Genetic variation in tree growth, stem form and mortality of *Guazuma crinita* in slower- and faster-growing plantations in the Peruvian Amazon

By J. C. WEBER[1),2),*)], C. SOTELO MONTES[1),2)], J. CORNELIUS[1),3)] and J. UGARTE[1)]

Abstract

Guazuma crinita is an important timber tree with a rotation age of 6–12 years in the Peruvian Amazon. A provenance/progeny test containing 200 families from seven locations (provenances) in the Aguaytía watershed of Peru was established in three zones in the Aguaytía watershed that differ in mean annual rainfall and soil fertility. Farmers managed the replications as plantations. Replications were divided into two groups at 24 months: faster- and slower-growing plantations. The faster-growing plantations were thinned at 32 months. The objectives of this paper are to determine if genetic variation in growth traits (tree height, stem diameter) is relatively greater in the faster-growing plantations, and if there are significant differences in tree mortality and stem bifurcations among provenances and families at 24, 36 and 48 months. Variation due to provenances and families and heritability of growth traits were consistently greater in the faster-growing plantations. At 48 months, heritability of growth traits was about twice as large in the faster- than in the slower-growing plantations. There were no significant interactions between zones and either provenances or families. Tree mortality and stem bifurcations in the faster-growing plantations generally did not differ significantly among families, but did differ significantly among provenances. Based on these results and considering its rotation age, we recommend that *G. crinita* families/trees could be selected at 48 months in the faster-growing plantations, the plantations could be transformed into seed orchards and the seed could be used for reforestation throughout the Aguaytía watershed. Results are compared with other tropical hardwoods.

Key words: tree improvement, provenance/progeny test, environment, heritability.

Introduction

Guazuma crinita Mart. (Sterculiaceae family) is a priority timber tree in the Peruvian Amazon (TOLEDO and RINCÓN, 1996). It grows rapidly and can be coppiced for successive harvests. Its moderately dense wood (WEBER and SOTELO MONTES, 2008) has useful properties for construction material (VALDIVIA and SOTELO MONTES, 1993) and is used primarily for wall panels and construction poles in Peru. The recommended rotation age is 6–12 years for these products, but younger trees are often harvested. Natural populations are the principal source of wood, but a rural association is producing seed and seedlings from selected trees for small-scale plantations in the Aguaytía and neighboring watersheds of Peru (PROSEMA, 2009).

G. crinita is a pioneer species that colonizes the floodplain and disturbed secondary forests in the lowland jungle of Peru, Ecuador and Brazil (ENCARNACIÓN, 1983; FAO, 2007). The breeding system has not been studied, but is assumed to be primarily out-crossing like the majority of tropical trees (BAWA *et al.,* 1990). Trees can begin flowering after 2–3 years in open-grown conditions, and the lightweight, feathered capsules are dispersed by both wind and water (WEBER and SOTELO MONTES, personal observations). These reproductive characteristics probably result in extensive gene flow which, at least for selectively neutral traits, would produce considerable genetic variation within populations but relatively little differentiation among populations (HAMRICK *et al.,* 1992).

As demand for *G. crinita* wood increases in the Peruvian Amazon, genetics research becomes increasingly important to identify superior germplasm for establishing plantations. A key research issue for tree improvement programs is to identify the most appropriate test environments for selecting faster-growing germplasm at an early age. CAMPBELL and SORENSEN (1978) hypothesized that genetic variation in tree growth traits would be relatively greater in test environments where trees grow more rapidly and, therefore, selection would be more effective in such environments.

A provenance/progeny test of *G. crinita* was established on farms in the Aguaytía watershed (Rochon *et al.,* 2007), which is representative in terms of environmental conditions of many other watersheds in the western Peruvian Amazon. Mean annual rainfall and soil fertility increase in general from the lower to the upper part of the watershed. Replications of the provenance/progeny test were established in the lower, middle and upper parts of the watershed, and managed as small-scale plantations. At 24 months, the plantations (i.e., replications) were divided into two groups based on mean growth of the trees: slower-growing and faster-growing plantations. In this paper, we present results of analyses of tree growth, stem bifurcations and mortality in the provenance/progeny test at 24, 36 and 48 months. The major objectives are to determine if genetic varia-

[1)] World Agroforestry Centre (ICRAF), CIP, Apartado Postal 1558, Lima 12, Peru.

[2)] World Agroforestry Centre (ICRAF), Sahel Office, B.P. E5118, Bamako, Mali.

[3)] Agroforestry and Novel Crops Unit, School of Marine and Tropical Biology, James Cook University, PO Box 6811, Cairns, Queensland 4870, Australia.

[*)] Author for correspondence: JOHN C. WEBER. Telephone: (223) 20235000. Fax: (223) 20228683. E-Mail: johncrweber@aol.com

tion in tree growth is relatively greater in the faster-growing plantations, and if there are significant differences in tree mortality and stem bifurcations among provenances and families. Results are compared with other tropical hardwood species, and some practical implications for tree improvement programs are discussed.

Materials and Methods

Sample region, study area, experimental design and management of the provenance / progeny test

Seeds were collected from 200 mother trees in seven natural stands, hereafter referred to as provenances, in the Aguaytía watershed and part of a neighboring watershed in the Peruvian Amazon (*Figure 1*). Natural stands and scattered individual trees of *G. crinita* occur throughout the sample region, so it is assumed that the sampled provenances are sub-populations of the same genetic population and are not genetically isolated. In addition, it is assumed that some inbreeding has occurred and continues to occur in these sub-populations. Farmers selected mother trees that had good bole form and no external disease symptoms. The number of selected trees per provenance (24, 63, 17, 35, 23, 17 and 21, respectively, for provenances 1 to 7) was roughly proportional to the total number of trees in each provenance. Selection intensity was only about 20%, so there was probably little difference between the selected trees and the entire population of trees in each provenance (WEBER *et al.*, 2009). To reduce the chance of sampling

siblings, at least 100 m was maintained between any two selected trees. Seedlings of the 200 families were grown in a randomized block experimental design in the nursery for 15 months before being transplanted to the test sites.

The provenance/progeny test was established in the lower, middle and upper parts of the Aguaytía watershed (*Figure 1*), hereafter called the lower, middle and upper zones. Soil fertility and mean annual rainfall increase in general from the lower to the upper zone, i.e. from Nuevo Requena to San Alejandro. The experimental design was a randomized complete block with 15 replications, hereafter referred to as plantations. The plantations were established on 15 different farms: four in the lower, five in the middle and six in the upper zone. The test was not replicated within farms. In each plantation, the 200 families were randomly assigned to 200 experimental plots, each plot containing two trees, for a total of 400 trees per plantation. Spacing was 2.5 by 2.5 meters within and between rows, and two rows of border trees completely surrounded each plantation. Dead trees were replaced during the first year, but data collected on replants were not included in the analyses.

The plantations were managed by the farmers. Management practices included fertilizer application, cover cropping and manual weeding. Organic compost and rock phosphate were placed in each planting hole, and a nitrogen-fixing cover crop was sown in and around each plantation to improve soil fertility and control soil erosion. Farmers weeded their plantations approximately every 4 weeks during the rainy season, and every 6–8
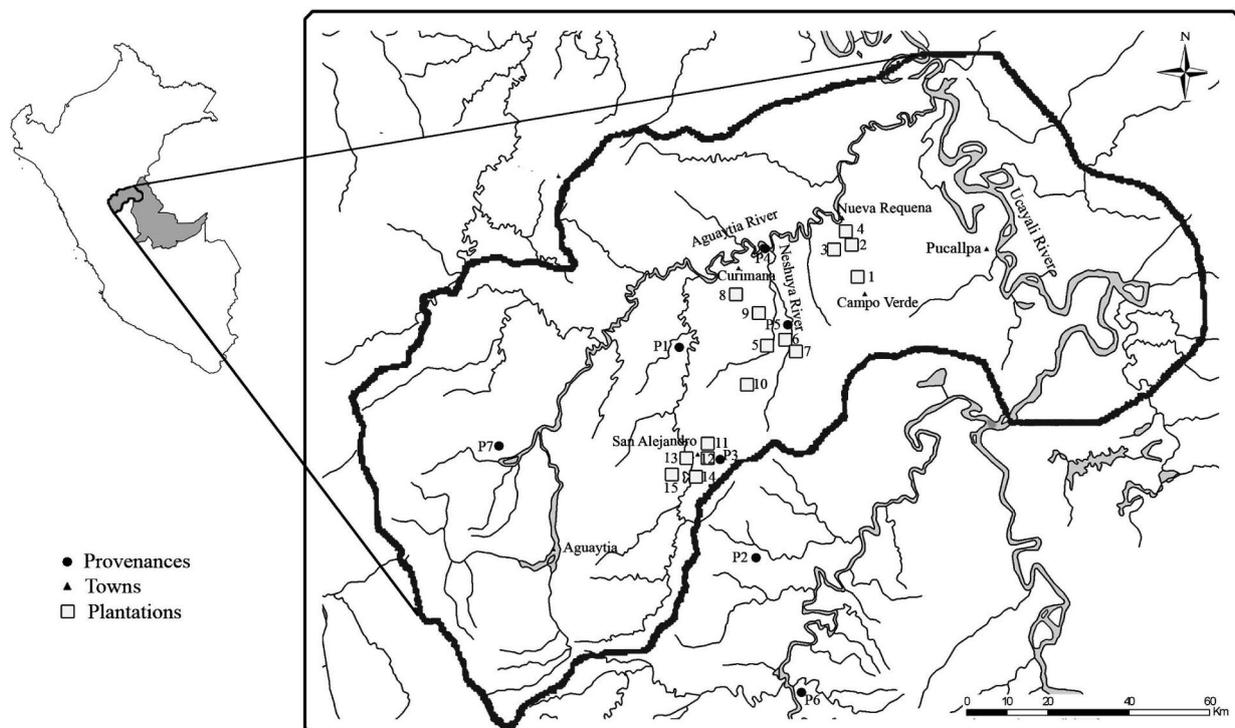
Figure 1. – Map showing the location of the Aguaytía watershed in Peru, the mean location of the mother trees from each provenance (solid circles) and the location of the plantations (open squares). Plantation refers to a replication in the provenance/progeny test. The slower-growing plantations were in the lower and middle zones of the watershed (numbers 1, 2, 3, 4 and 5, 6, 9, respectively), and the faster-growing plantations were in the upper and middle zones of the watershed (numbers 10, 11, 12, 13, 14, 15 and 7, 8, respectively).

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weeks during the dry season, but weeding was not systematically done due to time and labor constraints. The relatively large plantation size (about 0.3 ha) combined with farmers' erratic weeding practices probably affected the differences among plantations and among families within plantations, as well as the stability of provenance and family performance across plantations (ROCHON *et al.,* 2007).

Details about the sample region, study area, experimental design and management of the provenance/progeny test are provided elsewhere (Rochon *et al.,* 2007).

Faster- and slower-growing plantations in the provenance/progeny test

Based on mean tree growth at 24 months, the 15 plantations were divided into a faster-growing and a slower-growing group. The faster-growing group included all six plantations in the upper zone and two plantations in the middle zone, while the slower-growing group included all four plantations in the lower zone and three plantations in the middle zone (*Figure 1*). Plantations in the faster- and slower-growing groups are hereafter referred to as the faster- and slower-growing plantations.

The faster-growing plantations were thinned at 32 months. In plots with two living trees, the smaller, less vigorous tree with poorer stem form was cut. In plots with only one living tree, that tree was left even if it was small and had relatively poor stem form. The slower-growing plantations were not thinned.

Data collection and statistical analyses

Tree growth, stem bifurcations and mortality were evaluated at 24, 36 and 48 months. Tree height was measured to the nearest cm using a meter stick or telescopic measuring pole. Stem diameter was measured at 10 cm above ground (Dia-10) and at breast height (DBH, 1.3 m above ground, 36 and 48 months only): measurements were recorded to the nearest mm using callipers or diameter tape. Dia-10 was measured because many trees were too short to measure DBH, especially in the slower growing plantations at 24 months. In addition, *G. crinita* stems have relatively little taper and are typically coppiced between 10 and 30 cm above ground. The numbers of dead and living trees and trees with and without stem bifurcations were calculated for each family and provenance.

The SAS® statistical package (SAS INSTITUTE INC., 2004) was used for all analyses. Departure from the normal distribution and homogeneity of variance were tested for the residuals using statistics provided by the UNIVARIATE procedure. Data transformations were not considered necessary to satisfy the assumptions of analysis of variance. The significance level for all tests was $\alpha \leq 0.05$.

Analysis of variance (ANOVA) was used to determine if there were significant differences in tree height and stem diameter due to genetic and environmental factors (GLM procedure, partial sums of squares estimation method). Three sets of ANOVAs were carried out. The first set was based on all plantations at 24 months, and included the following sources of variation: zone (Z), plantation nested within zone [Plant(Z)], provenance (P), family nested within provenance [F(P)], interactions [P*Z, P*Plant(Z), F(P)*Z, F(P)*Plant(Z)] and residual variation. The second set was based on the slower-growing plantations at 24, 36 and 48 months: sources of variation were the same as above. The third set was based on the faster-growing plantations at 24, 36 and 48 months: sources of variation were the same as above at 24 months, but did not include F(P)*Plant(Z) at 36 and 48 months. In all ANOVAs, zone was fixed and the other factors were random, and F-ratios were used to test all factors. Some F-ratios involved more than one mean square in the denominator ("quasi" F-ratios), and were tested with approximate degrees of freedom (Satterthwaite approximation). Differences in least-squares means of zones were compared using Tukey's "honestly significant difference test".

Variance components were estimated using the restricted maximum likelihood method (VARCOMP procedure). The variance component for each random effect in the ANOVA model was expressed as a percentage of the total variance for the random effects (%VC).

Individual tree heritability (h_i^2) of growth traits was estimated at 24, 36 and/or 48 months only if there was significant variation due to families in the respective ANOVA. We assumed partial inbreeding and estimated additive genetic variance as $3\sigma^2_{F(P)}$ rather than $4\sigma^2_{F(P)}$, where $\sigma^2_{F(P)}$ is the variance component for families within provenances. We used the multiplier 3 rather than 4, as others have done (HODGE *et al.,* 2002; HODGE and DVORAK, 2004; SOTELO MONTES *et al.,* 2006), in order to provide a conservative estimate of h_i^2 under the assumption of partial inbreeding. The denominator of h_i^2 included the following variance components: $\sigma^2_{F(P)}$, $\sigma^2_{F(P)*Z}$, $\sigma^2_{F(P)*Plant(Z)}$ and $\sigma^2_{Residual}$ for all analyses at 24 months and for the slower-growing plantations at 36 and 48 months; and $\sigma^2_{F(P)}$, $\sigma^2_{F(P)*Z}$ and $\sigma^2_{Residual}$ for analysis of the faster-growing plantations at 36 and 48 months. Standard errors for h_i^2 were calculated using the formula provided by BECKER (1984).

The relationship between growth traits at 24 and 48 months was investigated using simple linear regression and Pearson *r* correlation coefficients (REG and CORR procedures). Analyses were carried out on family means and individual trees, using all data and separately for the slower- and faster-growing plantations. The independent variables for the regressions were height and Dia-10 at 24 months and the dependent variables were height and Dia-10 at 48 months.

The likelihood ratio chi-square statistic (G^2, FREQ procedure) was used to test whether the frequencies of tree mortality and stem bifurcations were statistically independent of provenances and families. Independence was tested separately for the slower- and faster-growing plantations at 24, 36 and 48 months.

The sample sizes in this test could have reduced the accuracy of some estimates of means and variances. The numbers of progeny per family (maximum 30 if no mortality) and families per provenance (< 20 in two provenances) were relatively low, reducing the accuracy of estimates of family means and some provenance means.

In addition, a minimum sample size of 40 is recommended to obtain accurate estimates of variance components (N. MANDEL, personal communication). The number of families (200) was adequate to obtain an accurate estimate of family variance, but the number of provenances (7) was too low to obtain an accurate estimate of provenance variance.

Results

Genetic and environmental variation in tree height and stem diameter

Judging from the coefficients of variation (CVs), the slower-growing plantations at 24 months had relatively greater variation in tree height and stem diameter (Dia-10) than the faster-growing plantations (*Table 1*). In the slower-growing plantations, CVs decreased between 24 and 48 months. In the faster-growing plantations, which were thinned at 32 months, CVs decreased between 24

and 36 months but increased slightly between 36 and 48 months.

In the analysis of all plantations at 24 months, there were significant differences in tree height and stem diameter between the three zones (*Table 2*). Both variables increased from the lower to the upper zone: height = 4.90, 8.08 and 10.58 m, and Dia-10 = 7.9, 10.2 and 12.5 cm, respectively, in the lower, middle and upper zone ($p < 0.001$ for all comparisons between zones).

There was also significant variation in tree height and stem diameter due to provenances and families within provenances in the analysis of all plantations at 24 months (*Table 2*). The percentage of the phenotypic variation (%VC) was greater for families than for provenances, but both were small. The majority of the phenotypic variation was due to plantations within zones and the residual. Provenance and family ranks were relatively stable across zones, judging from the non-signifi-

Table 1. – Descriptive statistics of tree height and stem diameter of *Guazuma crinita* in a provenance/progeny test in the Aguaytía watershed of Peru. Statistics are given for all plantations at 24 months and for the slower- and faster-growing plantations at 24, 36 and 48 months.

Variables	All plantations at 24 months			Slower-growing plantations			Faster-growing plantations		
	Mean	CV (%)	Range	Mean	CV (%)	Range	Mean	CV (%)	Range
Height (m)									
24 months	8.24	43.8	16.11	5.24	39.9	10.88	10.86	22.4	15.77
36 months	---	---	---	6.45	36.5	12.23	13.32	18.9	18.90
48 months	---	---	---	8.13	26.9	13.25	15.20	19.7	20.10
Dia-10 (cm)									
24 months	10.5	33.9	19.7	8.0	33.9	15.0	12.7	21.3	19.1
36 months	---	---	---	8.7	29.4	15.4	14.3	17.7	21.7
48 months	---	---	---	10.6	24.3	17.4	16.7	20.0	23.6
DBH (cm)									
36 months	---	---	---	6.3	34.5	13.8	11.7	20.6	18.2
48 months	---	---	---	7.2	28.9	14.3	12.9	21.4	19.1

Notes: Plantation = a replication in the provenance/progeny test. Height = tree height, Dia-10 = stem diameter at 10 cm above ground, DBH = stem diameter at breast height (1.3 m). CV = coefficient of variation. Sample sizes: all plantations at 24 months = 5057; slower-growing plantations = 2353 at 24 months, 2195 for height and Dia-10 and 2089 for DBH at 36 months, 1434 at 48 months; faster-growing plantations = 2704 at 24 months (before thinning), 1524 at 36 months, 1478 at 48 months.

Table 2. – Sources of variation of tree height and stem diameter of *Guazuma crinita* at 24 months in a provenance/progeny test in the Aguaytía watershed of Peru.

Source of variation	DF	Height		Dia-10	
		p	%VC	p	%VC
Z	2	0.012	---	0.014	---
Plant(Z)	12	<0.001	68.6	<0.001	42.8
P	6	0.012	0.1	0.032	0.3
F(P)	193	0.016	0.6	0.001	1.3
P*Z	12	0.977	0.0	0.783	0.0
P*Plant(Z)	72	0.027	0.2	0.010	0.5
F(P)*Z	386	0.099	0.6	0.408	0.4
F(P)*Plant(Z)	2201	<0.001	17.9	<0.001	18.2
Residual	2172	---	12.0	---	36.5

Notes: Plantation = a replication in the provenance/progeny test. Height = tree height, Dia-10 = stem diameter at 10 cm above ground. Source of variation: zone = Z, plantation nested in zone = Plant(Z), provenance = P, family nested in provenance = F(P), interactions = P*Z, P*Plant(Z), F(P)*Z and F(P)*Plant(Z). DF = degrees of freedom, p = probability of F ratio, %VC = variance component expressed as percentage of the sum of variance components for random effects (zone = fixed effect, so variance component not calculated).

Table 3. – Sources of variation of tree height and stem diameter of *Guazuma crinita* at 24, 36 and 48 months in a provenance/progeny test in the Aguaytía watershed of Peru. Analyses are given for the slower-growing and faster-growing plantations.

Slower-growing plantations

	24 months				36 months						48 months					
	Height		Dia-10		Height		Dia-10		DBH		Height		Dia-10		DBH	
Source	p	%VC	p	%VC	p	%VC	p	%VC	p	%VC	p	%VC	p	%VC	p	%VC
Z	0.436	---	0.731	---	0.227	---	0.614	---	0.327	---	0.241	---	0.294	---	0.737	---
Plant(Z)	<0.001	37.2	<0.001	24.5	<0.001	36.9	<0.001	24.5	<0.001	21.1	<0.001	17.4	<0.001	9.4	<0.001	11.5
P	0.354	0.0	0.150	0.2	0.350	0.0	0.180	0.2	0.167	0.1	0.390	0.0	0.157	0.4	0.108	0.5
F(P)	0.362	0.2	0.235	0.4	0.201	1.0	0.234	1.1	0.402	1.1	0.028	2.8	0.025	2.8	0.024	3.2
P*Z	0.931	0.0	0.840	0.0	0.939	0.0	0.807	0.0	0.865	0.0	0.721	0.0	0.858	0.0	0.876	0.0
P*Plant(Z)	0.002	1.2	<0.001	1.9	0.005	0.9	0.004	1.7	<0.001	2.1	0.067	1.0	0.015	1.5	0.002	2.3
F(P)*Z	0.160	1.2	0.612	0.0	0.071	1.3	0.088	1.4	0.053	1.7	0.991	0.0	0.988	0.0	0.972	0.0
F(P)*Plant(Z)	<0.001	34.2	<0.001	31.7	<0.001	30.5	<0.001	19.0	<0.001	22.0	<0.001	36.1	<0.001	18.2	<0.001	21.9
Residual	---	26.2	---	41.3	---	29.4	---	52.1	---	51.9	---	42.7	---	67.7	---	60.6

Faster-growing plantations

	24 months				36 months						48 months					
	Height		Dia-10		Height		Dia-10		DBH		Height		Dia-10		DBH	
Source	p	%VC	p	%VC	p	%VC	p	%VC	p	%VC	p	%VC	p	%VC	p	%VC
Z	0.560	---	0.557	---	0.517	---	0.752	---	0.791	---	0.427	---	0.630	---	0.816	---
Plant(Z)	<0.001	59.5	<0.001	27.0	<0.001	56.2	<0.001	24.7	<0.001	29.2	<0.001	52.7	<0.001	17.4	<0.001	23.6
P	0.002	0.3	0.035	0.3	0.014	0.2	0.186	0.0	0.145	0.0	0.039	0.2	0.406	0.0	0.316	0.0
F(P)	<0.001	1.8	<0.001	3.9	0.006	2.4	0.005	5.0	0.004	5.4	0.019	3.1	0.016	5.7	0.008	6.0
P*Z	0.958	0.0	0.838	0.0	0.910	0.0	0.852	0.0	0.853	0.0	0.903	0.0	0.870	0.0	0.892	0.0
P*Plant(Z)	0.534	0.0	0.551	0.0	0.485	0.0	0.123	0.2	0.112	0.2	0.326	0.1	0.081	0.5	0.219	0.0
F(P)*Z	1.000	0.0	1.000	0.0	1.000	0.0	0.999	0.0	0.999	0.0	0.990	0.3	0.596	3.1	0.864	2.4
F(P)*Plant(Z)	<0.001	24.4	<0.001	16.3	---	---	---	---	---	---	---	---	---	---	---	---
Residual	---	14.0	---	52.5	---	41.2	---	70.1	---	65.2	---	43.6	---	73.3	---	68.0

Notes: Plantation = a replication in the provenance/progeny test. Height = tree height, Dia-10 = stem diameter at 10 cm above ground, DBH = stem diameter at breast height (1.3 m). Source = sources of variation: zone = Z, plantation nested in zone = Plant(Z), provenance = P, family nested in provenance = F(P), interactions = P*Z, P*Plant(Z), F(P)*Z and F(P)*Plant(Z). p = probability of F ratio. Degrees of freedom for slower-growing plantations: Z = 1; Plant(Z) = 5 at 24 and 36 months, 4 at 48 months; P = 6; F(P) = 193; P*Z = 6; P*Plant(Z) = 30 at 24 and 36 months, 24 at 48 months; F(P)*Z = 193 at 24 and 36 months, 185 at 48 months; F(P)*Plant(Z) = 912 at 24 months, 861 for height and Dia-10 and 816 for DBH at 36 months, and 487 at 48 months; Residual = 1006, 899 and 527, respectively, at 24, 36 and 48 months. Degrees of freedom for faster-growing plantations: Z = 1; Plant(Z) = 6; P = 6; F(P) = 193; P*Z = 6; P*Plant(Z) = 36; F(P)*Z = 193; Residual = 1166, 1082 and 1036, respectively, at 24, 36 and 48 months. %VC = variance component expressed as percentage of the sum of variance components for random effects (zone = fixed effect, so variance component not calculated).

cant interactions with zones, but they were not stable across plantations within zones.

There was relatively greater genetic variation in the faster- than in the slower-growing plantations (*Table 3*). At 24 months, there was significant variation in height and Dia-10 due to provenances and families within provenances in the faster- but not in the slower-growing plantations. In all cases, %VC was greater for families than for provenances. In the faster-growing plantations at 36 and 48 months, variation due to provenances was significant for height, and variation due to families within provenances was significant for height, Dia-10 and DBH. In contrast, in the slower-growing plantations, variation due to provenances was not significant,

and variation due to families within provenances was significant for height, Dia-30 and DBH only at 48 months. The %VC of provenances and families within provenance was generally greater in the faster- than in the slower-growing plantations. The interaction between provenances and plantations within zones was not significant in the faster-growing plantations but was significant in the slower-growing plantations, whereas the interaction between families and plantations within zones was significant in both the slower- and faster-growing plantations.

Tree height and stem diameter had low h_i^2 at 24 months based on the analysis of all plantations (*Table 4*). It was notably higher in the faster-growing plantations,

Table 4. – Heritability and standard error (in parentheses) of tree height and stem diameter of *Guazuma crinita* in a provenance/progeny test in the Aguaytía watershed of Peru. Estimates are given only if there was significant variation due to families within provenances (*Tables 2* and *3*).

	Height	Dia-10	DBH
All plantations at 24 months	0.057 (0.025)	0.072 (0.027)	---
Slower-growing plantations			
48 months	0.103 (0.079)	0.096 (0.079)	0.111 (0.080)
Faster-growing plantations			
24 months	0.137 (0.054)	0.161 (0.057)	---
36 months	0.163 (0.092)	0.201 (0.095)	0.227 (0.097)
48 months	0.198 (0.096)	0.206 (0.097)	0.236 (0.099)

Notes: Plantation = a replication in the provenance/progeny test. Height = tree height (m), Dia-10 = stem diameter at 10 cm above ground (cm), DBH = stem diameter (cm) at breast height (1.3 m) measured only at 36 and 48 months.

and was not estimated in the slower-growing plantations because variance due to families was not significant (*Table 3*). In the faster-growing plantations, h^2_i of both height and diameter increased between 24 and 48 months (*Table 4*). At 48 months, h^2_i was approximately twice as large in the faster- than in the slower-growing plantations: however, considering the large standard errors of h^2_i, the difference cannot be considered statistically significant. Stem diameter, especially DBH, generally had higher h^2_i than tree height, but neither can this difference be considered statistically significant.

Relationships between growth traits at 24 and 48 months

Family mean height at 24 months explained about 34% of the variation in mean height at 48 months in the analysis of all plantations, but the relationship with stem diameter was not significant (*Table 5*). Family means at 24 months were stronger predictors of means at 48 months in the faster- than in the slower-growing plantations: they explained about 50% and 30% of the variation, respectively. To illustrate these relationships, the best 50 families were notionally "selected" based on tree height and stem diameter at 24 and 48 months. The number of families that were among the top 50 at both 24 and 48 months was 25 for height but only 12 for diameter in the analysis of all plantations, 27 for height and 28 for diameter in the slower-growing plantations, 30 for height and 31 for diameter in the faster-growing plantations.

In contrast to family means, individual tree height and stem diameter at 24 months explained about 88% of the variation in height and diameter at 48 months in the analysis all plantations (*Table 5*). The relationships were weaker in the separate analyses of the faster- and slower-growing plantations, explaining about 74% of the variation at 48 months in both cases.

Differences in tree mortality and stem bifurcations among provenances and families

Tree mortality increased from 16 to 34% between 24 and 48 months in the test. It was similar in the faster- and slower-growing plantations at 24 and 36 months, but lower in the faster- than in the slower-growing plantations at 48 months (27% versus 40%). Tree mortality differed significantly among provenances (G^2, p = 0.003, 0.009 and 0.030, respectively, at 24, 36 and 48 months; DF = 6) but not among families in the faster-growing plantations. Mortality did not differ significantly among provenances or families in the slower-growing plantations.

Stem bifurcations increased from 4 to 19% between 24 and 48 months in the test. The frequency of stem bifurcations differed significantly among families in the faster-growing plantations at 36 months and in the slower-growing plantations at 48 months (G^2, p = 0.043 and 0.024, respectively: DF = 199). It also differed significantly among provenances in the faster-growing plantations at 48 months (G^2, p = 0.043, DF = 6).

Table 5. – Simple linear regressions predicting tree growth of *Guazuma crinita* at 48 months from tree growth at 24 months in a provenance/progeny test in the Aguaytía watershed of Peru. Statistically significant regressions are given for family means and trees based on the combined analysis of all plantations, and the separate analyses within the slower- and faster-growing plantations.

Variable	Regression equation	R^2	SE	r
Family means				
All plantations				
Height	387.922 + 0.957*Ht	0.343	0.094	0.586
Slower-growing plantations				
Height	362.932 + 0.868*Ht	0.302	0.094	0.550
Dia-10	4.692 + 0.743*Dia	0.314	0.078	0.560
Faster-growing plantations				
Height	434.397 + 1.001*Ht	0.454	0.078	0.674
Dia-10	1.181 + 1.228*Dia	0.572	0.076	0.756
Trees				
All plantations				
Height	7.540 + 1.321*Ht	0.907	0.008	0.953
Dia-10	-0.167 + 1.221*Dia	0.848	0.010	0.921
Slower-growing plantations				
Height	104.600 + 1.135*Ht	0.747	0.017	0.864
Dia-10	2.071 + 0.941*Dia	0.708	0.016	0.841
Faster-growing plantations				
Height	135.391 + 1.225*Ht	0.759	0.018	0.871
Dia-10	-0.132 + 1.240*Dia	0.728	0.020	0.853

Notes: Plantation = a replication in the provenance/progeny test. Height = tree height (m) and Dia-10 = stem diameter (cm) at 10 cm above ground. Dependent variables = height and Dia-10 at 48 months. Independent variables = height and Dia-10 at 24 months, abbreviated as Ht and Dia, respectively. R^2 = coefficient of determination of regression model; SE = standard error of regression coefficient; r = Pearson correlation coefficient between height and Dia-10 at 24 and 48 months. Probability < 0.001 for t tests of regression coefficient and Pearson r. Sample sizes = 200 for families, 2912 for trees in the analysis of all plantations, 1434 for trees in slower-growing plantations, 1478 for trees in faster-growing plantations.

Discussion

Genetic and environmental variation in tree height and stem diameter

The larger coefficients of variation (CV) for tree height and stem diameter in the slower-growing plantations at 24 months were probably related to differences in micro-environmental variation and leaf abscission (ROCHON *et al.,* 2007). The faster-growing plantations were in the upper and middle zones while the slower-growing plantations were in the lower and middle zones of the watershed. Farmers' erratic weeding practices undoubtedly produced considerable spatial and temporal variation in soil moisture, fertility and temperature in the plantations, although these were not monitored. This micro-environmental variation would probably produce the greatest differences in tree growth in zones with the lowest rainfall and least fertile soils, such as the lower zone in this test, and the smallest differences in tree growth in zones with the highest rainfall and most fertile soils, such as the upper zone in this test (BOIVIN-CHABOT *et al.,* 2004). In addition, if there is phenotypic variation in leaf abscission, one would expect greater variation among trees planted in the drier zones. Partial leaf abscission was rarely observed among trees in plantations in the upper zone, but was common among trees in plantations in the lower zone during the dry season. Since leaf abscission reduces the photosynthetic surface, variation in leaf abscission among neighboring trees could produce substantial variation in growth rates (e.g., DVORAK *et al.,* 1998).

Changes in the CVs of growth traits of *G. crinita* over time were probably related to tree mortality. The slower-growing, less vigorous trees suffered greater mortality so as they died the standard deviations of height and diameter decreased. In the slower-growing plantations, tree mortality increased by about 24% between 24 and 48 months and the CVs of height and Dia-10 decreased by about 10%. The decrease in CVs of height and Dia-10 in the faster-growing plantations between 24 and 36 months was of course due primarily to the thinning at 32 months. In the faster-growing plantations, mortality increased by only 2% between 36 and 48 months and the CVs of height and Dia-10 increased by 1–2%, reflecting the fact that many of the smaller trees were able to survive in the less densely stocked plantations after thinning.

There were large, significant differences in mean growth of *G. crinita* trees among zones at 24 months, whereas the differences were not significant at 12 months (ROCHON *et al.,* 2007). This illustrates the fact that differences in tree growth among planting environments tend to increase over time (e.g., WEBER and SOTELO MONTES, 2005; SOTELO MONTES *et al.,* 2006; WEBER and SOTELO MONTES, 2008). Growth traits did not differ significantly among zones in the analyses of the faster- and slower-growing plantations because the slow/fast factors were confounded with zones, i.e. the slower-growing plantations were in the lower and middle zones and the faster-growing plantations were in the middle and upper zones. Much of the variation in growth was due to plantations and residual variation: this and the significant family by plantation interactions were proba-

bly due to the relatively large plantation size and farmers' erratic weeding practices, as reported earlier for this study (ROCHON et al., 2007) and for another provenance/progeny test established on farms in the same watershed (SOTELO MONTES *et al.,* 2006).

Growth of *G. crinita* trees differed significantly due to provenances and families within provenances at 24 months, but the two genetic components accounted for very little variation, as observed at 12 months (ROCHON *et al.,* 2007). Significant variation in tree growth due to provenances and/or families has also been detected at early ages in other tropical hardwoods in Latin America [e.g., *Alnus acuminata* Kunth. (CORNELIUS *et al.,* 1996); *Bombacopsis quinata* (Jacq.) Dugand (HODGE *et al.,* 2002); *Calycophyllum spruceanum* (Benth.) Hook. f. ex K. Shum (SOTELO MONTES *et al.,* 2003; WEBER and SOTELO MONTES, 2005; SOTELO MONTES *et al.,* 2006); *Prosopis flexuosa* D.C. (CONY, 1996); *Sterculia apetala* (Jacq.) Karst (DVORAK *et al.,* 1998); *Vochysia guatemalensis* Sm., J.D. (CORNELIUS and MESÉN, 1997)].

Families within provenances accounted for more variation in growth than did provenances. This is consistent with our assumption that there is considerable long-distance seed dispersal of *G. crinita* in the watershed, thereby increasing variation within and decreasing variation among provenances (HAMRICK *et al.,* 1992). This suggests that there is more to be gained by selecting the best families within provenances than by selecting the best provenances within the watershed. Similar results were reported for *C. spruceanum* sampled from and tested in the same watershed (SOTELO MONTES *et al.,* 2006).

As observed at 12 months (ROCHON *et al.,* 2007), provenance and family means for growth traits were relatively stable across zones at 24 months and in the separate analyses of slower- and faster-growing plantations through 48 months. This suggests that the best performing provenances/families of *G. crinita* could be used for reforestation throughout the watershed. Similar results were observed in the provenance/progeny test of *C. spruceanum* in the same watershed (SOTELO MONTES *et al.,* 2006).

Results were consistent with the hypothesis that the expression of genetic variation in growth traits is greater in test environments where trees grow more rapidly (CAMPBELL and SORENSEN, 1978). Variation in growth traits due to families within provenances was consistently greater and variation due to provenances was generally greater in the faster-growing plantations. Similar results were reported for this test at 12 months (ROCHON *et al.,* 2007) and for two tests of *C. spruceanum* in the Peruvian Amazon (SOTELO MONTES *et al.,* 2003; WEBER and SOTELO MONTES, 2005; SOTELO MONTES *et al.,* 2006). However, this was not the case in a test of *G. crinita* provenances sampled from several different watersheds in the Peruvian Amazon and established in the Aguaytía watershed (WEBER and SOTELO MONTES, 2008). In that test, variation due to provenances was relatively greater for growth traits in the zone with the slowest tree growth but for wood density in the zone with the fastest tree growth. In addition, tree growth and wood density were negatively correlated in general, but the magnitude of the correlation differed significant-

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ly among provenances and planting zones. Therefore, we cannot generalize and assume that the expression of genetic variation in growth, or traits correlated with growth, will always be greater in test environments where trees grow more rapidly. The expression of genetic variation in traits and correlations between traits depend on the specific traits, genetic population and test environment (FALCONER and MACKAY, 1996).

Although individual tree heritability (h_i^2) of height and stem diameter of *G. crinita* were relatively low in this test, they were within the range of values reported for other tropical hardwoods at an early age (e.g., CORNELIUS et al., 1996; GREAVES *et al.,* 1997; SHIMIZU *et al.,* 2002; SOTELO MONTES *et al.,* 2006). At 24 months, h_i^2 was too low for effective selection of faster-growing families across all plantations. As illustrated with the "selection" example, only 50% of the 50 families notionally "selected" at 24 months based on mean height across all plantations were among the best 50 families at 48 months.

Heritability of *G. crinita* growth traits was higher in the faster-growing plantations, as observed at 12 months in this test (ROCHON *et al.,* 2007). Similar results were reported for *C. spruceanum* (SOTELO MONTES *et al.,* 2006) and two *Eucalyptus* species (MACDONALD *et al.,* 1997; GINWALL *et al.,* 2004). Nevertheless, again using the "selection" example, only about 60% of the 50 *G. crinita* families notionally "selected" in the faster-growing plantations at 24 months were among the best 50 families at 48 months.

Estimated h_i^2 of tree height and stem diameter of *G. crinita* increased between 24 and 48 months in the faster-growing plantations and was 0.20–0.24 at 48 months. Based on these results and its rotation age (6–12 years), we recommend that selection of faster-growing *G. crinita* families/trees could be carried out at 48 months in environments where trees grow rapidly. Specifically, the faster-growing plantations could be transformed into seed orchards by roguing the less desirable families/trees. Since there was no significant family by zone interaction in this test, seed from the orchards could be used for reforestation throughout the Aguaytía watershed. Given the strong, positive correlations between growth of individual trees at 24 and 48 months, we assume that the correlations would also be strong between 48 and 72 months (i.e., the onset of the recommended rotation age).

Estimated h_i^2 of *G. crinita* growth traits was very low in the slower-growing plantations so selection would not be very effective in environments where trees grow slowly. Longer-term research is needed to assess whether h_i^2 increases significantly with time in these environments. However, it is unlikely that seed orchards derived from provenance/progeny tests would be economically feasible in these environments due to the slower growth and longer time required for evaluation of genetic variation.

Differences in tree mortality and stem bifurcations among provenances and families

Tree improvement programs must consider tree mortality and stem form if there is significant genetic varia-

tion in these traits. In the faster-growing plantations in the Aguaytía watershed, tree mortality and stem bifurcations were in general randomly distributed among families of *G. crinita*. This suggests that there is little (if any) genetic variation in mortality and stem bifurcations among families established in test sites where trees rapidly, at least up to 48 months. We cannot assume of course that there is little genetic variation in mortality and stem bifurcations among *G. crinita* families after 48 months in this test or in tests in other watersheds. In contrast to this test, there were significant differences in tree mortality and stem bifurcations among families of *C. spruceanum* in the Aguaytía watershed (WEBER *et al.,* 2009), and genetic variation in tree form has been reported in some other tropical hardwoods (e.g., CONY, 1996; CORNELIUS *et al.,* 1996; DVORAK *et al.,* 1998).

There were significant differences in tree mortality and stem bifurcations among provenances of *G. crinita* in the faster-growing plantations. Therefore, if tree improvement programs decide to select the best provenances and families within those provenances, then they should incorporate provenance mortality and stem bifurcations in the selection.

Recommendations for G. crinita tree improvement programs

Based on the results of this study, we recommend that tree improvement programs establish provenance/progeny tests of *G. crinita* in potential planting zones in other watersheds in the Peruvian Amazon and neighboring countries where it has potential for small-scale forestry plantations. The tests should evaluate tree growth, stem form, mortality and commercially important wood properties (such as density) of provenances and families originating from the same watershed in order to assess whether the results of this test can be generalized. The specific research questions of practical interest include the following. Is variation in tree growth and wood properties consistently greater within rather than among provenances in the watershed? Is genetic variation in growth traits consistently greater in planting zones where trees grow more rapidly? Are there significant interactions between provenances/families and planting zones in the watershed? Do genetic and phenotypic correlations between growth traits and wood density differ significantly among provenances and planting zones in the watershed? Do tree mortality and stem bifurcations differ significantly among provenances/families and planting zones in the watershed?

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