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GENETIC PARAMETERS AND PROVENENANCE VARIATION OF *PINUS TECUNUMANII* IN 78 INTERNATIONAL TRIALS

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ABSTRACT

Results from 78 international trials of *Pinus tecunumanii* in Brazil, Colombia, South Africa and Venezuela are presented. Measurements at ages 3, 5 and 8 were available, and all trials were measured at least once. Genetic material includes samples of essentially the entire range of *P. tecunumanii*, and includes 24 high-elevation and 16 low-elevation provenances from Mexico, Guatemala, Belize, Honduras and Nicaragua. High- and low-elevation provenances were tested separately. Volume growth of the species is commercially acceptable, with means across all provenances and families of approximately 14 $m^3 \cdot ha^{-1} \cdot year^{-1}$ on sites in Brazil and Venezuela, 15 $m^3 \cdot ha^{-1} \cdot year^{-1}$ in South Africa and 25 $m^3 \cdot ha^{-1} \cdot year^{-1}$ in the highlands of Colombia at 8 years of age. Provenance variation for volume growth is important, with the best provenances 10 to 15% better than the mean. Mean single-site estimates of heritability for volume growth are approximately 0.15, and substantial genetic variation exists among families within provenances. Potential genetic gain for age 8 volume from selection within provenance is around 35%. Quality traits such as straightness, stem breakage and forking also appear to be heritable, but these traits seem to be under a lower degree of genetic control, with heritabilities around 0.05. There was no evidence of strong adverse genetic correlations. Genotype × environment interaction for volume growth is stronger at the family level than at the provenance level, and higher for tests located in different countries than in the same countries. Selection for age 8 volume using age 5 data would be 89% as effective as selection at age 8. CAMCORE members have made over 200 selections of *P. tecunumanii* for advanced-generation breeding.

Keywords: *Pinus tecunumanii*, genotype × environment interaction, age-age correlations, tree breeding.

INTRODUCTION

Pinus tecunumanii Eguiluz and J. P. Perry, Jr. is a closed-cone pine in the Section Serotinae subsection Oocarpa (PERRY 1991). The main geographic range of the species extends from Chiapas, Mexico to central Nicaragua in a series of disjunct populations that occur between 400 and 2800 m elevation (DVORAK *et al.* 1993). CAMCORE (Central America and Mexico Coniferous Resources Cooperative), North Carolina State University, began seed collections of *P. tecunumanii* in 1981, and has now sampled more than 45 provenances in Belize, El Salvador, Guatemala, Honduras, Mexico, and Nicaragua (Figure 1). The seeds have been distributed to CAMCORE members in Brazil, Chile, Colombia, Guatemala, Indonesia, South Africa and Venezuela and established in provenance/progeny tests and conservation banks. *Pinus tecunumanii* has significant commercial potential in numerous regions throughout the tropics and sub-tropics (DVORAK *et al.* 1989, BIRKS & BARNES 1990, CROCKFORD 1990, DVORAK & DONAHUE 1992, DVORAK & SHAW 1992). The wood density of the species is acceptable for structural uses, and its pulping and paper-making properties compare favorably with other pines grown in the same environments (MALAN & HOON 1991, WRIGHT 1987).

To develop sound breeding strategies and maximize genetic gain, breeders need reliable information on provenance and family variation, genetic parameters, and the magnitude of genotype × site interaction. This is especially important in international forestry cooperatives like CAMCORE where one of the goals is to exchange the best genetic material between members on different continents to enlarge the size of breeding populations and improve productivity. *Pinus tecunumanii* provides tree breeders with an excellent opportunity to quantify patterns of genetic variation across locations because the species has been the most intensively sampled neotropical pine in Mexico and Central America over the last 15 years and the most widely tested in the tropics and subtropics. This paper reports 3 to 8 year results for 78 provenance/progeny tests of *P. tecunumanii* established in Brazil, Colombia, Venezuela and South Africa.

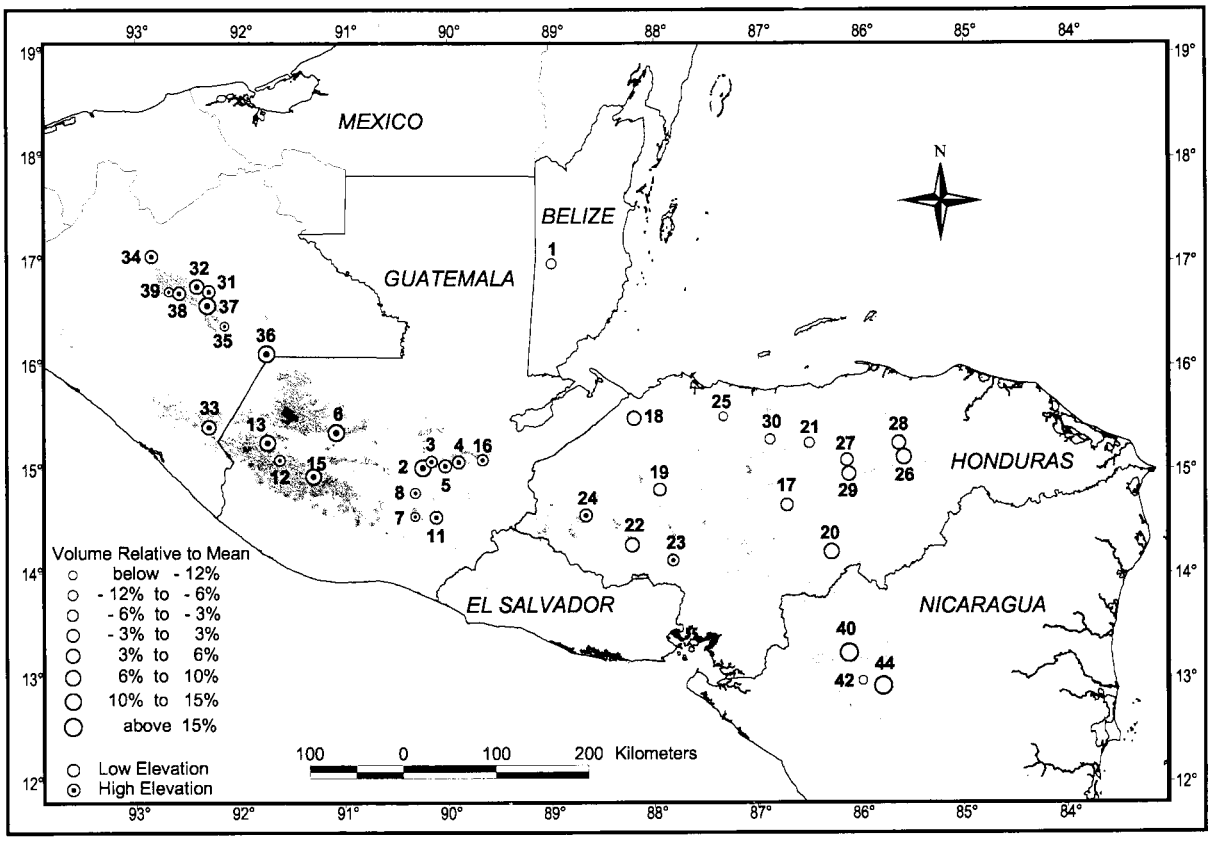

Figure 1. Locations and estimated effects for volume growth (%) at age 8 for provenances of *P. tecunumanii* included in CAMCORE tests. The provenance Juquila is not shown on the map. It is in the state of Oaxaca, nearly 5 ° further west than any other provenance. Provenances 18 (Cerro Cusuco) and 22 (La Esperanza) were included in the low-elevation tests, but are actually high-elevation (>1500 m) provenances.

MATERIALS AND METHODS

Plant Material and Genetic Tests

Twenty-four high-elevation provenances (above 1500 m) and 16 low-elevation provenances (generally below 1500 m) of *P. tecunumanii* were sampled in southern Mexico and Central America by the CAMCORE Cooperative between 1981 and 1995 (Table 1). Subsequent research has demonstrated significant variation in molecular markers between high- and low-elevation populations (FURMAN *et al.* 1996). In each provenance, seeds were collected from approximately 20–50 mother trees which had good volume growth and stem straightness. When provenance size was extremely small (< 5 ha) seed collections were made randomly in the stand. Seeds were kept separate by mother tree and distributed to CAMCORE members who established the provenance/progeny tests, and often included their own commercial controls. No attempt was made to select provenances within populations for specific members.

Provenances from the high- and low-elevation populations were usually established in separate tests with subsets of 3 to 6 provenances in each test. Two provenances of somewhat intermediate elevation (Cerro Cusuco and La Esperanza) were classified as low-elevation provenances and included in those tests, although it might have been more appropriate to include them with the high-elevation provenances.

A total of 48 tests containing over 73,000 trees were established using high-elevation provenances and 30 tests containing more than 54,000 trees were established using low-elevation provenances (Table 2). The high-elevation provenances have been tested more intensively because initial collection efforts began with these provenances.

The trial design was the same at all locations, a randomized complete block design, with provenances randomized in each replication, and families randomized within the provenance sub-plots. There were 9 replications and 6 trees per family planted in row-plots. Spacing was approximately 3 × 3 m in all tests. Test measurement was scheduled at ages 3, 5, and 8 with all trees assessed. Measurements were not available at all ages for all tests. Only growth traits were measured at

Table 1. Summary information for CAMCORE *P. tecunumanii* provenances.

Provenance	Code	Volume gain (%)	BTOP33	Country	Latitude	Longitude	Elevation (m)	Precip. (mm)
High-elevation Sources								
San Jeronimo	2	13.3	31.3 b	Guatemala	15° 00' N	90° 15' W	1620–1850	1200
Piedad	3	–5.2	32.9 b	Guatemala	15° 02' N	90° 06' W	1690–2200	2592
Chi San Vicente	4			Guatemala	15° 04' N	89° 54' W	2100–2770	1700
El Pinalon	5			Guatemala	15° 02' N	90° 02' W	2080–2230	2592
La Ul	6	11.2	29.2 c	Guatemala	15° 21' N	91° 05' W	2440–2680	1996
Km33	7	–14.5	31.6 b	Guatemala	14° 32' N	90° 19' W	2000–2200	1543
Km47	8	–9.1	26.2 b	Guatemala	14° 46' N	90° 19' W	2000–2200	1543
La Soledad	11	1.4	37.0 b	Guatemala	14° 32' N	90° 07' W	2390–2470	1543
Cabrican	12	–9.3		Guatemala	15° 05' N	91° 37' W	2510–2670	1010
San Miguel	13	9.7		Guatemala	15° 15' N	91° 44' W	2280–2370	2127
Pachoc	15	7.9	29.0 c	Guatemala	14° 56' N	91° 18' W	2000–2500	1350
San Lorenzo	16	–4.8	27.8 b	Guatemala	15° 05' N	89° 40' W	1900–2100	1700
Las Trancas	23	–4.7	31.0 b	Honduras	14° 07' N	87° 49' W	2075–2185	1579
Celaque	24	–2.4	41.2 b	Honduras	14° 33' N	88° 40' W	1540–2030	1273
Chanal	31	1.0	34.6 c	Mexico	16° 42' N	92° 23' W	2010–2350	1238
Chempil	32	3.6	30.4 a	Mexico	16° 45' N	92° 25' W	2020–2220	1146
El Carrizal	33	3.7	39.8 c	Mexico	15° 24' N	92° 18' W	2130–2280	2000
Jitotol	34	–1.9	32.3 a	Mexico	17° 02' N	92° 51' W	1660–1750	1701
Las Piedrecitas	35	–19.0	26.1 a	Mexico	16° 22' N	92° 09' W	2360–2500	1252
Montebello	36	10.5	43.6 a	Mexico	16° 06' N	91° 45' W	1660–1750	1909
Napite	37	10.7	37.8 c	Mexico	16° 34' N	92° 19' W	2070–2350	1350
Rancho Nuevo	38	1.3	28.7 c	Mexico	16° 41' N	92° 35' W	2280–2340	1238
San Jose	39	–11.5	32.1 a	Mexico	16° 42' N	92° 41' W	2245–2400	1252
Juquila	0	8.2	30.2 c	Mexico	16° 13' N	97° 14' W	2090–2260	1325
Low-elevation Sources								
Mountain Pine Range	1	–6.3	55.6	Belize	16 58' N		450–700	1558
Campamento	17	–1.6		Honduras	14° 39' N	86° 43' W	800–1300	1484
Cerro Cusuco	18	+4.5		Honduras	15° 29' N	88° 12' W	1400–1650	2287
Los Planes	19	+2.2		Honduras	14° 48' N	87° 57' W	1100–1800	2287
Villa Santa	20	+9.6	33.4	Honduras	14° 12' N	86° 17' W	800–1000	1302
Esquipulas del Norte	21	–7.7		Honduras	15° 15' N	86° 30' W	900–1000	1067
La Esperanza	22	+4.9		Honduras	14° 16' N	88° 13' W	1500–1800	1363
Locomapa	25	–26.2		Honduras	15° 30' N	87° 20' W	1100–1500	1166
Culmi	26	+7.6	46.2	Honduras	15° 07' N	85° 35' W	400–700	1491
Gualaco	27	–0.0		Honduras	15° 05' N	86° 08' W	600–800	1491
San Esteban	28	+5.3	31.0	Honduras	15° 15' N	85° 38' W	680–1200	1071
San Francisco	29	+5.0	29.4	Honduras	14° 57' N	86° 07' W	900–1590	1491
Jocon	30	–6.8	20.4	Honduras	15° 17' N	86° 53' W	775–1000	1166
San Rafael del Norte	40	18.0		Nicaragua	13 14' N	86 07' W	920–1040	1394
Cerro la Joya	42	–33.9		Nicaragua	12 58' N	89 59' W	940–1160	1394
Yucul	44	25.3		Nicaragua	12 55' N	85 47' W	900	1394

[1]BTOP33 expresses the amount of broken tops expected in a provenance, when the average provenance has 33% broken tops. Due to the structure of the data, BTOP33 for high-elevation provenances could only be compared in three disconnected subsets denoted by the letters a, b, and c following the estimate.

Table 2. Summary Information for CAMCORE *P. tecunumanii* tests. High-elevation sources.

Obs	Country	Test	Sitename	Lat	Long	Elev	Precip
1	Brazil	040102A	Pedreiras	20° 22' S	41° 00' W	900	1800
2		041103A	Morada Nova de Minas	18° 45' S	45° 10' W	570	1400
3		130102C	Santa Tereza	19° 56' S	40° 37' W	775	1600
4		130111E	Santa Tereza	19° 56' S	40° 37' W	775	1600
5		130602D	CPAC	15° 32' S	47° 39' W	1190	1546
6		130606B	Felixlandia	18° 45' S	44° 53' W	614	1220
7		130611D	Felixlandia	18° 45' S	44° 53' W	614	1220
8		130617A	CPAC	15° 32' S	47° 39' W	1190	1546
9		131538A	Fazenda Primavera	18° 38' S	42° 51' W	850	1400
10		131637A	Graõ Mogol	16° 30' S	42° 50' W	819	1081
11		131743D	Moquém	24° 07' S	50° 07' W	875	1660
12		132043E	Condessa	27° 31' S	50° 04' W	850	1769
13		132641A1	Imbauzinho	24° 16' S	50° 38' W	780	1473
14		132641A4	Capela	27° 32' S	50° 31' W	945	1463
15		132642A1	Imbauzinho	24° 16' S	50° 38' W	780	1473
16		132642A4	Campina Grande	27° 45' S	50° 23' W	830	1463
17	Colombia	040201A	Salinas	2° 12' N	76° 42' W	2500	2300
18		130202E	San José	2° 52' N	76° 06' W	1750	2046
19		130206A	San José	2° 52' N	76° 06' W	1750	2046
20		130211C	San José	2° 52' N	76° 06' W	1750	2046
21		130216B	San José	2° 52' N	76° 06' W	1750	2046
22		130232D	Peñas Negras	2° 15' N	71° 31' W	2490	2500
23		130233A	Peñas Negras	2° 15' N	17° 31' W	2490	2500
24		130234A	Peñas Negras	2° 15' N	17° 31' W	2490	2500
25		130243A	La Catana	2° 09' N	76° 36' W	2500	1968
26	S.Africa	130730A3	Mooiplaas	28° 38' S	31° 14' E	943	1200
27		130732C1	Mooiplaas	28° 38' S	31° 14' E	943	1200
28		130733B3	Mooiplaas	28° 38' S	31° 14' E	943	1200
29		131002A	Wilgeboom	24° 58' S	30° 57' E	960	1253
30		131002B	Tweefontein	25° 02' S	30° 47' E	1155	1953
31		131003A	Wilgeboom	24° 58' S	30° 57' E	960	1316
32		131003B	Tweefontein	25° 02' S	30° 47' E	1155	1953
33		131011A	Wilgeboom	24° 58' S	30° 57' E	960	1316
34		131011B	Tweefontein	25° 03' S	30° 45' E	1150	1254
35		131016A	Wilgeboom	24° 58' S	30° 57' E	960	1316
36		131020A	Tweefontein	25° 03' S	30° 45' E	1150	1953
37		131030A1	Tweefontein	25° 04' S	30° 49' E	1250	1953
38		131030A2	Hendriksdal	25° 11' S	30° 46' E	1450	1178
39		131032A1	Tweefontein	25° 04' S	30° 49' E	1250	1953
40		131032A2	Hendriksdal	25° 11' S	30° 46' E	1450	1178
41		131032A3	Ceylon	25° 04' S	30° 41' E	1590	1153
42		131032A4	Swartfontein	25° 15' S	30° 56' E	1080	1194
43		131032B1	Entabeni	23° 00' S	30° 17' E	1270	1810
44		131032B2	Woodbush	23° 59' S	29° 59' E	1600	1424
45		131033B1	Tweefontein	25° 04' S	30° 49' E	1250	1953
46		131033B2	Hendriksdal	25° 11' S	30° 46' E	1450	1178
47		131043C2	Wilgeboom	24° 58' S	30° 57' E	960	1316
48		131832C3	Ncula	30° 12' S	30° 05' E	1200	900

age 3, and all traits measured at ages 5 and 8 (scale listed in parentheses):

HT = height (m),

DBH = diameter at breast height, *e.g.*, 1.3 m (cm),

ST = stem straightness (1 = very crooked, 2 = average straightness, 3 = very straight),

BD = branch diameter (1 = thick, 2 = average, 3 = thin),

FORK = forking (0 = no fork, 1 = forked),

FOXT = foxtailing (0 = no foxtail, 1 = foxtail, *i.e.*,

Table 2 (cont.) Summary Information for CAMCORE *P. tecunumanii* tests. Low-elevation sources.

Obs	Country	Test	Sitename	Lat	Long	Elev	Precip
49	Brazil	030104A	Aracruz	19° 48' S	40° 17' W	550	1518
50		030104B	Sao Mateus	18° 40' S	39° 45' W	1060	1466
51		031105A	Morada Nova De Minas	18° 45' S	45° 10' W	570	1400
52		160101C	Aracruz	19° 48' S	40° 17' W	25	1518
53		160102B	Sao Mateus	18° 40' S	39° 45' W	35	1966
54		160603C	Moquém	24° 07' S	50° 09' W	840	1339
55		160801B	Quadra	0° 50' S	53° 00' W	75	2077
56		161502D	Fazenda Primavera	18° 38' S	42° 51' W	850	1400
57		161503B	Fazenda Primavera	18° 38' S	42° 51' W	850	1400
58		161707C	Ventania	24° 07' S	50° 07' W	310	1660
59	Colombia	030201A	La Arcadia	2° 30' N	76° 35' W	1750	2112
60		030202A	La Arcadia	2° 30' N	76° 35' W	1750	2112
61		030203A	La Arcadia	2° 30' N	76° 35' W	1750	2112
62		160203D	Los Alpes	4° 03' N	76° 29' W	1700	2702
63		160205B	Los Alpes	4° 03' N	76° 29' W	1700	2702
64		160211C	La Marı¡a	4° 10' N	76° 20' W	2160	1762
65		160213B	La Marı¡a	4° 10' N	76° 20' W	2160	1762
66	S. Africa	130731A3	Mooiplaas	28° 38' S	31° 14' E	943	1200
67		131031A1	Tweefontein	25° 04' S	30° 49' E	1250	1953
68		131031A2	Hendriksdal	25° 11' S	30° 46' E	1450	1178
69		161001E1	Wilgeboom	24° 58' S	30° 57' E	960	1316
70		161001E2	Kwambonambi	32° 10' S	28° 40' E	65	1201
71		161001G	Swartfontein	25° 11' S	30° 59' E	952	1194
72		161002C1	Wilgeboom	24° 58' S	31° 00' E	981	1316
73		161002C2	Kwambonambi	28° 40' S	32° 10' E	65	1200
74		161004A1	Witwater	25° 08' S	30° 52' E	1530	1154
75		161004A2	Dukuduku	28° 22' S	32° 19' E	70	1201
76	Venezuela	030407A	Ticoporo	7° 43' N	70° 56' W	200	1800
77		160301D	El Hierro	9° 10' N	69° 20' W	150	1520
78		160305A	Santo Tomás	10° 00' N	69° 05' W	300	1287

presence of an internode > 3 m), and

BTOP = broken top (0 = normal top, 1 = broken top).

A volume index was calculated using height and DBH using the formula

$$\text{Volume} = 0.00003\ (\text{DBH}_2 * \text{height})$$

As a part of the data preparation, a plot of height × DBH was inspected visually. Trees which were outliers (*i.e.*, those which had abnormal height-diameter ratios) were deleted from the data set. Thus, trees with heights severely affected by top breakage would not be included in volume calculations.

Single-site Analyses

Single site analyes were conducted for each test. The linear model was:

$$y_{ijklm} = \mu_i + B_j + P_k + F(P)_{kl} + B*f(P)_{jkl} + e_{ijklm}$$

where y_{ijklm} = phenotypic observation for the ijklmth tree, μ_i = mean in the ith test, B_j = fixed effect of the jth block, P_k = random effect of the kth provenance, $E[P_k] = 0$, $Var[P_k] = \sigma^2_{prov}$, $F(P)_{kl}$ = random effect of the lth family in the kth provenance, $E[f(P)_{kl}] = 0$, $Var[f(P)_{kl}] = ss^2_F$, r_{jkl} = random effect of the jklth row-plot, *i.e.* the interaction of the jth block and the lth family of the kth provenance, $E[r_{ikl}] = 0$, $Var[r_{ikl}] = \sigma^2_r$, e_{ijklm} = random error term associated with the ijklmth tree, $E[e_{ijklm}] = 0$, $Var[e_{ijklm}] = \sigma^2_e$,

Variance components for all traits were estimated using PROC VARCOMP METHOD = TYPE1 in SAS (Henderson's Method 3, SAS 1989). Phenotypic variance within-provenance (σ^2_T) was estimated as:

$$\sigma^2_T = \sigma^2_F + \sigma^2_r + \sigma^2_e$$

Single-site (or biased) heritability estimates within provenance (h_b^2) were estimated for all traits using the formula:

$$h_b^2 = \frac{3\sigma_F^2}{\sigma_T^2}$$

The covariance among open-pollinated families would typically be higher than ¼ of additive genetic variance; this could result from inbreeding and/or from a small number of effective male pollinators leading the to presence of some percentage of full-sibs with the OP family (SQUILLACE 1974). Thus a coefficient of 3 instead of 4 was multiplied by the family variance in the calculation of heritability. The "b" subscript indicates that the family variance is estimated on a single-site basis, and may be biased upward by the presence of family × environment interaction. Specifically, $\sigma_F^2 = \sigma_f^2 + \sigma_{fe}^2$, where σ_f^2 and σ_{fe}^2 are the family and family × environment variances in a multiple-site model (COMSTOCK & MOLL 1963, HODGE & WHITE 1992).

Lastly, provenance was considered a random effect in order to compare provenance variation to additive genetic variation. A parameter P_b^2 was estimated using the formula:

$$P_b^2 = \frac{\sigma_{prov}^2}{\sigma_T^2}$$

The *b* subscript indicates that the provenance variance was estimated on a single-site basis, and may be biased upward by the presence of provenance × environment variation, in the same manner as with families. Since both h_b^2 and P_b^2 are expressed relative to the phenotypic variance, they can be directly compared to indicate the relative importance of the two sources of variation.

Parameter means and empirical standard errors were calculated treating each test site as an independent estimate. As a general convention, parameter estimates in this paper will often be expressed as "mean ± standard error".

Age-Age Correlations

Age-age genetic correlations (the same trait at different ages) were estimated from single-site analyses. Between-age covariance components were calculated using a dummy variable approach (SEARLE 1992), and the genetic correlation estimated as

$$r_g = \frac{\hat{\sigma}_{F_1F_2}}{\hat{\sigma}_{F_1}\hat{\sigma}_{F_2}}$$

where $\hat{\sigma}_{F_1,F_2}$ = estimated family covariance between the trait measured at the different ages, $\hat{\sigma}_{F_1}$ = estimated family variance at the first age, $\hat{\sigma}_{F_2}$ = estimated family variance at the second age.

Paired-site Analyses and Genotype × Environment Interaction

Paired site analyses were conducted for all possible pairs of tests with at least 15 families in common. These analyses were conducted in order to quantify genotype × environment (G×E) interaction among families and provenances. Phenotypic observations were divided by the phenotypic standard deviation estimated for each test from the single-site analyses. This was done to remove most of the bias of the G×E interaction variances due to heterogeneous variances (EISEN & SAXTON 1983, HILL 1984). The linear model was

$$y_{ijklm} = \mu + E_i + B(E)_{ij} + P_k + PE_{ik} + f(P)_{kl} + f(P)E_{ikl} + r_{ijkl} + e_{ijklm}$$

where y_{ijklm} = phenotypic observation for the ijklmth tree, μ = overall mean, E_i = fixed effect of the ith test, $B(E)_{ij}$ = fixed effect of the jth block nested in the ith test, P_k = random effect of the kth provenance, $E[P_k] = 0$, $Var[P_k] = \sigma_{prov}^2$, PE_{ik} = random interaction of the kth provenance and the ith test, $E[PE_{ik}] = 0$, $Var[PE_{ik}] = \sigma_{pe}^2$, $f(P)_{kl}$ = random effect across sites of the lth family in the kth provenance, $E[f(P)_{kl}] = 0$, $Var[f(P)_{kl}] = \sigma_f^2$, $f(P)E_{ikl}$ = random interaction of the lth family in the kth provenance and the ith test, $E[f(P)E_{ikl}] = 0$, $Var[f(P)E_{ikl}] = \sigma_{fe}^2$, r_{ijkl} = random effect of the ijklth row-plot, *i.e.*, the interaction of the jth block of the ith test and the lth family of the kth provenance, $E[r_{ikl}] = 0$, $Var[r_{ijkl}] = \sigma_r^2$, e_{ijklm} = random error term associated with the ijklmth tree, $E[e_{ijklm}] = 0$, $Var[e_{ijklm}] = \sigma_e^2$, and all other terms defined as in the single-site model with blocks nested with tests.

For each pair of tests, estimates of Type B genetic correlations at the family and provenance level (r_{Bg} and r_{Bprov}, respectively) were calculated:

$$r_{Bg} = \frac{\sigma_f^2}{\sigma_f^2 + \sigma_{fe}^2}$$

$$r_{Bprov} = \frac{\sigma_p^2}{\sigma_p^2 + \sigma_{pe}^2}$$

Type B correlations measure the genetic or provenance correlation between the same trait expressed on two different sites (BURDON 1977). Type B correlations

over multiple sites range between 0 and 1; an $r_B \approx 1$ indicates a near perfect correlation between performance in different environments, or in other words, an absence of genotype (or provenance) × environment interaction. Type B correlations were only estimated if estimated h_B^2 exceeded 0.05 in both tests of a pair. Use of tests with extremely low h_B^2 estimates can result in seemingly very imprecise type B correlation estimates well out of the theoretical range. Parameter means and empirical standard errors were calculated using each pair of tests as an independent observation.

A second approach was used to estimate Type B correlations. Specifically, means of the variance component estimates were used in the general equation:

$$r^*_{Bg} = \frac{\bar{\sigma}^2_f}{\bar{\sigma}^2_f + \bar{\sigma}^2_{fe}}$$

$$r^*_{Bprov} = \frac{\bar{\sigma}^2_p}{\bar{\sigma}^2_p + \bar{\sigma}^2_{pe}}$$

where $\bar{\sigma}^2_f$ = mean of the family variance component estimates from paired test analyses, and similarly for other terms. This method can be described as a "function of the mean variance components" to calculate an average Type B parameter estimate, in contrast to the "mean of the function" approach described above. Use of a "function of the mean" approach to calculate an average genetic parameter has been shown to yield more precise estimates of genetic parameters (PEDERSON 1972). A typical CAMCORE provenance-progeny test might have from 3–6 provenances and from 30 to 60 families. Since for a given pair of tests, provenance and provenance × environment effects are estimated with only a few degrees of freedom, the advantage of r^*_B over r_B might be more important for estimates of the Type B provenance correlations than the Type B genetic correlations.

For all genetic parameters estimates (from both single-site and paired site analyses) analysis of variance was used to examine patterns of variation among genetic parameter estimates. Numerous models were utilized which included as main fixed effects elevational categories, countries and age, and two-way interactions of the main effects.

Provenance Effects

Provenance effects were estimated for both percent volume and percent stem breakage using ordinary least squares (OLS) across all tests. Least-squares means were estimated for each family in each test, and then divided by overall test mean; the resulting values were used as units of observation. Estimated provenance effects for volume can then be interpreted as percent differences in volume growth. Mean stem breakage in the tests used to calculate provenance effects was 34% in the high-elevation tests and 22% in the low elevation tests. Provenance effects for broken top were scaled to a common mean of 33% to facilitate comparison and to provide a meaningful measure of the importance of provenance differences for this trait.

RESULTS AND DISCUSSION

Species Productivity and Quality

Growth rates: Growth rates of *P. tecunumanii* in all countries were quite promising (Table 3). Heights were 3–4 m at age 3, 7–10 m at age 5, and 11–15 m at age 8, with the best height growth occurring in Colombia. Mean DBH ranged from 5–8 cm at age 3, 11–17 cm at age 5, and 16–21 cm at age 8. Assuming 1111 stems/ha with 85% survival, these growth rates correspond approximately to volumes (outside bark) of 14 m^3 of wood·ha^{-1}·yr^{-1} on sites in Brazil and Venezuela, 15 m^3·ha^{-1}·yr^{-1} in South Africa and 25 m^3·ha^{-1}·yr^{-1} in the highlands of Colombia at 8 years of age. These data represent the mean of unimproved material from all provenances on all sites, and substantially larger values should be expected from selected material from the best provenances planted on suitable sites.

It was difficult to compare high- and low-elevation populations as they were infrequently planted on the same types of sites, and checklots of the other population were not always included in the tests. The low-elevation provenances were generally established at lower elevations and latitudes than the high-elevation provenances, but there are a few tests planted on the same or very similar locations. As would be expected, site has a significant effect on which population performed better. For example, there were four high-elevation and three low-elevation tests established at sites with similar latitudes, elevation, and precipitation in Colombia (observations 18–21 and 59–61 in Table 2). The high-elevation tests had an average volume index of 0.252 m^3 versus 0.228 m^3 for the low-elevation tests (see Appendix 1), an advantage of approximately 10%. Note that this advantage is probably biased upward, as the low-elevation material was primarily from a single provenance, Mountain Pine Ridge in Belize, which appears to be about 6% below average among all low-elevation provenances (Table 1). In another comparison, there were three high-elevation tests and one low-elevation test established at the same site, Tweefontein, South Africa (observations 37, 39, 45, and 67 in Table 2). The average volume index of

Table 3. Means for growth traits in CAMCORE *P. tecunumanii* tests at ages 3, 5, and 8. Full data for all tests presented in Appendix 1.

Elevation	Country	HT3	HT5	HT8	DBH3	DBH5	DBH8	VOL3	VOL5	VOL8
high	Brazil	3.96	7.47	12.35	5.47	11.19	16.29	0.0041	0.0326	0.1155
	Colombia	5.02	7.26	13.31	7.93	14.33	20.97	0.0145	0.0536	0.1942
	S.Africa	3.88	7.91	12.84	4.90	11.95	18.08	0.0036	0.0396	0.1382
low	Brazil	5.58	9.53	13.13	7.66	14.31	16.78	0.0123	0.0639	0.1229
	Colombia	5.65	9.89	15.01	8.25	16.75	21.64	0.0161	0.0920	0.2283
	S.Africa	4.14	8.48	11.01	5.67	12.14	17.55	0.0057	0.0427	0.1226
	Venezuela	5.15	7.75	11.46	6.62	10.67	17.15	0.0084	0.0332	0.1163

Table 4. Means for quality traits in CAMCORE *P. tecunumanii* tests at ages 5 and 8. Full data for all tests presented in Appendix 2.

Elevation	Country	ST5	ST8	BD5	BD8	Fork5	Fork8	Foxt5	Foxt8	Btop5	Btop8
high	Brazil	2.11	2.10	1.88	2.14	9.37	15.0	3.7	0.7	1.8	0.4
	Colombia	1.64	1.41	1.76	1.50	11.1	24.7	4.4	7.5	23.5	31.7
	S.Africa	1.76	2.01	1.82	2.37	8.0	13.2	1.1	0.2	5.4	12.2
low	Brazil	1.93	1.68	2.03	2.53	6.51	18.8	0.9	0.1	8.8	3.2
	Colombia	1.14	1.55	1.32	1.93	8.3	28.1	1.2	1.5	8.6	14.1
	S.Africa	1.22	1.82	2.76	2.30	10.6	21.0	1.9	0.4	6.6	11.8
	Venezuela	1.81	1.40	2.26	1.71	4.8	3.4	0.4	1.7	0.2	0.2

the high-elevation tests and the low-elevation test were equal at 0.116 m^3 (Appendix 1). There was also one high-elevation and one low-elevation test established at Wilgeboom, South Africa (observations 31 and 69 in Table 2), and here the low-elevation material had an average volume index of 0.1605 m^3 versus 0.1482 m^3 for the high-elevation material (Appendix 1), an advantage of 8% for the low-elevation population. Lastly, there were two provenances that included in the low-elevation trials which could have could have been classified as high-elevation provenances: Cerro Cusuco (elev. 1400–1650 m) and La Esperanza (elev. 1500 –1800 m). Estimates of volume gain for these two provenances were quite similar, 4.5% and 4.9%, respectively (Table 1).

Broken Tops and Forking: Broken tops were most severe in tests of the high-elevation population in Colombia (Table 4). In eight tests, mean incidence of broken tops at age 5 was 23.5%, with two tests at 58% and 61% incidence. Mean incidence at age 8 was even higher. In seven tests, mean incidence was 31.7% and the minimum was 14.7%. The tests in Colombia are all between 2 and 2.5 ° latitude, and tests at higher latitudes in Brazil and South Africa did not have as high levels of incidence, with Brazil averaging less than 2% and South Africa averaging 5.4% at age 5 and 12.2% at age 8.

Low-elevation provenances in Colombia had lower incidence of broken tops than the high-elevation provenances. Mean incidence was 8.6% at age 5 and 14.1% at age 8. Similar, but slightly lower levels of broken tops were seen in South African low-elevation tests, with mean incidence 6.6% at age 5 and 11.8% incidence at age 8. In Brazil, incidence of broken tops was always low, with the exception of one test which had 35% broken tops at age 5. Subsequent inspection of field tests suggested that when *P. tecunumanii* is established on relatively fertile soils in the state of Parana in southern Brazil, stem breakage can be significant by age 5. However, when *P. tecunumanii* was established on relatively unfertile Oxisols in the Brazilian cerrado (characterized by well-defined dry seasons), stem breakage fell to less than 5% (MOURA & DVORAK 1998). It is unclear exactly what role environmental factors play in stem breakage.

Levels of forking in the four countries followed the same pattern as broken tops. For example, in 8-year-old measurements of the low-elevation population Colombia had the highest levels of forking with (28.1%), followed by South Africa (21%), Brazil (18.8%), and Venezuela (5.4%). It seems likely a high

proportion of forks would be caused by some top breakage, perhaps very high in the main stem, followed by competition among two or more new leaders. The two "traits", stem breakage and forking, may be different aspects of the same trait, and it may be more profitable to aggregate these defects into one score. For many of the tests in this study, this aggregate trait would have mean incidence in the 30–70% level, which is probably ideal for assessing genetic variance and heritability.

Single-site Heritability and Provenance Variation

Volume Growth: As might be expected for forest trees, single-site heritability for volume growth was lowest at the youngest age. Mean h_b^2 across all sites and both elevational categories was 0.12 ± 0.01 at age 3, 0.16 ± 0.01 at age 5, and 0.15 ± 0.01 at age 8 (Table 5). For each age, differences between elevational categories were not statistically significant. However, there was a slight tendency for the low-elevation population to have larger h_b^2 than the high-elevation population: 0.13 vs 0.11 at age 3 (p = 0.12), 0.18 vs 0.15 at age 5 (p = 0.14), and 0.15 vs 0.14 at age 8 (not significant). At ages 5 and 8, there was no effect associated with country, but at age 3 there were significant differences among countries for h_b^2. These appear to be primarily due to low age 3 heritability in South Africa. For example, in the low-elevation population in South Africa, mean h_b^2 = 0.06 vs 0.17 in Brazil and Colombia. A similar pattern exists in the high-elevation population, with mean h_b^2 = 0.08 in South Africa and approximately 0.15 in Brazil and Colombia. (Table 5). These lower heritabilities at an early age in South Africa may be partially associated with low growth rates in South Africa at age 3, with mean volumes substantially lower than in other countries, particularly in the low-elevation population (Table 3). Many of the South African tests were impacted by heavy deer browsing of seedlings shortly after planting, which would both reduce growth and increase error variance.

For volume growth, provenance variation apparently becomes relatively less important with age. When the estimated parameter P_b^2 is compared to estimated h_b^2, it provides a relative measure of the size of provenance variance and additive genetic variance on a single-site basis. Thus estimated provenance variance was roughly 0.05/0.12 = 42% of additive variance at age 3, 0.04/0.16 = 25% of additive variance at age 5, and 0.02/0.15 = 13% of additive variance at age 8.

Quality Traits: Straightness appears to be the most heritable of the quality traits with h_b^2 at both ages 5 and 8 approximately equal to 0.13 in both the high- and low-elevation populations (Table 5). There was no statistically significant effect of country on h_b^2 at age 5, but the effect of country was significant (p = 0.04) at age 8. This is probably due primarily to two tests in Venezuela which had mean h_b^2 = 0.01. There was some provenance variation in straightness, with estimated relative size about 23% of additive genetic variance.

Branch diameter was under a reasonable amount of genetic control, with mean h_b^2 = 0.09 at both ages 5 and 8. Provenance variation was very small, with mean P_b^2 = 0.01, on the order of 11% of the additive genetic variance. Heritability for branch diameter is significantly higher (p = 0.04) in the high-elevation population than in the low-elevation population (h_b^2 = 0.10 vs 0.04). In addition, there was a significant effect due to country; tests in South Africa had much lower levels of heritability for branch diameter in both low and high-elevation populations than in other countries (Table 5).

Stem breakage and forking appear to be under similar levels of genetic control. Since these traits are binomial (0 or 1), h_b^2 was only estimated if mean incidence in the tests exceeded 15%. There were 6 tests at age 5 which met this criteria for broken tops with a mean incidence across the tests of 35%, 11 tests for broken tops at age 8 with mean incidence of 29%, 9 tests of forking at age 5 with mean incidence of 24%, and 26 tests for forking at age 8 with mean incidence of 23% (Table 5). For both traits, mean h_b^2 is around 0.05 to 0.07, with forking having slightly higher heritability. There was a significant effect of high- and low-elevation on the heritability for broken tops at age 8, but this was probably due to one aberrant negative estimate of h_b^2 in one low-elevation test in Colombia. Provenance variation for both broken tops and forking is relatively low, with P_b^2 = 0.01 for both traits.

This level of genetic control for stem breakage is in general agreement with previous reports in the literature on family mean and plot mean heritabilities. Using variance component estimates consistent with an h_b^2 = 0.05 for broken tops, and assuming the standard CAMCORE design of 9 replications, 6 tree row-plots and 83% survival, plot heritability would be 0.20 and family heritability would be 0.69. These correspond to estimates of a plot mean heritability ranging from 0.20 to 0.36 (PARFITT 1996), and family mean heritability ranging from 0.17 to 0.63 (DVORAK *et al.* 1993).

Age-age Correlations

Age-age correlations (r_g) were estimated for volume, straightness and branch diameter (Table 6). There were never any significant differences between high-elevation and low-elevation populations for average age-age correlation for any trait.

Table 5. Trait means, minima and maxima, estimated within provenance heritabilities and provenance variation for different traits measured in CAMCORE *P. tecunumanii* tests. *N* = number of single sites where trait was assessed.

Trait	Elevation	Country	*N*	Mean	Min	Max	h_b^2	SE (h_b^2)	P_b^2	SE (P_b^2)
VOL3	high	Brazil	12	0.0051	0.0007	0.0104	0.16	0.04	0.05	0.012
	high	Columbia	9	0.0145	0.0015	0.0277	0.13	0.02	0.08	0.019
	high	S. Africa	22	0.0039	0.0007	0.0089	0.08	0.01	0.03	0.008
	high – across countries		43	0.0067	0.0007	0.0277	0.11	0.01	0.05	0.007
	low	Brazil	11	0.0113	0.0010	0.0242	0.17	0.03	0.03	0.007
	low	Columbia	7	0.0161	0.0021	0.0343	0.17	0.04	0.11	0.101
	low	S. Africa	9	0.0057	0.0009	0.0186	0.06	0.02	0.07	0.016
		Venezuela	2	0.0085	0.0064	0.0105	0.07	0.07	0.03	.
	low – across countries		29	0.0105	0.0009	0.0343	0.13	0.02	0.06	0.020
	Overall		72	0.0081	0.0007	0.0343	0.12	0.01	0.05	0.008
VOL5		Brazil	10	0.0326	0.0200	0.0525	0.18	0.04	0.07	0.025
		Columbia	8	0.0536	0.0158	0.0898	0.16	0.01	0.05	0.019
		S. Africa	17	0.0396	0.0145	0.0633	0.13	0.01	0.02	0.006
	high – across countries		35	0.0408	0.0145	0.0898	0.15	0.01	0.04	0.009
		Brazil	4	0.0639	0.0387	0.1002	0.24	0.04	0.00	.
		Columbia	5	0.0920	0.0550	0.1199	0.13	0.02	0.00	0.002
		S. Africa	6	0.0427	0.0241	0.0686	0.17	0.04	0.07	0.022
		Venezuela	3	0.0332	0.0141	0.0457	0.19	0.07	0.00	0.009
	low – across countries		18	0.0595	0.0141	0.1199	0.18	0.02	0.04	0.015
	Overall		53	0.0481	0.0141	0.1199	0.16	0.01	0.04	0.008
VOL8		Brazil	5	0.1155	0.0719	0.1927	0.11	0.02	0.02	0.008
		Columbia	7	0.1942	0.1139	0.2721	0.14	0.02	0.02	0.009
		S. Africa	13	0.1382	0.1141	0.1548	0.16	0.01	0.01	0.004
	high – across countries		25	0.1494	0.0719	0.2721	0.14	0.01	0.02	0.004
		Brazil	3	0.1229	0.0926	0.1534	0.19	0.04	.	.
		Columbia	3	0.2283	0.2070	0.2422	0.17	0.01	.	.
		S. Africa	8	0.1226	0.0971	0.1605	0.14	0.02	0.05	0.007
		Venezuela	3	0.1163	0.0655	0.1480	0.15	0.06	0.00	0.003
	low – across countries		17	0.1402	0.0655	0.2422	0.15	0.01	0.04	0.008
	Overall		42	0.1456	0.0655	0.2721	0.15	0.01	0.02	0.004
ST5		Brazil		2.11	1.62	2.84	0.13	0.02	0.02	0.007
		Columbia		1.64	1.17	2.07	0.16	0.02	0.03	0.012
		S. Africa		1.76	1.38	2.20	0.11	0.01	0.04	0.012
	high – across countries			1.83	1.17	2.84	0.13	0.01	0.03	0.007
		Brazil	4	1.93	1.02	2.43	0.20	0.05	0.00	.
		Columbia	2	1.13	1.09	1.17	0.13	0.07	0.00	0.005
		S. Africa	4	1.22	1.12	1.50	0.10	0.02	0.02	0.008
		Venezuela	2	1.81	1.67	1.96	0.12	0.08	0.01	0.014
	low – across countries			1.56	1.02	2.43	0.14	0.02	0.01	0.005
	Overall			1.75	1.02	2.84	0.13	0.01	0.03	0.005

Table 5. Trait means, minima and maxima, estimated within provenance heritabilities and provenance variation for different traits measured in CAMCORE *P. tecunumanii* tests. *N* = number of single sites where trait was assessed.

Trait	Elevation	Country	*N*	Mean	Min	Max	h_b^2	SE (h_b^2)	P_b^2	SE (P_b^2)
ST8	high	Brazil	5	2.10	1.87	2.24	0.11	0.02	0.01	0.008
	high	Columbia	7	1.41	1.19	1.81	0.14	0.02	0.02	0.010
	high	S. Africa	13	2.01	1.75	2.35	0.15	0.02	0.05	0.012
	high – across countries		25	1.88	1.19	2.35	0.1	0.01	0.03	0.007
	low	Brazil	3	1.68	1.63	1.72	0.14	0.04	.	.
	low	Columbia	3	1.55	1.36	1.76	0.20	0.05	.	.
	low	S. Africa	8	1.82	1.42	2.04	0.12	0.02	0.02	0.010
	low	Venezuela	2	1.40	1.01	1.80	0.01	0.04	0.00	0.002
	low – across countries		16	1.69	1.01	2.04	0.12	0.02	0.01	0.008
	Overall		41	1.81	1.01	2.35	0.13	0.01	0.03	0.006
BD5	high	Brazil	5	1.88	1.73	1.98	0.10	0.04	0.01	0.004
	high	Columbia	7	1.76	1.21	2.31	0.16	0.03	0.02	0.005
	high	S. Africa	14	1.82	1.26	2.71	0.07	0.01	0.01	0.006
	high – across countries		26	1.82	1.21	2.71	0.10	0.01	0.01	0.004
	low	Brazil	1	2.03	2.03	2.03	0.01	.	0.00	.
	low	Columbia	2	1.32	1.29	1.35	0.05	0.03	0.00	0.004
	low	S. Africa	5	2.76	1.89	2.99	0.01	0.01	0.00	0.002
	low	Venezuela	2	2.26	1.96	2.55	0.15	0.01	0.02	0.015
	low – across countries		10	2.30	1.29	2.99	0.04	0.02	0.01	0.003
	Overall		36	1.95	1.21	2.99	0.09	0.01	0.01	0.003
BD8	high	Brazil	5	2.14	1.82	2.92	0.07	0.02	0.00	0.004
	high	Columbia	7	1.50	1.18	1.84	0.11	0.01	0.01	0.004
	high	S. Africa	13	2.37	2.07	2.63	0.11	0.01	0.02	0.006
	high – across countries		25	2.08	1.18	2.92	0.10	0.01	0.01	0.003
	low	Brazil	3	2.53	1.76	2.97	0.02	0.04	.	.
	low	Columbia	3	1.93	1.87	1.98	0.12	0.05	.	.
	low	S. Africa	8	2.30	1.97	2.47	0.07	0.02	0.01	0.008
	low	Venezuela	2	1.71	1.56	1.86	0.11	0.02	0.01	0.000
	low – across countries		16	2.20	1.56	2.97	0.08	0.02	0.01	0.007
	Overall		41	2.13	1.18	2.97	0.09	0.01	0.01	0.003
BTOP5	high	Columbia	4	40.03	20.03	60.92	0.04	0.02	0.01	0.002
	high – across countries		4	40.03	20.03	60.92	0.04	0.02	0.01	0.002
	low	Brazil	1	34.99	34.99	34.99	0.07	.	0.00	.
	low	Columbia	1	16.84	16.84	16.84	0.03	.	0.01	.
	low – across countries		2	25.92	16.84	34.99	0.05	0.02	0.00	0.005
	Overall		6	35.33	16.84	60.92	0.04	0.01	0.01	0.002

Table 6. Mean age-age genetic correlation estimates for selected pairs of traits measured in the same CAMCORE *P. tecunumanii* tests.[a]

Trait 1	Trait 2	Elevation	Country	*N*	r_g	SE (r_g)
VOL3	VOL5	high	Brazil	4	0.95	0.03
		high	Columbia	7	0.79	0.06
		high	S. Africa	12	0.90	0.05
		high – across countries		23	0.88	0.04
		low	Brazil	4	0.90	0.02
		low	Columbia	4	0.57	0.11
		low	S. Africa	4	0.95	0.04
		low	Venezuela	1	1.10	.
		low – across countries		13	0.83	0.06
		overall		36	0.86	0.03
VOL3	VOL8	high	Brazil	2	0.87	0.13
		high	Columbia	6	0.59	0.04
		high	S. Africa	9	0.80	0.07
		high – across countries		17	0.73	0.05
		low	Brazil	3	0.81	0.04
		low	Columbia	2	0.70	0.06
		low	S. Africa	5	0.70	0.09
		low	Venezuela	1	1.02	.
		low – across countries		11	0.76	0.05
		overall		28	0.74	0.03
VOL5	VOL8	high	Brazil	2	0.84	0.10
		high	Columbia	7	0.80	0.05
		high	S. Africa	12	0.90	0.07
		high – across countries		21	0.87	0.05
		low	Brazil	3	0.95	0.03
		low	Columbia	3	0.97	0.07
		low	S. Africa	5	0.91	0.06
		low	Venezuela	2	0.85	0.12
		low – across countries		13	0.92	0.04
		overall		34	0.89	0.03
ST5	ST8	high	Brazil	2	0.85	0.05
		high	Columbia	6	1.02	0.05
		high	S. Africa	9	0.94	0.05
		high – across countries		17	0.96	0.03
		low	Brazil	3	0.80	0.13
		low	S. Africa	3	1.04	0.06
		low – across countries		6	0.92	0.08
		overall		23	0.95	0.03
BD5	BD8	high	Brazil	1	1.09	.
		high	Columbia	6	0.94	0.07
		high	S. Africa	6	0.65	0.13
		high – across countries		13	0.81	0.08
		low	Venezuela	2	0.84	0.13
		low – across countries		2	0.84	0.13
		overall		15	0.82	0.07

a) Genetic correlation estimated only if $h_B^2 > 0.05$ for both traits. Estimates of $r_g > 1.0$ were set equal to 1.10 when calculating means.

Age-age genetic correlation for volume growth averaged 0.86±0.03 across all tests for ages 3–5, 0.74 ±0.03 at ages 3–8, and 0.89 ±0.03 for ages 5–8. There was a significant country effect with age 3–5 and 3–8 correlations, presumably driven by the substantially lower correlations in Colombia than in other countries. For example, mean age 3–8 correlation for high-elevation population in Colombia was 0.59, while it was 0.87 in Brazil and 0.80 in South Africa (Table 6). Volume growth in Colombia was faster than anywhere else (Table 3), thus a higher age 3–8 correlation might have been expected. However, because of the fast growth, a given time interval would represent a greater interval in terms of stand development than in other countries; and this may be the cause of the lower age-age correlations.

Age 5–8 genetic correlations for straightness and branch diameter also appear to be quite high, with r_g = 0.95±0.03 for straightness and r_g = 0.82±0.07 for branch diameter.

Genotype × Environment Interaction

Volume Growth: Examination of genotype × environment interaction focused on volume growth. Mean Type B genetic correlations for different sub-classifica tions of test pairs were examined to try to identify patterns of G×E interaction. In general, the mean Type B correlations (r_B) were very similar to the "functions of the mean" (r_B^*) (Tables 7, 8, 9). Since each test could conceivably be measured at ages 3, 5, and 8, three different ways of aggregating the data were examined: 1) all possible data points were averaged together, thus each pair of tests could contribute up to three data points (*i.e.*, r_{Bg} at ages 3, 5, and 8), 2) each test pair contributes only one data point, which was the mean r_{Bg} for that test pair, and 3) each test pair contributes only one data point, which was the r_{Bg} for the oldest measurement for that test pair. The results of the three methods were nearly identical, and only results from method 1 are presented here.

Mean r_{Bg} for test pairs in the same country was 0.81 ± 0.02, while for test pairs in different countries mean r_{Bg} was 0.46 ± 0.03, which were significantly different according to analysis of variance. The estimates of r_{Bg}^* were similar (Table 7). This type of geographic effect on G×E has been found in *P. palustris* Mill. in the southeastern United States for pairs of tests in the same or different regions (east versus west) (ADAMS *et al.* 1994), but the magnitude of difference between "same" and "different" r_{Bg} was substantially lower (0.747 versus 0.610, respectively). In *P. elliottii* Engelm. var. *elliottii* a G×E pattern was found associated with site quality by HODGE & WHITE (1992) using open-pollinated data, but not by DIETERS *et al.* (1995) with a large control-pollinated data set.

The estimate of Type B provenance correlation from any one test is substantially less precise than the estimate of Type B genetic correlation due to many fewer degrees of freedom. Thus, mean Type B provenance correlations are relatively imprecise, with standard errors roughly twice as high as for the mean estimates of the genetic correlations (Tables 7–9).

Despite the lower precision of the estimates, in general, results for type B provenance correlations were similar to those for type B genetic correlations. Although mean r_{Bprov} for "same" versus "different" country class were not significantly different (0.60 and 0.58, respectively), r_{Bprov}^* were quite different, 0.84 for the "same" country class versus 0.54 for the "different" country class (Table 7). In general, it appears that provenances are more stable across environments than families. For example, across all pairs of tests from "different" countries, mean r_{Bprov} = 0.54 and mean r_{Bg} = 0.41 (Table 7). These results are in accord with earlier results based on 18 five-year-old *P. tecunumanii* trials, where there was moderate levels of family × location interaction, but little provenance × location interaction (DVORAK & SHAW 1992).

Further breakdowns of the data by country class become somewhat less reliable as number of data points decreases. However it appears that within the "same" country class, there is more G×E among pairs of tests in Brazil than in Colombia or South Africa (mean r_{Bg} = 0.67 versus 0.88 and 0.94, respectively). This may be due to a broader geographic range among sites in Brazil than in the other two countries, for example, there is over a 12° range in latitude among high-elevation tests in Brazil compared to less than 1° in Colombia and approximately 4° in South Africa. Within the "different" country class, South Africa and Colombia are moderately well correlated (r_{Bg} = 0.54), South Africa and Brazil somewhat less so (r_{Bg} = 0.46), and Brazil and Colombia more poorly correlated (r_{Bg} = 0.31).

Using country class to group pairs of tests is obviously a surrogate for other factors causing interaction among sites. A number of simple models were investigated in an attempt to explain variation in r_{Bg} and r_{Bprov}, including terms like test longitude, latitude, elevation, precipitation, general climatic and soil types, and various interactions. While many of these factors showed some relationship with the patterns of G×E, no one factor or model was found to be superior to the use of country class. However, it should be possible to utilize more sophisticated models to identify critical factors which lead to G×E.

Table 7. Mean type B genetic and provenance correlation estiamtes for volume growth in pairs of CAMCORE *P. tecunumanii* tests. All parameter estimates at ages 3, 5, and 8 are averaged together.

Country1	Country2	Type B genetic correlation				Type B provenance correlation			
		N	r^*_{Bg}	r_{Bg}	SE(r_{Bg})	N	r^*_{Bprov}	r_{Bprov}	SE(r_{Bprov})
Same country									
Brazil	Brazil	21	0.67	0.68	0.02	12	0.83	0.79	0.06
Colombia	Colombia	3	0.88	0.87	0.05	3	0.88	0.84	0.07
S. Africa	S. Africa	40	0.94	0.88	0.03	39	0.78	0.53	0.07
Mean		64	0.81	0.81	0.02	54	0.81	0.60	0.06
Different country									
Brazil	Colombia	23	0.21	0.31	0.07	13	0.54	0.53	0.09
Brazil	S. Africa	20	0.37	0.46	0.08	20	0.70	0.72	0.05
Brazil	Venezuela	8	0.48	0.47	0.10	2	0.64	0.76	0.23
Colombia	S. Africa	41	0.55	0.54	0.04	41	0.50	0.55	0.06
Colombia	Venezuela	4	0.02	0.17	0.12	2	-0.34	0.39	0.39
S. Africa	Venezuela	8	0.61	0.62	0.07	8	0.49	0.48	0.09
Mean		104	0.41	0.46	0.03	86	0.54	0.58	0.04

1) Type B genetic correlations estimated for a pair of tests only if $h^2_B > 0.05$ in both tests. Abbrevciations are as follow: N = number of pairs, r^*_{Bg} = ratio of means; r_{Bg} = mean of the ratios (negative variance components set to zero); se(r_{Bg}) = empirical standard error of the mean of the ratios.

Table 8. Mean type B genetic and provenance correlation estiamtes for volume growth in pairs of CAMCORE *P. tecunumanii* tests. All parameter estimates at ages 3, 5, and 8 are averaged together.

Elevation	Country class	Type B genetic correlation				Type B provenance correlation			
		N	r^*_{Bg}	r_{Bg}	SE(r_{Bg})	N	r^*_{Bprov}	r_{Bprov}	SE(r_{Bprov})
High	Same	40	0.88	0.85	0.03	39	0.75	0.51	0.07
	Different	61	0.40	0.45	0.03	60	0.53	0.58	0.04
Mean		101	0.58	0.61	0.03	99	0.59	0.56	0.04
Low	Same	24	0.75	0.75	0.03	15	0.90	0.84	0.05
	Different	43	0.42	0.48	0.05	26	0.59	0.57	0.07
Mean		67	0.53	0.57	0.04	41	0.73	0.67	0.05

1) Type B genetic correlations estimated for a pair of tests only if $h^2_B > 0.05$ in both tests. Abbreviations are as follow: N = number of pairs, r^*_{Bg} = ratio of means; r_{Bg} = mean of the ratios (negative variance components set to zero); se(r_{Bg}) = empirical standard error of the mean of the ratios.

Country class was the only significant factor affecting G×E as measured by type B correlations. There were no significant differences among high- and low-elevation populations for the type B genetic correlation with mean r_{Bg} = 0.59 and 0.55, respectively (Table 8). There was a difference among the elevational categories for the provenance correlation (significant at p = 0.09), with mean r_{Bprov} = 0.56 for the high-elevation population and 0.67 for the low-elevation population. Estimates using the alternative algorithm had the same pattern: r^*_{Bprov} = 0.59 for the high-elevation population and 0.73 for the low-elevation popula-

Table 9. Mean type B genetic and provenance correlation estiamtes for volume growth in pairs of CAMCORE *P. tecunumanii* tests. All parameter estimates at ages 3, 5, and 8 are averaged together.

Trait	Country class	Type B genetic correlation				Type B provenance correlation			
		N	r^*_{Bg}	r_{Bg}	SE(r_{Bg})	N	r^*_{Bprov}	r_{Bprov}	SE(r_{Bprov})
VOL3	Same	35	0.86	0.85	0.02	32	0.77	0.56	0.07
	Different	42	0.50	0.56	0.04	39	0.51	0.54	0.06
Mean		77	0.67	0.69	0.03	71	0.61	0.55	0.04
VOL5	Same	14	0.79	0.81	0.04	10	0.84	0.63	0.13
	Different	38	0.35	0.39	0.04	31	0.55	0.59	0.06
Mean		52	0.47	0.50	0.04	41	0.61	0.60	0.05
VOL8	Same	15	0.74	0.73	0.04	12	0.91	0.70	0.12
	Different	24	0.38	0.41	0.06	16	0.68	0.66	0.08
Mean		39	0.51	0.54	0.05	28	0.79	0.68	0.07

1) Type B genetic correlations estimated for a pair of tests only if $h^2_B > 0.05$ in both tests. Abbrevciations are as follow: N = number of pairs, r^*_{Bg} = ratio of means; r_{Bg} = mean of the ratios (negative variance components set to zero); se(r_{Bg}) = empirical standard error of the mean of the ratios.

tion. Age of the test pair did not have a statistically significant effect on r_{Bg} or r_{Bprov}, although there was some indication that r_{Bprov} increased with age (Table 9), with r_{Bprov} = 0.55, 0.60, and 0.68 at ages 3, 5, and 8, respectively. In *P. elliottii*, DIETERS *et al.* (1995) report r_{Bg} increasing with age with data at ages 5, 8 11, and 14.

Quality Traits: Country class ("same" versus "different") was also important in the type B correlations for the quality traits branch diameter and straightness. Both traits at both ages 5 and 8 had higher type B correlations for test pairs in the same countries than for test pairs in the different countries (Table 10). For example, mean r_{Bg} for straightness in the "same" country class was 0.69 versus 0.54 for the "different" country class. For straightness, type B provenance correlations are higher than the corresponding type B genetic correlations, which is the same pattern observed for volume growth. The correlations for branch diameter do not follow this pattern, but this may be an artifact due to the lower level of precision on the parameter estimates. The standard errors for the type B correlations for branch diameter are higher than for straightness, particularly for the provenance correlations. This probably reflects the lower heritability for branch diameter than for straightness, making it more difficult to estimate these kinds of parameters. There was insufficient data to examine patterns of G×E for forking and stem breakage.

Relationships among Stem Breakage, Volume and Branch Diameter

Trees with broken tops were included in the calculation of the volume means for a given family, except for trees with extremely aberrant height-diameter ratios. Nevertheless, since broken tops tend to decrease the height of a tree, there would also tend to be a negative relationship between the number of broken tops and volume. Interestingly, this negative relationship is stronger at age 5 than at age 8. For tests with high levels of broken tops at age 5 (*i.e.*, < 15%), the correlation between family means for volume and broken tops was –0.32±0.10. For tests with low levels of broken tops (*i.e.*, < 15%), the mean correlation was –0.08± 0.03. At age 8, the mean correlation between family means for volume and broken tops was –0.15±0.05 for tests with high incidence of broken tops, and –0.04± 0.04 for tests with low incidence. This may reflect a tendency for stem breakage to occur within a specific diameter range, say 9–10 cm. Breaks at that point in the stem would remove a larger percentage of 5-year-old tree's height than in an 8-year-old tree. PARFITT and VAN DER SIJDE (1993) comment that trees with broken tops quickly form new leaders and regain height growth, with little apparent impact on diameter growth. Although volume growth is reduced by stem breakage, there was no difference in single-site heritability for volume between tests with high and low levels of broken tops.

Table 10. Mean type B genetic and provenance correlation estiamtes for volume growth in pairs of CAMCORE *P. tecunumanii* tests. All parameter estimates at ages 3, 5, and 8 are averaged together.

Country class	Trait	Type B genetic correlation				Type B provenance correlation			
		N	r^{*}_{Bg}	r_{Bg}	SE(r_{Bg})	N	r^{*}_{Bprov}	r_{Bprov}	SE(r_{Bprov})
Same	BD5	6	0.91	0.87	0.06	6	0.74	0.46	0.21
	BD8	11	0.78	0.73	0.09	10	0.58	0.61	0.15
Mean		17	0.83	0.78	0.06	16	0.64	0.55	0.12
Different	BD5	14	0.37	0.40	0.07	14	0.46	0.61	0.13
	BD8	14	0.14	0.21	0.08	11	-0.04	0.60	0.14
Mean		28	0.26	0.30	0.06	25	0.18	0.61	0.09
Same	ST5	14	0.69	0.68	0.07	11	0.88	0.79	0.07
	ST8	15	0.71	0.70	0.06	12	0.90	0.77	0.10
Mean		29	0.71	0.69	0.04	23	0.89	0.79	0.06
Different	ST5	30	0.54	0.54	0.05	30	0.60	0.59	0.06
	ST8	17	0.53	0.54	0.07	13	0.74	0.73	0.07
Mean		47	0.54	0.54	0.04	43	0.64	0.64	0.05

1) Type B genetic correlations estimated for a pair of tests only if $h^2_B > 0.05$ in both tests. Abbrevciations are as follow: N = number of pairs, r^{*}_{Bg} = ratio of means; r_{Bg} = mean of the ratios (negative variance components set to zero); se(r_{Bg}) = empirical standard error of the mean of the ratios.

Low levels of broken tops have little effect on genetic parameter estimates for volume due both to the small percentage of trees with broken tops and the low level of genetic control on the trait. However, for tests with high incidence, the trait "volume" is perhaps better thought of as an aggregate trait incorporating both volume growth and stem breakage. For selection and breeding in regions where stem breakage is a problem, *e.g.*, Colombia, it might be beneficial to select on this "aggregate" trait.

Stem breakage appears to be correlated with branch diameter. DVORAK *et al.* (1993) reported a significant family-mean correlation between branch diameter and stem breakage in three of six tests in Colombia. The correlation ranged between 0.22 to 0.62, indicating that large branches were associated with stem breakage. In the present study, the correlation between family means for branch diameter and broken tops at age 5 was 0.48 ±0.09 in tests with high incidence of stem breakage, and 0.29±0.04 in tests with low incidence. At age 8, the correlation in high incidence tests was 0.30±0.07, and in low-incidence tests was 0.20±0.05. Typical branch architecture of *P. tecunumanii* is very distinct whorls and clear internodes, and stem breakage often occurs at a whorl with heavy branches.

PARFITT (1996) made a very detailed study of branch characteristics and stem breakage in Colombia and South Africa and found a significant relationship between stem breakage and both mean and maximum branch diameter. Interestingly, these two traits were negatively correlated with number of branches per whorl, *i.e.*, trees tended to have few heavy branches or many thin branches, with the latter state leading to fewer broken tops. There was also an undesirable correlation between branch angle and stem breakage, with flat branches (which produce less knot area) associated with higher stem breakage.

Estimated Effects for Specific Provenances

Volume growth, High-elevation: Since type B provenance correlations from country to country were moderately high (Table 7), one estimate of provenance volume gain was calculated using all data (Table 1, see also Figure 1). Among the high-elevation provenances, estimated volume gains range from +13.3% (San Jeronimo, #2) to –19.0% (Las Piedrecitas, #35). Other excellent provenances for volume growth include Chiul (#6, +11.2%), Napite (#37, +10.7%), Montebello (#36, +10.5%), and San Miguel (#13, +9.7%). San Jeronimo

and Montebello had been previously identified as very productive provenances (WRIGHT & OSORIO 1992, DVORAK & SHAW 1992). Very poor growing provenances include KM33 (#7, –14.5%), San Jose (#39, –11.5%), Cabrican (#12, –9.3%), and KM47 (#8, –9.1%).

Provenance performance varied greatly by geographic region (Figure 1). For example, all provenances from the San Cristobal de las Casas plateau in Chiapas (#31, 32, 34, 35, 37, 38, 39 in Figure 1) performed average to poorly, with the exception of Napite (#37). The overall poor performance may be the result of colder night-time temperatures on the plateau than in the highlands of Central America and a correspondingly earlier winter bud set. Phenotypically, however, these are some of the most beautiful natural stands of *P. tecunumanii* that exist.

The most productive provenances were located in western Guatemala (Chiul #6, San Miguel #13, and Pachoc #15) in the Sierra de los Cuchumantes (including Montebello #36 near the Mexican)/Guatemalan frontier) and central Guatemala in the western Sierra de las Minas (San Jeronimo #2). Two of the good provenances in the group, Montebello and San Jeronimo, occur between 1600 and 1800 m altitude in areas that are warmer than the other locations sampled in western and central Guatemala.

Some of the poorest-performing provenances from eastern Guatemala and western Honduras also happened to be the smallest physical size (~ 5 ha) like Km 33 (#7), Km 47 (#8), San Vicente (#3) and San Lorenzo (#16), and may be highly inbred. Small disjunct populations of Eucalyptus globulus have been observed to be more highly inbred and slower growing in field trials (HARDNER *et al.* 1996).

Juquila (Oaxaca) is not shown in Figure 1 as it is almost 5° further west than any other provenance. Besides being a geographic outlier, it is now suspected that this provenance is not pure *P. tecunumanii*, but is introgressed with *P. patula, P. herrerae*, and/or *P. lawsonii.* Molelcular marker research is currently underway to attempt to elucidate the status of this provenance; nevertheless, Juquila performed rather well in these trials, with +8.2% volume growth.

Volume growth, Low-elevation: Among the low-elevation population, estimated provenance effects for volume ranged from a high of +25.3% (Yucul, #44) to a low of –33.9% (Cerro la Joya, #42). Notable productive provenances include San Rafael del Norte (#40, +18.0%), Villa Santa (#20, +9.6%), and Culmi (#26, +7.6%), while Locomapa grew very poorly (#25, -26.3%) (Table 1, see also Figure 1). The provenances Yucul and San Rafael del Norte have been reported as the most productive in a single test in Zimbabwe (NYOKA & BARNES 1995), and Yucul was the best among four low-elevation provenances in a series of international trials coordinated by the Oxford Forestry Institute (BIRKS & BARNES 1990).

As with the high-elevation population, geographic location seems to be an important determinant of productivity for low-elevation provenances. The most productive provenances were from the southern and eastern extreme of the species distribution in southeastern Honduras and central Nicaragua (Yucul #44, San Rafael #40, Villa Santa #20) and in eastern Honduras (San Estaben #28 and Culmi #26) (Figure 1). The extremely poor performance of Cerro la Joya (#42) in this region is probably the result of introgression with *P. oocarpa.*

Northern Honduras populations of low-elevation *P. tecunumanii* generally performed very poorly. More inland provenances like Campamento (#17), were only average. Interestingly, the two populations of *P. tecunumanii* that exhibited the highest degree of introgression with *P. caribaea* var. *hondurensis* in field collections, Mountain Pine Ridge, Belize (#1) and Esquipulas del Norte, Honduras (#21), performed 6 to 8% below average in provenance trials.

Stem Breakage: Provenance effects for stem breakage are reported as BTOP33 (Table 1), which expresses the percent stem breakage expected for a bulk sample from that provenance planted on a site where an average provenance/family would have 33% stem breakage. Thus, high values of BTOP33 are undesirable. Among the high-elevation provenances, BTOP33 ranges from 43.6% (Montebello, a fast growing provenance) to 26.1% (Las Piedrecitas, the slowest growing provenance). This does not imply that fast volume growth is necessarily associated with high incidence of stem breakage. For example, San Jeronimo (fast) and KM33 (slow) both have BTOP33 around 31%, while Celaque is the second worst provenance for stem breakage (BTOP33 = 41.2%) and is below average for volume growth. Among low-elevation provenances, BTOP33 ranges from 55.6% (Mountain Pine Ridge) to 20.4% (Joc6n). The Jocón provenance was considered by SQUILLACE and PERRY (1992) to be mostly *P. oocarpa* on the basis of monoterpenes. *Pinus oocarpa* generally has much less stem breakage problems than does *P. tecunumanii*, so the field results are consistent with the monoterperne results. There was also no apparent relationship between BTOP33 and volume growth for the low-elevation provenances (Table 1).

Gene Conservation and Tree Breeding

Gene Conservation: The trial results identify several populations in Central America and Mexico that should be targeted for in-situ gene conservation effort. These include Napite and Montebello in Chiapas, Chiul and San Jeronimo in Guatemala, Villa Santa in Honduras, and San Rafael and Yucul in Nicaragua. Much work has already been done to protect the Yucul population in Nicaragua. The Montebello site is in a National Park and is protected. The Napite site is in the highland of Chiapas which is a politically sensitive area at present. The San Jeronimo population is now about one-third of its original 1980 size due to logging, and is greatly threatened as is San Rafael. The Villa Santa stand has easy road access and could be successfully managed for in-situ conservation, however, its easy access could also make it a target for wood cutters.

The poor performance of a number of small provenances may be related to inbreeding. Trees originating from these provenances may have good breeding values if they were to be outcrossed with unrelated material. Some selections will be made from all provenances and included in the next generation of genetic tests. In addition, progeny from all mother trees collected in the native range will be maintained in conservation banks by one or more members of the CAMCORE cooperative.

Potential for Plantation Forestry: *P. tecunumanii* has great potential as a plantation species in areas where severe frosts (lower than –1 to –2 °C) are infrequent. Its advantages are: (a) rapid development in the nursery (4 to 6 months to reach planting size), (b) fast growth in the field, relatively good drought resistance after establishment, (c) wood of medium density and suitable quality, (d) resistance to Sphaeropsis sapinea, formerly *Diplodia* (SWART & WINGFIELD 1991) in south-central Brazil, (e) apparent resistance to *Fusiarium subglutinans* f.sp *pini* (pitch canker) in the seedling stage (HODGE 1999, in preparation), (f) ability to hybridize with a number of other closed-cone neotropical pines as well as some temperate pines in the southern United States, and (g) the ease in which it can be vegetatively propagated as seedling cuttings.

As with most species, these advantages need to be weighed against its disadvantages. These include: (a) sensitivity to container size and shape in the nursery which affects root architecutre and stability in the field, (b) shallow rooting and susceptibility to wind throw, especially on sandy soils, (c) susceptibility to *Phytophora* root rot on some sites, and (d) susceptibility to suffer stem breakage.

Potential for genetic gain: Substantial genetic gains in volume growth can be made simply by selection of the best provenances. Both in the high- and low-elevation populations the best provenances will result in gains of 10 to 20% above the species mean, while the difference between the best and worst provenances is on the order of 35% in volume growth (Table 1). Genetic gain from within-provenance selection and breeding for volume growth is also expected to be substantial. The exact amount of genetic gain expected depends on many factors including breeding design, field test design, numbers of tests established, size of the breeding program, and selection intensity. However, with a large, well-designed program and high selection intensity it might be possible to identify an elite population with a mean breeding value that exceeds the population mean by two additive genetic standard deviations; these two standard deviations can be referred to as gain potential (ΔG_p). At age 8 in *P. tecunumanii* the mean within-provenance parameter estimates for tree volume index across 42 tests were $\bar{x}$ = 0.1456 m^3, σ_T^2 = 0.0055 m^6, h_b^2 = 0.15, and r_{Bg} = 0.81 for tests in the same country. One can then calculate the gain potential (ΔG_p) in a particular country (*i.e.*, breeding region) as:

$$\Delta G_p = 100\% \cdot 2\,\sigma_A / \bar{x} = 100\% \cdot 2\,(h_b^2\, r_{Bg}\, \sigma_T^2)^{1/2} / \bar{x}$$
$$= 100\% \cdot 2\,(0.15 \cdot 0.81 \cdot 0.00550)^{1/2} / 0.1456$$
$$= 35.5\%$$

The gain potential is intended only to indicate the level of genetic gain that is possible. It would of course be difficult to make this level of gain in a large breeding population of a few hundred members. On the other hand, it could conceivably be done with a production population, such as a seed orchard of 25–40 clones, or with a small group of 5 to 10 full-sib families in a vegetative propagation program. A gain of 35% in 8-year volume growth in *P. tecunumanii* would obviously be of very high economic value, but would require a very intensive and efficient breeding program. In addition, it would be much more difficult to achieve this level of gain if the breeding objective includes other traits such as wood quality, straightness, or resistance to stem breakage.

Provenance effects for stem breakage and other quality traits are not extremely large, but there does appear to be potential for genetic improvement through selection within provenances. For example, parameter estimates for stem breakage at ages 5 and 8 are very similar. Assuming values of $\bar{x}$ = 33%, σ_T^2 = 1950, h_b^2 = 0.05, and r_{Bg} = 0.70, one can estimate $\Delta G_p = -2 \cdot (0.05 \cdot 0.70 \cdot 1950)^{1/2} = -16.5\%$, where the –2 indicates that the objective is to reduce the mean by two genetic

standard deviations. Thus it might be possible to reduce stem breakage by half, to 16.5%, if selection were concentrated on this trait. Straightness and stem breakage would of course be high priorities for companies with sawtimber as the product objective. In some regions, it will be imperative to reduce stem breakage and/or foxtailing in order for the species to be widely utilized as a plantation species.

Selection age: Mean single-site heritability for volume at age 5 and age 8 are nearly identical (actually the age 5 estimates are slightly higher, Table 5), and the mean age 5–8 genetic correlation for volume is 0.89 and for straightness is 0.96 (Table 6). This indicates that selection for age 8 volume using age 5 data would be essentially as effective as selection at age 8. Typically, candidate trees are identified with a selection index, or best linear unbiased prediction from the measurements. These candidate trees are then inspected in the field for disease, re-assessment of straightness and other quality traits, to examine crown formation, and to examine for problems with spacing, missing neighbors, errors in measurement, etc., before the tree is accepted into the breeding population. Depending on the size of the trees in the test, assessing straightness and crown characteristics subjectively seems more difficult at age 5 then at age 8.

International exchange of genetic material: Due to seed limitations and logistical complications, not all families from all provenances have been tested by all organizations, or even within all countries. Many of the provenances are severely threatened, and it is difficult if not impossible to re-collect from outstanding mother trees in the field. Thus, exchange of genetic material among CAMCORE members is important to maintain a broad genetic base, and to transfer good genetic material which has been tested and selected in one country to another where it has not been tested. The relatively low type B genetic correlations between different countries ($r_{Bg} \approx 0.45$, Table 7) are somewhat disappointing, as the benefits of cooperative breeding and exchange of genetic material will be somewhat reduced. Some pairs of countries appear to have larger correlations, for example, for South Africa and Colombia the mean $r_{Bg} \approx 0.55$, and exchanges between two countries with higher Type B genetic correlations should be favored.

CAMCORE members have adopted a very flexible breeding strategy coupled with a structured breeding population. A small elite population (approximately 30 members) and a larger main population (say around 90 members) will be selected within each region which containing one or more members with an interest in breeding a particular species. There will be at least two and generally 3 to 4 regions (or countries) where a species has commercial utility. The selections made in other regions will comprise an additional 120 to 360 selections that can function as a second main population, providing additional genetic diversity for long term genetic gain. Currently, CAMCORE members in Brazil, Colombia and South Africa have made over 200 selections of high-elevation *P. tecunumanii*, and have just begun making selections from the low-elevation population.

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Appendix 1. Mean for growth traits in CAMCORE *P. tecunumanii* tests at ages 3, 5, and 8. High-elevation sources.

Obs	Country	Test	HT3	HT5	HT8	DBH3	DBH5	DBH8	VOL3	VOL5	VOL8
1	Brazil	040102A	5.25	.	16.07	6.93	.	19.24	0.0084	.	0.1927
2		041103A	3.60	7.15	11.92	4.26	9.99	14.39	0.0024	0.0249	0.0876
3		130102C	3.11	6.71	11.10	3.25	9.88	16.03	0.0012	0.0221	0.0980
4		130111E	3.45	7.64	12.96	3.90	10.85	16.92	0.0019	0.0312	0.1271
5		130602D	4.57	6.74	.	.	10.79	.	.	0.0260	.
6		130606B	3.31	8.37	.	.	10.92	.	.	0.0352	.
7		130611D	3.09	8.08	.	.	10.52	.	.	0.0314	.
8		130617A	50.4	7.63	.	7.05	11.28	.	0.0083	0.0323	.
9		131538A	4.60	.	.	6.19	.	.	0.0065	.	.
10		131637A	.	6.48	9.72	.	9.49	14.86	.	0.0200	0.0719
11		131743D	4.95	.	.	7.80	.	.	0.0104	.	.
12		132043E	3.04	.	.	4.33	.	.	0.0019	.	.
13		132641A1	4.69	7.93	.	6.83	14.28	.	0.0074	0.0525	.
14		132641A4	3.55	.	.	5.33	.	.	0.0037	.	.
15		132642A1	4.91	7.92	.	7.21	13.92	.	0.0087	0.0504	.
16		132642A4	2.16	.	.	2.56	.	.	0.0007	.	.
	Mean		3.96	7.47	12.35	5.47	11.19	16.29	0.0041	0.0326	0.1155
17	Colombia	040201A	3.27	6.78	9.98	4.74	13.09	19.43	0.0025	0.0377	0.1208
18		130202E	6.55	10.08	15.89	10.45	16.25	21.37	0.0233	0.0870	0.2466
19		130206A	6.57	10.21	16.78	10.97	16.46	22.25	0.0255	0.0898	0.2721
20		130211C	6.20	9.41	15.55	10.93	16.13	21.39	0.0238	0.0788	0.2330
21		130216B	6.32	9.61	17.04	10.30	15.90	21.44	0.0218	0.0782	0.2555
22		130232D	3.31	4.21	.	4.68	12.78	.	0.0025	0.0219	.
23		130233A	2.94	3.81	8.69	3.69	11.40	20.57	0.0015	0.0158	0.1139
24		130234A	3.26	3.95	9.27	4.36	12.64	20.37	0.0022	0.0198	0.1175
25		130243A	6.80	.	.	11.29	.	.	0.0277	.	.
	Mean		5.02	7.26	13.31	7.93	14.33	20.97	0.0145	0.0536	0.1942
26	S.Africa	130730A3	2.63	5.75	.	2.78	8.61	.	0.0007	0.0145	.
27		130732C1	3.53	6.62	.	4.60	10.74	.	0.0026	0.0250	.
28		130733B3	3.30	6.33	.	3.99	10.07	.	0.0019	0.0212	.
29		131002A	4.14	8.61	14.16	6.23	13.21	18.34	0.0055	0.0485	0.1548
30		131002B	4.63	8.80	13.75	6.27	13.45	18.02	0.0065	0.0517	0.1440
31		131003A	4.30	8.55	14.14	6.43	13.48	17.93	0.0059	0.0501	0.1482
32		131003B	4.62	8.66	13.83	6.55	13.71	18.11	0.0067	0.0529	0.1473
33		131011A	3.97	8.43	14.12	5.40	12.29	17.80	0.0040	0.0413	0.1447
34		131011B	4.50	8.44	12.80	5.89	13.65	18.27	0.0053	0.0514	0.1416
35		131016A	3.72	7.95	13.97	4.93	11.85	17.97	0.0031	0.0364	0.1457
36		131020A	4.00	7.77	11.88	5.29	12.88	18.08	0.0041	0.0423	0.1285
37		131030A1	3.96	7.83	11.67	4.11	11.40	17.34	0.0024	0.0336	0.1141
38		131030A2	3.91	.	.	4.62	.	.	0.0030	.	.
39		131032A1	3.67	7.43	11.66	3.56	10.99	17.80	0.0017	0.0301	0.1197
40		131032A2	3.55	.	.	3.96	.	.	0.0021	.	.
41		131032A3	4.12	8.69	12.46	5.01	9.34	19.43	0.0035	0.0251	0.1489
42		131032A4	5.41	8.84	.	7.02	13.30	.	0.0089	0.0508	.
43		131032B1	.	8.99	11.97	.	14.51	19.12	.	0.0633	0.1441
44		131032B2	3.11	.	.	4.05	.	.	0.0018	.	.
45		131033B1	3.90	7.79	11.58	4.46	11.58	17.46	0.0027	0.0343	0.1154
46		131033B2	3.65	.	.	4.06	.	.	0.0023	.	.
47		131043C2	4.11	.	.	5.45	.	.	0.0042	.	.
48		131832C3	2.82	.	.	3.89	.	.	0.0015	.	.
	Mean		3.88	7.91	12.84	4.90	11.95	18.08	0.0036	0.0396	0.1382

Appendix 1. Mean for growth traits in CAMCORE *P. tecunumanii* tests at ages 3, 5, and 8. Low-elevation sources.

Obs	Country	Test	HT3	HT5	HT8	DBH3	DBH5	DBH8	VOL3	VOL5	VOL8
49	Brazil	030104A	4.93	7.66	11.15	7.02	11.89	15.31	0.0089	0.0387	0.0926
50		030104B	5.45	9.30	12.85	7.61	13.36	17.28	0.0107	0.0532	0.1227
51		031105A	4.50	10.55	15.39	7.10	13.78	17.75	0.0090	0.0635	0.1534
52		160101C	5.18	.	.	6.70	.	.	0.0082	.	.
53		160102B	6.63	.	.	9.38	.	.	0.0193	.	.
54		160603C	5.74	9.53	.	8.94	18.19	.	0.0155	0.1002	.
55		160801B	3.80	.	.	4.16	.	.	0.0025	.	.
56		161502D	5.83	.	.	7.33	.	.	0.0111	.	.
57		161503B	6.01	.	.	8.14	.	.	0.0133	.	.
58		161707C	6.73	.	.	10.26	.	.	0.0242	.	.
	Mean		5.58	9.53	13.13	7.66	14.31	16.78	0.0123	0.0639	0.1229
59	Colombia	030201A	5.64	10.21	15.52	8.23	16.76	22.08	0.0128	0.0911	0.2422
60		030202A	5.30	9.79	15.43	7.55	15.58	21.78	0.0105	0.0755	0.2356
61		030203A	3.49	8.84	14.09	3.98	13.67	21.05	0.0021	0.0550	0.2070
62		160203D	7.47	10.36	.	11.34	18.81	.	0.0318	0.1199	.
63		160205B	7.70	10.23	.	11.70	18.93	.	0.0343	0.1184	.
64		160211C	4.37	.	.	6.36	.	.	0.0071	.	.
65		160213B	5.60	.	.	8.62	.	.	0.0144	.	.
	Mean		5.65	9.89	15.01	8.25	16.75	21.64	0.0161	0.0920	0.2283
66	S.Africa	130731A3	3.82	6.69	.	4.69	10.52	.	0.0030	0.0241	.
67		131031A1	.	8.17	11.82	.	11.56	17.42	.	0.0359	0.1164
68		131031A2	3.75	.	.	4.44	.	.	0.0026	.	.
69		161001E1	6.29	10.34	14.41	9.53	14.32	18.52	0.0186	0.0686	0.1605
70		161001E2	3.02	.	11.30	3.93	.	17.75	0.0017	.	0.1127
71		161001G	4.30	8.29	12.60	6.21	12.39	18.08	0.0058	0.0432	0.1359
72		161002C1	5.46	10.43	13.90	6.91	12.68	17.26	0.0086	0.0555	0.1357
73		161002C2	2.37	.	11.36	3.18	.	17.81	0.0009	.	0.1145
74		161004A1	4.35	6.98	11.55	6.34	11.35	17.06	0.0057	0.0288	0.1077
75		161004A2	3.88	.	11.14	5.79	.	16.48	0.0048	.	0.0971
	Mean		4.14	8.48	11.01	5.67	12.14	17.55	0.0057	0.0427	0.1226
76	Venezuela	030407A	5.44	9.34	14.15	7.15	11.81	17.90	0.0105	0.0457	0.1480
77		160304D	4.85	7.82	11.61	6.10	12.47	19.02	0.0064	0.0396	0.1353
78		160305A	.	6.09	8.63	.	7.71	14.55	.	0.0141	0.0655
	Mean		5.15	7.75	11.46	6.62	10.67	17.15	0.0084	0.0332	0.1163

Appendix 2. Mean for quality traits in CAMCORE *P. tecunumanii* tests at ages 5, and 8. High-elevation sources.

Obs	Country	Test	ST5	ST8	BD5	BD8	FORK5	FORK8	FOXT5	FOXT8	BTOP5	BTOP8
1	Brazil	040102A	.	2.10	.	1.91	.	25.1	.	0.7	.	1.1
2		041103A	1.62	1.87	.	2.92	0.0	0.0	0.0	0.0	0.0	0.0
3		130102C	.	2.06	.	1.82	0.0	21.7	0.0	0.0	0.0	0.0
4		130111E	.	2.23	.	1.96	0.0	17.5	0.0	0.0	0.0	0.6
5		130602D	1.85	.	1.97	.	15.7	.	1.9	.	0.7	.
6		130606B	2.42	.	.	.	0.0	.	0.0	.	0.0	.
7		130611D	2.50	.	.	.	0.0	.	0.0	.	0.0	.
8		130617A	1.91	.	1.98	.	8.1	.	2.5	.	0.5	.
9		131538A	.	.	.	.	.	.	.	.	.	.
10		131637A	2.84	2.24	1.96	2.11	10.3	10.8	1.9	2.7	0.6	0.2
11		131743D	.	.	.	.	.	.	.	.	.	.
12		132043E	.	.	.	.	.	.	.	.	.	.
13		132641A1	1.85	.	1.73	.	35.3	.	20.5	.	9.6	.
14		132641A4	.	.	.	.	.	.	.	.	.	.
15		132642A1	1.89	.	1.75	.	23.3	.	9.8	.	6.5	.
16		132642A4	.	.	.	.	.	.	.	.	.	.
Mean			2.11	2.10	1.88	2.14	9.37	15.0	3.7	0.7	1.8	0.4
17	Colombia	040201A	.	1.20	.	1.55	0.0	49.8	0.0	1.1	0.0	14.7
18		130202E	1.87	1.38	2.07	1.52	15.0	15.0	4.8	0.0	20.0	36.5
19		130206A	1.93	1.56	2.31	1.57	21.0	18.3	6.6	12.0	21.4	30.9
20		130211C	1.89	1.81	1.80	1.84	14.2	20.1	10.9	16.8	14.1	43.0
21		130216B	2.07	1.57	2.10	1.60	12.2	19.4	10.8	19.2	13.8	17.5
22		130232D	1.23	.	1.21	.	0.0	.	0.0	.	0.0	.
23		130233A	1.17	1.19	1.46	1.21	14.2	22.5	0.9	1.2	57.8	40.8
24		130234A	1.30	1.19	1.38	1.18	12.4	27.6	1.6	2.3	60.9	38.4
25		130243A	.	.	.	.	.	.	.	.	.	.
	Mean		1.64	1.41	1.76	1.50	11.1	24.7	4.4	7.5	23.5	31.7
26	S.Africa	130730A3	1.86	.	1.91	.	6.8	.	1.1	.	1.7	.
27		130732C1	1.89	.	1.98	.	14.5	.	2.0	.	7.3	.
28		130733B3	1.90	.	1.94	.	14.1	.	0.8	.	4.7	.
29		131002A	1.65	1.92	1.44	2.48	7.0	11.2	0.4	0.3	6.2	10.5
30		131002B	1.66	2.10	1.62	2.52	8.0	8.3	0.6	0.1	2.9	14.9
31		131003A	1.65	2.01	1.55	2.45	7.1	10.7	0.6	0.0	5.3	7.6
32		131003B	1.38	1.97	1.26	2.56	2.0	9.7	0.3	0.1	1.7	9.8
33		131011A	1.91	2.25	1.56	2.59	6.3	10.1	0.7	0.1	2.3	9.5
34		131011B	1.82	2.33	1.69	2.28	7.1	17.8	0.9	0.0	6.0	26.7
35		131016A	1.92	2.35	1.86	2.63	0.0	11.7	0.0	0.1	0.0	9.4
36		131020A	1.70	2.29	1.58	2.46	5.4	14.7	0.3	0.0	1.8	30.1
37		131030A1	.	1.84	.	2.07	8.5	20.4	0.1	0.2	3.8	5.7
38		131030A2	.	.	.	.	.	.	.	.	.	.
39		131032A1	.	1.75	.	2.16	4.9	16.5	0.3	0.0	4.1	4.5
40		131032A2	.	.	.	.	.	.	.	.	.	.
41		131032A3	1.75	2.00	2.71	2.17	5.4	11.5	0.0	0.2	1.6	8.1
42		131032A4	2.20	.	2.33	.	7.7	.	1.0	.	9.4	.
43		131032B1	1.61	1.98	1.96	2.28	4.1	9.5	0.7	0.3	11.4	19.5
44		131032B2	.	.	.	.	.	.	.	.	.	.
45		131033B1	.	1.88	.	2.20	5.4	15.3	0.1	0.1	4.8	5.5
46		131033B2	.	.	.	.	.	.	.	.	.	.
47		131043C2	.	.	.	.	.	.	.	.	.	.
48		131832C3	.	.	.	.	.	.	.	.	.	.
Mean			1.76	2.01	1.82	2.37	8.0	13.2	1.1	0.2	5.4	12.2

Appendix 2. Mean for quality traits in CAMCORE *P. tecunumanii* tests at ages 5, and 8. Low-elevation sources.

Obs	Country	Test	ST5	ST8	BD5	BD8	FORK5	FORK8	FOXT5	FOXT8	BTOP5	BTOP8
49	Brazil	030104A	1.90	1.70	.	2.86	0.0	18.1	0.0	0.0	0.0	1.0
50		030104B	2.35	1.63	.	1.76	0.0	27.1	0.0	0.1	0.0	2.4
51		031105A	2.43	1.72	.	2.97	0.0	11.3	0.0	0.1	0.0	6.2
52		160101C	.	.	.	.	.	.	.	.	.	.
53		160102B	.	.	.	.	.	.	.	.	.	.
54		160603C	1.02	.	2.03	.	26.1	.	3.7	.	35.0	.
55		160801B	.	.	.	.	.	.	.	.	.	.
56		161502D	.	.	.	.	.	.	.	.	.	.
57		161503B	.	.	.	.	.	.	.	.	.	.
58		161707C	.	.	.	.	.	.	.	.	.	.
Mean			1.93	1.68	2.03	2.53	6.51	18.8	0.9	0.1	8.8	3.2
59	Colombia	030201A	.	1.76	.	1.93	0.0	42.5	0.0	0.6	0.0	14.8
60		030202A	.	1.36	.	1.98	0.0	20.8	0.0	1.2	0.0	10.2
61		030203A	.	1.54	.	1.87	0.0	21.0	0.0	2.8	0.0	17.3
62		160203D	1.09	.	1.29	.	18.5	.	3.3	.	16.8	.
63		160205B	1.17	.	1.35	.	22.8	.	2.5	.	26.0	.
64		160211C	.	.	.	.	.	.	.	.	.	.
65		160213B	.	.	.	.	.	.	.	.	.	.
	Mean		1.14	1.55	1.32	1.93	8.3	28.1	1.2	1.5	8.6	14.1
66	S. Africa	130731A3	1.50	.	1.89	.	33.9	.	11.6	.	19.4	.
67		131031A1	.	1.52	.	1.97	4.4	16.8	0.1	1.3	8.1	8.7
68		131031A2	.	.	.	.	.	.	.	.	.	.
69		161001E1	1.18	1.82	2.95	2.36	7.3	21.1	0.0	0.0	0.0	13.1
70		161001E2	.	2.01	.	2.31	.	18.1	.	0.0	.	11.2
71		161001G	1.30	1.81	2.99	2.19	4.3	34.9	0.0	0.9	6.6	20.1
72		161002C1	1.12	1.93	2.99	2.47	3.9	18.4	0.0	0.4	0.0	11.2
73		161002C2	.	2.04	.	2.38	.	18.1	.	0.0	.	10.5
74		161004A1	1.00	1.42	2.96	2.43	9.7	27.2	0.0	0.3	5.3	8.8
75		161004A2	.	2.00	.	2.26	.	13.3	.	0.1	.	11.0
Mean			1.22	1.82	2.76	2.30	10.6	21.0	1.9	0.4	6.6	11.8
76	Venezuela	030407A	.	.	.	.	0.0	0.0	0.0	0.0	0.0	0.0
77		160301D	1.67	1.01	1.96	1.56	12.9	15.1	1.1	5.0	0.5	0.6
78		160305A	1.96	1.80	2.55	1.86	1.5	1.2	0.1	0.2	0.0	0.1
Mean			1.81	1.40	2.26	1.71	4.8	3.4	0.4	1.7	0.2	0.2