

GENOTYPE-BY-ENVIRONMENT INTERACTION AND DEPLOYMENT CONSIDERATIONS FOR FAMILIES FROM FLORIDA PROVENANCES OF LOBLOLLY PINE

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ABSTRACT

Open-pollinated families of *Pinus taeda* L. from Marion County and Central Florida provenances were planted at seven sites in the lower coastal plain of the southeastern United States. Data for mean annual increment in volume at age – 15 were analyzed. The results indicated that these families were more interactive with environment than previously reported for families from other loblolly pine provenances. Multivariate restricted maximum likelihood was used to define deployment zones with little genotype by-environment interaction within a zone and high interaction between zones. The two statistically defined zones were biologically pleasing with one zone consisting of the western-most tests and the other zone of the tests along the Atlantic Coast. Two sites with aberrant soils failed to group with either zone. Evaluation of deployment and selection options across and between zones indicated that considerable gain in mean annual increment for volume was available through use of these zones. Further research is required to understand the causes and nature of these genotype-by-location interactions.

Keywords: *Pinus taeda*, Florida source, genotype-by-environment interaction, type B genetic correlation, deployment.

INTRODUCTION

Loblolly pine (*Pinus taeda* L.) is the most important timber species in the southeastern United States making up 80% of the 10 million ha of forest plantations in this region (KELLISON 1992). Several studies have examined genotype-by-environment interactions for loblolly pine and found differences among genotypes across various environments for traits such as growth rate, rust resistance, and sweep (WELLS & SWITZER 1971; OWINO 1977; LA FARGE & KRAUS 1981; YEISER *et al.* 1981; LI & MCKEAND 1989; DOUGLASS *et al.* 1993).

When genotype-by-environment interactions are significant, it is important to define how many families contribute to the interaction, the nature of the interaction, and also how economically significant it is, before making any decision about future breeding, testing and deployment (BURDON 1977; LINDGREN 1984; AASTVEIT & AASTVEIT 1993; COOPER & DELACY 1994). A better understanding of genotypic stability or conversely, responsiveness, of selected families over various locations can increase genetic gain by allowing breeders

to deploy families to specific environments to maximize forest productivity (LI & MCKEAND 1989). In addition, breeding and progeny testing programs could be altered to produce greater gain if genotype-by-environment interactions are important.

Several statistical methods for assessing genotype-by-environment interactions have been proposed in the field of agriculture and forestry such as variance components, regression, genetic correlations, multivariate analyses and cluster techniques (SHELBOURNE 1972; BARNES *et al.* 1984; SKRØPPA 1984; LIN *et al.* 1986; PSWARAYI *et al.* 1997). In forestry the primary methods that have been used are genetic correlations (BURDON 1977; HODGE & WHITE 1992; PSWARAYI *et al.* 1997) and regression analysis (OWINO 1977; BARNES *et al.* 1984; LI & MCKEAND 1989). Both of these types of methods have important advantages (such as being easy to compute and having a strong statistical basis).

Genetic parameters such as heritabilities and interactions of family and environment have not been well studied for the Florida provenances compared to

provenances from other geographic areas of the loblolly pine natural distribution, and these Florida provenances are important both in the southeastern USA as well as in other parts of the world (SCHULTZ 1999; BRIDGWATER *et al.* 1997). There is also a strong indication that the Florida provenances perform better than those from the Atlantic Coastal Plain and Gulf Coastal Plain when planted in the Lower Coastal Plain (SIERRA-LUCERO 1999). This paper focuses exclusively on 31 families from two Florida provenances, Marion County (MC) and Central Florida (CF).

The objectives of the paper are, for mean annual increment for volume at age 15, to:

1. Estimate genetic parameters including heritability, type B genetic correlations and trait-trait genetic correlations;
2. Examine the family-by-environment interactions within the Florida sources and develop deployment and testing regions homogeneous for genetic performance to improve genetic gains;
3. Compare deployment gains for a potential region based on parental performance in the same and other regions.

MATERIALS AND METHODS

The data

Data were available from seven provenance-progeny tests located in four states: Alabama, Florida, Georgia, and Mississippi (Figure 1, Table 1). The provenances planted in these experiments are from three Coastal Plain areas in the southeastern USA (see Figure 1): South Carolina and Georgia, Florida (CF and MC), and Alabama and Mississippi. Open-pollinated seed-orchard seed was collected from approximately 15 families from each of the four sources (about 60 open-pollinated families). Within each provenance the lightly-rogued or unrogued grafted orchards consisted of wild selections from within the specific provenance and the orchards were physically located within the zone of origin. At each field location, 38 to 60 families were planted in a randomized complete block design in a split-plot experiment with 3 to 5 complete blocks. Provenances were arranged as whole plots and each family within a whole plot was represented by a 10-tree row sub-plot. Families from the same provenance were grouped together in a whole-plot within each block to minimize competition among provenances; however, there were no internal border rows. In total, the seven

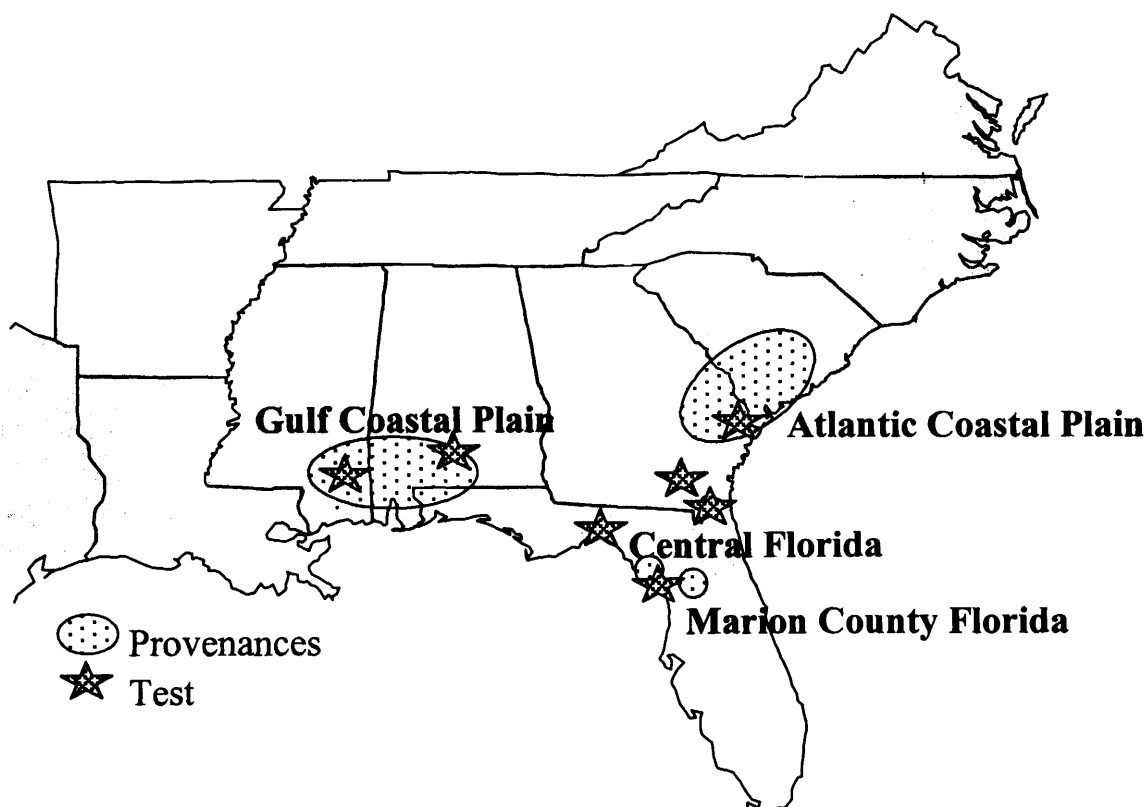


Figure 1. Test numbers and locations for the seven provenance-progeny studies used in this experiment and zone of origin for the Florida sources.

Table 1. Test location, site description^a and significance of family within provenance effect for Mean Annual Increment for Volume (MAIV, m³·ha⁻¹·yr⁻¹) for the seven open-pollinated loblolly pine progeny trials established in 1982 and 1983.

Test ID	280	281	284	285	286	287	288
County	Levy	Butler	Wayne	Nassau	Effingham,	Jefferson	Green
State	FL	AL	GA	FL	GA	FL	MS
Latitude	29 14	31 54	31 44	31 38	32 26	30 40	31 21
Longitude	82 70	86 45	81 79	81 37	81 28	83 81	88 64
Rainfall (mm)	1320	1441	1490	1391	1510	1350	1460
AAMT (°C) ^b	-6.7 to -9.4	-9.5 to -12.2	-6.7 to -9.4	-6.7 to -9.4	-6.7 to -9.4	-6.7 to -9.4	-9.5 to -12.2
MAIV ^c m ³ ·ha ⁻¹ ·yr ⁻¹	15.6	21.1	15.6	12.9	11.3	14.5	18.3
FAM(PROV) ^d	0.36	0.0001	0.0001	0.01	0.001	0.001	0.0001

^{a)} There was less than 100 meter difference in elevation among the sites.

^{b)} Average Annual Minimum Temperature (USDA Plant Hardiness Zone Map 1990).

^{c)} Average Mean Annual Increment for Volume for the Florida families.

^{d)} Significance (α level) of family within provenance for mean annual increment for volume, Equation 3 by site.

sites included approximately 14,500 trees.

Only the age-15 data from the two Florida provenances were used in these analyses, i.e. data from Georgia and South Carolina, and Mississippi and Alabama sources were deleted. Each tree was measured for height in meters (HT), diameter at breast height in centimeters (DBH), rust presence or absence, and survival. Tree volume in cubic meters (VOL) (LAMBETH *et al.* 1983; HODGE *et al.* 1996) and mean annual increment for volume in cubic meters per hectare per year (MAIV) (SIERRA-LUCERO 1999) were computed as:

$$\text{VOL (m}^3\text{)} = (0.25)(3.14)(\text{DBH}^2)(1.37 + 0.33(\text{HT} - 1.37)) \quad [1]$$

$$\text{MAIV (m}^3\text{ha}^{-1}\text{yr}^{-1}\text{)} = ((\text{VOL})(\text{Survival})(\text{Trees per hectare}))/\text{Age} \quad [2]$$

where:

Survival = the decimal equivalent of survival of the family row plot at age 15;

Trees per hectare = planting density of the tests;

Age = measurement age in years, 15.

Before analysis, data were checked for errors by examining suspected outliers in each block of each site. Outliers are data points outside the normal range of measurement that produce inflated variances (MAGNUSSEN 1993; WHITE 1996). A total of 2.2 % of the observations were deleted as suspected outliers for various reasons such as recording errors during data collection or being runts that were likely due to selfing (WHITE *et al.* 1986). Individual MAIV's were standardized by the square root of the mean square error of each associated test-block combination to remove scale effects and homogenize variances across sites (HODGE *et al.* 1996;

WHITE 1996; DUTILLEUL & CARRIERE 1998; LU 1999). Hence the error variance of the standardized data was approximately 1.0 for all sites, and when pooled across sites.

Statistical analyses and genetic parameter estimates

The univariate linear model used in the statistical analysis was:

$$y_{ijklm} = \mu + S_i + B(S)_{ij} + P_k + PS_{ik} + PB(S)_{ijk} + f(P)_{kl} + f(P)S_{ikl} + f(P)B(S)_{ijkl} + w_{ijklm} \quad [3]$$

where:

μ is an overall mean;

S_i is the fixed effect of the i^{th} site, $i = 1$ to 7;

$B(S)_{ij}$ is the fixed effect of the j^{th} block within the i^{th} site, $j = 1$ to 5;

P_k is the fixed effect of the k^{th} provenance, $k = 1$ to 2;

PS_{ik} is the fixed interaction between provenance and site;

$PB(S)_{ijk}$ is the fixed interaction between provenance and block within site;

$f(P)_{kl}$ is the random effect of the l^{th} family within the k^{th} provenance, $k = 1$ to 15, $\sim \text{NID}(0, \sigma_{f(P)}^2)$;

$f(P)S_{ikl}$ is the random interaction between family within provenance and site, $\sim \text{NID}(0, \sigma_{f(P)S}^2)$;

$f(P)B(S)_{ijkl}$ is the random interaction between family within provenance and block within site, i.e. plot, $\sim \text{NID}(0, \sigma_{f(P)B(S)}^2)$; and

w_{ijklm} is random error, $\sim \text{NID}(0, \sigma_w^2)$.

Variance component estimates from the above model were used to calculate individual-tree heritabilities and type B genetic correlations (YAMADA 1962) for

MAIV.

Unbiased individual tree heritabilities (h^2) were estimated from pooled sites measured at 15 as:

$$h^2 = V_A / V_p \quad [4]$$

where: V_A = additive genetic variance estimated as $4\sigma_{f(P)}^2$ from equation 3. V_p = phenotypic variance within provenance estimated as

$$\sigma_{f(P)}^2 + \sigma_{f(P)S}^2 + \sigma_{f(P)B(S)}^2 + \sigma_w^2$$

from equation 6. The coefficient of relationship was assumed to be 4. This implies that the open-pollinated seed-orchard seed were produced by unrelated and non-inbred parents, although more conservative values for the coefficient of relationship for open-pollinated seed have been described (SQUILLACE 1974; SORENSEN & WHITE 1988).

The YAMADA (1962) method was used to estimate type B genetic correlations by families (r_{Bf}) for each of the regions (various groupings of the seven sites). This method estimates (using a univariate linear model) the genetic correlation of the same trait in different environments (FERNANDO *et al.* 1984; LU 1999).

$$r_{Bf} = \frac{\sigma_{f(p)}^2}{\sigma_{f(p)}^2 + \sigma_{f(p)s}^2} \quad [5]$$

When $r_{Bf}=1$, there is no family-by-site interaction, and when $r_{Bf}=0$, family-by-site interaction is strongly indicated. SHELBORNE (1972) suggested a limiting value of 0.67 to indicate the presence of severe genotype-by-environment interaction, *i.e.* values lower than 0.67 compromise the genetic gain and the breeder should consider regionalisation (MATHESON & RAYMOND 1984; HODGE 1996).

The major focus of this paper was to examine the family-by-site interactions for the Florida families. Many indices has been suggested to identify relatively interactive or stable families across sites. These indices and their interrelationships were described by LIN *et al.* (1986) and WEBER *et al.* (1996), and some of these indices have been used in forestry (LI & MCKEAND 1989; ADES & GARNIER-GÉRÉ 1996).

Because of the data imbalance in this study, a stability index, p_i , was used to indicate reactive and stable families. This index uses mixed model theory as implemented in Proc Mixed (SAS® INSTITUTE 1996), WHITE & HODGE (1989) and LITTELL *et al.* (1996), following the theory discussed by LIN *et al.* (1986). Best Linear Unbiased Prediction (BLUP) was used to predict values for all random effects in the linear model

[eq. 3]. The predictions for the genotype-by-environment interaction ($G \times E$) in the form of the family within provenance by site interaction were used as data for the calculation of the index. When p_i is greater than one, the family is more interactive than the average family in the provenance. When p_i is less than one, the family is more stable than the average family within a provenance.

The formula for p_i for each family is:

$$p_i = \frac{\sum_{i=1}^a (f(P)S_{ikl})^2}{\frac{n_i}{N} \sum_{i=1}^a \sum_{l=1}^d (f(P)S_{ikl})^2} \quad [6]$$

where:

p_i is the index value for family 'i' within provenance 'k';

$f(P)S_{ikl}$ is the BLUP of the each random interaction of family within provenance with site ($G \times E$, eq. 1) for MAIV at age 15;

n_i is the number of $G \times E$ predictions for family 'i' within provenance 'k' across 'a' sites; and

N is the total number of $G \times E$ predictions across all sites for all 'd' families within a given provenance.

Various groupings of the seven sites were formed to identify possible homogeneous areas for deployment based on the premise that the type B correlation within a homogeneous area should be at or above the value suggested by SHELBORNE (1972) of 0.67. When found, these homogeneous areas for genetic performance were called "regions". MTDFREML (BOLDMAN *et al.* 1995) was the software used to identify regions and to calculate the genetic correlations between regions. With this program MAIV on sites within the same region was considered one trait and on sites in different regions as considered a distinct trait (even though MAIV at age 15 was the only variable analyzed, LU *et al.* 2001).

Genetic correlations between MAIV measured in different regions were estimated using MTDFREML as:

$$r_{g(\text{region 1, region 2})} = \frac{\sigma_{f(P)\text{region 1, region 2}}}{\sqrt{\sigma_{f(P)\text{region 1}}^2 \sigma_{f(P)\text{region 2}}^2}} \quad [7]$$

where $\sigma_{f(P)}$ is the estimate of the covariance for families within provenance between regions 1 and 2; $\sigma_{f(P)}^2$ is the estimate of family within provenance variance for region 1 or 2, respectively from eq. 3.

Genetic gain estimates

Deployment gains that quantify the results of using the

best parents were calculated using (1) estimated marginal family values (*MFV*), which are the estimated family performance across all sites and regions, and (2) estimated family values (*FV*), which are the estimated family performance in a specific region. The *MFV* for each family was estimated, using the results from eq. 3, as:

$$MFV_{kl} = LSM_k + f(P)_{kl} \quad [8]$$

where:

LSM_k is the least square mean for MAIV for a provenance (either MC or CF) across all sites; and

$f(P)_{kl}$ is the BLUP prediction for family 'l' within provenance 'k' across all sites.

The *FV*, which is specific to a particular family-site combination, was calculated, using the results from analysis using eq. 3, as:

$$FV_{ikl} = LSM_{ik} + f(P)_{kl} + f(P)S_{ikl} \quad [9]$$

where:

LSM_{ik} is the least squares mean for a site-provenance combination;

$f(P)_{kl}$ is the BLUP prediction for family performance across all sites; and

$f(P)S_{ikl}$ is the BLUP prediction of the family within provenance by site interaction, which assumes the interaction is repeatable.

A regional value for a family was calculated as the mean of the *FV*'s for the family across all sites in the region.

The above least square means and family values were used to predict genetic gains across all sites and also for regional deployment. Deployment gains across all sites were estimated as the average *MFV*'s of the five best marginal parents over the mean of the two provenance means, converted to a percentage [eq. 8]. Regional deployment gains were calculated as the average of the top five *FV*'s for a region divided by the mean of the two provenances for the region, converted to a percentage [eq. 9].

RESULTS AND DISCUSSION

Family-by-environment interaction for Florida provenances

In by-site analyses for MAIV, family within provenance was highly significant for all sites except 280 (Table 1). Analysis across the seven sites, Eq. 3, yielded significant site by family within provenance interaction, not shown, and very low heritability (Table

Table 2. Estimates of individual heritabilities (h^2) and type B genetic correlations (r_B) for mean annual increment for volume at age 15 across seven tests for the families within the Marion County and Central Florida provenances. The analysis was run with all 31 families and then again with the eight most interactive families with sites removed, based on the stability index [eq. 6].

All 31 Families		Eight Most Interactive Families Removed	
h^2	r_B	h^2	r_B
0.08	0.27	0.11	0.64

2). The type B genetic correlation for families within provenances across all sites [eq. 5] was 0.27 indicating significant rank changes for the Florida families across the seven sites in this study (Table 2). Due to the importance of family-within-provenance by site interactions for MAIV for the Marion County and Central Florida provenances, analyses were conducted to aid in understanding these genotype-by-environment interactions.

First, graphical analyses (not shown) were performed by plotting the FV_{ikl} 's for each provenance separately [eq. 9], arrayed by site according to the site index. The graph of the MC source showed strong rank changes across sites, while families of the CF source showed fewer rank changes.

The second analysis used p_l [eq. 6] to identify the most reactive families. Eight very reactive families (out of a total of 31 families) with $p_l > 1.6$ accounted for 48% of the sum of the weighted squared family-within-provenance by site predictions for MAIV at age 15 [eq. 6]. Five of the eight reactive families were from the MC provenance and these accounted for 34% of the weighted squared predictions. This proportion of highly reactive families, 26 %, is greater than other authors have reported for loblolly pine (LI & MCKEAND 1989; MCKEAND *et al.* 1990; STONECYPHER *et al.* 1996; PSWARAYI *et al.* 1997).

When these eight reactive families were dropped from the analysis, the type B genetic correlation increased substantially from 0.27 to 0.64, for the combined analysis across seven sites. Further, the individual heritability [eq.4] for MAIV increased from 0.08 to 0.13.

Regionalisation to capture family-by-environment interaction

The low value for heritability and the very low value for type B genetic correlation (Table 2) for the analysis

Table 3. Estimates of type B genetic correlations (r_B) and heritabilities (h^2) for Central Florida and Marion County source loblolly pine for mean annual increment for volume at age 15, when sites are grouped to raise the type B correlation within a group.

Region	Sites	r_B	h^2
R1	281,288	0.71	0.26
R2	284, 286, 287	0.72	0.20

Note: Region 1 (R1) represent the two sites in Alabama and Mississippi and Region 2 (R2) contains the three sites in the Atlantic Coastal Plain (Florida and Georgia). The genetic correlation between regions was 0.37.

of all 31 families indicate that these families do not rank consistently across the seven sites. For this reason, it seemed important to find groupings of sites (called regions) such that there was consistent family performance.

Several different runs of MTDFREML were conducted with potential groupings of sites. In each multivariate run, MAIV from different sites within a grouping (region) was treated as the same trait, while MAIV was treated as a different trait between regions. Two groupings of sites were identified as potential deployment regions (Table 3).

Region 1 (R1) contained the two western most sites which were located in Alabama and Mississippi (281 and 288, see Fig. 1). Family performance was consistent across these sites with type B genetic correlation of 0.71. Region 2 (R2), located in the Atlantic Coastal Plain (Florida and Georgia), contained three sites (284–286–287, see Figure 1) with a type B genetic correlation of 0.72 (Table 3).

The remaining two sites (280 and 285, see Figure 1) failed to group in any of the defined regions or with each other. There were *a priori* reasons that may have caused these sites to fail to group with the others. The site in Nassau County, Florida was extremely phosphorus deficient to the point that parts of the test were discarded and block boundaries redrawn (MCKEAND pers. comm.). The other site in Levy County, Florida is located on high pH calcareous soils. If these soil characteristics were sufficient to cause rank changes in family performance, then the fact that these two sites failed to group with any of the others seems reasonable.

Grouping sites into regions substantially improved both the narrow sense heritabilities (> 0.2 vs < 0.1) and the type B genetic correlations (> 0.7 vs < 0.3) over those from the seven site pooled analysis for MAIV (Tables 1 and 2). Multivariate analysis of this data structure also yielded a genetic correlation [eq.7]

between the two candidate regions for MAIV of 0.37. This low correlation adds further support to considering MAIV as a single trait within each of these regions and a different trait between regions. These results strongly suggest that considerable effort should be given to developing a better understanding of the causes and nature of these genotype-by-environment interactions.

Genetic gains for deployment

Having developed candidate regions with reasonable genetic correlations and heritabilities within a region and a low genetic correlation between the two regions, it seems appropriate to survey possible genetic gains for deployment from this regionalisation. Using equations 5 and 6, gains from deployment of this population of open-pollinated families were assayed by choosing the top five families (out of 31) for two scenarios: (1) Using the selections from the pooled analysis ignoring regions (MFV) and deploying them across the two regions (FV); and (2) Using the results from each of the regions to choose families to deploy in the other (FV). These results are summarized as follows: (1) Using the overall analysis to choose families resulted in a reduction of 2 to 3 % in MAIV per hectare in R1 and R2, respectively; (2) Selecting families in R1 for deployment in R2 resulted in an 8 % reduction in MAIV per hectare; and (3) Selecting families in R2 to deploy in R1 produced a 4 % loss in MAIV per hectare. These values further confirm that, based on this data, regionalisation did improve gains for MAIV at age 15.

CONCLUSIONS

The 31 loblolly families from Central Florida and Marion County exhibited much more family-by-site interaction ($r_B = 0.27$) than would have been anticipated based on previous reports and on the performance of Atlantic Coastal Plain and Gulf Coastal Plain provenances in these same experiments (SIERRA-LUCERO 1999). Further, a higher proportion of these families than expected were responsible for this interaction. These genotype-by-environment results prompted an examination of the data to determine if there were site groupings within which genotypes performed consistently.

The statistically defined regions which resulted from the groupings enquiry were biologically pleasing:

- (1) Two sites with aberrant soil types failed to group;
 - (2) The western-most sites grouped together, R1; and
 - (3) The Atlantic coastal sites formed a group, R2.
- While interesting, these groupings are based on

genotype-by-environment interaction predictions assumed to be repeatable. To the extent that these genotype-by-environment interactions are not repeatable, the pattern of regionalization would not be repeatable. Further, the results are based on few families (31) and few sites (7).

The Central Florida and Marion County materials have been shown to have high mean productivity (SIERRA-LUCERO 1999), but the optimal use of this material in the lower coastal plain seems hindered by a lack of understanding of the genotype-by-environment interactions which are present. Further study is needed to define the environmental factors causing repeatable interaction. When these causes are known, regionalisation can be assessed in a more elegant and practical manner.

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