

Realized Genetic Gains of Rust Resistant Selections of Slash Pine (*Pinus elliottii* var. *elliottii*) Planted in High Rust Hazard Sites

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Summary

Realized gains from selection for resistance to the fungal disease fusiform rust caused by *Cronartium quercuum* f. sp. *fusiforme* were estimated using data from five field trials planted on large rectangular plots in high rust-hazard sites. These five realized gain trials, planted as a Best Management Practices study (BMP), compared resistant and susceptible mixtures of families from the first-generation breeding population of slash pine (*Pinus elliottii* var. *elliottii* Engelm.) in southeastern North America.

Analyses of variance (Proc Mixed using REML in SAS), conducted to test the significance of realized gains and interactions contrasting resistant with susceptible seedlots, detected important and highly significant realized gains in both rust resistance and mid-rotation yield. Significant gains were obtained for rust resistance at age 5 and stand yield at age 16 with high stability across sites and across silvicultural treatments, indicating that gains in rust resistance and the associated influence on gains in stand yield were consistent under many environmental conditions. Additionally, the values of realized gains in stand yield steadily increased with age, primarily due to increased rust associated mortality with age in the susceptible material. The 25% realized gain for rust resistant material compared to rust susceptible material obtained at age 16 was conservatively extrapolated to a 25-year-old rotation-age gain of 51.4 m³ ha⁻¹ (735 feet³ acre⁻¹) in inside-bark volume.

Key words: Tree improvement, forest genetics, block plots, mean annual increment, tree volume.

Introduction

Fusiform rust (*Cronartium quercuum* f. sp. *fusiforme*) is the most serious pine disease in southeastern North America (SCHMIDT *et al.*, 1981; HODGE *et al.*, 1990; SCHMIDT, 1998), and slash pine (*Pinus elliottii* var. *elliottii* Engelm.) is highly susceptible to this pathogen. Fusiform rust causes stem galls that decrease product values and cause growth reduction, deformations, and mortality which produce significant losses in stand yield (SOHN and GODDARD, 1979; SCHMIDT *et al.*, 1981; WEBB and PATTERSON, 1984; SCHMIDT, 1998; BRAWNER *et al.*, 1999). Those yield losses account for hundreds of millions of dollars in economic costs across southeastern

North America (PHELPS and CHELLMAN, 1975; ANDERSON *et al.*, 1986; CUBBAGE *et al.*, 2000).

The increase in disease incidence and area seriously affected by fusiform rust in southeastern North America since 1930 (PHELPS and CHELLMAN, 1975; GRIGGS and SCHMIDT, 1977) was caused by factors related to increased management intensity (SCHMIDT, 1998). Reduction of wildfires, coupled with more abundant and dense young plantations, resulted in a historical annual rust increment of 2–3%. More recently, fertilization and weed control have exacerbated the problem, because unlike some pathogens, rust infection increases in rapidly-growing trees (SCHMIDT *et al.*, 1981; PYE *et al.*, 1997; BRAWNER, 1998; SCHMIDT, 1998).

Many efforts have been aimed at controlling rust incidence in plantations, but the most effective and economically-viable tool for managing rust epidemics and reducing damage is selection, breeding, and planting of genetically-resistant material (PYE *et al.*, 1997; SCHMIDT, 1998; WALKINSHAW, 1999; CUBBAGE *et al.*, 2000). Selection in high-rust-hazard sites, testing, and breeding have produced substantial rust resistance in some families of slash pine (HODGE *et al.*, 1990; WHITE *et al.*, 1993; BRAWNER *et al.*, 1999). Commercial production of rust-resistant seedlings began around 1980 and by 1997, almost half of the planted seedlings of slash pine contained increased resistance to fusiform rust (PYE *et al.*, 1997).

The assessment of realized gains is important to justify the investment in genetic improvement (ZOBEL and TALBERT, 1984; ELDRIDGE *et al.*, 1994), and the evaluation of the impact of rust resistance on stand yield is important to quantify those realized gains. Differential rust resistance among slash pine families and seedlots has been demonstrated using row-plots. A study assessing rust incidence in three-tree row plots from an intensely-selected population, at three and five years after planting, found significant realized gain above unimproved controls (SOHN and GODDARD, 1979). *I/U* ratios (total rust incidence in the improved material divided by total rust incidence in the unimproved control) ranged from 0.50 to 0.77 depending on rust hazard (defined as total percentage rust incidence on unimproved material).

Additionally, a study using material from seed production areas and a seed orchard created from selections made in heavily rust infected stands evaluated in 17 row-plot progeny tests showed significant gain in rust resistance at all rust hazard levels (HODGE *et al.*, 1990).

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The seed production areas and seed orchard material had I/U ratios of 0.67 and 0.80, respectively. The evaluations made at ages between 3 and 10 years showed relatively constant I/U ratios across rust hazard levels indicating little genotype-by-environment interaction. Another study corroborating the low interaction across sites tested improved versus unimproved families in row-plots on 11 sites (LOPEZ-UPTON *et al.*, 2000). The I/U ratios obtained ranged from 0.35 to 0.80, and the adjusted model between improved and unimproved material was highly significant with a slope (I/U ratio) of 0.71 and $R^2 = 0.91$.

A broader study conducted by DHAKAL *et al.* (1996) evaluated realized genetic gains for rust resistance using 175 control-pollinated tests with 2051 first-generation families arranged in row and single-tree plots. The I/U ratios ranged from 0.53 to 1.37 depending of the level of improvement in the families. For example, seedlots representing unrogued and rogued seed orchards had 1.24 and 0.81 I/U ratios, respectively.

To date, most evaluations of rust resistance in slash and loblolly pine (*Pinus taeda* L.) have estimated differences in rust incidence between families or seedlots (SOHN and GODDARD, 1979; HODGE *et al.*, 1990; DHAKAL *et al.*, 1996; LOPEZ-UPTON *et al.*, 2000). It is clear that tree improvement programs have successfully produced material that incurs less disease on a wide range of sites. However, these studies have not generally quantified the effect of rust resistance on growth and stand yield. To provide an unbiased estimate for the effect of rust resistance on per unit area volume yield requires experiments planted in large rectangular plots (WHITE, 1987; FOSTER, 1992; LAMBETH *et al.*, 1994). Rust-associated mortality on high-rust-hazard sites (ANDERSON *et al.*, 1986) can alter competition patterns in row-plot trials, thereby magnifying the competitive advantages of resistant families growing near susceptible families. Large rectangular plots avoid this problem since they allow each seedlot to express its genetic potential without interference from other seedlots (ZOBEL and TALBERT, 1984; LOWERTS, 1986; WILLIAMS and MATHESON, 1994). However, large plots have low statistical precision and a large number of sites is needed to precisely estimate the magnitude of genetic differences (DHAKAL *et al.*, 1996).

The effects of rust resistance on slash pine growth and stand yield have been evaluated extensively in only one large rectangular-plot study installed between 1985 and 1987 (HODGE *et al.*, 1993). This Best Management Practices (BMP) study has been measured and analyzed at different ages from five years after planting (HODGE *et al.*, 1993; SCHMIDT and ALLEN, 1997) to mid-rotation age (12-year) (BRAWNER, 1998; BRAWNER *et al.*, 1999), finding significant gains in rust resistance (average $RR/RS=0.37$, where RR represents a selected rust-resistant seedlot and RS represents a rust-susceptible seedlot worse than unimproved material) and stand yield (17% at age 12 and a projected gain of 25 and 33% at ages 20 and 25, respectively).

The present study contains new information from the BMP experiment, using 5, 12, and 16-year data to assess the impact of slash pine rust resistance on

growth and stand yield. The original BMP study was installed with slash and loblolly pine on eight sites across high-rust-hazard environments in the southeastern USA (SCHMIDT and ALLEN, 1997). The present study evaluated slash pine on the five available trials for the species planted in high rust hazard locations.

The objectives of this study were to: (1) evaluate the effect of rust-resistance in slash pine on growth and stand yield at mid-rotation using large rectangular plots; (2) estimate and compare the effects of rust resistance on growth and stand yield across ages; and (3) assess the impact of silviculture and rust hazard on the effect of rust resistance for growth and stand yield.

Materials and Methods

Breeding Population and Genetic Trials

The plant material in the BMP study consists of selections from a first-generation breeding population of slash pine (*Pinus elliottii* var. *elliottii* Engelm.) in southeastern North America. The five companion trials analyzed in this study were planted by the Integrated Forest Pest Management Cooperative on high-rust-hazard sites located in north Florida and south Georgia between 1985 and 1987 (SCHMIDT *et al.*, 1995) (Figure 1, Table 1).

These trials compare rust-resistant (RR) with rust-susceptible (RS) seedlots. RR and RS are bulk-mixes of six rust-resistant and six rust-susceptible wind-pollinated families, respectively. The predicted rust resistance of the six families included in each seedlot was obtained from the predicted breeding values for rust resistance, designated as $R50$ values (WHITE *et al.*, 1996). $R50$ values indicate the percentage of total rust incidence expected for a particular seedlot, when unimproved material would incur 50% rust in the same environment (HODGE *et al.*, 1989). Best linear prediction (BLP) (WHITE and HODGE, 1988) was used to predict breeding values for approximately 2500 first-generation parents

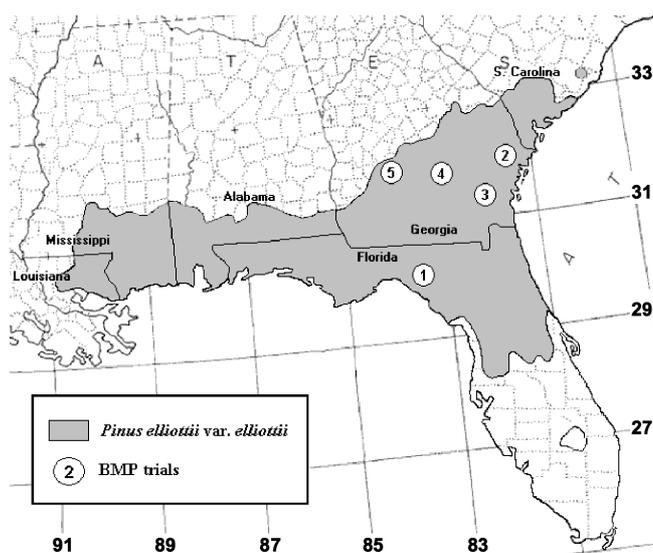


Figure 1. – Natural range of slash pine (CRITCHFIELD and LITTLE, 1966) and location of the five BMP trials used in the analysis.

Table 1. – Best Management Practices (BMP) trials used in the analysis.

#	Trial	County, State (place)	Rust hazard ¹	Site index (m) ²	Date planted	Measure ages	Rep # ³	No. of seedlots	Density (tree/ha)
1	551	Taylor, FL (Perry)	28.3 %	22.5	1985	5, 12, 17	3	2	1796
2	552	Bulloch, GA (Statesboro)	63.7 %	23.8	1986	5, 12, 16	3	2	1796
3	553	Wayne, GA (Screven)	41.8 %	22.2	1986	5, 12, 16	3	2	1495
4	554	Wheeler, GA (Mc Rae)	44.1 %	23.1	1986	5, 12, 16	3	2	1796
5	555	Sumter, GA (Americus)	36.3 %	20.1	1987	5, 12, 15	3	2	1796

¹) Realized total rust incidence at age five averaging rust-resistant (*RR*) and rust-susceptible (*RS*) seedlots with the formula $((RR + RS)/2) + RS/2$ in order to represent an unimproved seedlot (i.e. $R50 = 50$).

²) Site index on a 25-year basis (PIENAAR *et al.*, 1990) estimated at age 16 and based on *RR* performance in the trial.

³) Number of replications in the trial.

in 1995 (WHITE *et al.*, 1996). The *R50* averages for the six parents producing the offspring of the *RR* and *RS* seedlots were 17.8% and 68.8%, respectively⁴). Because the seeds were harvested from wind-pollinated seed orchards, an *R50* of 45% is assumed for pollen contribution (HODGE *et al.*, 1993). Therefore, the mean predicted *R50*s for the *RR* and *RS* seedlots are 31% ($17.8 * 0.5 + 45 * 0.5$) and 57% ($68.8 * 0.5 + 45 * 0.5$), respectively. These seedlots have approximately the same mean predicted gains in growth rate based on their BLP values for volume (WHITE *et al.*, 1996). Predicted parental breeding values in growth rate for the six parents in *RR* and in *RS* averaged 19.5% and 14.4% above unimproved material, respectively (VERGARA, 2003; Table A-4). Considering a pollen contribution with a predicted gain in growth rate of 7% (considering 30% pollen contamination, FRIEDMAN and ADAMS, 1985; EL-KASSABY *et al.*, 1989), the mean predicted gains in growth rate for the *RR* and *RS* seedlots are 13% ($19.5 * 0.5 + 7 * 0.5$) and 11% ($14.4 * 0.5 + 7 * 0.5$), respectively.

Experimental Design and Data Organization

The original BMP study was installed to assess the effect on rust resistance of eight sites, two oak treatments (presence or absence), two species (slash and loblolly pine), two seedlots (*RR* and *RS*), three cultural treatments, and three replications (SCHMIDT and ALLEN, 1997). However, the information utilized in this study (Table 1) included only five sites due to low survival or absence of slash pine on three of the original sites, one species, and two of the three cultural treatment. Therefore, the final experimental design at each of the five sites was a $2 \times 2 \times 2 \times 3$ randomized complete block split-plot design with two oak treatments, two seedlots, two cultural treatments, and three replications nested within oak treatment (Figure 2).

Before site preparation at each site, two areas of approximately 25 ha were located to apply the oak treat-

ments. All oaks were removed in the “oak-free” area, and the “oak-present” area as a control. Within each area, three replications of whole-plots with two seedlots (*RR* and *RS*) were randomly located. Finally, within each whole-plot, three cultural treatments were randomly assigned as sub-plots. The two cultural treatments included in this paper were “growth”, consisting of fertilization and herbicide applied in the planting year only, and “control”, without treatment.

In 2001, a total of 120 rectangular plots and nearly 4,000 trees were measured in five trials. Each gross plot had 0.1 ha with approximately 180 planted trees having between two and four buffer rows planted with non-

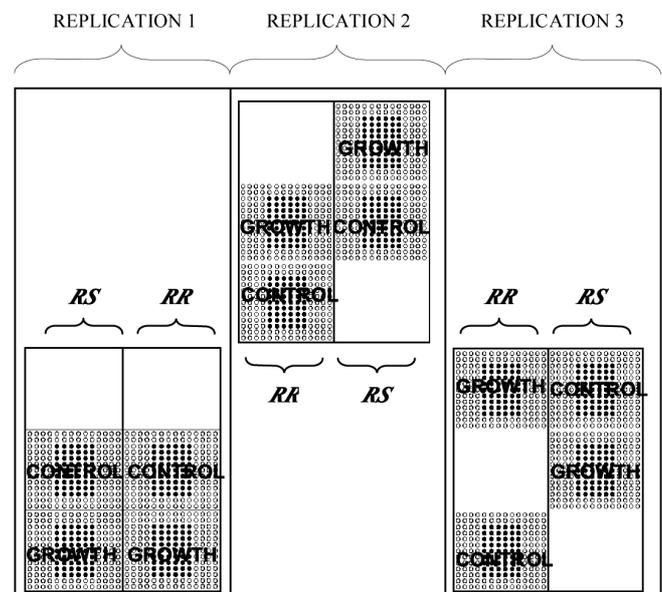


Figure 2. – BMP study experimental design. Example of an oak-treatment area with three replications, two seedlots as whole-plot (rust-resistant = *RR* and rust-susceptible = *RS*), and two cultural treatments as sub-plot (Growth = fertilizer and herbicide in year 1. Control = no treatment). Blank areas in the drawing represent the cultural treatment and loblolly pine plots excluded. ● = inner measure trees. ○ = outer trees (buffer). Only the inner trees were measured.

⁴) The individual breeding values can be found in VERGARA (2003, Table A-4).

measure trees (*Figure 2*). Only trees in the inner area of plots were measured, and these areas averaged 33 trees per plot at age 16. Trees were measured in each trial at five, 12 and 16 (15–17) years from planting (*Table 1*).

Variables measured were dbh (stem diameter outside bark at 1.4 m), total height, and branch or stem galls (0 = healthy, 1 = only branch galls, or 2 = at least one stem gall) for each measure tree. Inside bark volume (bole) (FANG *et al.*, 1999) and height-dbh ratio were calculated for each tree. The individual tree information was summarized on a per unit area basis obtaining one record per plot (experimental unit) for the following variables: percentage survival obtained as the fraction of planted trees (SURV), percentage total rust incidence (including trees with galls on branches or stem) (RUST), percentage stem rust incidence (including trees with at least one stem gall) (STEM), site index on a 25-year basis estimated using the anamorphic site index equation of PIENAAR *et al.* (1990) (SI25) (m) representing the seedlot's dominant height, average height-dbh ratio of living trees in the plot (HDR) (m cm^{-1}), average volume of living trees in the plot (TREEVOL) (m^3), and mean annual increment (MAI) ($\text{m}^3 \text{ ha}^{-1} \text{ year}^{-1}$) which represents stand yield. To employ the site index equation, dominant height was defined as the average height of the largest half of the trees in the plot based on dbh (*pers. comm.* Dr. BARRY SHIVER, modified from BAILEY and BROOKS (1994)).

Site indices were estimated using last-measured heights of the *RR* seedlot only, as the BMP study does not have a conventional unimproved control, i.e. the *RS* seedlot is disease susceptible. Therefore, site indices may be slightly overestimated, because the volume breeding value for *RR* is approximately 13% above seedlots that are unimproved for volume. Rust hazard in each trial was estimated using total rust incidence at age five (DHAKAL *et al.*, 1996) with the formula $((RR + RS)/2) + RS/2$ in order to obtain an estimation nearer than expected for unimproved material. This is because the mean predicted R50s for *RR* = 31%, *RS* = 57%, and $((31 + 57)/2) + 57/2$ is approximately 50%. The values of site index and rust hazard obtained in each trial are shown in *Table 1*.

Data Analysis

Site-by-site analysis

Evaluation of seedlot effects and the interaction of seedlot effects with other treatments on tree performance was conducted by analysis of variance (ANOVA) on each site at each measurement age utilizing restricted maximum likelihood analysis (REML) in Proc Mixed (SAS, 1996). Plot means or totals for each variable were used as the unit of observation. In the analyses, replications were treated as random effects, while oak treatments, seedlots, and cultural treatments were treated as fixed effects. Before analysis in Proc Mixed, a full linear model was run in Proc GLM (SAS, 1990) in order to locate non-significant interaction effects using Satterthwaite approximate *F* tests (SATTERTHWAITE, 1946). Non-significant terms were dropped from the model using the sometimes-pooling technique when *p*-values were greater than 0.25 (BOZIVICH *et al.*, 1956), to increase the

power of the tests of significance. Finally, a reduced model was run for each variable at each age. The full model used in Proc GLM was:

$$y_{ijkl} = \mu + \tau_i + \beta_{j(i)} + \gamma_k + (\tau\gamma)_{ik} + (\gamma\beta)_{kj(i)} + \varphi_l + (\tau\varphi)_{il} + (\gamma\varphi)_{kl} + (\tau\gamma\varphi)_{ikl} + \epsilon_{ijkl}$$

where

- y_{ijkl} = RUST, STEM, SI25, HDR, TREEVOL or MAI for the i^{th} oak treatment in the j^{th} replication within the i^{th} oak treatment, k^{th} seedlot, and l^{th} cultural treatment,
- μ = Overall mean,
- τ_i = Fixed effect of the i^{th} oak treatment (i = oak-free or oak-present),
- $\beta_{j(i)}$ = Random effect of the j^{th} replication nested within the i^{th} oak treatment (j = 1, 2 or 3 in each oak treatment),
- γ_k = Fixed effect of the k^{th} seedlot (k = *RR* or *RS*),
- $(\tau\gamma)_{ik}$ = Fixed effect of the interaction of oak treatment and seedlot,
- $(\gamma\beta)_{kj(i)}$ = Random whole-plot error which is the seedlot by replication within oak treatment interaction,
- φ_l = Fixed effect of the l^{th} cultural treatment (l = control or growth),
- $(\tau\varphi)_{il}$ = Fixed effect of the interaction of oak treatment and culture,
- $(\gamma\varphi)_{kl}$ = Fixed effect of the interaction of seedlot and culture,
- $(\tau\gamma\varphi)_{ikl}$ = Fixed effect of the interaction of oak treatment, seedlot and culture, and
- ϵ_{ijkl} = Random sub-plot error.

In the model, total rust incidence (RUST), stem rust incidence (STEM), and height-dbh ratio (HDR) were analyzed without transformation, because evidence shows that REML estimates are robust to violations of normality (BANKS *et al.*, 1985; WESTFALL, 1987).

Using least square means (lsmeans), realized gains were calculated for each variable at each site and age. Significance of *RR*'s genetic superiority was obtained looking at the seedlot effects in the ANOVA. The *RR*'s genetic superiority (realized gain) for SI25, HDR, TREEVOL and MAI was estimated comparing the *RR*'s seedlot performance against *RS*, with the formula $\text{Gain}\% = ((RR - RS)/RS) * 100$, where *Gain%* is the percentage of realized gain. Rust resistance realized gains were calculated as a measure of seedlot incidence adjusted to the rust hazard level in each site as follows. Total rust incidence per plot (RUST) and stem rust incidence per plot (STEM) were transformed to adjusted incidence (I50 and S50, respectively) using the hypothesis of proportional resistance (HODGE *et al.*, 1993). The transformation of STEM to S50 was made supposing that the hypothesis of proportional resistance to total rust incidence applies to stem rust incidence as well, which has not been documented. Consequently, results related to S50 must be taken with caution. The formulas used were $I50 = (RUST * 50) / (\text{rust hazard})$ and $S50 = (STEM * 50) / (\text{rust hazard})$ at each age, where rust hazard is defined as the observed total rust incidence on *RR* and *RS* seedlots combined by the formula

$((RR + RS)/2) + RS)/2$. For example, if in a given site the average RUST for *RR* and *RS* is 30% and 70%, respectively, rust hazard would be $((30 + 70)/2) + 70)/2 = 60\%$, and the observed incidence for *RR* would be $(30 \cdot 50)/60 = I50 = 25\%$. This value represents the percentage of total rust incidence an *RR* seedlot would get in a 50% rust hazard site, i.e. in a site where unimproved material would incur 50% total rust incidence.

Across-site analysis

The same type of analysis was conducted pooling all data from the plot means of a single variable across

sites. Site and site interactions were included in the full model as random effects (VERGARA, 2003). To improve the fit of the model, the REML analysis in Proc Mixed was conducted specifying the error variance in each site separately to allow for heterogeneous variances by site. An asymptotic *t* test from Proc Mixed was used to evaluate significance of random effects. Tests of seedlot effects, interactions of seedlot with other treatments, and interaction of seedlot with site were conducted for each variable at each measurement age. Using the sometimes-pooling technique, non-significant interactions with *p-values* greater than 0.25 (BOZIVICH *et al.*,

Table 2. – Significance levels for contrasts between rust-resistant (*RR*) and rust-susceptible (*RS*) seedlot mixtures. Realized Gain%, realized I50 and S50 calculated from the site-by-site analyses.

a) RUST		Contrast Significance Levels			I50		
Trial	Age 5	Age 12	Age 15-17	Age 5	Age 12	Age 15-17	
551	<.001**	<.001**	<.001**	22.2	21.3	18.2	
552	<.001**	<.001**	<.001**	24.9	20.4	21.1	
553	<.001**	<.001**	0.001**	20.2	20.2	14.6	
554	<.001**	<.001**	<.001**	19.8	23.8	25.4	
555	0.001**	0.009**	0.003**	17.9	23.3	20.1	
b) STEM		Contrast Significance Levels			S50		
551	0.003**	0.007**	0.005**	13.7	16.4	14.0	
552	0.001**	<.001**	<.001**	10.5	16.7	19.3	
553	0.001**	0.001**	<.001**	13.2	14.5	11.6	
554	<.001**	<.001**	<.001**	10.8	17.4	15.3	
555	0.004**	0.004**	0.004**	7.1	14.9	18.7	
c) SI25		Contrast Significance Levels			Gain%		
551	0.321	0.095 ⁺	0.199	-2.8	-4.4	-3.6	
552	0.256	0.076 ⁺	0.049*	8.4	3.0	3.9	
553	0.640	0.387	0.404	-2.3	-2.0	3.1	
554	0.291	0.670	0.097 ⁺	-1.9	0.4	2.6	
555	0.529	0.271	0.258	-2.8	2.4	2.3	
d) HDR		Contrast Significance Levels			Gain%		
551	0.296	0.191	0.155	-3.1	2.7	3.1	
552	0.330	0.003**	0.002**	-6.3	7.9	8.5	
553	0.995	0.085 ⁺	0.051 ⁺	0.0	3.1	3.8	
554	0.439	0.781	0.081 ⁺	-1.6	-0.7	4.1	
555	0.534	0.375	0.048*	4.6	4.4	5.8	
e) TREEVOL		Contrast Significance Levels			Gain%		
551	0.387	0.038*	0.040*	-8.6	-17.0	-19.3	
552	0.235	0.857	0.687	23.4	-0.7	-2.1	
553	0.901	0.523	0.734	1.5	-5.5	4.5	
554	0.723	0.279	0.977	-1.9	8.0	-0.2	
555	0.923	0.780	0.426	1.5	1.5	-4.7	
f) MAI		Contrast Significance Levels			Gain%		
551	0.942	0.335	0.785	0.8	-7.1	-2.8	
552	0.048*	0.007**	0.002**	57.3	48.0	50.5	
553	0.998	0.351	0.035*	0.0	9.1	22.0	
554	0.904	0.083 ⁺	0.007**	1.0	13.6	21.1	
555	0.688	0.425	0.110	8.0	21.4	28.3	

a) RUST = total rust incidence (%).

b) STEM = stem rust incidence (%).

c) SI25 = site index on a 25-year basis (m) (PIENAAR *et al.*, 1990) representing the seedlot's dominant height.

d) HDR = average height-dbh ratio of living trees in the plot (m cm⁻¹).

e) TREEVOL = average volume of living trees in the plot (m³).

f) MAI = mean annual increment (m³ha⁻¹year⁻¹) representing stand yield.

Gain% = $((RR - RS)/RS) \cdot 100$. I50 = estimated total rust incidence on *RR* when rust hazard is 50%. S50 = estimated stem rust incidence on *RR* when rust hazard is 50%. Significance levels: ⁺ $\alpha = 0.1$, * $\alpha = 0.05$, ** $\alpha = 0.01$.

1956) were dropped from the full model and a final reduced model was run for each variable at each age. Realized gains and significance of *RR*'s genetic superiority were estimated in the same way as for the site-by-site analysis.

Age-seedlot interactions

To compare gains assessed at different trial ages, age was added as a repeated measures factor in the across-sites linear model, testing age x seedlot interactions following the methodology of BOZIVICH *et al.* (1956) in order to drop non-significant interactions (VERGARA, 2003). Significant age x seedlot interactions were plotted to examine biological meaning in each trial.

Results and Discussion

Realized Gains in Rust Incidence

To evaluate rust incidence on the two seedlots *RR* and *RS*, data from five-year-old measurements were used, because at early ages some of the rust incidence is not evident and after age five, the effect of mortality can bias rust incidence estimations (PHELPS and CHELLMAN, 1975; ANDERSON *et al.*, 1986; SCHMIDT and ALLEN, 1997). Realized gains in rust resistance at five years have already been evaluated in the BMP study by HODGE *et al.* (1993), SCHMIDT and ALLEN (1997) and BRAUNER (1998). However, the current evaluation used only a portion of the same data and a different methodology in the analysis.

Individual site analysis

The differences in RUST and STEM between *RR* and *RS* were highly significant ($\alpha=0.01$) at all sites. In all

sites, *RR* had consistently lower rust incidence than *RS* (Table 2a and b). In addition, consistency in *RR* superiority was found in every combination of silvicultural treatments in all sites. Moreover, significant interactions between seedlot and silvicultural treatments were not found at any site ($\alpha=0.1$ level, data not shown). This absence of interactions denotes a high stability of genetic resistance in rust-resistant seedlots across silvicultural treatments.

The expression of genetic resistance is given by I50 and S50 values (realized percentage of total rust incidence and stem rust incidence, respectively, of the *RR* seedlot, when rust hazard is 50% as estimated by $((RR + RS)/2) + RS/2$). The average realized I50s by site at age five ranged between 17.9 and 24.9% (Table 2a), and the individual values for each site/oak/culture combination ranged between 7.2 and 30.0%. Average realized S50s by site at age five ranged between 7.1 and 13.7% (Table 2b), and values among treatment combinations ranged between 3.6 and 22.3%. Therefore, we would expect a maximum total rust incidence of 30% and a maximum stem rust incidence of 22% when planting this rust-resistant material on 50% rust hazard sites, i.e. sites where unimproved material have 50% total rust incidence.

Impact of site, silviculture and age on realized gains for RUST and STEM

Across-site analysis at each age. An across-site analysis allowing for heterogeneous variances by site was conducted for each variable at each age to confirm tendencies found in the site-by-site analysis and to test for interactions across sites (Table 3). The results at five years for RUST and STEM (Figure 3a and b) confirmed

Table 3. – *P-values* obtained in the REML-Proc Mixed (SAS 1996) run for the BMP study across sites fitting separate error variances at each site. For random effects the *p-values* were obtained from asymptotic *t* tests. Only effects with a *p* value of 0.25 or less for at least one response variable are shown.

Source	Effect	Df	Age	RUST	STEM	SI25	HDR	TREE VOL	MAI
Seedlot	Fixed	1	5	<.001**	0.001**	0.346	0.203	0.974	0.320
			12	<.001**	0.002**	0.956	<.001**	0.728	0.133
			16	<.001**	0.001**	0.003**	<.001**	0.348	0.003**
Seedlot x site	Random	4	5	<i>D</i>	0.205	<i>D</i>	<i>D</i>	<i>D</i>	<i>D</i>
			12	0.110	0.095 ⁺	0.999	<i>D</i>	<i>D</i>	0.180
			16	0.999	0.150	<i>D</i>	<i>D</i>	<i>D</i>	0.999
Seedlot x site x oak	Random	4	5	<i>D</i>	<i>D</i>	<i>D</i>	<i>D</i>	<i>D</i>	<i>D</i>
			12	<i>D</i>	<i>D</i>	0.110	<i>D</i>	<i>D</i>	<i>D</i>
			16	0.170	<i>D</i>	<i>D</i>	<i>D</i>	<i>D</i>	0.130
Seedlot x culture	Fixed	1	5	<i>D</i>	0.051 ⁺	<i>D</i>	<i>D</i>	<i>D</i>	<i>D</i>
			12	0.023*	0.146	<i>D</i>	<i>D</i>	<i>D</i>	<i>D</i>
			16	<i>D</i>	0.062 ⁺	0.278	<i>D</i>	<i>D</i>	<i>D</i>

Variables. RUST = total rust incidence (%), STEM = stem rust incidence (%), SI25 = site index on a 25-year basis (m) (PIENAAR *et al.*, 1990) representing the seedlot's dominant height, HDR = average height-dbh ratio of living trees in the plot (m cm⁻¹), TREEVOL = average volume of living trees in the plot (m³), MAI = mean annual increment (m³ ha⁻¹ year⁻¹) representing stand yield.

Factors. seedlot (rust-resistant mixture and rust-susceptible mixture), site (tests growing on five different environments), oak (oak-free and oak-present), culture (growth = fertilizer plus herbicide and control = no culture).

D = Non-significant interaction dropped in the model with $p > 0.25$ (BOZIVICH *et al.*, 1956). In the cases when the three factor interaction had a $p < 0.25$, the interaction seedlot x site was never dropped. Significance levels: ⁺ $\alpha=0.1$, * $\alpha=0.05$, ** $\alpha=0.01$.

that the difference in rust resistance between *RR* and *RS* was highly significant at $\alpha=0.01$ with realized values $I50=21.9\%$ and $S50=11.2\%$, corroborating the result obtained when the same study was analyzed by HODGE *et al.* (1993), SCHMIDT and ALLEN (1997), and BRAUNER (1998).

Consistent superiority of rust-resistant material over unimproved seedlots has been reported in virtually

every study for slash pine. Realized $I50s^{5)}$ of 25–39% (SOHN and GODDARD, 1979), 34–40% (HODGE *et al.*, 1990), 26–35% (DHAKAL *et al.*, 1996), 18–40% (LOPEZ-UPTON *et al.*, 2000), and 22% from this study demon-

⁵⁾ Values were transformed in $I50s$ in order to compare them with our results. By definition $I50 = 50(R_i/R_u)$, where R_i = rust incidence in improved seedlots and R_u = rust incidence in unimproved seedlots).

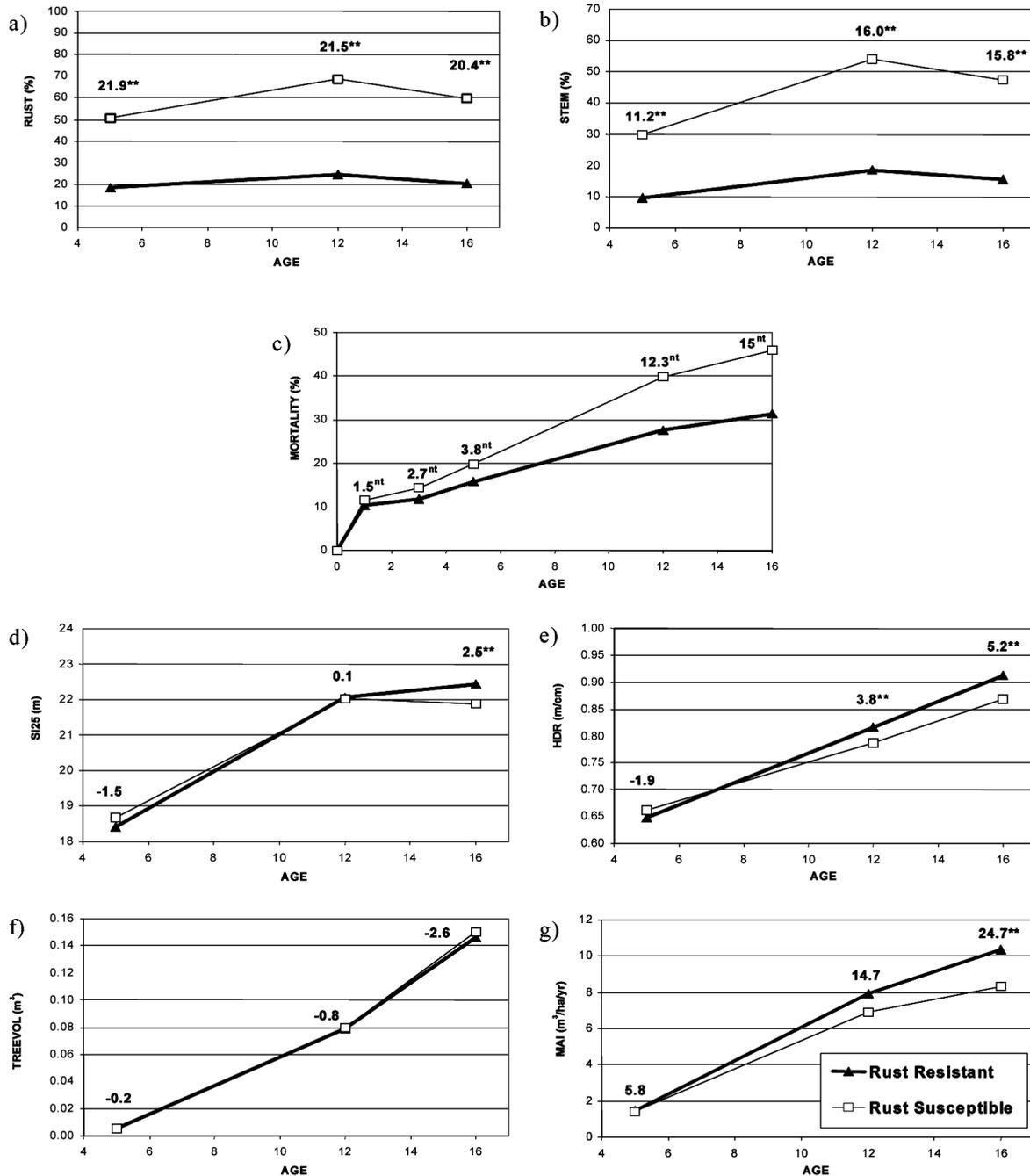


Figure 3. – Least square means from across-site analyses at ages five, 12 and 16 years old. Rust-resistant mixture (*RR*) and rust-susceptible mixture (*RS*) average performance for a) RUST = total rust incidence (%), b) STEM = stem rust incidence (%), c) Mortality (%), d) SI25 = site index on a 25-year basis (m) (PIENAAR *et al.*, 1990), representing the seedlot’s dominant height. e) HDR = average height-dbh ratio of living trees in the plot ($m\ cm^{-1}$), f) TREEVOL = average volume of living trees in the plot (m^3), g) MAI = mean annual increment ($m^3\ ha^{-1}\ year^{-1}$) representing stand yield. The values above the lines are $I50s$ (realized total rust incidence on *RR* when rust hazard is 50%) in a, $S50s$ (realized stem rust incidence on *RR* when rust hazard is 50%) in b, differences in mortality (*RS-RR*) in c, and realized gains ($Gain\% = ((RR-RS)/RS)*100$) in d, e, f, and g. Significance levels in gain: $^+\alpha=0.1$, $^*\alpha=0.05$, $^{**}\alpha=0.01$, nt = not tested.

strated the highly significant gain for first-generation selections. Thus, depending on the genetic quality of the seedlots planted, resistant material incurred 20–40% total rust incidence on sites in which unimproved material is 50%.

The stability of rust resistance across sites was evidenced by consistently non-significant seedlot x site interactions for RUST and STEM at all ages (*Table 3*). In one case, a weak interaction for STEM was significant at 12 years old, but not at five years old. Additionally, the three way interactions of seedlot x site x silvicultural effects were non-significant at $\alpha=0.1$ (*Table 3*). Similar to site effects, interactions of seedlots with silvicultural treatments were tested in the across-site analysis to assess the impact of oak removal and culture on rust resistance responses. In general, neither oak treatment nor culture had a significant impact on the realized gains obtained. Seedlot x culture was the only significant interaction for RUST at 12 years old and significant for STEM at five and 16 years old (*Table 3*). However, the graphic analysis of these significant interactions (VERGARA, 2003; *Figure 3–4*) did not show a change in the general tendencies, where rust susceptible seedlots were always more successfully attacked by fusiform rust than rust resistant seedlots. These results are consistent with those from other studies in slash pine indicating that rust-resistant seedlot mixtures are consistently resistant across sites (SCHMIDT and GODDARD, 1971; GODDARD and SCHMIDT, 1979; HODGE *et al.*, 1990; DHAKAL *et al.*, 1996) and silvicultural treatments (LOPEZ-UPTON *et al.*, 1999; LOPEZ-UPTON *et al.*, 2000). Nevertheless, this tendency is not always true when analyzing single families. In that case, family x environment interactions, especially in low-rust-hazard sites, can be significant with rank changes in slash pine (KUHLMAN *et al.*, 1995; DIETERS *et al.*, 1996; SCHMIDT *et al.*, 1999) and in loblolly pine (MCKEAND *et al.*, 2003).

There were substantial and consistent gains in rust resistance, and the magnitude of these gains should be directly predictable from the best linear prediction (BLP) breeding values (mean predicted R50s). Correspondingly, the overall realized rust resistance (I50) should be close to the mean predicted R50s for *RR* calculated by WHITE *et al.* (1996). However, the mean predicted BLP breeding value for the *RR* seedlot, $R50 = 31.4\%$, was larger than the realized $I50 = 21.9\%$ in this study. This implies that the BLP-predicted breeding values under-predicted the true rust-resistance of the *RR* seedlot. Curiously, in the validation done by HODGE *et al.* (1993) in the same study that used the previous 1988 BLP breeding values (R50s, HODGE *et al.*, 1989), overall realized rust resistance agreed very well with the mean predicted value ($I50 = 25.3\%$ vs $R50 = 23.7\%$). The most plausible explanation for the lack of agreement of predicted and observed realized gains in this study is an altered assumption regarding additive genetic variance in the 1995 BLP analysis. In 1995, the assumption of variance among open-pollinated families was modified from the traditional one-fourth of the additive variance to one-third of the additive variance (WHITE *et al.*, 1996) reducing the spread of predictions. Therefore, with the 1995 BLP predictions, the mean predicted R50 value of

RR was higher than with the 1988 predictions. Following the approach of DHAKAL (1995), the mean prediction of rust resistance for the *RR* seedlot would be $R50 = 23.25\%$ using the previous assumption of one-fourth, which is much closer to the realized $I50 = 21.9\%$.

Age-seedlot interactions. In order to compare realized I50s and S50s assessed at three trial ages, an across-site analysis was performed using age as a repeated measure. In that analysis, a highly significant ($\alpha=0.01$) influence of age on realized rust resistance was found. Nevertheless, *Figure 3a* and *b* shows that realized I50s and S50s do not follow any clear age trend. The statistically significant differences in rust resistance among ages were probably because assessments of rust incidence at ages 12 and 16 are very difficult and masked by mortality, due to the failure to install permanent plots, making later measures less reliable. Additionally, realized I50 and S50 are always significantly smaller than 50% (which indicates more resistance than unimproved material), meaning a positive and stable assessment of realized gain across ages. Few studies have analyzed the effect of age on rust resistance in slash pine, and our results agree with the only reference showing that realized gains for rust resistance was not influenced by age (DHAKAL *et al.*, 1996).

Realized Gains in Growth and Stand Yield

The analysis of growth and stand yield variables was conducted using data from the last measurement (approximately 16 years old) nearing rotation age. Realized gains in dominant height (SI25), tree volume (TREEVOL) and stand yield (MAI) were last evaluated in this same set of trials at 12 years, and projected gains from a growth model were estimated at rotation-age for volume (BRAWNER, 1998; BRAWNER *et al.*, 1999). Goals of this analysis were to estimate actual gains in growth traits at the older age and to validate the previous growth model projections.

Individual site analysis

As mentioned previously, gains for growth and stand yield traits in this study were not thought to be due to genetic differences in growth rates, because the mean volume breeding values predicted for seedlots *RR* (mixture of 6 rust-resistant families) and *RS* (mixture of 6 rust-susceptible families) are nearly identical (13% and 11%, respectively). Therefore, any gain in growth detected should be attributed to the seedlots' differences in rust resistance. Examination of seedlot differences for growth variables in the site-by-site analysis at 16 years old evidenced very consistent, although not necessarily significant, results in the four high-rust-hazard⁶ sites (trials 552, 553, 554, and 555). However, trial 551, the only trial growing on a moderate-rust-hazard site (*Table 1*), had an opposing trend (*Table 2*).

Realized gains for dominant height (SI25) were slightly positive (3%) on the average of high-rust-hazard sites (*Table 2c*). These gains might have been positive

⁶ Low, moderate, and high rust hazard represents <10%, 10–30%, and >30% of rust incidence, respectively, according to SCHMIDT (1998).

because on high-rust-hazard sites rust infection eventually reduced height growth in the *RS* seedlot more than in the *RR* seedlot. In contrast, slightly and non-significant negative gains (-3.6%) in the moderate-rust-hazard site (trial 551) could have been produced because the lower infection would not be enough to express a difference on SI25 between seedlots.

Height-dbh ratio (HDR) was consistently higher for the *RR* seedlot compared to the *RS* seedlot across all trials (Table 2d), indicating less taper in the *RR* seedlot. The nature of this index is highly influenced by other variables like stand density or height, and therefore, the differences could be due to genetic differences for these other variables.

In the case of individual tree volume (TREEVOL), differences between seedlots were not generally significant except in trial 551 (Table 2e). The significant and negative gain (-19.3%) obtained in TREEVOL at trial 551 (moderate-rust-hazard) could be the effect of lower mortality in *RR* (30%) than in *RS* (42%) without a detrimental effect of rust on growth rate in the remaining trees. But it is unclear why this happened only in the moderate-rust-hazard site.

The gains in MAI (mean annual increment in $\text{m}^3 \text{ha}^{-1} \text{year}^{-1}$), which represent gains in stand yield, were almost always large and positive in all sites (Table 2f), demonstrating higher stand yield for the *RR* seedlot. The only slightly negative gain was obtained, again, in the moderate-rust-hazard site (trial 551, -2.8%). In contrast, the high-rust-hazard sites averaged gains of 30.5% for the *RR* seedlot. Further, gains were consistently positive in each combination of oak and culture treatments, including three of the four treatments in trial 551 (data not shown for the two culture and oak treatments). In trial 551, only the combination oak-free plus no-culture treatment had a negative gain (-18.7%), which accounts for the small negative gain for the entire trial. This generally positive gain in MAI is likely due to the combined effects of rust susceptibility, which lead to higher mortality in the *RS* compared to the *RR* seedlot and slightly slower growth due to more stem galled trees in the *RS* seedlots.

The impact of site, silviculture and age on realized gains for growth and stand yield

Across-sites analysis at each age. Results from the across-sites analysis are shown in Figure 3 (d, e, f, and g) and generally represent the average gains to be obtained when deploying rust-resistant seedlots on high-rust-hazard sites. The small, but highly significant realized gain, obtained for SI25 (2.5%, Figure 3d) is strong evidence of the effect of rust on height growth, given that the inherent genetic growth rates of the *RR* and *RS* seedlots are identical. Therefore, the gain obtained is probably due to lower growth rate for the *RS* seedlot caused by more stem-galled trees, which has been found in other studies (SCHMIDT *et al.*, 1981; BRAUNER, 1998; LOPEZ-UPTON *et al.*, 2000).

No gains were found for individual tree volume (Figure 3f), most likely because individual volume of living trees was influenced by both mortality and reduced

growth when rust infection was present. Rust associated mortality (Figure 3c) generated lower survival, and therefore, lower stand density on *RS* plots, allowing remaining trees to grow faster in dbh than trees on *RS* plots with higher stand density. Conversely, those trees with stem galls probably suffered reduced individual tree growth (SCHMIDT *et al.*, 1981; BRAUNER, 1998) and more of these stem-galled trees occurred in the *RS* seedlot. As a result of this balance between faster and slower growth rate, realized gains for TREEVOL close to zero on high-rust-hazard sites seems reasonable. The fact that *RS* trees grew faster in dbh and slower in height than *RR* trees probably explains the 5.2% in HDR gain obtained in this study (Figure 3e).

Finally, stand yield, as represented by MAI, was the most important outcome of the differential rust resistance between seedlots. The highly significant gain in MAI (24.7%, Figure 3g) is likely the result of two factors related to rust susceptibility. Stand yield loss is primarily associated with stem-galled trees that die and or grow more slowly throughout the rotation (SCHMIDT *et al.*, 1981). In this study, both increased rust-associated mortality and reduced height growth are clear (Figure 3c and d).

The 24.7% gain in MAI obtained in the BMP study for slash pine represents an absolute gain in stand yield of $32.9 \text{ m}^3 \text{ha}^{-1}$ (inside-bark volume) at age 16. This value can be conservatively extrapolated to 25-year-rotation age. At that age the absolute gain in stand yield would be $51.4 \text{ m}^3 \text{ha}^{-1}$ ($735 \text{ feet}^3 \text{acre}^{-1}$) above a rust susceptible yield of about $205 \text{ m}^3 \text{ha}^{-1}$ ($2940 \text{ feet}^3 \text{acre}^{-1}$), without considering intensive silvicultural management. The 24.7% gain in MAI compares favorably with the 25% gain in stand yield projected to age 20 using growth models by BRAUNER *et al.* (1999) from 12-year-old data in the same study. Although the gains in this study compare rust-resistant and rust-susceptible seedlots and therefore, could over-estimate the genetic gains of rust-resistant seedlots compared to unimproved material, our conservative extrapolation of gains to rotation age would ameliorate the effect. Additionally, the impact of these realized gains would be even more important considering the additional effect of rust resistance on wood quality and marketability (WEBB and PATTERSON, 1984; ANDERSON *et al.*, 1986; PYE *et al.*, 1997; CUBBAGE *et al.*, 2000). Realized gains for MAI varied substantially among sites (Table 2f) and between oak treatments (data not shown). The interactions, however, were never statistically significant ($\alpha=0.1$) as confirmed by lack of significance of seedlot x site and seedlot x oak (Table 3). This absence of seedlot x environment interaction might not be true when analyzing single families, particularly in low-rust-hazard sites (KUHLMAN *et al.*, 1995; DIETERS *et al.*, 1996; SCHMIDT *et al.*, 1999).

Predicted volume breeding values for *RS* and *RR* are 11% and 13%, respectively. This difference of only 2% cannot account for the 24.7% realized gain obtained in MAI. WHITE *et al.* (1996) predicted yield indices that combine R50 and tree volume, putting more weight on R50 in high-rust-hazard stands. In order to use these indices, rust hazard for these five sites was categorized in low, moderate, and high-rust-hazard representing

<20%, 20–60%, and >60% of total rust incidence, respectively, on unimproved material at five years of age. Under this criterion, in general, the BMP trials are placed in moderate-rust-hazard sites where the yield index earned predicted gains in yield of 8% and 17% for *RS* and *RR*, respectively. Furthermore, supposing high-rust-hazard sites for the BMP study, predicted values would be 6% and 21% for *RS* and *RR*, respectively. These predicted differences of 9% (moderate rust hazard) and 15% (high rust hazard) considerably underestimate the 24.7% gain of the *RR* seedlot in this study. The devastating effects of rust infections on stand yield seem to be more serious than predicted at these rust hazard levels.

Age-seedlot interactions. The across-site analysis, using age as a repeated measure, demonstrated highly significant age x seedlot interactions for SI25 and HDR. The significance of those interactions for the variables TREEVOL and MAI was not available, because the algorithm used did not converge to a solution. Nevertheless, looking at the site-by-site analysis, age x seedlot interactions appeared to have little importance for TREEVOL and highly important meaning for MAI.

Figure 3d illustrates the change of ranking for SI25. Although the negative gain at age 5 was not significant, it occurred consistently in four of five trials (*Table 2c*). Later, there were no differences in seedlots at age 12, and at age 16 there were positive and significant gains of the *RR* seedlot for SI25. This variable is not influenced directly by mortality (i.e. by density) (PIENAAR and RHENEY, 1996; PIENAAR and SHIVER, 1984); hence, the age x seedlot interaction might be due to fast early height growth in the *RS* seedlot followed by reduced growth rate after stem infection. Supporting this idea, evidence that rust susceptibility is related to higher availability of succulent tissue in the plants (SCHMIDT *et al.*, 1981) could mean that genotypes with a high initial growth rate are more susceptible to rust. However, this correlation between high initial growth rate and rust susceptibility has never been supported by progeny test analysis in slash pine.

The change of ranking for HDR (*Figure 3e*) had the same pattern as SI25, but this interaction was likely caused by mortality. Small differences in mortality at age 5 (*Figure 3c*) between seedlots allowed *RS* to have similar diameters but larger heights than *RR* generating higher HDR in *RS* than in *RR*. Later at ages 12 and 16, mortality and reduced height growth in the *RS* seedlot changed the HDR by allowing a faster diameter growth rate than in *RR* and therefore, positive gains.

In the case of MAI, the age x seedlot interactions had a scale effect, steadily increasing gain with age (*Figure 3g*). This pattern was very consistent among sites, and it was coincident with the pattern of mortality in the study (*Figure 3c*). The projected gains obtained by BRAWNER *et al.* (1999) for slash pine in the BMP study (25% at age 20 and 33% at age 25) follows about the same tendency across time, but apparently that projection still underestimated the realized gains in stand yield. Following the tendency shown in *Figure 3g*, the 24.7% realized gain in MAI obtained at age 16 in this

study, should be larger at age 20 than the 25% projected for BRAWNER *et al.* (1999).

Conclusions

Rust resistance was substantially improved in slash pine in this study by using a rust-resistant seedlot (mixture of 6 rust-resistant families) on high-rust-hazard sites. The results were consistent across sites and silvicultural treatments with no seedlot x environment interaction, supporting the idea of stability of genetic rust resistance across different environments, at least when using seedlot mixtures with several families. Additionally, assessments of rust resistance were consistent across ages with small changes in the observed realized gains. The consistently lower total rust incidence in the *RR* seedlot (realized I50 = 21.9%) is smaller than the expectation (mean predicted R50 = 31.4%), although there is an agreement among realized and predicted values for substantial and positive gains.

Realized rust resistance in slash pine had a positive, but small, effect on dominant height (SI25) and the height-dbh ratio (HDR), but no effect on individual tree volume (TREEVOL). Nevertheless, it had a significant and positive effect on stand yield (MAI). At age 16, the realized gain in stand yield was approximately 25%, consistent across sites and silvicultural treatments. If this realized gain is extrapolated conservatively to a 25-year-rotation age, the realized gain in stand yield (inside-bark volume) obtained by planting rust resistant material in high-rust-hazard sites would be at least 51.4 m³ ha⁻¹ (735 feet³ acre⁻¹) above a rust susceptible yield of about 205 m³ ha⁻¹ (2940 feet³ acre⁻¹). Realized gain in stand yield was primarily influenced by rust-associated mortality and slower individual tree height growth in the rust susceptible seedlot. This amount of realized gain reflects a larger impact of rust resistance in stand yield than projected by growth models or predicted by yield indices in high-rust-hazard sites. The devastating effects of rust infection on stand yield, and possibly on wood quality and marketability, are clearly overcome by genetic rust resistance.

Realized gains for growth and stand yield traits varied across ages. The accumulated effect of rust infection across age generated increasing gains in dominant height, height-dbh ratio, and stand yield from age 5 to age 16, indicating that assessing realized gains for these traits must be done near rotation age. In particular, differences of realized gains in stand yield were large across ages, coinciding with the pattern of mortality due to rust infection. The assessing of age-age correlations in order to predict gains in stand yield due to rust resistant seedlots will be an important challenge when this study reaches the rotation age in five or 10 more years.

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Age-related Trends in Genetic Parameters for Jack Pine and Their Implications for Early Selection

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Abstract

Trends in genetic parameters for height growth of jack pine (*Pinus banksiana* Lamb.) were examined over three series of family tests throughout New Brunswick. Data were analyzed for each site and across sites within each series. Although individual narrow sense heritability estimates from single-site analyses varied substantially

from site to site and showed no consistent age-related pattern, the estimates from across-site analyses showed an increasing trend to age 20. Similar as individual narrow sense heritability, the coefficient of additive genetic variance estimated from single site showed more variation than those estimated from across site analyses. Age-age (type-a) genetic correlations for height were high and could be well predicted by a LAR^2 model, where LAR is the natural logarithm of the ratio between two ages at assessment. Type-b genetic correlations were high and of similar magnitude at different ages. Genetic correlations between height at different ages and volume at one-half rotation age were generally high. Taking the volume at one-half rotation age as the target trait, the selection for target trait from early selection at

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