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Effects of Site and Intensive Culture on Family Differences in Early Growth and Rust Incidence of Loblolly and Slash Pine

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Summary

Eleven field tests with two silvicultural treatments (intensive and less intensive) with open-pollinated families of improved *P. taeda,* and improved and unimproved *P. elliottii* were established by the Cooperative Forest Genetics Research Program in the Lower Coastal Plain of the southeastern USA. Results for third-year fusiform rust infection indicated highly consistent family rankings across sites ($r_{B\text{-site}}$=0.90) and across management intensities ($r_{B\text{-treat}}$=0.97). Single-site heritabilities for rust in the binary scale ($h^2_{B\ 0,1}$) and in the underlying scale ($h^2_{B\ und}$=0.29) were not affected by site nor by the increase in management intensity.

For third-year height growth, family rankings were less influenced by environmental differences among treatments ($r_{B\text{-treat}}$=0.87) than by differences among sites ($r_{B\text{-site}}$=0.57). These early results imply that stable rankings for height may be expected as cultural intensity increases. However, a few families were more responsive to culture than others. Differences in susceptibility to fusiform rust and seedling quality caused some instability in height rankings across sites. The intensive culture had a smaller site by family interaction (higher $r_{B\text{-site}}$ value) than less intensive culture, meaning family ranking for height were more stable across sites for intensive culture.

In the intensive treatment, additive variance was reduced by 6% and environmental error decreased by 25%. This resulted in higher heritability for the intensive treatment as compared to non-intensive treatment (h^2_B = 0.3 *vs.* 0.2, averaged over all three taxa and all sites). The higher heritability for height growth in the intensive management treatment implies that genetic gains from progeny testing are higher in intensive culture. Further, the higher heritability in the intensive culture along with little GxE between treatments ($r_{B\text{-treat}}$=0.87) implies that progeny testing with intensive culture could have advantages for operational deployment in either culture.

Key words: Pinus elliottii, Pinus taeda, cultural intensity, heritability, GxE, type B genetic correlation, early growth, rust resistance, genetic gain.

1. Introduction

Loblolly pine (*P. taeda* L.) and slash pine (*Pinus elliottii* ENGELMAN var. *elliottii*) are the two most important commercial timber species in the southeastern United States (BORDERS and HARRISON, 1989). Several studies have examined the response of loblolly and slash pine to cultural practices at levels considered „operational" by forest industries, but few have included intensive silviculture (e.g., HAINES and GOODING, 1983; BLAKESLEE *et al.,* 1987; COLBERT *et al.,* 1990). Such comparisons are important, because of the increasing interest in intensive culture to produce larger volumes of wood per unit area (HAGLER, 1996).

Moreover, genetic improvement has occasionally been incorporated into studies with both fertilization and weed control to compare genotypes of both species (BORDERS and HARRISON, 1989; SWINDEL *et al.,* 1988; NEARY *et al.,* 1990). Fertilization and competition affect growth and can increase susceptibility to physical damage and pest incidences on trees in both loblolly and slash pine, e.g., fusiform rust, caused by *Cronartium quercuum* (BERK.) MIYABE ex SHIRAI f. sp. *fusiforme* (BLAKESLEE *et al.,* 1987; SWINDEL *et al.,* 1988; SHOULDERS *et al.,* 1990). Genotypes may respond differentially to these challenges in disparate silvicultural treatments.

Genetic parameters such as family variances, heritabilities and the interaction of family with environment may also be affected by cultural practices. For example, heritabilities are greatly influenced by environmental homogeneity of the test, and homogeneity may be impacted by management activities. Further, since heritabilities are population-specific, studies with intensive and less intensive culture may provide a good opportunity to explore how genotypes within species respond to culture by examining genetic expression and genotype by environment interaction.

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There are many estimates of heritabilities for these species, for height growth (HODGE and WHITE, 1992; BALOCCHI *et al.,* 1993; BRIDGWATER and MCKEAND, 1997), and resistance to fusiform rust (ROCKWOOD and GODDARD, 1973; SOHN and GODDARD, 1979; HODGE *et al.,* 1990; DIETERS *et al.,* 1996). There is less information on the impact of silvicultural management on heritabilities in both loblolly and slash pine (LI and MCKEAND, 1989; SURLES *et al.,* 1995; MCKEAND *et al.,* 1997).

Using third-year data, the primary objectives of this paper are to: 1) Estimate heritabilities (h^2) for height growth and resistance to fusiform rust and examine whether these heritabilities are affected by management intensity under two levels of cultural practices across 11 sites in the Lower Coastal Plain of the USA; and 2) Examine patterns of environment by family interaction across these sites and management intensities to determine whether intensive culture affects family ranking in improved loblolly, improved slash and unimproved slash pine.

2. Materials and Methods

Taxa

A large series of field experiments was established in 1994 by the Cooperative Forest Genetics Research Program (CFGRP), in which seven different pine taxa are being tested: three slash x *P. caribaea* hybrids; the slash x loblolly F1 hybrid, improved slash (PEE), unimproved slash (PEU) and improved loblolly pine (PTA). In this paper only the results from PEE, PEU and PTA are presented.

The improved slash taxon consisted of open-pollinated seed from 18 slash pine trees which are outstanding for volume growth or disease resistance. Since these families are open-pollinated, the average breeding values for the seedlots were calculated considering the breeding values of the clones (females parents) and all trees in the seed orchard (assuming 30% pollen contamination). The PEE seedlot was estimated to have means of 18.3% for volume gain and 37.1% for rust (R50), as predicted by the CFGRP (LÓPEZ-UPTON, 1999). The 18.3% volume gain is expressed for 15-yr volume above unimproved material. Lower R50 values indicate more resistance to fusiform rust (WHITE and HODGE, 1988; WHITE *et al.,* 1988). For example, a breeding value of 37% means that on a given site where unimproved material exhibit 50% rust infection, the PEE families are predicted to average 37% infection.

The unimproved slash pine families consisted of open-pollinated seed from 17 parents intended to represent slash pine as it existed in 1955, before domestication. For comparison, the PEU seedlot was estimated to have a 4.9% volume gain and a R50 of 51.3%. The improved loblolly taxon consisted of open-pollinated seed from 17 superior parents mostly from the Atlantic Coastal Plain. Details are not available on breeding values of these parents.

Field implementation phase

Four seedling growers were used to supply the seedlings, and each grower produced the plants for two or three test sites. Each group of two or three test locations that shared the same grower is denoted as a series. No special greenhouse cultural practices were used. The taxa were allowed to grow at different rates in order to permit genetic differences in growth to be expressed. So, seedlings were of different sizes at outplanting. Eleven field test locations were planted in December 1994 in the Lower Coastal Plain, which includes north Florida and the southern portions of Georgia and Alabama. These sites covered a wide range of soil groups (LÓPEZ-UPTON, 1999), from well to poorly drained and site index from 16 to 21 (meters at base age = 25 yrs.).

At each location, the field design consisted of a Randomized Complete Block, nested split-plot design, with three complete blocks nested within each of two treatment levels labeled as High (intensive) and Low (less intensive culture), 7 taxa (including the 3 taxa analyzed here: PEE, PEU and PTA), 16 open-pollinated families per taxon and 5 trees per family as a row plot (see LÓPEZ-UPTON, 1999, for details). Each taxon whole-plot within a given treatment level consisted of 80 trees (16 families x 5 trees per family row plot). Per taxa, 480 trees were planted at each site (2 treatments x 3 blocks x 16 families x 5 trees/family). Sixteen families in each taxon were planted per location, but the families varied slightly among sites. Overall, 18 PEE, 17 PEU and 17 PTA families were represented in these 11 tests, while 11 PEE, 15 PEU and 14 PTA families were common to all sites. The sites in each series (same nursery grower) shared the same 16 families of each taxon.

Tree spacing varied by location from 1.5 m x 3.0 m to 1.8 m x 3.0 m. A buffer strip of 21 m or more was used to separate the two management treatments to contain the effects of fertilizer and insecticide applications. Also, two to four border rows of treated trees surrounded each treatment plot. Herbaceous weed control was part of the pre-planting site preparation in both cultural treatments across all 11 sites. Chopping, raking, burning and bedding were done as needed.

In the low treatment, cultural practices were applied at levels considered operational by forest industries in the southeastern USA. No fertilization was used, except for one location where phosphorus was added in both treatments. No weed control was used during the first three growing seasons. However, to facilitate data recording, all plots on four sites were mown once.

In the high treatment, fertilizer, weed control and insecticides for tip moth were applied in 1995, 1996 and 1997 at different rates among sites (see LÓPEZ-UPTON, 1999, for details). The objective was to create differential growth between treatments, although specific management varied by site depending on site requirements.

Variables measured and statistical analysis

The following variables were measured on all 11 sites: 1) Height was assessed at age 3 years in the winter of 1997 to 1998, and was measured as height of the highest terminal bud; and 2) Rust incidence was assessed at age 3 years and scored as 0 (absence of rust) and 1 (presence of rust).

Data editing and standardization

Rust incidence data from eleven sites were obtained. However, two sites with less than 15% of the trees infected were excluded because low rust incidence levels have small variances (WHITE and HODGE, 1987). Data from ten sites were used for height analyses. One site was eliminated from the height analyses due to extensive deer damage, resulting in large experimental error. For height analyses, an average of 2.5% of the data points in each block were outliers, distinctly outside the range of measurements. These were assumed to be inbred trees or recording errors, and were deleted prior to analysis (MOSTELLER and TUKEY, 1977). To remove the effects of scale, height was standardized by dividing each observation in a site-treatment-block combination by the corresponding square root of the phenotypic variance for that block (VISSCHER *et al.,* 1991; HODGE *et al.,* 1996).

General analysis of variance

All analyses of variance (ANOVA) were done based on individual tree data with the model:

$$Y_{tijkmn} = \mu + s_t + \alpha_i + s\alpha_{ti} + b_{j(ti)} + \tau_k + s\tau_{tk} + \alpha\tau_{ik} + s\alpha\tau_{tik} + b\tau_{tijk} + f_{m(k)} + sf_{tkm} + \alpha f_{ikm} + s\alpha f_{tikm} + bf_{tijkm} + e_{tijkmn} \quad (1)$$

where Y_{tijkmn} is the n^{th} tree observation in the m^{th} family of the k^{th} taxa in the j^{th} block of the i^{th} treatment at the t^{th} site,

μ is the population mean,

s_t is the random variable for site ~*NID* $(0, \sigma^2_s)$,

α_i is the fixed effect for treatment (High *vs.* Low),

$s\alpha_{ti}$ is the random interaction of site by treatment ~*NID* $(0, \sigma^2_{s\alpha})$,

$b_{j(ti)}$ is the random variable for block within site and treatment ~ *NID* $(0, \sigma^2_b)$,

τ_k is the fixed effect for taxa (PEE, PEU and PTA),

$s\tau_{tk}$ is the random interaction of site by taxa ~*NID* $(0, \sigma^2_{s\tau})$,

$\alpha\tau_{ik}$ is the fixed effect for the interaction treatment by taxa,

$s\alpha\tau_{tik}$ is the random three-way interaction of site by treatment by taxa ~ *NID* $(0, \sigma^2_{s\alpha\tau})$,

$b\tau_{tijk}$ is the random interaction block within site and treatment by taxa ~ *NID* $(0, \sigma^2_{b\tau})$,

$f_{m(k)}$ is the random variable for family within taxa ~*NID* $(0, \sigma^2_f)$,

sf_{tkm} is the random interaction of site by family within taxa ~*NID* $(0, \sigma^2_{sf})$,

αf_{ikm} is the random interaction of treatment by family within taxa ~*NID* $(0, \sigma^2_{\alpha f})$,

$s\alpha f_{tikm}$ is the random three way interaction of site by treatment by family within taxa ~ *NID* $(0, \sigma^2_{s\alpha f})$,

bf_{tijkm} is the random interaction of block within site and treatment by family within taxa ~*NID* $(0, \sigma^2_{bf})$,

e_{tijkmn} is the error term ~*NID* $(0, \sigma^2_e)$;

where t = 1,...9 or 10 sites; i = 1,2 management treatments; j = 1,2,3 blocks; k = 1,2,3 taxa; m = 1,...16 families per taxon; and n = 1, ...5 trees per plot.

PROC GLM (SAS Institute Inc., 1988) was used to test the significance of random effects. After the general ANOVA, three analyses of variance were performed per trait, one for each of the three taxa, to estimate the significance of family, site by family, treatment by family, and site by treatment by family interaction. The model was obtained by dropping the taxa effect from model (1) (i.e., dropping all terms with subscript *k*). Thus the ANOVA for each taxon was performed with:

$$Y_{tijmn} = \mu + s_t + \alpha_i + s\alpha_{ti} + b_{j(ti)} + f_m + sf_{tm} + \alpha f_{im} + s\alpha f_{tim} + bf_{tijm} + e_{tijmn} \quad (2)$$

where all effects are as described in model (1).

Heritabilities

To estimate single-site heritabilities (h^2_B) for both rust resistance and third-year height growth for all combinations of sites, treatment, and taxa, single-site analyses were accomplished using the individual tree data. With so few families in each taxon, the goal in h^2 estimation was not to add to the wealth of existing estimates of heritabilities already in the literature for these species (Rockwood and Goddard, 1973; Sohn and Goddard, 1979; Hodge *et al.,* 1990; Hodge and White, 1992; Balocchi *et al.,* 1993; Dieters *et al.,* 1996; Bridgwater and McKeand, 1997). Rather, the interest is in how silvicultural management affects h^2_B.

Variance components were estimated by PROC MIXED with the restricted maximum likelihood method, REML (Littell *et al.,* 1996). The model using individual data for each site-treatment-taxa combination was the following:

$$Y_{jmn} = \mu + b_j + f_m + bf_{jm} + e_{jmn} \quad (3)$$

where Y_{jmn} is the n^{th} tree observation of the m^{th} family in the j^{th} block,

μ is the population mean,

b_j is the fixed effect for blocks,

f_m is the random variable for family ~*NID* $(0, \sigma^2_f)$,

bf_{jm} is the random interaction of block by family ~*NID* $(0, \sigma^2_p)$,

e_{jmn} is the error term ~ $(0, \sigma^2_w)$;

where j = 1,2,3 blocks; m = 1,...16 families; and n = 1,...5 trees.

The open-pollinated families in each taxon were assumed to be half-sib families; hence the variance component for families (σ^2_f) can be interpreted as an estimate of one quarter of the additive genetic variance (σ^2_A) (Falconer and Mackay, 1996). Actually, σ^2_f is upwardly biased when obtained from single site analyses due to the confounding effects of genotype by environment interaction ($\sigma^2_f = \frac{1}{4}\,\sigma^2_A + \frac{1}{4}\,\sigma^2_{AE}$) (Comstock and Moll, 1963). A total of 66 estimates of h^2_B for rust (11 sites x 2 treatments x 3 taxa) and 60 estimates for h^2_B third year height (10 sites) were obtained as follows:

$$h^2_B = 4 * \sigma^2_f \,/\, \sigma^2_f + \sigma^2_p + \sigma^2_w \quad (4)$$

For height, standardized values as indicated before were used. For rust, both untransformed values of 0 and 1, and transformed data were used to calculate heritabilities. Binary heritability or heritability with untransformed values ($h^2_{B\,0,1}$) is appropriate for traits of low heritability ($h^2 \leq 0.3$) and for traits of high heritability with mean incidence levels less than 75% (Lopes, 1998). However, to obtain heritability estimates that are independent of the frequency of the trait, the binary heritability was converted to an underlying continuous scale, ($h^2_{B\,un}$), by Dempster and Lerner's (1950) method:

$$h^2_{B\,un} = [\, h^2_{B\,0,1} * p\,(1-p)\,] \,/\, c^2 \quad (5)$$

where: $h^2_{B\,un}$ is the heritability on the underlying scale;

$h^2_{B\,0,1}$ is the individual heritability on the binary scale estimated from 0/1 data;

p is the percentage of rust infection in each site-treatment-taxa combination;

c is the ordinate of the normal density function at the threshold.

Linear regression analyses were used in an attempt to explain trends in height and rust heritabilities associated with treatments and site. For rust incidence, the 66 estimates of h^2_B were used as the dependent variable and various transformations and combinations of mean rust incidence, treatments, and taxa as regressors (Sohn and Goddard, 1979). For height, the 60 estimates of h^2_B were used as the independent variable with combinations of mean height growth, treatment and taxa as regressors.

Further, for third year height, the ratio of h^2_B in high treatment to h^2_B in low treatment was calculated for each site and used as a dependent variable (h^2_B-High to h^2_B-Low, a value larger than 1 means that h^2_B is larger in high treatment at that site). The ratio of mean height in high treatment to mean height in low treatment was used as a measurement of effectiveness of the silviculture treatment on each site in causing growth differences. Thus, effectiveness and various transformations of this ratio and in combination with taxa were used as independent variables. Two heritabilities of zero were removed from the analysis.

Preliminary regressions indicated that the heritability for height was affected by management intensity. Thus, a linear regression was used to examine if the change in heritability was due to changes in genetic variance (additive variance) or less environmental variance. First, to reduce dependence of these variances on scale, coefficients of variation (CV) were created for both additive and environmental error variances (CV-Add and CV-Error) as:

$$\text{CV-Add} = \sqrt{4^*\sigma^2_f} / \text{height and CV-Error} = \sqrt{\sigma^2_w - [3^*\sigma^2_f]} / \text{height}$$

where height = mean height of a given site-treatment-taxa combination.

Thus, for height 60 CV-Add and 60 CV-Error values were created (2 treatments x 10 sites x 3 taxa). For both CV-Add and CV-Error, a ratio of CV in the high treatment to CV in the low treatment was created to be the dependent variable (30 observations of CV-Add High to CV-Add Low, and 30 observations of CV-Error High to CV-Error Low). As before, effectiveness (mean of height in the high treatment to mean of height in the low treatment) was considered an independent variable for regressions with taxa as a class variable. Several models were used to examine the importance of management.

Genotype by environment interaction

The goal of these analyses was to determine if silvicultural treatments caused rank changes among families and if these rank changes across treatments were larger than rank changes of families across sites. A change in relative performance across environments is called genotype x environment interaction (GxE). Type-B genetic correlation was used to examine the stability of family performance across environments (Burdon, 1977; Lu, 1999). It is defined as the genetic correlation for the same trait measured in different environments (Yamada, 1962; Burdon, 1977). The procedure for standardization for height trait (mentioned in Data Editing and Standardization) was used to homogenize phenotypic variances across tests and treatments (Dickerson, 1962; Yamada, 1962). Then, a genetic correlation near one indicates that interaction is negligible (i.e., family rankings are stable). On the other hand, a genetic correlation less than one means changes in family ranking in different sites or treatments. Type B genetic correlations were estimated (r_B) (Yamada, 1962) for each taxa as:

$$r_{\text{B-treat}} = \sigma^2_f / (\sigma^2_f + \sigma^2_{\alpha f}), \text{ and} \qquad (6)$$

$$r_{\text{B-site}} = \sigma^2_f / (\sigma^2_f + \sigma^2_{sf}) \qquad (7)$$

All analyses were done separately by taxa to see if trends were consistent for PEE, PEU and PTA. To estimate $r_{\text{B-treat}}$, the variance components for family and treatment by family (σ^2_f and $\sigma^2_{\alpha f}$) were obtained from a pooled analysis (model 2), but site, treatment, and block were considered fixed effects. To estimate $r_{\text{B-site}}$, one ANOVA was performed for each treatment-taxa combination (six ANOVAs in total) to investigate whether genetic correlations among sites were consistent across treatments and taxa. The variance components for family and site by family (σ^2_f and σ^2_{sf}) were obtained using the pooled analysis model (2), but treatment was dropped from the model (i.e., dropping all terms with subscript *i*). Thus the model was:

$$Y_{tjmn} = \mu + s_t + b_{j(t)} + f_m + sf_{tm} + bf_{tjm} + e_{tjmn} \qquad (8)$$

where all term were described in model 1, but site and block effects were considered fixed effects and t = 1,...9 or 10 sites; j = 1,2,3 blocks; m = 1,...17 or 18 families per taxon; n = 5 trees.

Where important GxE interaction existed (r_B<0.7, as suggested by Shelbourne, 1972), several analyses were performed to identify the responsive families in each taxa or to find which sites were causing the GxE. Furthermore, some analyses were performed by including the effect of the seedling grower (series). Series was added to model 8 and site was nested in series. To examine whether rust was causing the GxE on height, some analyses were done using only data from rust-free trees. Lastly, the GxE analyses were redone with series in the model and with data from rust-free trees.

Finally, a relative gain estimation for third-year height growth was performed to compare gains from progeny testing in one culture and deployment in another culture. Relative genetic gains, which is the ratio of indirect gain to direct gain, for each taxon were calculated with the formula developed by Falconer and Mackay (1996). This ratio measures the relative gains from choosing families or parents based on their performance in Low and then planting those chosen families in High (or vice versa). For progeny testing in the Low intensity and deployment in High intensity culture, the final formula was derived from Relative Gain = Indirect gain / Direct gain as:

$$RG_{\text{L to H}} = i_L \, r \, h_{fL} \, h_{fH} \, \sigma_H \; / \; i_H \, h^2_{fH} \, \sigma_H,$$

Assuming that the intensity of selection is the same in both environments ($i_L = i_H$), the relative genetic gains for third-year height growth for comparing gains from progeny testing in low and deployment in high intensity were:

$$RG_{\text{L to H}} = r_{\text{B-Treat}} \text{ x } (h_{fL} / h_{fH}) \qquad (9)$$

Similarly for progeny testing in high and deployment in low intensity:

$$RG_{\text{H to L}} = r_{\text{B-Treat}} \text{ x } (h_{fH} / h_{fL}) \qquad (10)$$

where: $r_{\text{B-Treat}}$ is the type B genetic correlation for treatments averaged over all three taxa, and h_f is the square root of family heritability for height growth in High and Low culture (derived below).

Ratios of gains $RG_{\text{L to H}}$ and $RG_{\text{H to L}}$ were performed by pooling taxa (not conducted separately for each taxa). Since heritability estimates were based on few families, it was assumed that all taxa were similar and differences in estimates for PEE, PEU and PTA were errors from sampling a small number of families in each taxa. Thus, single-site heritabilities were taken as h^2_{BH}=0.30 and h^2_{BL}=0.20. Then h^2_B has $4\sigma^2_F$ in numerator and $\sigma^2_F * r_{\text{B-site}} = \sigma^2_f$ and $\sigma^2_{fe} = \sigma^2_F - \sigma^2_f$ (White and Hodge, 1992). Thus σ^2_f and σ^2_{fe} were substituted in :

$$h^2_f = \sigma^2_f / (\sigma^2_f + \sigma^2_{fe}/t + \sigma^2_e/tb) \qquad (11)$$

where: σ^2_f is the variance due to average family effects;

σ^2_{fe} is the variance due to family by environment interaction effects;

σ^2_e is the error term in a single-tree plot design;

t is the number of test locations; and

b is the number of blocks assuming single-tree plots.

To predict the ratios of relative gains, a simulation was performed substituting number of sites from 1 to 20 and assuming 15 blocks per site.

3. Results and Discussion

Family effects and interaction with sites and treatments

Rust incidence

Significant differences were found among families within taxa for rust incidence in all pooled analysis performed. The non significant interaction of site by family in each treatment pooled analyses showed that families performed consistently across sites in both cultural treatments. This supports the results of many researchers, that genotype by environment interaction for fusiform rust infection is of little practical importance in either slash or loblolly pine (KINLOCH and STONECYPHER, 1969; GODDARD and SCHMIDT, 1979; WELLS *et al.,* 1982; HODGE *et al.,* 1990, 1993; DIETERS *et al.,* 1996). Also, no significant treatment by family interaction was detected, i.e., resistant families have less rust incidence than susceptible families whether growing in operational or intensively managed areas. Therefore, if considering only the rust incidence, deployment of families to intensive management sites may be based on their resistance evaluations like R50 (HODGE *et al.,* 1993), i.e., for most families there is no need for matching specific families to either sites or management regimes.

Height

Significant differences were found among families within taxa for height in all pooled analyses performed. On average across sites, all 18 PTA families were superior to the very best PEE family in both treatments (data not shown). Meanwhile, 11 and 9 out of 18 PEE families were superior to the best PEU family in the high and low treatments, respectively.

Treatment by family interaction was significant in the pooled analysis. Site by family interactions were highly significant for height in both pooled analyses (pooling all three taxa and separately by taxa for models (1) and (2)). Genotype by site interaction for height has been noted to occur in slash pine progenies, where some progenies did not perform consistently in low, medium, and high productivity sites (GODDARD and ROCKWOOD, 1982).

Heritabilities

Rust incidence

With so few families from selected parents, these heritabilities should be used with caution, although some conclusions may be drawn. Regression analysis indicated that single-site rust heritabilities both for the untransformed values 0 and 1 ($h^2_{B\ 0,1}$) and in the underlying scale ($h^2_{B\ und}$) were not affected by the change in management intensity (*Table 1*).

On the observed binary scale, the single-site heritabilities for rust ($h^2_{B\ 0,1}$) were well predicted by a quadratic function of the mean rust incidence in the test including taxa as class variable (*Figure 1*). This behavior has been noted by other researchers when using heritability on the binary scale (SOHN and GODDARD, 1979; HODGE *et al.,* 1990, 1993; SOUZA *et al.,* 1991; DIETERS *et al.,* 1996). The predicted maximum biased heritability occurred at 60.5% of rust incidence, which is close to that reported by SOHN and GODDARD (1979) and DIETERS *et al.* (1996). The maximum h^2 values were predicted to be 0.33 for PEE, 0.21 for PEU and 0.27 for PTA, but these differences among taxa may reflect the few families upon which the estimates are based and different taxa rust incidences.

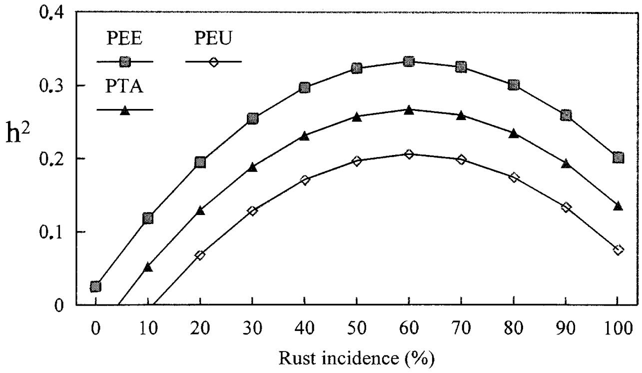

Figure 1. – Predicted models for single site heritability of rust incidence for the three taxa tested. For the full model including taxon as a main effect the $R^2 = 0.40$. The final model is $h^2_{B\ 0,1} = a + 0.010133\ r - 0.00008371\ r^2$, where a is 0.0254, –0.1004 and –0.0398 for PEE, PEU and PTA, respectively, and r = rust incidence (in percent) at the site.

The heritability on the underlying continuous scale ($h^2_{B\ und}$) is better for taxa comparisons, and the $h^2_{B\ und}$ are quite similar both among taxa and treatments (*Table 1*). In fact, when modeled as the dependent variable in the regression, $h^2_{B\ und}$ was not affected by the change in the management intensity nor environments. Regression analysis with 66 $h^2_{B\ und}$ estimates indicated a significant taxa effect, but a non significant effect of management intensity. The taxa effect explained 12% of the variability among estimates of $h^2_{B\ und}$ (p=0.023). Although the site effect was significant (p=0.026), this effect explained only 0.2% of the variability among estimates of $h^2_{B\ und}$.

Height

Overall, the increase in management intensity increased single site heritability as well as height growth (*Table 2*). This higher heritability for height growth in the intensive management treatment implies that genetic gains may be improved

Table 1. – Mean and range (in parentheses) of single-site heritability estimates for rust by treatment and taxon. Heritabilities were obtained using 0 to 1 data ($h^2_{B\ 0,1}$) and in the underlying scale ($h^2_{B\ und}$) by DEMPSTER and LERNER's (1950) method.

		High Treatment	**Low Treatment**
$\mathbf{h_B{}^2{}_{0,1}}$	PEE	0.29 (0.0-0.61)	0.28 (0.0-0.57)
	PEU	0.17 (0.0-0.42)	0.13 (0.0-0.32)
	PTA	0.12 (0.0-0.35)	0.10 (0.0-0.47)
	Average	0.19	0.17
$\mathbf{h_B{}^2{}_{und}}$	PEE	0.38 (0.0-0.91)	0.40 (0.0-0.87)
	PEU	0.29 (0.0-0.66)	0.24 (0.0-0.59)
	PTA	0.20 (0.0-0.65)	0.21 (0.0-0.71)
	Average	0.29	0.28

Table 2. – Mean and range (in parenthesis) of single-site heritability estimates for height by treatment and taxon. Analyses used third-year data with standardized values obtained by dividing raw data by the square root of the phenotypic variance in each block.

Taxa	**High Treatment**	**Low Treatment**
PEE	0.29 (0.08-0.57)	0.19 (0.00-0.44)
PEU	0.31 (0.00-0.47)	0.23 (0.00-0.54)
PTA	0.32 (0.04-0.46)	0.23 (0.09-0.49)
Average h^2_B	0.31	0.22

through selection of genotype under intensive management practices. For example, through cultural practices intensively managed tests have been successful in increasing juvenile mature correlations in *P. taeda* (LI *et al.,* 1992).

Both the additive variance and the error variance for height were lower in the high treatment. The reduction of additive variation (6% reduction in CV-Add from 0.1891 in Low to 0.1783 in High) may be due to reduced genetic expression in the uniform environment. In any case, the environmental error was more strongly reduced with the increase of management treatments (25% reduction in CV-Error from 0.3186 in Low to 0.2386 in High), and this resulted in increased h^2 values in the high treatment.

The difference in h^2_B between High and Low was partially associated with the effectiveness of the increased management intensity, measured as the ratio of mean height in High divided by mean height in Low at each site (*Figure 2*). This was consistent for all three taxa, since no significant taxa effect was detected in the regression analyses. The phenotypic correlation coefficient between the ratio of h^2_B in the High to h^2_B in the Low treatment and effectiveness was 0.61 (*Table 3*), and this ratio of heritabilities was positively associated with the ratio of the coefficient of variation for additive variance in High to the coefficient of variation for additive variance in Low (CV-Add High to CV-Add Low, r=0.66). The heritability ratio was negatively associated with the ratio of the coefficient of variation for environmental error in High to the coefficient of variation for environmental error in Low (CV-Error High to CV-Error Low, r= -0.73).

The intensive cultural treatment was effective in increasing heritability for height by decreasing the coefficient of variation for environmental error (CV-Error). The CV-Error High to CV-Error Low ratio was closely associated with a linear function of effectiveness (r=0.90 in *Table 3* and see *Figure 3*). No significant taxa effect was detected in the regression.

On the other hand, additive variance was not related to the effectiveness of the management intensity. That is, variation in the ratio of CV-Add High to CV-Add Low among sites and taxa as dependent variable was not explained by regressions including taxa or by a linear or quadratic function of effectiveness or any combination of them. Further, the correlation of effectiveness with the ratio of CV-Add High to CV-Add Low was -0.17 (*Table 3*).

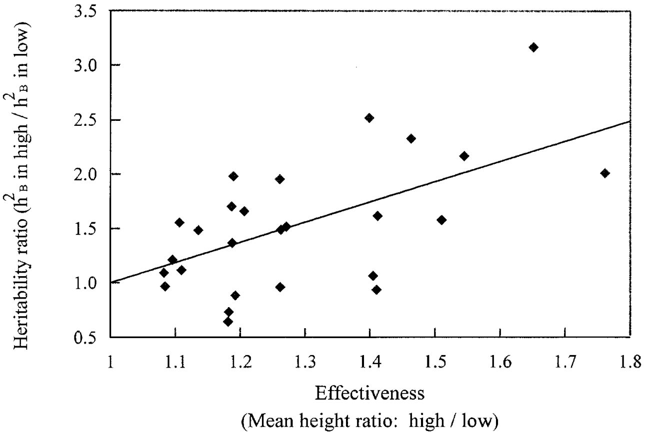

Figure 2. – Single-site heritability ratio (h^2_B in High / h^2_B in Low) as a function of the effectiveness of cultural treatment. For the full model h^2_B-High / h^2_B-Low = –0.86 + 1.86 (Effectiveness). R^2 = 0.37 and taxon was not significant as a regressor.

Intensive silviculture, e.g., fertilization, drainage improvement, weed competition control, have been shown to reduce microenvironmental variation (KISS and YEH, 1988; BOUVET and VIGNERON, 1995; WOODS *et al.,* 1995). Also, any kind of biotic or mechanical injury to the plants can also contribute to the

Table 3. – PEARSON correlation coefficients of heritability ratio for height, effectiveness, the ratio coefficient of variation for additive variance in High to coefficient of variation for additive variance in Low (CV-Add High to CV-Add Low) and the ratio coefficient of variation for environmental error in High to coefficient of variation for environmental error in Low (CV-Error High to CV-Error Low). There were 30 observations (3 taxa x 10 sites).

	Effectiveness (High to Low Height ratio)	CV-Add High to CV-Add Low	CV- Error High to CV-Error Low
h^2_B High / **h^2_B** Low ratio	0.6070*	0.6562**	-0.7281**
CV-Add High to CV-Add Low	-0.1700n.s.	--------	--------
CV- Error High to CV-Error Low	-0.9002**	-0.0736n.s.	--------

** = P<0.001; * = P<0.01; N.S. = Not significant.

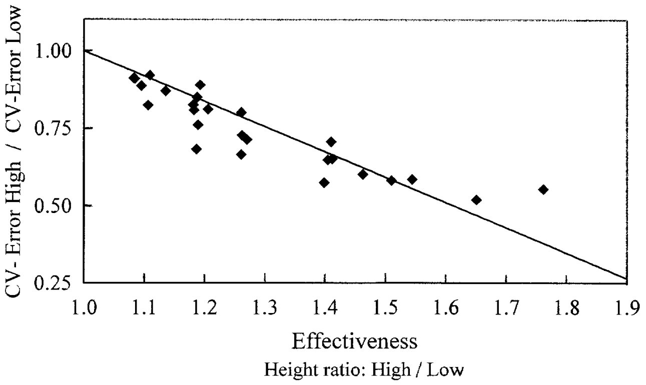

Figure 3. – Predicted models for the coefficient of variation of environmental error expressed as a ratio of the High and Low management (CV-Error High / CV-Error Low) for height as a function of the effectiveness in the three taxa tested. For the full model: (CV-Error High / CV-Error Low) = 1.82 – 0.82 (Effectiveness), $R^2 = 0.81$. Taxon and taxon interaction with effectiveness were not significant. A value of >1 for effectiveness means that third-year height in the High treatment is larger than the height in the Low treatment.

large within-plot variance (KISS and YEH, 1988). The insecticide application to reduce tip moth (*Rhyacionia* spp.) damage, greater control of weeds and fertilizer applications in the intensive treatment apparently reduced the environmental error and hence increased heritability for height growth.

Genotype by environment interaction

Rust incidence

In agreement with the non significant treatment by family interaction in the ANOVA, type B genetic correlations for treatments ($r_{B\text{-treat}}$) indicate highly stable rankings for rust resistance across the two management intensities (*Table 4*). The selection of families for commercial plantations based on rust incidence may be done irrespective of silvicultural activities.

The estimates of type B genetic correlations for sites ($r_{B\text{-site}}$) indicate high stability of family rankings for rust resistance across sites (*Table 4*). Both treatments showed similar and very low levels of GxE, indicating that GxE is not important for rust. A similar result was found by DIETERS *et al.* (1996), who stated that GxE interaction appeared to be of little importance for rust resistance in slash pine.

Height

Although caution is needed in drawing inferences with relatively few families, family rankings for height were less influenced by environmental differences among treatments than by differences among sites (*Tables 5* and *6*); this was consistent for all three taxa. Overall, values of type B genetic correlations for treatments ($r_{B\text{-treat}}$) indicate high stability of rankings for height across the two management intensities (*Table 5*). For both PEE and PTA the tallest family in the High treatment (one family out of 18 and 17 for PEE and PTA, respectively) appeared more responsive to more intense silviculture. When this single family was dropped, the type B correlation estimates were 1.0 for PTA and 0.94 for PEE. Although evaluation at mature ages is necessary, the selection of families for commercial plantations at this age is little influenced by silviculture activities.

Site by family interaction was high (low values of $r_{B\text{-site}}$), i.e., families were changing rank across sites (*Table 6*). GxE across sites may be very sensitive to the small number of trees per family planted in each site-treatment combination (5 trees x 3 blocks = 15 trees) and the arrangement in five-tree plots.

However, the high treatment had less GxE. The larger genotype by environmental interaction in the low treatment indicates a lack of consistency in the relative performance of genotypes when growing in different environments (sites) under operational cultural conditions (*Table 6*). Conceivably, the intensive culture practices in high treatment ameliorated the site and may have removed some limiting factors. This may explain the smaller GxE in the high treatment.

Two other factors appeared to influence GxE for height: rust incidence and series (sites in same series were grown in the same nursery). In general, when trees free of rust were analyzed, GxE was lower ($r_{B\text{-site}}$ higher) than when all trees were included and this was true for both management treatments (*Table 6*). Rust is known to affect height growth in this study (LÓPEZ-UPTON *et al.,* 1999) and differences among families in rust resistance could alter family rankings for height. When series (seedling grower effect) was included in the model, GxE was significantly reduced for slash pine in the high treatment. This reduction in GxE was greater for the improved slash pine families. Apparently, seedling quality differences from the different growers carried over through three years in the field and altered family ranking among growers.

Relative gains in height growth

Additional genetic gain in early height growth is expected if family selection is performed in one single site managed with intensive culture followed by operational deployment in plantations managed with less intensive culture. This is due to higher h^2_B in the high treatment and the high $r_{B\text{-treat}}$. However, the relative benefit of testing families in intensive culture for deployment in operational culture ($RG_{H\ \text{to}\ L}$) decreases as the number test locations increases (*Figure 4*). Therefore, with a

Table 4. – Estimates of Type B genetic correlation for rust incidence for both the site by family interaction and the treatment by family interaction. Values were obtained from equations 6 and 7 using nine sites with greater than 15% of rust incidence.

Taxa	$r_{B\text{-treat}}$	$r_{B\text{-site}}$	
		HIGH	LOW
PEE	1.0	1.0	0.96
PEU	0.95	0.86	0.93
PTA	0.96	0.85	0.83
Average	0.97	0.90	0.91

Table 5. – Estimates of type B genetic correlations for height for the treatment by family interaction. Values were obtained from equation 6.

Taxa	$r_{B\text{-treat}}$	
	RAW	Dropping the most responsive family
PEE	0.76	0.94
PEU	0.91	0.94
PTA	0.93	1.0
Average	0.87	0.96

Table 6. – Estimates of type B genetic correlation for height for site by family interaction. Values were obtained from equation 7 using standardized data in three different analyses: Including all trees (All); using only rust-free trees (Rust-free) and adding seedling grower to the model (Series). The value when dropping the most responsive single family is in parentheses.

Taxa	$r_{B\text{-site}}$					
	HIGH			LOW		
	All	Rust-free	Series	All	Rust-free	Series
PEE	0.41 (0.63)	0.74 (0.81)	0.91 (1.0)	0.38 (0.61)	0.82 (0.86)	0.41 (0.75)
PEU	0.69 (0.75)	0.89 (0.99)	0.80 (0.87)	0.50 (0.67)	0.57 (0.61)	0.57 (0.69)
PTA	0.80 (0.94)	0.95 (1.0)	0.82 (0.97)	0.65 (0.76)	0.59 (0.67)	0.57 (0.69)
Average	0.63 (0.77)	0.86 (0.93)	0.84 (0.95)	0.51 (0.68)	0.66 (0.71)	0.52 (0.71)

large number of test locations, there is no benefit of testing families in intensive silviculture for subsequent planting under operational conditions. On the other hand, the relative benefit of testing families in less intensive for deployment in intensive culture increases as number of sites planted increases. The relative gains approach the same value from either direction as number of tests increases, and gains depend only on the treatment by genotype interaction ($r_{B\text{-treat}}$=0.87, *Figure 4*).

If the difference in height growth between intensive culture and operational plantations were large and GxE became large, it is conceivable that the increase in h^2 in intensive culture may not be enough to offset the reduced correlations (see equations 9 and 10). Thus, additional gains from testing in high intensity treatments could conceivably be nullified. In our study no evidence for the latter hypothesis was found. Even when differences in early height growth between intensive and less intensive culture were on average 31% (from 10% to 72% at individual sites), the average $r_{B\text{-treat}}$ was 0.87. Furthermore no significant model was detected in regression analyses to corroborate an increase of GxE when treatment effectiveness increased to produce larger height differences between intensive and less intensive treatment. Further research is needed comparing intensive versus non-intensive culture and evaluation at mature ages to corroborate these early results; however, our results suggest that all genetic tests could be managed intensively (to achieve higher heritabilities) even when planned culture of operational plantations is less intensive.

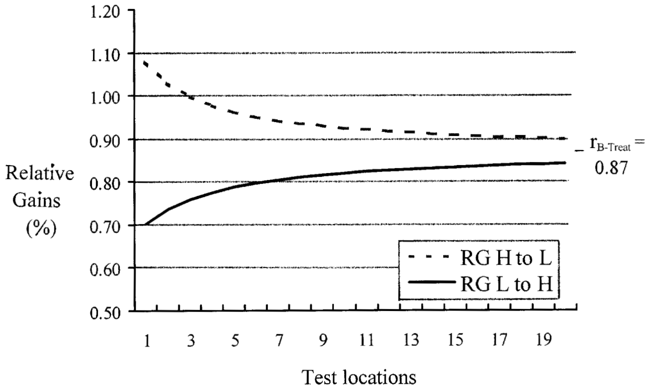

Figure 4. – Predicted model for the relative genetic gains in early height growth from family selection if testing in high treatment to deploy in low treatment (RG H to L) and from testing in low treatment to deploy in high treatment (RG L to H). Values were obtained combining information across taxa with formula 11.

4. General Discussion and Conclusions

The type B genetic correlations ($r_{B\text{-site}}$=0.90 and $r_{B\text{-treat}}$=0.97) indicate highly consistent family rankings for rust incidence across sites and management intensities. This supports the results of many researchers that genotype by environment interaction for fusiform rust infection is of little practical importance in either slash or loblolly pine (KINLOCH and STONECYPHER, 1969; GODDARD and SCHMIDT, 1979; WELLS *et al.*, 1982; HODGE *et al.*, 1990, 1993). Therefore, if considering only rust incidence, deployment of families in both intensive and operational management regimes may be done based on their resistance evaluations based on testing in either or both management regimes.

While these results for rust resistance suggest that there is no need to match specific families to either sites or management regimes, recent results based on a very small number of families indicated that slash pine families were not always stable in rust resistance across sites and planting years (Schmidt *et al.,* 1999). Even though results as those of Schmidt *et al.* (1999), with few families should be used with caution, decisions on single-family deployment in commercial plantations may consider potential instability for rust resistance.

With few families from selected parents (52 families in total for this experiment), the heritability estimates should be interpreted cautiously, although some conclusions may be drawn. Single-site heritabilities for rust in the binary scale ($h^2_{B\ 0,1}$) and in the underlying scale ($h^2_{B\ und}$) were not affected by site nor by the increase in management intensity, even though rust incidence was somewhat increased by intensive management (López-Upton, 1999). Conversion to the underlying scale reduced parameter dependency on rust incidence and indicates a $h^2_{B\ und}$ of 0.29. This value is in the range of other estimates for single-site heritability for rust when transformed to the underlying scale by Dempster and Lerner's (1950) method ($h^2_{B\ und}$=0.26 in Rockwood and Goddard, 1973; $h^2_{B\ und}$=0.33 in Dieters *et al.,* 1996). Taken together, these estimates indicate that rust resistance is one of the more heritable traits of commercial importance other than wood properties. From information on many studies, single-site heritabilities for growth traits range from 0.1 to 0.25, while for wood specific gravity h^2_B is above 0.3 (Cornelius, 1994). So, resistance to fusiform rust is more heritable than most traits.

For third-year height growth, family rankings for height were less influenced by environmental differences in management intensity than by differences among sites; this was consistent for all three taxa ($r_{B\text{-}treat}$=0.87 while $r_{B\text{-}site}$=0.57, averaged over all three taxa). Although evaluation at mature ages is necessary, these early results imply that stable rankings for height may be expected when cultural intensity increases. However, a few families were more responsive and in some cases the tallest in the High treatment, and these may be useful for deployment under intensive culture conditions.

Site by family interactions for height were significant and important (low values of $r_{B\text{-}site}$), meaning that families were changing rank across site. Some general observations may be drawn. First, loblolly pine families were more stable across sites than slash pine families (*Table 6*). Second, differences in rust incidences caused some instability in height rankings in the analysis across sites, because more resistant families had relatively better performance for height on highly infected sites. Third, seedling quality also affected the GxE. Height of improved slash pine seemed particularly sensitive to the different quality of seedlings from different growers. Fourth, the intensive culture had smaller site by family interaction (higher $r_{B\text{-}site}$ value) than less intensive culture, meaning more stable family rankings across sites for intensive culture (*Table 6*). Conceivably, intensive cultural practices in the intensive treatment ameliorated the site and may have removed some limiting factors. The decreased environmental differences across sites may have increased the apparent stability of genotypes.

The increase of management intensity increased average third-year height growth and its single-site heritability. Both additive variance and environmental error for height were lower in the intensive treatment. The reduction of 6% in additive variation may be due to reduced genetic expression in the uniform environment. In any case, the environmental error was more strongly reduced (by 25%) in the intensive management treatment and this resulted in higher heritability (h^2_B = 0.3 *vs.* 0.2, averaged over all three taxa in high and low, respectively). The greater control of weeds and insecticide applications to reduce tip moth (*Rhyacionia* spp.) damage in the intensive treatment may have contributed to the reduced environmental error and hence increased heritability for height growth for all three taxa.

The higher heritability for height growth in the intensive management treatment implies that genetic gains from progeny testing are higher in intensive culture (when selected families are deployed back to the environment in which they are tested). This means testing in intensive to deploy in intensive achieves more gain than testing in less intensive to deploy in less intensive. Moreover, this higher heritability in the intensive culture along with little GxE between treatments ($r_{B\text{-}treat}$=0.87, averaged over all three taxa) indicates that gains from indirect testing favor testing families in intensive management for subsequent deployment in operational management regimens. These conclusions for height growth need confirmation with later results since they are based on data at three years of age. However, it appears that progeny testing with intensive culture could have advantages for deployment in either culture, although as the number of sites increases, the advantage of testing in intensive culture decreases.

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Genetic Variation in *Pinus brutia* Ten. in Turkey

II. Branching and Crown Traits

By K. Isik[1]) and F. Isik[2])

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Abstract

The nature and extent of variation in certain crown (crown diameter, live crown ratio, crown shape index) and branching traits (branch angles, number of growth cycles, length of the longest branch) of *Pinus brutia* Ten. were investigated in this study. The data were collected destructively by thinning a provenance-progeny trial, first at age 13 and then at age 17 years. There were six natural populations each represented by 10 open-pollinated families, and each family by 10 half-sibs in the experiment. Populations were significantly different for all the branching and crown traits. Similarly, there were significant differences among families within populations for most traits. Populations from higher altitudes showed relatively wider branch angles, shorter branches and longer and narrower crowns. Crowns get narrower ($r= -0.59$, $p<0.0001$) and longer ($r=0.45$, $p<0.0001$) with the increase of altitude of origins. Families with straighter stems had narrower crowns ($r= -0.72$, $p<0.0001$). The percent of genetic variation due to populations in crown and branching traits was considerable, ranging from 2.4% (crown diameter) to 24.5% (crown shape index). Variance components due to families were in general below 10% for each trait, showing increasing tendency with age. Individual heritabilities for the branching traits were moderately high, ranging from 0.23 to 0.53. On the other hand, heritabilities for crown traits were weak at age 13, but for crown diameter and for crown shape index were comparatively high at age 17. The results indicated that combined population, family and within-family selection for branching and crown traits would result in considerable gain in *Pinus brutia*.

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