

Provenance and family variation of *Pinus caribaea* var. *hondurensis* from Guatemala and Honduras, grown in Brazil, Colombia and Venezuela⁽¹⁾

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Abstract – *Pinus caribaea* var. *hondurensis* (Sénécl) Barr. & Golf. is a tropical pine that naturally occurs in lowland areas of Belize, El Salvador, Guatemala, Honduras, Nicaragua, and eastern Mexico. It has been one of the most studied tropical pines and the one with the most commercial importance in Brazil. The objective of this work was to select the best provenances for plantations and best trees in families for the establishment of seed orchards. For that a trial with five provenances and 47 open-pollinated families was planted near Planaltina, Federal District, in the Cerrado Region of Brazil. The provenances tested were Poptun (Guatemala), Gualjoco, Los Limones, El Porvenir and Santa Cruz de Yojoa (Honduras) and assessed at 12 years of age. Poptun and Gualjoco had larger volume, and Los Limones and El Porvenir the lowest incidence of forks and foxtails. Individual tree heritabilities for volume, stem form and branch diameter were 0.34, 0.06, and 0.26 respectively. More than 90% of the trees had defects, common in unimproved *P. caribaea*. Selection criteria for quality traits need to be relaxed in the first generation of breeding to allow for larger genetic gains in productivity. Results from this test compared with *P. caribaea* var. *hondurensis* trials in other Brazilian, Colombian and Venezuelan sites suggest that provenance x site and family x site interactions are not as strong as in other pine species.

Index terms: pinus, selection criteria, genetic gain, heritability, breeding methods.

Varição em procedências e famílias de *Pinus caribaea* var. *hondurensis* da Guatemala e Honduras, testadas no Brasil, Colômbia e Venezuela

Resumo – *Pinus caribaea* var. *hondurensis* (Sénécl) Barr. & Golf. é uma espécie tropical que ocorre naturalmente nas terras baixas de Belize, El Salvador, Guatemala, Honduras, Nicarágua e no leste do México. Esta espécie tem sido uma das mais estudadas entre os pinos tropicais e uma das mais importantes comercialmente no centro e norte do Brasil. O objetivo deste trabalho foi selecionar as melhores procedências para plantios e também as melhores árvores dentro de famílias para o estabelecimento de pomares de semente. Para isso, um experimento com cinco procedências e 47 famílias de polinização aberta de *P. caribaea* var. *hondurensis* foi instalado próximo a Planaltina, DF, Região do Cerrado. As procedências testadas foram Poptun (Guatemala), Gualjoco, Los Limones, El Porvenir e Santa Cruz de Yojoa (Honduras), e foram medidas aos 12 anos de idade. Poptun e Gualjoco apresentaram maior volume; Los Limones e El Porvenir apresentaram a menor incidência de plantas bifurcadas e com “foxtails”. As herdabilidades individuais do volume, forma de fuste e diâmetro dos ramos foram 0,34, 0,06 e 0,26, respectivamente. Mais de 90% das árvores tinham defeitos, fato comum em *P. caribaea* não melhorado. Os critérios de seleção dos caracteres qualitativos devem ser flexíveis na primeira geração de melhoramento, para se garantir maiores ganhos genéticos em produtividade. Os resultados deste teste, comparados com testes de *P. caribaea* var. *hondurensis* em outros locais do Brasil, Colômbia e Venezuela, indicam que as interações procedência x local e família x local não são tão fortes como em outras espécies de pinos.

Termos para indexação: pinus, critérios de seleção, ganho genético, herdabilidade, métodos de melhoramento.

Introduction

Pinus caribaea var. *hondurensis* (Sénécl) Barr. & Golf. is a tropical pine that occurs in lowland areas of Belize, El Salvador, Guatemala, Honduras, Nicaragua, and in one location in the state of Quintana Roo, Mexico. The species has great com-

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mercial importance in places like Queensland, Australia, central and northern Brazil, the Fiji Islands, and Venezuela. The largest plantation area of *P. caribaea* is in Venezuela where approximately 600,000 ha have been established and 30,000 ha are planted annually. In Brazil, up to the 1980's, more than 50,000 hectares were planted with this species of which, more than 50% was in the Cerrado Region (Golfari et al., 1978), during the period of fiscal incentives for forestry programs. The Cerrado is a savanna that covers an area of 204 million hectares or approximately 25% of the Brazilian territory. The topography in the Cerrado Region ranges from flat to low rolling hills, which facilitates the use of mechanical tools for agricultural purposes. The soils are highly leached and are low in calcium, magnesium, potassium and sodium but have high aluminum content and high soil acidity (Goedert et al., 1980). The climate in the Cerrado is mostly tropical. It has an average rainfall varying from 750 to 2,000 mm/year and, over most of the region, it ranges between 1,100 and 1,600 mm (Eiten, 1990).

In the 1970's, a number of *P. caribaea* provenances were tested throughout the tropics under the auspices of the Oxford Forestry Institute (OFI). Provenance/progeny tests of *P. caribaea* were subsequently established in a second phase seed collection program by both the OFI and the Central America and Mexico Coniferous Resources Cooperative (CAMCORE), North Carolina State University, in the early 1980's (Dvorak & Donahue, 1992). The objectives of the second set of trials were to better determine family and within-family variation and to establish *ex situ* conservation plantings. CAMCORE made collections in 24 provenances and sampled well over 1,000 mother trees in Mexico and Central America, including material from sites with less than 1,400 mm annual rainfall (dry sites) in Guatemala and Honduras, such as from Poptun, Los Limones, Gualjoco and El Porvenir. These are classified as dry sites because they have at least a four-month period when rainfall is less than 30 mm/month. These provenances of *P. caribaea* var. *hondurensis* have been distributed to cooperative members since 1983 and were planted across multiple sites in Brazil, Colombia, and Venezuela.

One trial of the CAMCORE *P. caribaea* var. *hondurensis* dry site material was established at Planaltina, Brazil, located at 15°35' S and 1,000 m altitude in the Cerrado Region of the country. This paper reports also on the growth, heritability, and expected genetic gain from selections in the *P. caribaea* var. *hondurensis* material at Planaltina and discusses the performance of similar material planted in other areas of Brazil, Colombia and Venezuela.

The objective of this study was to determine if adaptable provenances may be better chosen by matching soil qualities of donor and receptor countries, rather than rainfall amounts, as well as to select provenances for plantations and trees in families for the establishment of seed orchards.

Material and Methods

Seeds were collected from 172 mother trees of *P. caribaea* var. *hondurensis* in Honduras and Guatemala by CAMCORE Cooperative and the National School of Forest Science (ESNACIFOR) in Siguatepeque, Honduras. The trees selected in the original stand were of average to excellent phenotypic quality and were separated by a distance of 100 m whenever possible following CAMCORE guidelines (Balocchi, 1990).

The Santa Cruz, Honduras provenance, which is considered as a wet site source was included in the study to determine if selection of provenances by total rainfall amounts is a practical way of broadening the genetic base for adaptability. Set of seeds from the collection was sent to CAMCORE member organizations in Brazil, Colombia, and Venezuela. One trial in Brazil was established by Embrapa-Centro de Pesquisa Agropecuária dos Cerrados at Planaltina, Federal District, with five provenances (Table 1). Forty-seven open-pollinated families were included in this test. A bulk control lot of commercial seeds of *P. caribaea* var. *hondurensis* from the Companhia Agroflorestal Monte Alegre (Brazil control) and others representing four families from La Mosquitia, San Nicolas, San Estéban and Los Limones, Honduras, (CAMCORE control) were also included in the test. The trial was planted in a compact family block design, replicated nine times, with six trees per family row plots. The spacing was 3 m x 3 m. The number of families in each provenance varied from 7 to 16. In a compact family design, families of one provenance are grouped together within each provenance/replication plot; family positions within the provenance block are randomized in each replication.

Table 1. Provenances information for *P. caribaea* var. *hondurensis* sources included in the CAMCORE genetic trials.

Provenance	Country	Latitude	Elevation (m)	Annual rainfall (mm)
Poptun	Guatemala	16°21' N	470-580	1,688
Gualjoco	Honduras	14°55' N	240-355	1,200
Los Limones	Honduras	14°8' N	660-750	616
El Porvenir	Honduras	14°23' N	550-600	805
Santa Cruz de Yojoa	Honduras	14°53' N	530-720	2,758

The trial was assessed at 12 years of age for survival, height, diameter at breast height (dbh), volume, stem form, branch diameter, broken tops, forking, foxtails, and multistems. Both branch diameter and stem form were scored using a subjective scale of 1-3, with 1 being the largest branch diameter or most crooked stem and 3 being the smallest branch diameter or straightest stem (Balocchi, 1990). For broken tops, forking, foxtails, and multistems, the score used was either a "yes" or a "no". A tree was classified as multistem when it had two or more stems coming from the base. Volume was calculated from a general formula for juvenile trees derived by Ladrach (1986) as volume (m³) = 0.00003 d²h.

The statistical model used was:

$$Y_{ijkm} = u + r_i + p_j + rp_{ij} + f(p)_{k(j)} + e_{ijkm},$$

where:

u = grand mean;

r_i = (i = 1..r) effect of the *i*th block;

p_j = (j = 1..p) effect of the *j*th provenance;

rp_{ij} = the interaction of the *i*th block and the *j*th provenance;

f(p)_{k(j)} = (k = 1..k) the *k*th family effect within each *j*th provenance;

rf(p)_{ik(j)} = the interaction of the *i*th block and the *k*th family within provenance;

e_{ijkm} = the interaction of the *m*th tree in the *i*th block and the *k*th family in the *j*th provenance.

Individual tree values were used in the analyses for all traits except for survival, broken tops, multistem and forking. The data for survival, broken tops, multistem and forking were transformed into arcsine-square roots values prior to conducting the analyses of variance (Steel & Torrie, 1980). The analyses of these four traits were conducted on plot means. Therefore, rf(p) term was not included in the model and the error term was e_{ijk} that is the interaction of the *i*th block and the *k*th family in the *j*th provenance.

Provenance effects were considered fixed and all other effects were considered random. The analyses of variance

(ANOVA) for all traits were conducted with the Statistical Analysis System (SAS) Generalized Linear Model (GLM) procedure type III sums of square. Waller Duncan multiple range test (SAS Institute, 1990) was used to determine if differences among provenances and families were significant. Approximate F tests were made using the procedure proposed by Satterthwaite (1946). Variance components were estimated by the VARCOMP procedure (SAS Institute, 1990). Individual, family and within family heritabilities for all traits were calculated in the usual way, except that the coefficient of relationship was assumed to be 0.33 because some degree of inbreeding (about 10%) was thought to be occurring in the relatively small populations from which the open-pollinated seed was collected in Central America and Mexico (Vasquez & Dvorak, 1996). By increasing the coefficient of relationship from 0.25 to 0.33 the heritability estimates became more conservative (Squillace, 1974).

The formulae used to estimate heritability were:

Individual tree heritability:

$$h^2_i = (3 * \sigma^2_{f(p)}) / (\sigma^2_{f(p)} + \sigma^2_{rf(p)} + \sigma^2);$$

Family heritability:

$$h^2_f = \sigma^2_{f(p)} / (\sigma^2_{f(p)} + \sigma^2_{rf(p)} / r + \sigma^2 / nr);$$

Within family heritability:

$$h^2_w = (2 * \sigma^2_{f(p)}) / (\sigma^2_{rf(p)} + \sigma^2);$$

where:

σ²_{f(p)} = components of variance for families within provenances;

σ²_{rf(p)} = components of variance for block*family within provenances;

σ² = error component of variance;

n = number of trees in plot;

r = number of blocks.

Heritabilities for survival, broken top, multistem and forking, based on plot means were calculated according to the following model:

Family heritability:

$$h^2_{f(p)} = (\sigma^2_{f(p)}) / (\sigma^2_{f(p)} + \sigma^2 / r);$$

where:

σ²_{f(p)} = components of variance for families within provenances;

σ² = error component of variance;

r = number of replications.

Phenotypic correlations between growth and quality traits were calculated using Pearson's product-moment method (SAS Institute, 1990). Correlation analyses were based on family and provenance means.

The best trees in volume growth in each study were selected based on an index that combines individual phenotypic value with the family performance and weights them

based on family and within-family heritability (Balocchi, 1990). The index has the form of:

$$I = pm + (h^2_f P_f + h^2_w P_w)$$

where:

I = index value;

pm = provenance mean;

h^2_f = family mean heritability;

P_f = deviation of a family mean from the provenance mean;

h^2_w = within-family heritability;

P_w = deviation of an individual value from the family mean.

Independent culling levels were set for stem straightness and branch diameter. Trees with forks, and other defects were deleted from consideration.

In addition, single-site analysis at 12 years of age at Planaltina and eight other sites in Brazil, Venezuela and Colombia were also analyzed and compared (Table 2). The traits assessed at five years were height, diameter at breast height, stem volume, foxtail, forking, broken-top, and survival.

Table 2. The site description of the *P. caribaea* var. *hondurensis* CAMCORE tests.

Site	Country	Latitude	Elevation (m)	Annual rainfall (mm)
Planaltina	Brazil	15°35' S	1,100	1,554
Felixlândia	Brazil	18°45' S	614	1,220
Chaguaramas	Venezuela	8°42' N	40	1,000
Coloradito	Venezuela	8°50' N	70	1,060
El Amparo	Colombia	3°5' N	120	2,208
São Mateus	Brazil	18°40' S	10	1,466
Jari (G126)	Brazil	0°50' S	75	1,800
Jari (Q37)	Brazil	0°50' S	75	1,981

Table 3. Provenance trial means of *P. caribaea* var. *hondurensis*, assessed for height, diameter breast height (dbh), volume, survival, stem form, branch diameter, forking, foxtail, multistem, broken-top at 12 years of age, at Planaltina, Federal District, Brazil.

Provenance	Height	Dbh	Volume	Survival	Stem form	Branch diameter	Forking	Foxtail	Multistem	Broken-top
	(m)	(cm)	(m ³)	(%)			------(%)-----			
Gualjoco	16.8	21.3	0.25	97	1.0	1.7	7.2	7.0	25.2	0.7
Los Limones	17.0	20.9	0.24	91	1.2	1.8	2.8	2.3	13.5	0.3
Poptun	17.3	21.3	0.25	94	1.2	1.9	5.0	12.9	11.6	0.6
El Porvenir	16.1	20.7	0.22	94	1.1	2.0	3.4	1.7	13.8	0.3
Santa Cruz de Yojoa	16.0	20.4	0.21	99	1.0	1.8	2.3	6.8	12.9	0.9
CAMCORE control	16.0	20.6	0.22	90	1.1	2.0	7.7	6.2	17.9	1.5
Brazil control	17.7	23.4	0.30	94	1.1	1.9	9.8	3.9	19.6	13.7
Overall mean ⁽¹⁾	16.6	20.9	0.23	94	1.1	1.8	4.1	6.1	15.4	0.6

⁽¹⁾ The controls are not included in the overall mean.

Results and Discussion

The average survival of *P. caribaea* var. *hondurensis* at Planaltina was 94% and there were no significant differences among provenances. There were significant differences in height, diameter at breast height, volume, stem form, forking, and foxtail, but not in branch diameter, multistem and broken top. The average height growth was 16.6 m and the mean difference between the fastest (Poptun) and the slowest growing source (Santa Cruz de Yojoa) was almost 1.5 m (Table 3). Poptun provenance produced the greatest volume but it was not significantly different from Gualjoco and Los Limones. El Porvenir and Santa Cruz de Yojoa produced the smallest volumes. The control (CAFMA) grew significantly higher than all the other provenances (Table 3). It is possible that this control comes from a population that has already gone through a selection process and the original seed source might be from Poptun.

The differences in stem form among *P. caribaea* var. *hondurensis* provenances were small. The average score was 1.1 with provenance means ranging from 1.0 to 1.2. Poptun and Los Limones provenances had better form than all the others.

There were important differences among provenances of *P. caribaea* var. *hondurensis* in both forking and foxtail. El Porvenir and Los Limones had significantly less forking and foxtail than other

sources, including the controls. Poptun seems to be highly susceptible to foxtailing in the Cerrado Region. The control (CAFMA) had 13.7% of its trees with broken tops. This was more than ten times higher than in the other provenances.

There were significant differences among families in most growth and quality traits. The stem volume of the fastest growing family was 0.32 m³ while the stem volume of the slowest growing family was 0.17 m³. Almost 50% difference between one and other.

Individual tree heritabilities for growth traits varied from 0.29 to 0.34 and family heritabilities from 0.81 to 0.86 (Table 4). Stem form, branch diameter and multistem had lower heritabilities (0.06, 0.16 and 0.26, respectively). The family heritabilities for forking and foxtail was 0.36 and 0.63, respectively.

Survival of *P. caribaea* var. *hondurensis* across locations varied from 86.2% to 98.9% (Table 5). The poorest survival was at El Amparo, Colombia, a site with sandy soils, high rainfall, but a pronounced dry season. However, in almost all sites, survival was around 95%. There were few differences in survival within-sites. At Aracruz, the Santa Cruz de Yojoa provenance had lower survival than the others, particularly the El Porvenir provenance.

Volume growth varied considerably depending on the planting site (Table 5). At São Mateus and Aracruz, in the east coast of Brazil, where rainfall is well distributed along the year and the soils are more fertile than in other planting sites, the average volume growth was nearly, or more than double of those

Table 4. Individual tree heritability (h^2_i) and standard error (SE), within-family (h^2_w) and family heritability (h^2_f) for volume of *P. caribaea* var. *hondurensis* growing in Planaltina, Federal District, Brazil, at 12 years of age.

Traits	h^2_i	SE (h^2_i)	h^2_w	h^2_f
Height	0.31	0.08	0.23	0.81
Dbh	0.29	0.07	0.22	0.84
Volume	0.34	0.09	0.26	0.86
Stem form	0.06	0.03	0.05	0.47
Branch diameter	0.26	0.07	0.19	0.77
Multistem	0.16	0.04	0.11	0.73
Forking	-	-	-	0.36
Foxtail	-	-	-	0.63

Table 5. Provenances means of survival (%) / stem volume (m³) of *P. caribaea* var. *hondurensis*, at sites in Brazil, Venezuela and Colombia at five years of age.

Provenance	Brazil					Venezuela			Colombia	
	S ^o Mateus	Aracruz	Planaltina	Felixl ndia	Jari (G126)	Jari (Q37)	Chaguaramas	Coloradito	El Amparo	
Gualjoco	97 / 0.069	86 / 0.072	97 / 0.047	98 / 0.047	95 / 0.036	94 / 0.029	87 / 0.039	100 / 0.056	83 / 0.018	
Los Limones	96 / 0.061	86 / 0.072	94 / 0.043	98 / 0.044	96 / 0.036	91 / 0.030	99 / 0.037	99 / 0.057	88 / 0.015	
Poptun	96 / 0.060	92 / 0.080	95 / 0.050	97 / 0.032	96 / 0.041	96 / 0.033	99 / 0.036	99 / 0.057	84 / 0.017	
El Porvenir	90 / 0.060	96 / 0.061	95 / 0.039	-	-	-	93 / 0.033	-	86 / 0.012	
Santa Cruz de Yojoa	90 / 0.058	75 / 0.069	99 / 0.041	98 / 0.039	97 / 0.033	94 / 0.029	98 / 0.032	98 / 0.052	90 / 0.016	
Overall mean	94 / 0.062	87 / 0.071	96 / 0.044	98 / 0.040	96 / 0.036	94 / 0.030	95 / 0.035	99 / 0.055	86 / 0.016	

in other locations. The volume growth at Coloradito and Venezuela were also good and slower only in comparison to the last mentioned sites. The Cerrado sites at Planaltina and Felixlândia also showed good growth compared to those at Jari (Amazon region, Brazil), El Amparo (Colombia) and Chaguaramas (Venezuela).

Provenances ranked differently from site to site, indicating G x E interactions (Table 5). The Poptun provenance was unstable across sites. It had the fastest growth at Aracruz, Planaltina, Jari, and Coloradito. At the other sites, it was replaced by Gualjoco provenance. El Porvenir and Santa Cruz de Yojoa were the slowest growing provenances across all sites.

The frequency of forking was high in all sites. Provenances means varied considerably within sites (Table 6). It was higher at Coloradito (Venezuela), and São Mateus (Brazil), than at Planaltina, Brazil. Poptun and Gualjoco were among provenances with the highest percentage of forked trees across sites.

Conversely, Los Limones and El Porvenir were among those with the lowest percentage in all test sites.

Percentage of foxtail varied considerably across sites (Table 6). At São Mateus, Brazil, and El Amparo, Colombia, the percentage of foxtailed trees was extremely low. At the other sites, foxtail percentages varied from 15.0% at Jari (Q37), to 36.3 at Coloradito. Los Limones and El Porvenir provenances consistently had the lowest percentages of foxtailed trees across sites. Poptun had the highest percentages at all sites.

The percentage of crooked trees varied considerably across and within sites (Table 7). The lowest percentages were found at Jari, Brazil, and the highest at Coloradito, Venezuela, and Planaltina, Brazil. The Gualjoco provenance had the highest percentage of crooked trees at all sites, and Poptun the lowest, except at Coloradito, Chaguaramas and Jari (G126).

Table 6. Percentage means of forked / foxtailed trees of *P. caribaea* var. *hondurensis* provenances in Brazil, Venezuela and Colombia at five years of age.

Provenance	Brazil			Venezuela		Colombia	
	São Mateus	Planaltina	Jari (G126)	Jari (Q37)	Chaguaramas	Coloradito	El Amparo
Gualjoco	47.0 / 0.3	30.7 / 26.7	41.1 / 23.8	33.8 / 15.6	42.9 / 28.8	42.8 / 39.8	- / 0.8
Los Limones	36.2 / 0.0	20.7 / 11.1	33.3 / 10.0	33.9 / 6.5	29.3 / 18.4	31.0 / 16.6	- / 0.5
Poptun	48.8 / 2.7	19.5 / 39.9	44.6 / 26.8	44.9 / 25.1	32.6 / 42.9	52.0 / 49.8	- / 2.0
El Porvenir	24.7 / 0.0	19.4 / 9.7	-	-	33.3 / 12.9	-	- / 0.0
Santa Cruz de Yojoa	47.9 / 0.5	15.1 / 24.7	35.0 / 23.7	35.3 / 13.9	34.2 / 31.6	41.3 / 39.2	- / 0.5
Overall mean	40.9 / 0.7	21.3 / 22.4	38.5 / 21.0	36.9 / 15.3	34.5 / 26.8	41.7 / 36.3	- / 0.8

Table 7. Percentage means of crooked / thick branched trees of *P. caribaea* var. *hondurensis* provenances in Brazil and Venezuela at five years of age.

Provenance	Brazil			Venezuela	
	Planaltina	Jari (G126)	Jari (Q37)	Chaguaramas	Coloradito
Gualjoco	73.1 / 23.6	46.3 / 3.5	25.2 / 1.3	62.1 / 23.7	56.7 / 28.5
Los Limones	40.5 / 12.3	21.1 / 1.5	13.3 / 2.3	39.1 / 9.3	39.2 / 9.3
Poptun	36.1 / 11.1	23.8 / 0.7	10.6 / 2.1	39.5 / 11.3	55.8 / 11.3
El Porvenir	46.7 / 14.4	-	-	42.9 / 6.9	-
Santa Cruz de Yojoa	57.7 / 17.2	36.4 / 1.0	20.4 / 1.5	47.4 / 15.0	50.7 / 21.7
Overall mean	50.8 / 15.7	31.9 / 1.7	17.4 / 1.8	46.2 / 13.2	53.1 / 17.7

Branching habit was also variable across and within sites. The lowest percentage of trees with thick branches was found at Jari, Brazil. The Gualjoco provenance had a larger number of trees with thick branches at all sites, except at Jari (Q37) and Poptun, the smallest at Planaltina and Jari (G126) (Table 7).

The highest number of trees with defects (forked, foxtailed, crooked) was found at the Cerrado of Planaltina, Brazil, and the lowest number at El Amparo, Colombia. At this site the trees had the lowest rate of growth. Within sites, the highest contrast was between the Gualjoco and Los Limones provenances at Planaltina and Jari (G126); El Porvenir and Santa Cruz at São Mateus; Los Limones and Poptun at Jari (Q37) and Coloradito; and Poptun and El Porvenir at El Amparo (Table 8).

Individual tree heritabilities for volume across sites varied from 0.15 to 0.40, and family heritabilities from 0.69 to 0.87. It seems that heritability values are positively associated with rate of growth. The lowest individual and family heritabilities were found at El Amparo, Colombia and Chaguaramas, Venezuela, where survival and volume growth were the lowest (Table 9).

Spearman rank correlations were estimated on sub-samples of the nine tests where a minimum of twelve families were in common in each pair of sites in order to examine the magnitude of family x site interaction. Family x site interactions for volume growth was of the highest importance in some pairs of locations but not in others. For instance, the rank correlation coefficient (r) was significant between El Amparo, Colombia, and the other test sites. Con-

versely, the ranking of family means for volume in Felixlândia, Brazil, was not related to the rank of families in other sites (Table 10).

Up to the late 70's *P. caribaea* var. *hondurensis* was the most planted tropical pine in Brazil and the provenances from Poptun and Peten (Guatemala), were the most widely used in plantations (Golfari et al., 1978). This species has potential to grow well in the wet and tropical parts of Brazil, as recommended by Golfari et al. (1978). Those authors also recommend to look for seed at sources in areas where climate is analogous to those at the plantation sites, considering that this species grows naturally under a large range of rainfall (600 to 4,000 mm) with dry seasons ranging from two to six months (Dvorak et al., 1993). The results at Planaltina, reinforce the recommendations made by Golfari et al. (1978). The best performing provenances in the Cerrado area of Planaltina were Poptun and Gualjoco, which come from areas of rainfall (between 1,000 and 1,700 mm) and latitude similar to those at Planaltina. However, similarity in latitude and rainfall between plantation and source sites *per se* can not explain growth rate. The Guanaja provenance, from area of high rainfall (above 2,000 mm) grew faster than the Poptun provenance at Planaltina (Moura & Dvorak, 1997). In other tests in the Brazilian Cerrados, height growth of the Poptun provenance was similar to the other provenances, such as Los Limones and Culmi, but slower growing than Mountain Pine Ridge provenance (Moura et al., 1991). At Planaltina, Poptun and Los Limones provenances had the best stem form. However in natural stands while Poptun is considered to have one of the best phenotypes, Los Limones

Table 8. Percentage means of imperfect trees of *P. caribaea* var. *hondurensis* provenances in Brazil, Venezuela and Colombia at five years of age.

Provenance	Brazil				Venezuela		Colombia
	São Mateus	Planaltina	Jari (G126)	Jari (Q37)	Chaguaramas	Coloradito	El Amparo
Gualjoco	47.3	85.5	77.1	57.4	75.5	74.5	3.3
Los Limones	36.2	61.5	52.0	44.4	53.0	50.8	2.7
Poptun	51.9	71.4	68.0	62.8	68.1	78.1	6.9
El Porvenir	25.3	65.8	-	-	51.2	-	0.6
Santa Cruz de Yojoa	48.5	74.0	68.0	54.9	66.2	72.9	2.3
Overall mean	41.8	71.6	66.3	54.9	62.8	69.1	3.1

is known to be one of the worst (Dvorak et al., 1993). Therefore, one can not rely on the quality of the natural stands for selection and even the phenotypically worst material should be tested. Los Limones has shown a slow growth in several sites (Gibson et al., 1983; Cornelius & Ponce, 1990) but in this study, it showed a good growth, particularly in height at Planaltina. The use of Poptun provenance in commercial plantations in Brazil was a right choice. This provenance had the fastest growth in volume at Planaltina, second only to the Brazil control (presumably from Poptun).

It seems that no provenance is outstanding at all sites. However, Poptun, Gualjoco and Los Limones, grew faster than El Porvenir and Santa Cruz de Yojoa provenances at all sites. It is possible that a large proportion of the total variation in growth is attributable to variations between and within families, rather than to variations between provenances, which tend to

mask real differences among provenances (Robbins & Hughes, 1983). It is apparent that the qualitative traits are under more genetic control than the quantitative traits. Provenances varied considerably across sites in quality traits, showing strong site influence, but they tended to be more susceptible to defects than other across sites. The Gualjoco provenance was one of the most productive at all sites, but it had consistently the highest percentage of imperfect trees across sites. Therefore, it is advantageous to include more than one provenance in a commercial breeding population, but care should be taken when choosing trees for selection, since productive provenances can show a high proportion of malformed trees.

The provenance from Santa Cruz de Yojoa, where rainfall is much higher than in other provenances (wet site), did not do well at any of the sites, regardless of the rainfall. Soil condition seems to influence the growth of *P. caribaea* var. *hondurensis* more than the amount of rainfall. El Amparo is the test site where the amount of rainfall is the highest of all but had the slowest growth. Even the provenance from Santa Cruz (wet site) grew less than those from drier sites. In drier sites, such as Chaguaramas, Venezuela (1,000 mm) this species did not grow well.

The fastest growing families of *P. caribaea* var. *hondurensis* chosen at Planaltina may be also the best in other sites, but surprisingly not the fastest growing at a similar area in the Cerrado of Felixlândia. A *P. caribaea* var. *hondurensis* breeding program for extensive areas appears to be more feasible than local ones, contrary to the program suggested for *P. oocarpa* (Moura et al., 1998). The results from the present study confirm, in certain ways, the results found in an across country assessment of *P. tecunumanii* (Hodge, 1996). This author suggested

Table 9. Individual tree heritability (h^2_i) and standard error (SE), within-family (h^2_w) and family heritability (h^2_f) for stem volume of *P. caribaea* var. *hondurensis* growing in sites in Brazil (Br), Venezuela (Ven) and Colombia (Col) at five years of age.

Site	h^2_i	SE(h^2_i)	h^2_w	h^2_f
São Mateus, Br	0.24	0.08	0.17	0.77
Aracruz, Br	0.27	0.10	0.20	0.79
Planaltina, Br	0.40	0.10	0.31	0.87
Felixlândia, Br	0.25	0.07	0.18	0.74
Jari (Q37), Br	0.22	0.07	0.16	0.74
Jari (G126), Br	0.17	0.05	0.12	0.70
Chaguaramas, Ven	0.15	0.05	0.11	0.69
Coloradito, Ven	0.30	0.08	0.22	0.81
El Amparo, Col	0.16	0.05	0.12	0.63

Table 10. Spearman rank correlation table for pairs of common families between locations in Brazil (Br), Colombia (Col) and Venezuela (Ven)⁽¹⁾.

Site	Planaltina, Br	Chaguaramas, Ven	Jari (Q37), Br	Jari (G126), Br	Coloradito, Ven
Felixlândia, Br	0.30 ^{ns} (18)	0.35 ^{ns} (12)	0.10 ^{ns} (12)	0.08 ^{ns} (30)	
El Amparo, Col	0.64 ^{**} (15)	0.44 [*] (19)	0.73 ^{***} (16)		0.67 ^{**} (15)
Jari (Q37), Br	0.60 ^{***} (20)	0.64 ^{**} (17)			
Chaguaramas, Ven	0.33 [*] (36)				

⁽¹⁾ Number within brackets are family pairs. ^{ns} Nonsignificant. *, ** and *** Significant at 5%, 1% and 0.1% probability level, respectively.

that marginal gains could still be obtained by exchanging genetic material across wide geographic regions through forestry cooperatives like CAMCORE.

The variation in heritabilities across sites was not as strong as verified in *P. oocarpa* growing in similar sites (Moura et al., 1998). The decreasing trend in heritability values with decrease in the rate of growth as observed in this study, may be the result of the differences in stages of ontogeny of the trees, as well as in environmental conditions where they are growing.

Populations of unimproved *P. caribaea* var. *hondurensis* are considered to have a high proportion of poor quality trees, which is a disadvantage to their use in commercial plantations (Golfari et al., 1978). In the Planaltina test, more than 90% of the trees had some type of defect. Therefore, heavy selection intensity in quality traits should be avoided in the first generation of selection. If not, most of the good candidate trees for volume production would be eliminated. For instance, if trees with foxtails, forks, multistem, broken tops and crooked stems (index "1") are discarded, less than 10% of a population of 2.600 individuals will be left for further selection.

In estimating genetic gain, it was assumed that the best 25 trees would be selected in the trial for the production (elite) population. However, in actual practice, more trees than just 25, would be selected in the trial; those not placed in the production orchard would be grafted into a breeding orchard along with other CAMCORE selections of *P. caribaea* var. *hondurensis* and then further tested. It is also expected that some genetic material of *P. caribaea* var. *hondurensis* would be obtained from other CAMCORE members.

Conclusions

1. The best performing provenances for planting in the Cerrado are Poptun and Gualjoco at Planaltina, while Poptun and Los Limones are most promising in Felixlândia.

2. Among the fastest growing provenances at Planaltina, Poptun has the best stem form, together with Los Limones provenance.

3. None of the tested provenances is outstanding at all sites.

4. Sites factors have strong influence on quality traits among *P. caribaea* var. *hondurensis* provenances.

5. Santa Cruz de Yojoa provenance does not grow well at any of the test sites.

6. The fastest growing families of *P. caribaea* var. *hondurensis* chosen at Planaltina may also be the fastest growing in other countries.

7. The heritabilities in growth traits across sites decrease with decrease in the rate of growth.

8. More than 90% of *Pinus caribaea* var. *hondurensis* trees have some type of defect (forking, foxtailing, crookedness).

9. Heavy selection intensity in quality traits in *Pinus caribaea* var. *hondurensis* should be avoided in the first generation of selection.

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References

- BALOCCHI, C. E. **CAMCORE tree improvement program**. Raleigh : North Carolina State University, 1990. 36 p. (CAMCORE Bulletin on Tropical Forestry, 7).
- CORNELIUS, J. P.; PONCE, E. G. Provenances trials of *Pinus caribaea* Morelet var. *hondurensis* (Sencl.) Barr. & Golfari and *P. oocarpa* Schiede in the Republic of Honduras. **Commonwealth Forestry Review**, Oxford, v. 69, n. 3, p. 227-246, 1990.
- DVORAK, W. S.; DONAHUE, J. K. **CAMCORE research review 1980-1992**. Raleigh : North Carolina State University, 1992. 93 p.
- DVORAK, W. S.; ROSS, K. D.; LIU, Y. **Performance of *Pinus caribaea* var. *hondurensis* in Brazil, Colombia and**

- Venezuela.** Raleigh : North Carolina State University, 1993. 47 p. (CAMCORE Bulletin on Tropical Forestry, n. 11).
- EITEN, G. Vegetação do cerrado. In: PINTO, M. N. (Org.). **Cerrado:** caracterização, ocupação e perspectivas. 2. ed. Brasília : Editora da UnB, 1990. p. 17-73.
- GIBSON, G. L.; BARNES, R. D.; BERRINGTON, J. Provenance productivity in *Pinus caribae* and its interaction with environment. **Commonwealth Forestry Review**, Oxford, v. 62, n. 2, p. 93-106, 1983.
- GOEDERT, W. J.; LOBATO, E.; WAGNER, E. Potencial agrícola da região dos cerrados. **Pesquisa Agropecuária Brasileira**, Brasília, v. 15, n. 1, p. 1-17, jan. 1980.
- GOLFARI, L.; CASER, R. L.; MOURA, V. P. G. **Zoneamento ecológico esquemático para reflorestamento no Brasil** (2a. aproximação). Brasília : PRODEPEF, PNUD/FAO/IBDF/BRA-45, 1978. 66 p. (Série Técnica, 11).
- HODGE, G. R. Marginal gains from regionalization to utilize genotype x environment interactions. In: TREE IMPROVEMENT FOR SUSTAINABLE TROPICAL FORESTRY CONFERENCE, 1996, Caloundra. **Proceedings...** Caloundra : Queensland Forest Research Institute/International Union of Forestry Research Organizations, 1996. v. 2, p. 323-327.
- LADRACH, W. E. **Comparaciones entre procedencias de siete coníferas en la Zona Andina al finalizar los ochos años.** Bogotá : Smurfit Cartón de Colombia, 1986. 8 p. (Informe de Investigación, 105).
- MOURA, V. P. G.; DVORAK, W. S. Variation among open-pollinated families of *Pinus caribaea* var. *hondurensis* from Guanaja Island, Honduras, grown in Brazil. In: BIENNIAL SOUTHERN FOREST TREE IMPROVEMENT CONFERENCE-SFTIC, 24. , 1997, Orlando. **Proceedings...** Orlando : University of Florida, 1997. p. 275-284.
- MOURA, V. P. G.; DVORAK, W. S.; HODGE, G. R. Provenance and family variation of families of *Pinus oocarpa* Schiede, grown in the Brazilian Cerrado. **Forest Ecology and Management**, Amsterdam, v. 109, p. 315-322, 1998.
- MOURA, V. P. G.; PARCA, M. L. S.; SILVA, M. A. **Variação da densidade da madeira de espécies e procedências de *Pinus* centro-americanos em três locais na região dos Cerrados.** Colombo : Embrapa-CNPQ, 1991. p. 29-44. (Embrapa-CNPQ. Boletim de Pesquisa Florestal, 22/23).
- ROBBINS, A. M. J.; HUGHES, C. E. **Provenance regions for *Pinus caribaea* and *P. oocarpa* within the Republic of Honduras.** Oxford : University of Oxford, 1983. 77 p. (Commonwealth Forestry Institute. Unit of Tropical Silviculture. Tropical Forestry Paper, 18).
- SAS INSTITUTE (Cary, Estados Unidos). **SAS/STAT user's guide:** version 6. 4. ed. Cary, 1990. v. 2.
- SATTERTHWAITE, F. E. An approximate distribution of estimates of variance components. **Biometric Bulletin**, Washington, v. 2, p. 110-114, 1946.
- SQUILLACE, A. E. Average genetic correlations among off-spring from open-pollinated forest trees. **Silvae Genetica**, Frankfurt, v. 23, p. 149-156, 1974.
- STEEL, R. G. D.; TORRIE, J. H. **Principles and procedures of statistics.** New York : McGraw-Hill, 1980. 633 p.
- VASQUEZ, J.; DVORAK, W. S. Trend in variances and heritabilities with stand development of tropical pines. **Canadian Journal of Forest Research**, Ottawa, v. 26, p. 1473-1480, 1996.