were numerous examples of differential family performance in mixed versus pure plots manifested as significant deployment \times family interactions for diameter at breast height, height, basal area, volume, survival, disease, and damage traits. Significant and consistent interactions of several families with mixed versus pure deployment led to the identification of putative crop and competition ideotypes in both loblolly and slash pine. Tree-level crown architectural traits and an index of growth efficiency for the identified families were consistent with the hypothesized ideotypes.

Résumé : Peu d'études réalisées dans l'aire naturelle de répartition du pin à encens (*Pinus taeda* L.) et du pin de Floride (*Pinus elliottii* Engelm. var. *elliottii*) ont permis de comparer le rendement et la dynamique de peuplement de familles plantées seules dans des blocs distincts et de familles plantées en mélange dans un même bloc et ce, sous différents régimes sylvicoles. Une meilleure compréhension des interactions de nature compétitive entre génotypes est importante afin de prédire la performance phénotypique, définir les stratégies de croissance et les idéotypes et déployer la bonne combinaison de familles dont les caractéristiques sont complémentaires pour améliorer le rendement et la résistance aux ravageurs. En l'an 2000, des dispositifs expérimentaux répétés ont été établis dans le sud-est des États-Unis pour étudier les effets de l'agencement des génotypes (sept familles biparentales de pin à encens et six familles biparentales de pin de Floride plantées séparément ou en mélange), de la densité de plantation (1334 versus 2990 arbres/ha) et de l'intensité du régime sylvicole (opérationnel versus intensif). Les auteurs ont mesuré quatre cortèges de ces dispositifs. Plusieurs familles ont eu des performances différentes selon qu'elles étaient plantées séparément ou en mélange, ce qui se traduisait par des interactions significatives entre la famille et l'agencement des génotypes dans le cas du DHP, de la surface terrière, du volume, de la survie et des caractères relatifs aux maladies et aux dommages. Des interactions significatives et constantes entre quelques familles et l'agencement des génotypes ont permis d'identifier des idéotypes présumés correspondant aux conditions de culture intensive ou opérationnelle, tant chez le pin à encens que chez le pin de Floride. Chez ces familles, les caractères d'architecture de la cime individuelle des arbres et l'indice d'efficacité de la croissance étaient cohérents avec les idéotypes précédemment identifiés.

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Introduction

Forest resource managers in the southern United States are faced with important decisions regarding deployment of elite genetic materials across a variety of soil types and local climatic regimes and potential interactions with endemic pests (Nance et al. 1983; Williams et al. 1983). Deployment op-

tions used in current plantation management systems range in genetic variability from open-pollinated half-sibling families to vegetatively propagated clones (Fox et al. 2007). Comparative studies examining interspecific mixtures versus monospecific plantations on forest yield and pest damage have been the focus of considerable research. In particular, numerous examples of facilitative interactions can be found in the literature, whereby improved yields in mixed species stands (sometimes called "overyielding") have been manifest when one species directly benefits from the presence of another species (e.g., N-fixing species; Binkley 2003).

Overyielding may also occur when the species being combined have characteristics that facilitate complementary resource use (Kelty 2006). For example, Amoroso and Turnblom (2006) compared productivity of pure and mixed moderately shade tolerant Douglas-fir (*Pseudotsuga menziesii*

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(Mirb.) Franco) and very shade tolerant western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) plantations and suggested that spacing played an important role on the productivity of the mixed stands. They invoked the “competitive production principle” as a possible mechanism (Vandermeer 1989), whereby less interspecific competition occurred in the mixed stands than intraspecific competition in the pure stands.

Less common are studies examining productivity differences associated with intraspecific variation (e.g., mixed-family vs. single-family plantings or polyclonal vs. single clone plantations; Heybroek and Van Tol 1985; Perry 1985; Knowe et al. 1994). Understanding intergenotypic competitive interactions is important for not only predicting phenotypic performance, but also in deploying the correct mix of families and (or) clones that possess complementary characteristics for enhanced yield and pest resistance (Adams et al. 1973). Matching genetic materials to a site, in conjunction with site specific silvicultural treatments, can potentially aid in enhancing stand yields by understanding the growth strategies of different genetic source materials (McKeand et al. 2006).

Only limited information is available on genetic \times environment interactions for southern pine species using family block experiments (McCrary and Jokela 1998; Roth et al. 2007). Thus, assessing the performance and stability of different genetic source materials deployed in mixed and pure arrangements in varying environments is critical and necessary. Given that intertree competition is related to the relative abilities of adjacent trees to exploit spatially and temporally varying resources (niches; Vandermeer 1989), it is plausible to hypothesize that shifts in stand-level genetic variability may impact intertree competition dynamics and, as a result, patterns of stand-level variability and production. Limited evidence suggests that stand-level production could vary depending on the genetic composition of plots. For example, Foster et al. (1998) found that some mixtures of *Populus* clones outperformed pure plots of the best-performing clones by as much as 27%. Williams et al. (1983) found that stand-level production varied in pure versus mixed-family plots of loblolly pine (*Pinus taeda* L.). However, our understanding of how competitive interactions are influenced by genetic composition is still limited (von Euler et al. 1992), particularly at the stand level. In contrast, considerably more research has been conducted comparing pure versus mixed species plantings, along with the possible competitive mechanisms contributing to differential growth performances (DeBell and Radwan 1979; Garber and Maguire 2004).

Understanding competitive interactions in mixed versus pure family plots is important for several reasons. Firstly, studies of this kind give insight into the relative performance of families when grown in competition with other families, as compared with competition within the same family. This would help improve genetic selection and deployment decisions, because most family-level genetic selection programs select families based on performance in single-tree progeny trials, but these families usually are deployed in pure family blocks.

Secondly, the intensity of genetic selection and silvicultural treatments is expected to increase as the pressure to produce more wood products on a shrinking landbase becomes greater (Youngquist and Hamilton 1999; Jokela et al. 2004). Therefore, quantifying growth and yield differences between

mixed- and pure-family plantings, and investigating which combinations of planting and silvicultural regimes maximize volume and value production, pose pressing research needs.

Finally, studies addressing competition mechanisms may provide better insight into the utility of the ideotype concept for tree breeding and deployment (Martin et al. 2001). Briefly, an ideotype is a conceptual model that explicitly describes the characteristics of plants that are hypothesized to produce greater yields (Donald 1968; Cannell 1978; Dickmann et al. 1994). The competition ideotype rapidly exploits site resources, aggressively expanding its crown and root structure to the detriment of neighboring genotypes; in other words, it is a strong competitor. The crop ideotype efficiently obtains resources but does not compete aggressively with its neighbors. Because of elevated production efficiency and other factors, it is hypothesized that the crop ideotype will produce the greatest yield per unit ground area in intensively managed monocultures (Cannell 1978), but crop or competition ideotypes have not been conclusively identified in southern pines.

This paper explores competition dynamics within species by comparing stand dynamics characteristics in plots composed of individuals from single full-sibling families of loblolly and slash pine (*Pinus elliottii* Engelm. var. *elliottii*), as well as plots containing mixtures of several full-sibling families grown under two levels of initial spacing and two levels of silvicultural intensity across multiple sites.

Methods

Study description

Data for this study comes from the Pine Productivity Interactions on Experimental Sites (PPINES) trials, a set of large-scale experimental installations that serve as field laboratories for addressing questions related to the productivity and sustainability of intensively managed plantations of loblolly and slash pine. These trials were established in January 2000 by the Forest Biology Research Cooperative (<http://fbrc.ifas.ufl.edu>) at the University of Florida. The eastern series of PPINES locations were established in southeastern Georgia and northeastern Florida with the intent of examining interactions between silviculture, planting density, and genotype (full-sibling families) in loblolly and slash pine plantations (Roth et al. 2007).

The study locations in this trial series share a subtropical and humid climate, with long hot wet summers and mild dry winters (NOAA 2002). All locations have nearly flat topography, and all but one site occurs on soils in the Spodosol order (Table 1). Common understory woody vegetation included sawtooth palmetto (*Serenoa repens* (B.) Small.), wax myrtle (*Myrica cerifera* L.), runner oak (*Quercus pumila* Walt.), blueberries (*Vaccinium* spp.), gallberry (*Ilex glabra* (L.) Gray), St. John's-wort (*Hypericum fasciculatum*); common herbaceous plants were bluestem grasses (*Andropogon* spp.), panic grasses (*Panicum* spp.), sedges (*Carex* spp. and *Cyperus* spp.), and dogfennel (*Eupatorium capillifolium* (Lam.) Small).

Experimental design

The PPINES data used in this study were obtained from two loblolly pine and two slash pine installations. Loblolly pine installations were located in Sanderson, Florida, and

Table 1. Characteristics of the Pine Productivity INteractions on Experimental Sites.

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

Note: All sites were planted in January 2000.

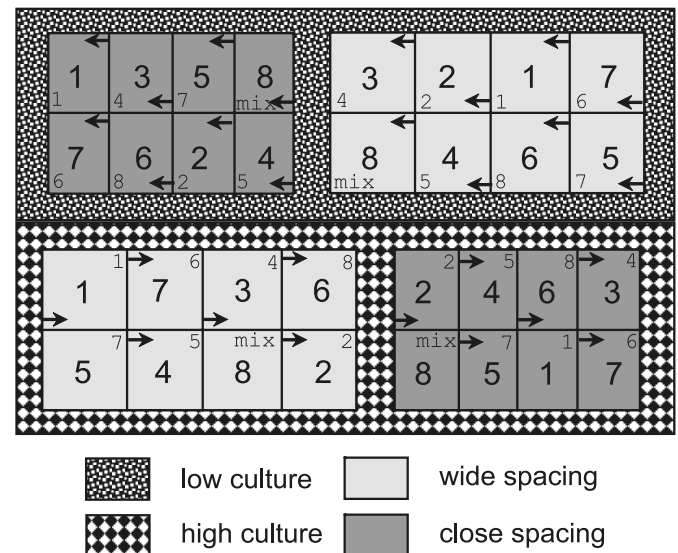
Waverly, Georgia; slash pine installations were located in Perry, Florida, and Waldo, Florida. Each installation was laid out as a randomized complete block design in four blocks with treatments applied in a split-split plot design. Each block was first split into intensive and operational silvicultural treatment zones (the main plot), and then, each zone was split into a high- and low-density planting area (the subplot). Each density area was then split into eight plots (the split-split plots; hereafter referred to simply as “plots”), which were considered the experimental units for the analysis (Fig. 1). Each plot was planted with a single family with one plot designated as a mixture of elite families for the species of interest, which allowed for a family × deployment comparison.

In the loblolly trials, seven plots were pure-planted in each of seven full-sibling families: six elite, fast-growing families and one family with “average” growth. The eighth plot was planted with a mixture of the six elite families, with the family identity of each tree in the mixed plots mapped and recorded. For the slash pine trials, six plots were pure-planted in each of six full-sibling families: five elite families and one family with “average” growth. Similar to the loblolly pine installations, the seventh plot was planted with a mixture of the five elite families. The eighth plot in the slash pine installations was planted with a mixture of the six elite loblolly pine families, which provided a species contrast on the two slash pine installations. Families selected in these trials were chosen based on their aboveground growth performance from long-term genetic progeny tests. Because our interest was only in comparing mixed versus pure plantings of elite pine families, our analyses were restricted only to those plots with elite families for the species of interest, making six families plus their mixture available for analysis within each silvicultural intensity – planting density combination at the loblolly pine locations. Similarly, five families plus their mixture within each treatment combination were analyzed at the slash pine locations. All references to our analyses of “mixed” versus “pure” stands in this paper refer to mixed-family and pure-family stands.

At the whole-plot level, the two contrasting silvicultural treatments were operational versus intensive. At the subplot level, the two planting density treatments were 1334 trees/ha (wide spacing) versus 2990 trees/ha (narrow spacing). Genetic entries were alphanumerically coded using the prefix letter L for loblolly pine and S for slash pine to aid in field identification. Each plot had a treated buffer; given the plot eliminations discussed above, there were 5376 trees available for measurement at each loblolly pine location and 4608 trees available at each slash pine location.

Treatment descriptions

All plots, including both the intensive and operational silvicultural treatments, were bedded at time of planting. In

Fig. 1. Schematic diagram of experimental layout for one block at one location.

addition, all plots received a chemical site preparation treatment consisting of Arsenal (imazapyr, 1.02 L/ha) and Garlon (triclopyr, 7.02 L/ha) to remove woody and herbaceous competition (Roth et al. 2007). The operational silviculture treatment included nutrient management practices commonly used by the forest industry in the southeastern United States and consisted of 280 kg/ha diammonium phosphate applied at the time of planting. The contrasting intensive treatment was driven mainly by early and complete vegetation control, along with annual fertilization. Competing vegetation for this treatment was controlled using directed applications of Arsenal (imazapyr) at 0.28 L/ha (limited to loblolly pine installations) and Oust (sulfometuron methyl) at 0.14 L/ha on all installations. Directed applications of Roundup (glyphosate) in a 2% solution were also used to inhibit development of herbaceous competition. The fertilization regime for the intensive plots included 660 kg/ha of 10:10:10 (N:P:K) fertilizer plus micronutrients applied at time of planting, followed by annual applications of macro- and micro-nutrient fertilizers using prescriptions based on foliar analyses.

The narrow-spacing plots (1.22 m × 2.75 m) were arranged in eight beds of 16 planting positions each for a total of 128 trees in each gross treatment plot; a two-tree border around the perimeter was not analyzed, resulting in a 48-tree interior measurement plot of 0.016 ha. The wide-spacing plots (2.75 m × 2.75 m) were arranged in eight beds of 10 planting positions each for a total of 80 trees in each gross plot; a single-tree buffer around the perimeter was not analyzed, resulting in a 48-tree interior measurement plot of 0.036 ha.

Seedlings were grown in Ray Leach Cone-tainer cells (Stuewe and Sons, Inc., Corvallis, Oregon) consisting of 66 mL/cell. Each site was hand planted with 1-year-old containerized seedlings over a 2 day period in January 2000. Mixed plots were balanced in terms of numbers of individuals by family where possible. However, because of low numbers of seedlings available from some families, the number varied from 2 to 14 individuals in mixed plots. All genetic entries in the study were resistant to fusiform rust (*Cronartium quercum* (Berk.) Miyabe ex Shirai f. sp. *fusiforme*), which likely reduced the confounding effects from disease incidence. Because of the high quality of the containerized planting stock and site-preparation treatments, survival was >95% in all treatments at the end of the first growing season, despite an ongoing drought in the southeastern United States.

Inventory

Diameter at breast height (DBH; 1.37 m) was measured at ages 2, 3, and 5–7 years for each surviving tree within the interior measurement plot. Height (HT) was measured on every tree at ages 1, 2, and 3 years and on a random subsample of trees at age 7 years. At age 5 years, height to the base of the live crown and maximum crown diameter parallel and perpendicular to the planting rows was measured on a 20% subset of the trees. These data were used to calculate a growth efficiency index at age 5 years as stem volume divided by crown volume (calculated as a cone). Crown width and growth efficiency variables were analyzed with stem volume as a covariate to account for differences in tree size. Mortality, condition, and damage were assessed on each tree during each inventory. Each tree was scored for the presence or absence of damage in four categories: fusiform rust infection, pitch canker (*Fusarium circinatum* Nirenberg & O’Donnell) infection, tropical storm wind damage, and stem forking (Roth et al. 2007).

Statistical analyses

Response variables of interest included annual tree DBH (cm) and HT (m), as well as measures of stand occupation, such as basal area per hectare (BAHA; m²/ha), volume per hectare (VOLHA; m³/ha), growth efficiency, crown width, trees per hectare (TPH), mortality (%), and disease and damage (%). Individual tree volumes (outside bark, 15 cm stump) were calculated using the following equations for site-prepared slash and loblolly pine growing in the lower Coastal Plain, respectively (Bailey et al. 1982; Clutter et al. 1984):

$$[1] \quad \text{VOL}_{\text{tree}} = 6.222 \times 10^{-5} \text{DBH}^{2.0578} \text{HT}^{0.7468}$$

$$[2] \quad \text{VOL}_{\text{tree}} = 5.7757 \times 10^{-5} \text{DBH}^{1.8945} \text{HT}^{0.9288}$$

where VOL_{tree} is the volume in cubic metres of an individual tree.

Only year 7 volumes were considered in this analysis. Basal area and volume were first calculated on a tree-level basis and then averaged at the family level by plot. To facilitate comparisons between families grown in mixed versus pure plots, family-level estimates of basal area, volume, and number of surviving trees were scaled to a per-hectare basis to obtain estimates of BAHA, VOLHA, and TPH. Annual

mortality was calculated on a per-plot basis by family, as were disease and damage, which were assessed as the proportion of trees in the plot affected by fusiform rust, pitch canker, wind, and stem forking since planting. For the plot-level variables of TPH, annual mortality, and presence of disease or damage, observations were weighted by the initial number of stems in each family in each plot. Thus, family-level observations from mixed-family plots were given, on average, one-sixth as much weight as those of pure-family plots.

The change in response variable was modeled as a function of deployment and its interactions with spacing, silviculture, family, and location; however, interactions were limited to second- and third-order effects to promote model parsimony and so that biological interpretation was possible. To test for differences in stand-level attributes among treatments, separate analyses were performed for loblolly and slash pine locations using linear mixed models. For the tree-level attributes height, DBH, BAHA, and VOLHA, the basic model (shown excluding interactions for easier presentation) was

$$[3] \quad X_{ijklmfrt} = \mu + L_i + C_k + S_l + D_m + F_f + T_t + bL_{j(i)} + bLC_{jk(i)} + bLCS_{jkl(i)} + bLCSD_{jklm(i)} + bLCSD_{jklm(i)} + \varepsilon_{(ijklmfr)t} + \tau_{(ijklmfr)t}$$

where $X_{ijklmfrt}$ is the DBH, BAHA, height, or VOLHA of the r th tree at the t th time in the i th location, j th block, k th silvicultural intensity, l th spacing, m th deployment (mixed versus pure), and f th family ($i = 1, 2; j = 1, 2, 3, 4; k = 1, 2; l = 1, 2; m = 1, 2; f = 1, 2, \dots, 6$ for slash and 7 for loblolly pine; $r = 1, 2, \dots, n_{ijklmf}; t = 2, 3, 5, 6, 7$ for DBH and BAHA, and $t = 1, 2, 3, 7$ for height); n_{ijklmf} is the number of trees in the i th site, j th block, k th silvicultural intensity, l th spacing, m th deployment, f th family; μ is the overall mean; L_i is the fixed effect of the i th location; C_k is the fixed effect of the k th silvicultural intensity; S_l is the fixed effect of the l th spacing (planting density); D_m is the fixed effect of the m th deployment; F_f is the fixed effect of the f th family; T_t is the fixed effect of the t th time; $bL_{j(i)}$ is the random effect of the j th block nested within the i th site; $bLC_{jk(i)}$ is the random effect of the k th silvicultural intensity, and j th block nested within the i th site; $bLCS_{jkl(i)}$ is the random effect of the k th silvicultural intensity, l th spacing, and j th block nested within the i th site; $bLCSD_{jklm(i)}$ is the random effect of the k th silvicultural intensity, l th spacing, m th deployment, and j th block nested within the i th site; $bLCSD_{jklm(i)}$ is the random effect of the k th silvicultural intensity, l th spacing, m th deployment, f th family, and j th block nested within the i th site; $\varepsilon_{(ijklmfr)t}$ is the random error of the r th tree in the i th site, j th block, k th silvicultural intensity, l th spacing, m th deployment, f th family; and $\tau_{(ijklmfr)t}$ is the random error of the t th time for the r th tree in the i th site, j th block, k th silvicultural intensity, l th spacing, m th deployment, f th family.

The last seven terms in the model represent random effects that are used to hierarchically test the fixed effects in the model. For instance, the random effect of block and silvicultural intensity nested within site, $bLC_{jk(i)}$, is used as an error term to test the effect of silvicultural intensity. The last two terms in the model, $\varepsilon_{(ijklmfr)t}$ and $\tau_{(ijklmfr)t}$, are error terms that account for the spatial and temporal repeated measures

nature of the data, respectively. Because the tree-level attribute VOLHA was tested using year 7 data only, the basic model was modified from eq. 3; the time effect and final error term (T_t and $\tau_{(ijklmfr)t}$) were dropped from the model.

Interactions in the model are also hierarchical and are based on this error structure. Thus, all combinations of interactions of location, silviculture, spacing, deployment, and family are valid and are tested with the highest-level hierarchical error. For instance, the interaction of deployment, family, and silviculture would be tested versus $bLCSDF_{jklmf(i)}$. Because our research questions focused on questions relating to mixed- versus pure-family performance, only significant ($P < 0.10$) effects that involved the deployment effect, D_m , were investigated and reported in this paper.

For the stand-level attributes TPH and annual mortality, the basic linear model (shown excluding interactions) is

$$[4] \quad Y_{ijklmft} = \mu + L_i + C_k + S_l + D_m + F_f \\ + T_t + bL_{j(i)} + bLC_{jk(i)} + bLCS_{jkl(i)} \\ + bLCS_{D_{jklm(i)}} + bLCSDF_{jklmf(i)} + \tau'_{(ijklmf)t}$$

where $Y_{ijklmft}$ is the stand level variable (TPH or annual mortality rate) at the t th time of the trees in the i th location, j th block, k th silvicultural intensity, l th spacing, m th deployment (mixed versus pure), and f th family; $\tau'_{(ijklmf)t}$ is the random error of the t th time for the i th site, j th block, k th silvicultural intensity, l th spacing, m th deployment, f th family; and all other variables as previously defined.

For disease and damage occurrence, trees were evaluated with one response (presence or absence) over the entire 7 year time period, and with a covariate to account for tree size. Therefore, the model (shown excluding interactions) was

$$[5] \quad Z_{ijklmf} = \mu + L_i + C_k + S_l + D_m + F_f \\ + H_{ijklmf} + bL_{j(i)} + bLC_{jk(i)} + bLCS_{jkl(i)} \\ + bLCS_{D_{jklm(i)}} + \varepsilon'_{(iklmf)j}$$

where Z_{ijklmf} is the stand level variable proportion of disease or damage (pitch canker, rust, weather, or forking) of the trees in the i th location, j th block, k th silvicultural intensity, l th spacing, m th deployment (mixed versus pure), and f th family; H_{ijklmf} is the stand level year 1 or year 2 mean tree HT in the i th location, j th block, k th silvicultural intensity, l th spacing, m th deployment (mixed versus pure), and f th family; $\varepsilon'_{(iklmf)j}$ is the random error of the j th block in the i th site, k th silvicultural intensity, l th spacing, m th deployment, f th family; and all other variables are as previously defined.

To support crop and competition ideotype identification, post hoc analyses of growth efficiency and crown width were also conducted using a model similar to eq. 5. Year 5 growth efficiency and crown width were modeled using year 5 stem volume instead of height as a covariate.

As in the model in eq. 3, errors in eqs. 4 and 5 are hierarchical, and interactions are tested within this hierarchical error structure. Because the response variables in eq. 4 are computed at the plot level, there is no error term associated with individual tree measurements. Because the response variables in eq. 5 are considered over the entire 7 year period, there was no time effect and no error term associated with measurements repeated over time.

Analyses were conducted in a mixed-models framework using the SAS procedures MIXED and GLIMMIX (Littell et al. 2006). First, data from the response variable were tested for normality using the Kolmogorov–Smirnov test in the SAS UNIVARIATE procedure. Where data were not significantly different from normal ($P > 0.05$), they were analyzed with the MIXED procedure. Where data departed significantly from normality, a log transformation resulted in approximately normal data. For these cases, analyses with the GLIMMIX procedure were conducted assuming a log-normal response. In either case, error covariance structures were explicitly defined to account for correlation among trees in each plot (spatial correlation), and a repeated-measures structure for annual measurements by tree was included where appropriate (temporal correlation). Several models of error covariance structures were investigated to account for temporal correlation, including first-order autoregressive and compound symmetric structures. For all models, a compound symmetric error covariance structure was deemed most appropriate.

To test the assumptions of proper model specification and homogeneous variation necessary for analysis of variance, probability plots of the residuals were constructed, as well as plots of residuals versus predicted values. Where models revealed significant effects ($P < 0.05$), least squares means were generated between levels of the factors of interest. Back-transformation was performed to present means in their original units where necessary. The overall significance level was kept at $\alpha = 0.05$ by using Bonferroni's multiple comparison test.

Results

DBH and BAHA

Both DBH and BAHA were significantly affected by deployment in the slash and loblolly pine trials of this experiment, with significant deployment \times family \times time interactions detected in years 5, 6, and 7 (Table 2). At age 7 years, variation in DBH among families within a species was similar for slash and loblolly, ranging from approximately 12.6 to 14.4 cm (Figs. 2a and 2b). Slash pine families S2 and S6 had significantly larger mean diameters in the mixed-family plots compared with the pure-family plots (approximately 0.6 and 0.35 cm, respectively), whereas family S4 had smaller mean diameters (approximately -0.4 cm) in the mixed-family plots. In loblolly pine, families L4 and L7 had larger diameters in the mixed-family and pure-family plots, respectively (approximately 0.8 and -0.6 cm; Fig. 2b); similar trends were found in years 5 and 6.

BAHA at age 7 ranged from 22 to 28 m²/ha in slash and from 24 to 31 m²/ha in loblolly (Figs. 2a and 2b). Slash pine family S2 had significantly higher BAHA in the mixed-family plots (3 m²/ha) compared with the pure-family plots, and family S1 accrued 10% lower BAHA (3 m²/ha) in the mixed- versus pure-family plots (Fig. 2a). Similarly, loblolly pine family L4 had 3 m²/ha more BAHA in mixed plots, whereas no other family showed a significant basal area difference by deployment effect.

In loblolly pine, both DBH and BAHA had additional significant location \times deployment \times family, and spacing \times de-

Table 2. Summary of *F* values, statistical significance, and associated degrees of freedom from mixed model testing for slash and loblolly pine DBH and BAHA (all years), and VOLHA (year 7 only).

Effect	df		DBH		BAHA		Volume	
	Numerator	Denominator	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Slash pine								
D	1	25	0.05	0.817	3.16	0.088	0.43	0.516
L × D	1	25	0.08	0.786	3.55	0.071	14.32	0.001*
C × D	1	25	0.11	0.747	0.51	0.481	0.51	0.484
L × C × D	1	25	0.34	0.564	1.52	0.230	1.29	0.267
S × D	1	25	0.07	0.789	0.02	0.903	1.21	0.282
L × S × D	1	25	0.03	0.875	0.01	0.931	0.13	0.724
C × S × D	1	25	0.18	0.672	0.77	0.390	0.48	0.494
D × F	4	209	6.56	<0.0001	18.43	<0.0001	10.62	<0.0001*
L × D × F	4	209	2.00	0.095*	1.10	0.360	1.03	0.390
C × D × F	4	209	2.14	0.078*	3.22	0.014*	1.62	0.169
S × D × F	4	209	0.97	0.422	1.11	0.354	1.25	0.292
D × T	4	1144	0.18	0.947	2.05	0.0854		
L × D × T	4	1144	0.05	0.996	2.10	0.0793*		
C × D × T	4	1144	0.14	0.968	0.47	0.7543		
S × D × T	4	1144	0.01	1.000	0.28	0.8935		
D × F × T	16	1144	2.61	0.001*	8.30	<0.0001*		
Loblolly pine								
D	1	25	1.98	0.171	0.36	0.551	0.01	0.918
L × D	1	25	0.95	0.339	0.04	0.837	0.02	0.894
C × D	1	25	0.27	0.610	2.21	0.150	1.57	0.222
L × C × D	1	25	0.02	0.878	0.38	0.544	0.05	0.824
S × D	1	25	0.25	0.620	0.02	0.880	0.00	0.974
L × S × D	1	25	0.82	0.373	0.03	0.867	0.73	0.401
C × S × D	1	25	0.33	0.569	0.13	0.724	0.00	0.964
D × F	5	265	7.19	<0.0001	6.39	<0.0001	4.04	0.002
L × D × F	5	265	8.70	<0.0001*	9.16	<0.0001*	4.60	0.001*
C × D × F	5	265	1.53	0.180	2.03	0.075*	1.09	0.365
S × D × F	5	265	3.39	0.006*	5.44	<0.0001*	2.82	0.017*
D × T	4	1297	0.38	0.826	0.08	0.990		
L × D × T	3	1297	1.13	0.337	0.22	0.885		
C × D × T	4	1297	0.28	0.891	1.41	0.229		
S × D × T	4	1297	0.54	0.709	0.12	0.975		
D × F × T	20	1297	3.72	<0.0001*	3.74	<0.0001*		

Note: Values with asterisks are significant ($P < 0.10$) effects associated with deployment (D) at their highest order interaction. Effects are as follows: L, site; C, silvicultural intensity; S, planting spacing; D, deployment; F, family; T, time.

ployment × family interactions; however, these interactions were significant in magnitude only, i.e., all effects were consistent with those of Fig. 2b in terms of direction. Significant differences were only detected for family L4, which over all years had significantly larger DBH and more BAHA when planted in mixed-family plots under narrow spacing (Fig. 2c), and when planted in Waverly, Georgia (Fig. 2d). In comparison, there was weak evidence of a location × deployment × family interaction in slash pine (Table 2; $P = 0.095$).

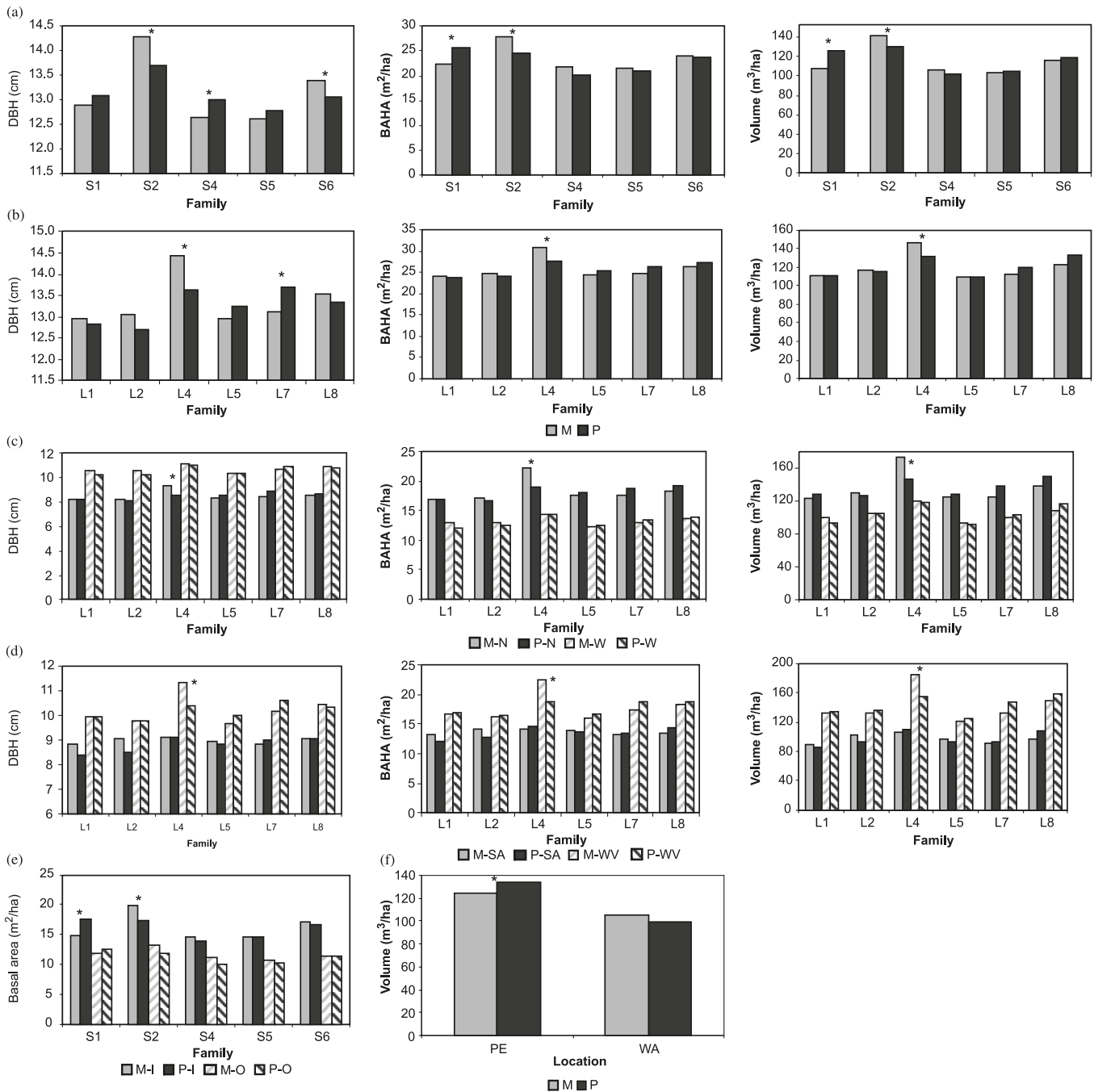
Similarly, BAHA in slash pine had additional significant silvicultural intensity × deployment × family interaction and a weak location × deployment × time interaction (Table 2); these interactions were consistent in direction with the responses of DBH (Fig. 2a). The silvicultural intensity × deployment × family interaction was driven by family S2, which had significantly more BAHA in mixed versus pure plots under intensive culture, and by family S1, which had

significantly less BAHA in mixed versus pure plots under intensive culture (Fig. 2e). In both cases, the magnitude of difference by deployment was approximately 2.5 m²/ha. In comparison, there was weak evidence of a silvicultural intensity × deployment × family interaction in loblolly pine ($P = 0.075$; Table 2).

Volume

The range in VOLHA among families within a species was similar for slash and loblolly pine at year 7, ranging from approximately 105 to 144 m³/ha (Figs. 2a and 2b). Within a species, the patterns of variation in VOLHA were similar to BAHA, with a significant deployment × family interaction observed for slash pine (Table 2). VOLHA was significantly higher for family S2 in the mixed-family plots (approximately 12 m³/ha) and significantly lower for family S1 in the mixed-family plots (approximately -18 m³/ha; Fig. 2a).

Fig. 2. DBH, BAHA, and VOLHA least square means for significant interactions with deployment (a) by family in year 7 for slash pine, (b) by family in year 7 for loblolly pine, (c) by family and spacing for loblolly pine, (d) by family and location for loblolly pine, (e) by family and silvicultural intensity for slash pine, and (f) by location for slash pine. Bars with asterisks are significantly different at the 0.05 level. M, mixed; P, pure; N, narrow, W, wide; SA, Sanderson Florida; WV, Waverly Georgia; PE, Perry Florida; WA, Waldo Florida; O, operational; I, intensive.



Additionally, there was a location × deployment interaction, whereby mixed plots had marginally less VOLHA than pure plots in Perry, Florida (Fig. 2f).

For loblolly pine in year 7 the statistical effects on VOLHA were identical to BAHA and DBH, with significant spacing × deployment × family, and location × deployment × family interactions (Table 2). The results (Figs. 2b, 2c, and 2d) were consistent with those of BAHA,

with family L4 having more VOLHA in mixed deployment under narrow spacing and at the Waverly, Georgia, location.

Height

For slash pine HT, there was a significant location × deployment × time interaction (Table 3). Mean slash pine HT was consistently higher for trees planted in mixed deployment in all years and sites, except in year 7 at Perry, Florida

Table 3. Summary of *F* values, statistical significance, and associated degrees of freedom from mixed model testing for slash and loblolly pine height.

Effect	df		Height	
	Numerator	Denominator	<i>F</i>	<i>P</i>
Slash pine				
D	1	25	0.34	0.565
L × D	1	25	1.09	0.306
C × D	1	25	0.06	0.806
L × C × D	1	25	0.61	0.443
S × D	1	25	0.28	0.603
L × S × D	1	25	0.01	0.944
C × S × D	1	25	1.66	0.209
D × F	4	209	0.13	0.971
L × D × F	4	209	0.27	0.899
C × D × F	4	209	0.46	0.764
S × D × F	4	209	0.90	0.466
D × T	3	858	0.20	0.897
L × D × T	3	858	3.13	0.025*
C × D × T	3	858	0.01	0.998
S × D × T	3	858	0.75	0.522
D × F × T	12	858	0.18	0.999
Loblolly pine				
D	1	25	0.27	0.606
L × D	1	25	0.01	0.923
C × D	1	25	0.16	0.693
L × C × D	1	25	0.12	0.733
S × D	1	25	0.02	0.903
L × S × D	1	25	0.31	0.581
C × S × D	1	25	0.12	0.731
D × F	5	265	2.58	0.027
L × D × F	5	265	1.40	0.226
C × D × F	5	265	0.94	0.459
S × D × F	5	265	2.53	0.029*
D × T	3	949	0.08	0.969
L × D × T	2	949	0.16	0.851
C × D × T	3	949	0.53	0.663
S × D × T	3	949	0.11	0.956
D × F × T	15	949	1.43	0.127

Note: Values with asterisks are significant (*P* < 0.10) effects associated with deployment (D) at their highest order interaction. See Table 2 for effect abbreviations.

(Fig. 3a). In loblolly pine, there was a significant spacing × deployment × family interaction (Table 3). For the wide spacing, trees planted in pure deployments were significantly taller for family L4 and significantly shorter for family L5 (Fig. 3b). However, these differences may be of little practical significance, as they accounted for a mean HT difference of <10 cm.

TPH and annual mortality

Survival in these trials was >90%, with annual mortality generally <2.5% (Fig. 3a). In slash pine, there was no significant effect of deployment on TPH, with the exception of the deployment × time interaction (*P* = 0.083) for annual mortality (Table 4). For loblolly pine annual mortality, significant location × deployment × time and spacing × deployment × time interactions were observed (Table 4). A small absolute

increase in mortality was evident in the loblolly pine data, and it occurred 1 year earlier in the mixed- versus pure-family plots (Fig. 4). This increase was also more evident in the widely spaced plots and in Sanderson Florida, where mortality increased from about 1% to almost 5% (Fig. 4a). Further, there were significant deployment × time and spacing × deployment × family interactions for loblolly pine TPH (Table 4). This three-way interaction was driven by two families: in the narrow spacing, family L7 had modestly higher TPH in the mixed-family plots, whereas family L8 had higher TPH in the pure-family plots (Fig. 4b).

Disease and damage

Statistical models for disease and damage did not include a time effect, because these impacts were evaluated with one response (presence or absence) over the life of the experiment. Height was a significant predictor of fusiform rust and forking incidence in both species: taller trees sustained less rust damage but had more forking. With the inclusion of mean tree height for the plot in the model, no disease or damage incidence was significantly related to deployment at the *P* = 0.05 level in slash pine. However, the deployment × family interaction for fusiform rust incidence and the spacing × deployment × family interaction for pitch canker in slash pine were marginally significant (*P* = 0.054 for fusiform rust, *P* = 0.069 for pitch canker; Table 5). There were also several significant interactions for fusiform rust and pitch canker in loblolly pine (Table 6, Figs. 5a and 5b). Nevertheless, the absolute differences among families, deployment, and spacing for these disease traits were small, which reflects the genetic improvement for both species. For example, the significant location × silvicultural intensity × deployment interaction for pitch canker in loblolly pine was driven by an increase in incidence from 0.5% to 2.3% in Sanderson, Florida (Fig. 5b).

In 2004, tropical storm winds impacted portions of the southeastern United States, including these experiments. Although damage to these studies was not extensive, there was a significant location × spacing × deployment interaction for wind damage with loblolly pine (Table 6). In all locations and spacings, mixed-family plots sustained significantly more wind damage than pure-family plots (Fig. 5c). As was the case with disease incidence, absolute differences in wind damage varied by <1%. The significant deployment × family interaction for forking in loblolly pine was caused by family L5, which had higher forking in the mixed-family plantings (17% vs. 12%), compared with family L8, where forking was higher in the pure-family plantings (28% vs. 19%; Fig. 5d).

Discussion

Previous work with the PPINES experiments has demonstrated significant interactions of elite loblolly and slash pine families deployed in pure plots with silvicultural and site factors (Roth et al. 2007). In the current study, we were interested primarily in the performance of elite families in mixture and in pure plots and how these competitive relationships interacted with silvicultural and site factors. The type and number of interactions evident in these studies reflects the nature of the elite genetic materials selected, the

Fig. 3. Height by deployment versus (a) location by time for slash pine and (b) family and spacing for loblolly pine. Bars with asterisks are significantly different at 0.05 level. See Fig. 2 for abbreviations.

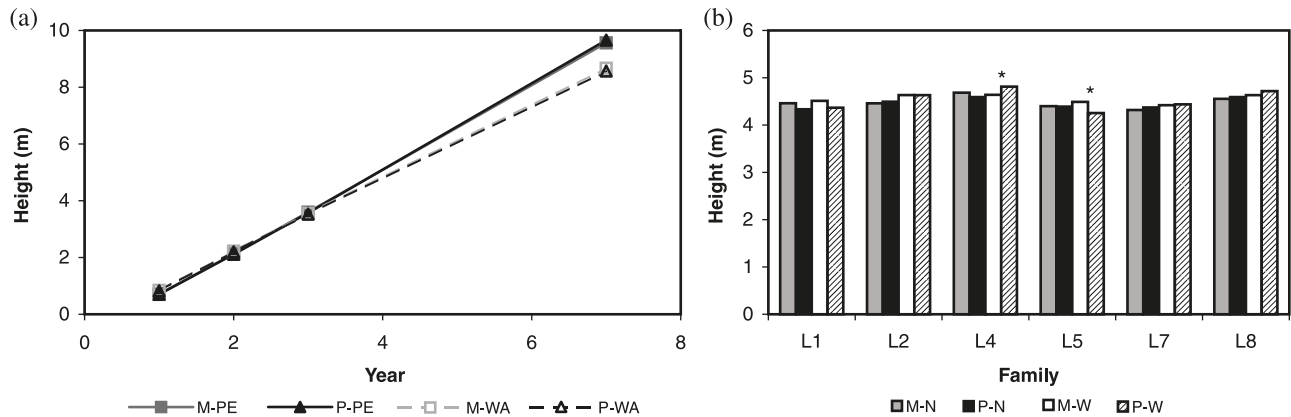


Table 4. Summary of *F* values, statistical significance, and associated degrees of freedom from mixed model testing for slash and loblolly pine annual mortality and trees per hectare (TPH).

Effect	df		Annual mortality		TPH	
	Numerator	Denominator	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Slash pine						
D	1	25	2.38	0.136	2.07	0.163
L × D	1	25	1.46	0.239	1.42	0.245
C × D	1	25	0.37	0.551	0.41	0.527
L × C × D	1	25	0.06	0.804	1.25	0.275
S × D	1	25	0.51	0.483	0.01	0.935
L × S × D	1	25	0.00	0.958	0.01	0.939
C × S × D	1	25	0.44	0.512	0.07	0.801
D × F	4	209	0.05	0.995	0.06	0.994
L × D × F	4	209	0.09	0.984	0.17	0.953
C × D × F	4	209	0.05	0.994	0.61	0.658
S × D × F	4	209	0.20	0.936	0.34	0.854
D × T	5	1430	1.95	0.083*	0.73	0.623
L × D × T	5	1430	1.37	0.233	0.87	0.514
C × D × T	5	1430	0.97	0.436	0.17	0.986
S × D × T	5	1430	0.46	0.806	0.46	0.839
D × F × T	20	1430	0.40	0.992	0.41	0.995
Loblolly pine						
D	1	25	1.37	0.254	1.22	0.280
L × D	1	25	1.05	0.315	0.00	0.984
C × D	1	25	2.26	0.146	4.08	0.054
L × C × D	1	25	1.42	0.244	0.97	0.334
S × D	1	25	0.02	0.896	0.35	0.562
L × S × D	1	25	0.66	0.425	0.76	0.392
C × S × D	1	25	0.02	0.877	2.38	0.136
D × F	5	265	0.88	0.496	1.63	0.153
L × D × F	5	265	1.84	0.106	1.19	0.314
C × D × F	5	265	0.65	0.659	0.93	0.461
S × D × F	5	265	1.03	0.399	2.60	0.026*
D × T	5	1800	13.16	<0.0001	3.35	0.003*
L × D × T	5	1800	6.65	<0.0001*	1.66	0.127
C × D × T	5	1800	0.76	0.578	0.36	0.903
S × D × T	5	1800	2.92	0.012*	0.49	0.817
D × F × T	25	1800	0.67	0.892	1.22	0.191

Note: Values with asterisks are significant (*P* < 0.10) effects associated with deployment (D) at their highest order interaction. See Table 2 for effect abbreviations.

Fig. 4. Loblolly pine least squares means for significant interactions with deployment: (a) annual mortality per hectare by year and spacing and by year and location and (b) live trees per hectare by family and spacing and by year. Bars with asterisks are significantly different at the 0.05 level. See Fig. 2 for abbreviations.

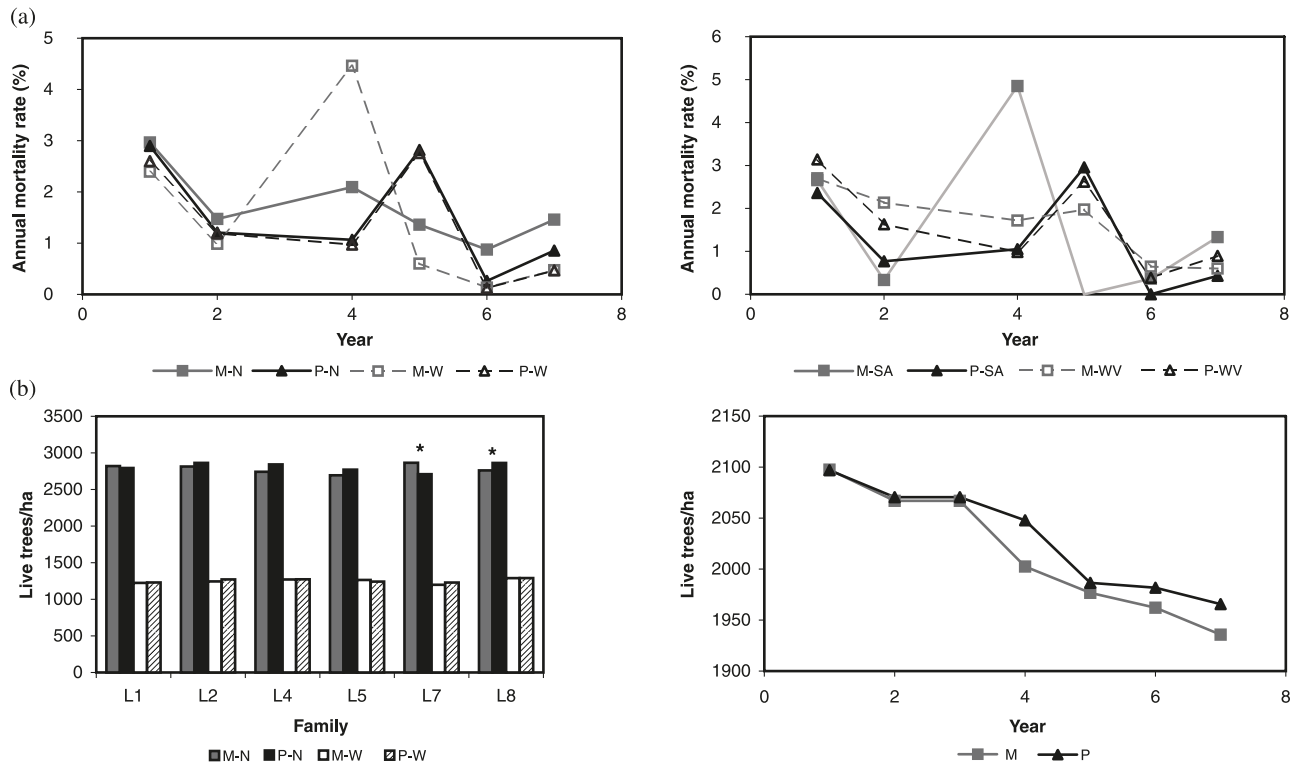


Table 5. Summary of *F* values, statistical significance, and associated degrees of freedom from mixed model testing for slash pine disease and damage.

Effect	df		Fusiform rust		Pitch canker		Weather damage		Forking	
	Numerator	Denominator	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Height	1	208	5.53	0.020*	0.09	0.767	0.90	0.343	13.26	<0.001*
D	1	25	2.87	0.102	1.09	0.307	0.15	0.704	0.31	0.585
L × D	1	25	0.17	0.684	0.00	0.968	0.52	0.476	0.60	0.447
C × D	1	25	0.88	0.357	2.24	0.147	0.10	0.753	2.11	0.158
L × C × D	1	25	0.01	0.918	1.36	0.254	0.96	0.336	0.24	0.630
S × D	1	25	0.17	0.684	0.30	0.587	0.53	0.473	0.00	0.966
L × S × D	1	25	0.13	0.720	0.07	0.791	0.87	0.359	0.34	0.564
C × S × D	1	25	1.96	0.174	0.37	0.549	0.77	0.388	0.00	0.975
D × F	4	208	2.36	0.054*	0.25	0.909	1.42	0.227	0.06	0.993
L × D × F	4	208	1.07	0.372	0.52	0.722	1.01	0.402	0.15	0.961
C × D × F	4	208	1.08	0.366	0.19	0.946	0.52	0.725	0.66	0.621
S × D × F	4	208	1.42	0.229	2.21	0.069*	0.51	0.728	0.93	0.448

Note: Values with asterisks are significant (*P* < 0.10) effects associated with deployment (D) at their highest order interaction. See Table 2 for effect abbreviations.

range in silvicultural treatments applied (planting density, fertility), and the high statistical power and precision associated with the experimental design.

In field experiments comparing mixed-genotype plots with pure plots, trees in mixed plots tend to more rapidly differentiate and develop dominance because of increasingly asymmetric competition among genotypes with contrasting growth potential. For example, DeBell and Harrington (1997) reported that in plantings containing four *Populus* clones, the two fastest growing clones (as measured by growth in pure plots) tended to grow even faster in mixed

plots, suppressing growth of the two slower growing clones. We observed similar responses in mixed-family plots in the current study. DBH differentiation between the mixed- and pure-family deployments did not occur until year 6, except in families S2, S4, and L4, which also showed significant differences in year 5. These differences were fairly consistent by year but not consistent by family: certain families performed better in mixtures than in pure plots and vice versa. The largest and smallest families were the same in the mixed and pure plots (i.e., there was no rank change at the extremes). However, mixed plots had a wider range of

Table 6. Summary of *F* values, statistical significance, and associated degrees of freedom from mixed model testing for loblolly pine disease and damage.

Effect	df		Fusiform rust		Pitch canker		Weather damage		Forking	
	Numerator	Denominator	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Height	1	274	17.72	<0.0001*	0.00	0.998	0.16	0.689	12.42	0.001*
D	1	25	1.27	0.271	1.15	0.294	8.74	0.007	0.09	0.767
L × D	1	25	1.52	0.228	3.39	0.077	0.19	0.667	0.17	0.685
C × D	1	25	4.58	0.042	0.60	0.446	0.13	0.725	1.64	0.213
L × C × D	1	25	0.69	0.415	0.86	0.363	1.50	0.232	1.49	0.234
S × D	1	25	1.55	0.225	2.36	0.137	1.79	0.192	1.05	0.314
L × S × D	1	25	2.11	0.159	4.69	0.040*	5.77	0.024*	0.30	0.590
C × S × D	1	25	3.02	0.095*	0.57	0.459	2.13	0.157	0.25	0.623
D × F	5	274	0.33	0.895	1.42	0.216	1.78	0.117	3.16	0.009*
L × D × F	5	274	1.64	0.151	2.48	0.032*	0.28	0.924	1.42	0.217
C × D × F	5	274	0.45	0.813	0.81	0.542	1.11	0.357	0.99	0.425
S × D × F	5	274	0.71	0.616	1.10	0.362	0.63	0.678	1.77	0.120

Note: Values with asterisks are significant ($P < 0.10$) effects associated with deployment (D) at their highest order interaction. See Table 2 for effect abbreviations.

DBH than pure plots by year 6: more rapidly growing families grew larger at the expense of the smallest ones when growing in an intimate mixture. In some cases, this response was only apparent under the most extreme competitive environments. For example, loblolly pine family L4 had higher DBH in mixed plots under the narrow spacing treatment.

Overyielding has been observed numerous times in species mixing trials (Kelty 2006; Amoroso and Turnblom 2006) and, occasionally, at the intraspecific level when clones are grown in mixture (Foster et al. 1998). In the current study, there was no evidence of overyielding; there was no difference in stand yield between mixed- and pure-family plantings of slash pine at the Waldo location and slightly higher yields in pure plots at the Perry location.

When analyzed by year, slash pine annual mortality rates and the number of live TPH were not significantly different in mixed versus pure plantings over the time period. However, there were significant deployment interactions with site and year and with silvicultural intensity and year for loblolly pine mortality rates. At Sanderson and in the wide spacings, a mortality pulse occurred in the mixed-family plots at year 4, whereas this pulse occurred in year 5 for the mixed plots. This difference was also reflected in the annual estimates of the numbers of live TPH, which showed a decline in mixed plantings earlier than those of pure-family plots. There was also a significant interaction between deployment, spacing, and family; for loblolly pine family L7, the mixed-family plots had significantly more TPH, whereas the opposite was observed for loblolly pine family L8.

Although BAHA was marginally higher in the mixed plots (as was demonstrated previously in eastern cottonwood, *Populus deltoides* Bartr.; Foster et al. 1998), tree survival was higher in pure plots. In part, these differences may be explained by differences in disease susceptibility. Trees in mixed plots were more susceptible to pitch canker, wind damage, and forking. This was somewhat unexpected given the widespread perception that diverse forests are more resistant to insects and pests (Carnus et al. 2006). However, Burdon (2001) and Koricheva et al. (2006) have pointed out that the relationships between forest pathogens and genetic

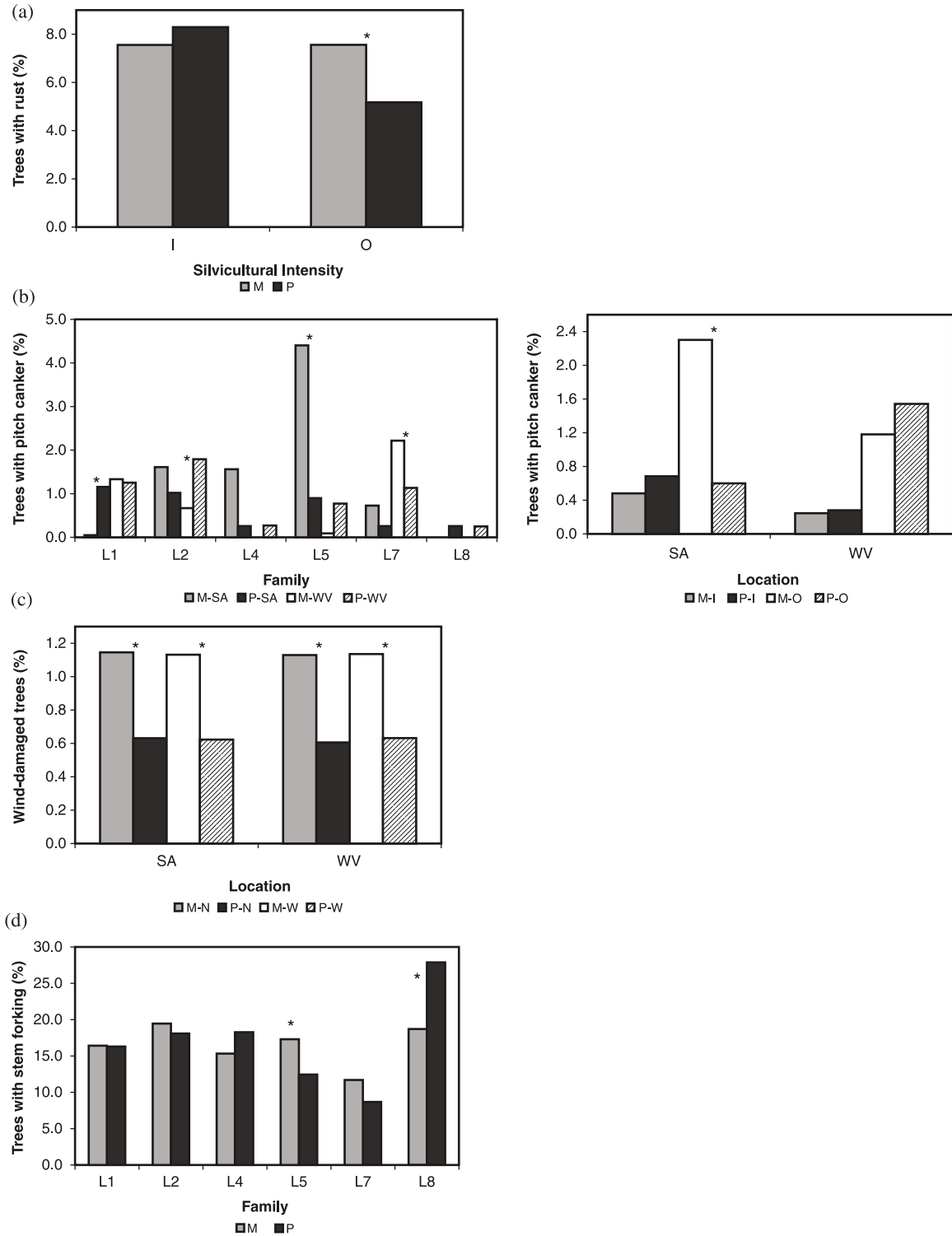
diversity is complex and that published studies have been inconsistent in supporting this hypothesis.

Based on the proposed characteristics of tree crop and competition ideotypes described in the literature (Cannell 1978; Martin et al. 2001), we can make some predictions about the stand dynamics responses that might be observed in field-grown examples of the respective ideotypes. We predict that, when grown in mixture with a wide range of families, competition ideotypes would outcompete most of their neighbors resulting in higher performance for the competition ideotypes in mixed-family plots than when grown with their full sibs in pure-family plots. In contrast, crop ideotypes are predicted to be poor competitors and, thus, would perform better when grown in pure plots than when grown in mixtures with other, more aggressively competitive families.

In our analyses, these dynamics would be apparent as a deployment × family (D × F) interaction for stand-level growth and survival traits, which occurred in both loblolly and slash pine. These D × F interactions were driven primarily by two families in each species: S1 and S2 in slash pine and L4 and L8 in loblolly pine. In slash pine, families S1 and S2 manifest stand dynamics characteristic of crop and competition ideotypes, respectively. When grown in pure plots, the performance of both families was nearly identical, but when grown in mixture, VOLHA and BAHA production of slash pine family S1 declined, whereas production in family S2 increased relative to that in pure plots. Similar dynamics occurred for loblolly families L4 and L8, which exhibited growth and survival dynamics characteristic of competition and crop ideotypes, respectively.

In most cases, family and deployment interacted with a third factor: spacing and time for loblolly pine BAHA, VOLHA and live TPH, and silvicultural intensity and time for slash pine BAHA were additional significant interaction terms with family and deployment. In all cases, these additional interaction terms resulted from the manifestation or enhanced manifestation of the D × F interaction in situations where stand development was more advanced or where competition was more intense. For instance, with loblolly

Fig. 5. Loblolly pine disease and damage incidence least squares means for significant interactions with deployment: (a) percentages with rust by silvicultural intensity, (b) percentages with pitch canker by family and location, and by location and silvicultural intensity, (c) percentages with wind damage by location and spacing, and (d) percentages with stem forking by family. Bars with asterisks are significantly different at the 0.05 level. See Fig. 2 for abbreviations.



pine VOLHA and BAHA, the $D \times F$ interaction was only apparent in the narrow spacing treatment and at the more nutrient-rich Waverly study location. Similarly, for slash pine BAHA, the $D \times F$ interaction was only apparent under the intensive silvicultural intensity treatment.

Stand dynamics result from interactions among individual trees; therefore, we were interested in determining whether tree-level traits could help explain the contrasting dynamics exhibited by the putative crop and competition ideotype families identified from the stand-level data. It has been hypothe-

sized that crop ideotypes would have narrow, compact crowns as opposed to competition ideotypes, which would have wide, spreading crowns (Cannell 1978; Martin et al. 2001). Because crop ideotypes perform well without aggressively occupying growing space, we would also predict that crop ideotypes should have higher efficiency of resource conversion, i.e., higher radiation or nutrient use efficiency (Cannell 1978; Dickmann and Keathley 1996). Based on post hoc analyses of crown structure, we investigated if family-level characteristics were consistent with these predictions. The putative slash pine crop ideotype, family S1, had a 13% greater stemwood growth efficiency (stem volume/crown volume) than family S2 ($P = 0.008$); similarly, loblolly pine family L8 had a 14% greater stemwood growth efficiency than family L4 ($P = 0.003$). Crown widths were also consistent with theory predictions, with the putative crop ideotypes (S1 and L8) having narrower crowns (slash pine, $P = 0.0421$; loblolly pine, $P = 0.0350$) than the putative competition ideotypes (S2 and L4). Taken together, the tree-level crown architecture data and stand-level shifts in production patterns support the identification of families S1 and L8 as crop ideotypes and families S2 and L4 as competition ideotypes. To our knowledge, these are the first examples where crop and competition ideotypes have been identified in loblolly and slash pine. As the stands in the present study develop, it will be informative to examine patterns of density-dependent mortality, allowing us to determine whether crop ideotypes exhibit increased carrying capacity (DeBell et al. 1997).

The prospect of ideotype breeding in trees has been discussed for several decades (Cannell 1978; Martin et al. 2005), but implementation has only been attempted in a few agronomic crops and in Scandinavian conifers (Kärki and Tigerstedt 1985). Although the current study demonstrates the probable existence of crop and competition ideotypes in southern pines, further research is needed to determine the characteristics of putative crop ideotypes under various silvicultural scenarios. Potential advantages of deploying crop ideotypes include the ability to plant at closer spacing while maintaining or enhancing stand-level productivity and more efficient production of biomass per unit resource input. Stem architectural characteristics like crown volume and crown width are moderately heritable in southern pines (Lambeth and Huber 1997; Emhart et al. 2007), so breeding for crown traits guided by ideotype models is possible.

The development of clonal forestry may provide additional opportunities to further explore the potential of crop ideotypes, because individual genotypes can be selected for promising crown architectural and competition traits and can be deployed in pure plots with no genetic variation. Given the importance of branch and crown characteristics for determining stem and wood product quality (Amateis et al. 2004; Briggs et al. 2007), it will be logical to incorporate wood quality considerations into any crop ideotype screening or breeding program.

Conclusions

In conclusion, we examined the performance of elite loblolly and slash pine families growing in pure-family plots and in family mixtures under contrasting silvicultural and spacing treatments. Intertree competition occurred fairly

early in intimate mixtures, resulting in rapid stratification in the mixed-family plots. From a progeny test perspective, this may bias the prediction of rapidly growing families upward compared with pure plots as early as 5 years at densities between 1334 and 2990 trees/ha, further illustrating the need to test genetic material in block plots. In addition, predictions from mixed plots may be confounded by mortality due to diseases, such as fusiform rust, that interact with deployment method, although the absolute magnitude of most disease and mortality interactions at this stage was quite small.

The reactions of families to competition in mixed plots varied from positive to negative. Significant and consistent interactions of several families with mixed versus pure deployment led to the identification of putative crop and competition ideotypes in both loblolly and slash pine. Tree-level crown architectural traits and an index of growth efficiency for the identified families were consistent with the hypothesized ideotypes. As the stands develop, further investigation of the carrying capacity of these families should be informative.

Acknowledgments

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