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GENETIC PARAMETERS AND PROVENANCE VARIATION OF *PINUS MAXIMINOI* IN BRAZIL, COLOMBIA AND SOUTH AFRICA

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ABSTRACT

Twenty-nine provenance/progeny tests of *Pinus maximinoi* were assessed at ages 3, 5 and 8 years of age in Brazil, Colombia and South Africa as part of the CAMCORE, North Carolina State University, testing program. The genetic material included 22 provenances and 439 open-pollinated families collected in southern Mexico, Guatemala and Honduras. Mean productivity values of unimproved *P. maximinoi* are approximately twice that of improved *P. taeda* in subtropical Brazil and *P. patula* in Colombia and 17 % better than improved *P. patula* in South Africa. Mean single-site heritability estimates were approximately 0.21 for diameter at breast height, 0.11 for branch diameter, 0.18 for stem straightness and 0.21 for foxtailing at age 8 years. There was no evidence of adverse genetic correlations between growth and quality traits. Age-age correlations for dbh were high (0.87). Genotype by environment interaction is similar at both family and provenance level, with more interaction between tests located in different countries than in same countries. Selection for age 8 dbh using age-5 data would be 83 % as effective as selection at age 8. Potential genetic gain for basal area growth at 8 years from selection within provenance is around 20 %.

Keywords: *Pinus maximinoi*, heritability, genotype × environment interaction, age-age genetic correlations, genetic gain.

INTRODUCTION

The natural distribution of *Pinus maximinoi* H. E. Moore includes northwestern, central and southern Mexico and the Central American countries of Guatemala, Hondurus, Nicaragua and El Salvador (Figure 1). Timber and pulpwood are major products of both natural and exotic forests of *P. maximinoi.* Initial tests of *P. maximinoi* in the tropics and sub-tropics showed that the species has great potential with yields usually surpassing those of the traditionally planted species of *Pinus patula* Schiede ex Schlechtendal & Chamisso var. *patula*, *Pinus elliottii* Engelm, *Pinus taeda* L. and *Pinus kesiya* Royle (LADRACH 1984; CROCKFORD, *et al.* 1991; NYOKA 1994).

However the genetics of this species have not been well studied. The initial testing activities in the 1970s and early 1980s were oriented to establish basic information on provenance variation and the influence of site on growth and productivity (LADRACH 1984; CROCKFORD *et al.* 1991; NYOKA 1994). CAMCORE (International Cooperative for Gene Conservation and Tree Improvement), North Carolina State University, USA carried out individual tree seed collections from 785 trees in 22 provenances of *P. maximinoi* in Mexico, Guatemala and Honduras beginning in 1984.

The material was distributed to some of the CAMCORE members in Colombia, South Africa, Brazil, Honduras, Mexico and Venezuela. A total of 41 tests were established across a range of environments (DVORAK & DONAHUE 1988), principally in areas where commercial forest plantations are sited. The objectives of the provenance/progeny tests were to provide information about the commercial potential of the species, to permit estimation of genetic parameters and genotype × environment interaction, and to develop predictions of provenance and family genetic value. This paper reports 3 to 8-year results for 29 provenance/progeny tests of *P. maximinoi* established in Brazil, Colombia, and South Africa.

MATERIALS AND METHODS

Plant Material and Genetic Tests

From 1984 to 1986, 29 provenance/progeny tests were established as the test and selection population for the genetic improvement of *P. maximinoi* in Brazil, Colom-

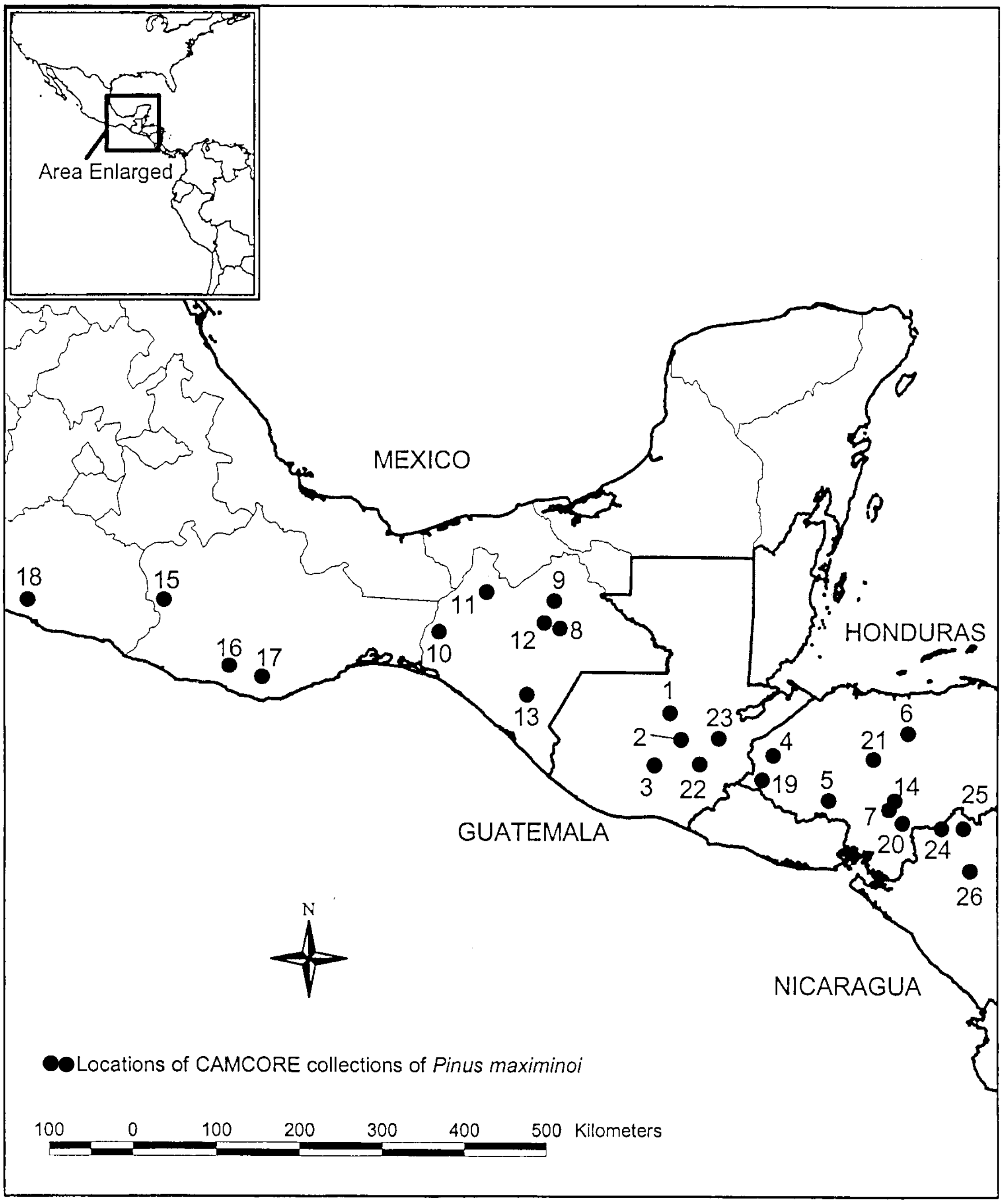

Figure 1. Location of the CAMCORE *Pinus maximinoi seed* collection sites in Mexico and Central America.

bia and South Africa. The details of the test sites in Brazil, Colombia and South Africa are shown in Table 2.

The commercial controls in the respective countries against which *P. maximinoi* was tested were *P. taeda* and *P. elliottii* in Brazil, *P. patula, P. elliotti, P. tecunumanii* and *P. kesiya* in Colombia, and *P. patula* and *P. elliottii* in South Africa. Each of the test was a randomized complete block design at provenance level, and families were randomly nested within provenances. There were nine replications and six trees per family planted in row-plots. Spacing was approximately 3 x 3 meters in all tests. Test measurement was scheduled at ages 3, 5, and 8 years with all trees assessed. Height and breast-height diameter at ages 3, 5 and 8 years were measured on all trees, and a volume index was calcu lated as 0.0003 x height x dbh^2. At ages 5 and 8 years, stem straightness and branch diameters were assessed

Table 1. Summary information for CAMCORE *Pinus maximinoi* provenances.

Prov. Code	Provenance	Dept/State, Country	Lat 0	Long	Altitude (m)	Annual Prec (mm) 0	No. of families	Provenance Gains[1] (% Basal Area Gains, age 8)		
								Brazil	Colombia	S.Africa
1	Coban	Alta Verapaz, Guatemala	15° 28'	90° 24'	1420–1440	2109	31	4.1	2.2	6.6
2	San Jerónimo	Baja Verapaz, Guatemala	15° 04'	90° 14'	1280–1590	970	30	4.8	5.3	4.8
3	San Juan Sacateqequez	Guatemala, Guatemala	14° 41'	90° 38'	1580–2000	1138	30	2.1	–5.4	4.6
4	Dulce Nombre de Copan	Copan, Honduras	14° 50'	88° 51'	1100–1300	1386	50	5.4	4.9	0.8
5	Marcala	La Paz, Honduras	14° 10'	88° 01'	1600–1800	1670	40	–3.5	–1.9	–0.7
6	Tapiquil	Yoro, Honduras	15° 10'	86° 50'	1500–1769	1069	50	–2.6	–2.2	–8.3
7	Tatumbla	Fco. Morazan, Honduras	14° 01'	87° 07'	1400–1600	908	112	–1.3	4.6	–2.7
8	Altamirano	Chiapas, Mexico	16° 43'	92° 03'	1280–1350	1750	39	3.6	2.5	1.6
9	San Jerónimo	Chiapas, Mexico	17° 09'	92° 08'	940–1020	1750	24	3.5	4.5	7.1
10	Ciénaga de León	Chiapas, Mexico	16° 41'	93° 52'	1050–1240	1750	18	–4.1	–4.8	–5.5
11	Coapilla	Chiapas, Mexico	17° 17'	93° 09'	1300	1250	36	–2.6	–5.5	–4.3
12	La Cañada	Chiapas, Mexico	16° 49'	92° 17'	1270–1360	1750	20	7.4	6.2	7.0
13	Monte Cristo	Chiapas, Mexico	15° 44'	92° 33'	800	2000	29	–1.3	–4.7	1.5
14	Valle de Angeles	Fco. Morazan, Honduras	14° 10'	87° 02'	1200–1600	908	50	–3.6	–1.1	–8.4
15	San Juan Copala	Chiapas, Mexico	17° 10'	97° 58'	1370–1560	1350	22	–2.8	–1.1	0.0
16	San Jerónimo	Oaxaca, Mexico	16° 10'	97° 00'	1220–1480	1950	32	–4.5	–2.0	–0.5
17	Candelaria	Oaxaca, Mexico	16° 00'	96° 31'	1370–1480	1350	23	–1.6	0.6	3.1
18	Las Compuertas	Guerrero, Mexico	17° 10'	99° 59'	1050–1200	1400	29	1.2	1.0	1.2
19	El Portillo	Ocotepeque, Honduras	14° 28'	89° 01'	1400–1600	1325	30	–3.3	–4.1	–6.8
20	Yuscaran	El Paraíso, Honduras	13° 50'	86° 55'	1500–1700	1300	30	1.7	–0.7	–3.3
21	La Lagunilla	Jalapa, Guatemala	14° 42	89° 57'	1540–1860	1017	20	2.1	2.4	2.8
22	San Lorenzo	Zacapa, Guatemala	15° 05'	89° 40'	1900–2100	1500	10	0.3	0.0	0.8

[1] Provenance gains are Best Linear Unbiased Predictions of the provenance effect expressing percent gain in individual tree basal area at age 8. BLUPS for specific countries were calculated.

using a three-point scale, and foxtailing was assessed as a binary trait (a tree with an internode greater than 2 meters was classified as a foxtail). In total, this allowed for an examination of 439 open- pollinated families and approximately 74,000 trees included in the 29 tests.

Single-site Analyses

Variance components for all traits were estimated using the PROC VARCOMP (METHOD = REML) procedure (SAS Institute Inc. 1990). The linear model used for the single site analyses was:

$$Y_{ijklm} = \mu_i + B_j + P_k + F(P)_{kl} + BF(P)_{jkl} + e_{ijklm} \quad [1]$$

where: Y_{ijklm} = phenotypic observation for the ijklm th tree, μ_i = mean of the ith test, B_j = 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, $E[F(P)_{kl}] = 0$, $Var[F(P)_{kl}] = \sigma^2_{f(p)}$, $BF(P)_{jkl}$ = random effect of the jkl th row-plot, i.e. the interaction of the jth block and the lth family of the kth provenance, $E[BF(P)_{jkl}] = 0$, $Var[BF(P)_{jkl}] = \sigma^2_{bf(p)}$, e_{ijklm} = random error term associated with the ijklm th tree, $E[e_{ijklm}] = 0$, $Var[e_{ijklm}] = \sigma^2_e$,

The formulas used to estimate heritability were those suggested by BECKER (1985). Individual tree heritability was estimated as:

$$h^2_b = 3\,\sigma^2_{f(p)} / (\sigma^2_{f(p)} + \sigma^2_{bf(p)} + \sigma^2_e) \quad [2]$$

Note that the heritability estimate (h^2_b) is calculated on a within-provenance basis, and that family, plot and within-family variance are assumed to be equal in all provenances. The "b" subscript indicates that the family variance is estimated on a single-site basis, and may be biased upward by the possible presence of family × environment interaction (COMSTOCK & MOLL 1963; HODGE & WHITE 1992). The covariance among sibs of open-pollinated families will often be higher than ¼ of additive genetic variance; this could result from inbreeding and/or from a small number of effective male pollinators leading to the presence of some percentage of full-sibs with the open-pollinated family (SQUILLACE 1974). Thus, the coefficient of relationship was assumed to be 0.33 instead of the normal 0.25 for half-sib family analysis.

Family heritability was estimated as:

$$h^2_f = \sigma^2_{f(p)} / [\sigma^2_{f(p)} + \sigma^2_{bf(p)} / b + \sigma^2_e / n_h\, b] \quad [3]$$

Table 2. Summary information for CAMCORE *P. maximinoi* tests.

Test	Country	Sitename	Latitude	Longitude	Elevation (m)	Precipitation (mm)
15–06–07E	Brazil	Pisa 17 T–17	24° 07' S	50° 09' W	840	1339
15–06–09A		Pisa 17 T–13	24° 07' S	50° 09' W	840	1339
15–15–19A		Fazenda Primavera Gn	18° 38' S	42° 51' W	850	1400
15–16–07D		G. Mogol / Cancela	16° 30' S	42° 50' W	810	1080
15–16–15C		G. Mogol / Cancela	16° 30' S	42° 50' W	810	986
15–16–18A		G. Mogol / Cancela	16° 30' S	42° 50' W	810	985
15–02-01Y	Colombia	Aguaclara	03° 41' N	76° 33' W	1400	1185
15-02-01Z		Samaria	04° 03' N	76° 29' W	1750	2859
15-02-02C		San Jose	02° 36' N	76° 34' W	1750	2058
15-02-03A		La Paz	02° 31' N	76° 37' W	1750	2112
15-02-07B		El Retiro	02° 38' N	76° 32' W	1750	2046
15-02-08C		La Arcadia	02° 31' N	76° 37' W	1750	2089
15-02-16A		Romerito/c	02° 15' N	71° 39' W	2450	2090
15-10-01A1	S. Africa	Swartfontein D40	25° 15' S	30° 56' E	1080	1194
15-10-01A2		Mariti A3	24° 55' S	30° 57' E	980	1316
15-10-02A1		Swartfontein C22	25° 14' S	30° 56' E	1080	1194
15-10-02A2		Mariti A3	24° 55' S	30° 57' E	980	1316
15-10-03B1		Wilgeboom C2	24° 57' S	30° 56' E	980	1316
15-10-03B2		Swartfontein C22	25° 14' S	30° 56' E	1080	1194
15-10-07A1		Swartfontein D40	25° 15' S	30° 56' E	1080	1194
15-10-07A2		Mariti A3	24° 55' S	30° 57' E	980	1316
15-10-08B1		Mariti A3	24° 55' S	30° 57' E	980	1316
15-10-08B2		Swartfontein C22	25° 14' S	30° 56' E	1080	1194
15-10-15A1		Wilgeboom C2	24° 57' S	30° 56' E	980	1316
15-10-15A2		Swartfontein C22	25° 14' S	30° 56' E	1080	1194
15-10-17A1		Swartfontein C22	25° 14' S	30° 56' E	1080	1194
15-10-17A2		Mariti A3	24° 55' S	30° 57' E	980	1316
15-10-21B1		Mariti A3	24° 55' S	30° 57' E	980	1316
15-10-21B2		Swartfontein D24	25° 15' S	30° 56' E	1080	1194

where: n_h = harmonic mean for number of trees per plot, and b =number of blocks.

The family heritability is considered approximate in the sense that different families had different h^2_f estimates because of different number of trees and blocks for a particular family.

Within-family heritability was estimated as:

$$h^2_w = (2\,\sigma^2_{f(p)}) / (\sigma^2_{bf(p)} + \sigma^2_e) \qquad [4]$$

Family heritability for fox-tailing based on plot means was calculated according to the following model:

$$h^2_f = \sigma^2_{f(p)} / [\sigma^2_{f(p)} + \sigma^2_e / b] \qquad [5]$$

Age-Age Correlations

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

$$r_g = \sigma_{F1,F2} / (\sigma^2_{F1}\sigma^2_{F2})^{1/2} \qquad [6]$$

where $\sigma_{F1,F2}$ = estimated family covariance between the trait measured at different ages, σ^2_{F1} = estimated family variance observed at an early age,σ^2_{F2} = estimated family variance observed at a later age.

Paired-site Analyses and Genotype × Environment Interaction

The paired-site analyses included data from 5 tests in Brazil, 3 in Colombia and 15 tests in South Africa, and 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 ***gei*** variances due to heterogenous variances (EISEN & SAXTON 1983; HILL 1984). The linear model used for the paired-site analysis was:

$$\gamma_{ijklm} = \mu + S_i + B(S)_{ij} + P_k + PS_{ik} + F(P)_{kl} + F(P)S_{ikl} + r_{ijkl} + e_{ijklm} \qquad [7]$$

where γ_{ijklm} = phenotypic observation for the ijklmth tree, = overall mean, S_i = random effect of the ith site, $B(S)_{ij}$ = random effect of the jth block nested in the ith site, P_k = random effect of the kth provenance, $E[P_k] = 0$, Var-$[P_k] = \sigma^2_p$, PS_{ik} = random interaction of the kth provenance and the ith site, $E[PS_{ik}] = 0$, $Var\ [PS_{ik}] = \sigma^2_{ps}$, $F(P)_{kl}$ = random effect across site of the lth family in the kth provenance, $E[F(P)_{kl}] = 0$, $Var\ F(P)_{kl} = \sigma^2_{f(p)}$, $F(P)S_{ikl}$ = random interaction of the lth family in the kth provenance and the ith site, $E[F(P)S_{ikl}] = 0$, Var $[F(P)S_{ikl}] = \sigma^2_{f(p)s}$, r_{ijkl} = random effect of the ijklth row-plot, i.e. the interaction of the jth block, of the ith site and the lth family of the kth provenance, $E[r_{ijkl}] = 0$, Var $[r_{ijkl}] = \sigma^2_r$, e_{ijklm} = random error term associated with the ijklmth tree, $E[e_{ijklm}] = 0$, Var $[e_{ijklm}] = \sigma^2_e$.

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

$$r_{Bg} = \sigma^2_{f(p)} / \sigma^2_{f(p)} + \sigma^2_{f(p)s} \qquad [8]$$

$$r_{Bp} = \sigma^2_p / \sigma^2_p + \sigma^2_{ps} \qquad [9]$$

Type B correlations measure the genetic or provenance correlation between the same trait expressed on two different sites (YAMADA 1962; BURDON 1977). Assuming homogeneous variances (or adjustments for heterogeneity as mentioned above), the Type B correlation will measure the type of G x E interaction that is due to rank changes across environments. It is this type of interaction that is of most interest to tree breeders selecting provenances or families which will perform well across the range of sites.

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) x environment interaction. Type B correlations were only estimated if estimated h^2_b exceeded 0.05 in both tests of a pair. Use of tests with extremely low h^2_b estimates can result in seemingly very imprecise type B correlation estimates which can fall well out of the theoretical range.

Provenance effects for diameter were converted to percent differences in basal area growth (expressed on a percent of the grand mean) using Best Linear Unbiased Prediction (BLUP) across all tests, and are expressed relative to the grand mean across all unimproved native provenances. Specifically, SAS Proc Mixed was utilized to predict provenance effects for each country (SAS 1990). Least squares means for DBH were used as units of observation.

Efficiency of early selection

The genetic gain for mature performance from individual tree selection based on a juvenile trait (e.g., dbh5) is given by FALCONER & MACKAY (1996):

$$\Delta G = i_5\, h_5 \times h_8\, r_{g5,8}\, \sigma_{T8} \qquad [10]$$

where ΔG = genetic gain at age 8 based on selection for the trait at age 5; i_5 = selection intensity in the juvenile trait (dbh5); h_5 = square root of heritability estimates for dbh5; h_8 = square root of heritability estimates for dbh8; $r_{g5,8}$=additive genetic correlation of juvenile and mature trait (dbh5 and dbh8); σ_{T8} =phenotypic standard deviation of the mature trait (dbh8).

The genetic gain from (mature) selection at age 8 from individual tree selection (FALCONER & MACKAY 1996):

$$\Delta G = i_8\, h^2_8\, \sigma_{T8} \qquad [11]$$

The ratio of gains based on the juvenile trait (dbh5) and the mature trait (dbh8) gives the equation for genetic efficiency, and assuming that $i_5 = i_8$, can be simplified to:

$$E = 100 \times h_5\, r_{g5,8} / h_8 \qquad [12]$$

Gain efficiency per generation (E) expressed as a percent was compared between dbh at age 8 years and dbh at age 5 years.

RESULTS AND DISCUSSION

Species survival and productivity

Survival of *P. maximinoi* in the CAMCORE tests at eight years averaged 70 % in Brazil, 86 % in Colombia and 68 % in South Africa. Survival differences were great between test plantings in tropical and subtropical Brazil. The CAMCORE trials planted in Brazil were established in two distinct climates. One group of trials was planted at Grão Mogol, Minas Gerais at latitude 16° S and the second group was established 860 km to the south in Paraná state at approximately 24° S latitude (DVORAK *et al.* 2000). The Grão Mogul site is tropical but with a six-month dry season and 1000 mm of annual rainfall. At the tropical site, average survival was only 64 % after 8 years of age. Most of the mortality at the tropical site occurred during the first several months after planting the trials because of the drought that persisted in the following months. No trend was ob-

Table 3. Means for growth traits of *Pinus maximinoi* at 5 and 8 years by country. Height and volume calculations were performed only on trees without broken tops.

Country	DBH5 (cm)	DBH8 (cm)	HT5 (m)	HT8 (m)	VOL5 (m^3)	VOL8 (m^3)
Brazil	14.4 ± 0.04	15.7 ± 0.05	9.3 ± 0.02	12.3 ± 0.02	0.07 ± 0.01	0.10 ± 0.01
Colombia	16.2 ± 0.03	21.7 ± 0.05	10.5 ± 0.02	14.9 ± 0.05	0.09 ± 0.02	0.21 ± 0.05
South Africa	12.7 ± 0.02	17.8 ± 0.03	9.0 ± 0.02	12.6 ± 0.03	0.05 ± 0.03	0.12 ± 0.02
Overall Mean	14.4 ± 0.03	18.4 ± 0.04	9.6 ± 0.02	13.3 ± 0.04	0.07 ± 0.02	0.14 ± 0.03

Table 4. Means for quality traits of *Pinus maximinoi* at 5 and 8 years by country.

Country	ST5	ST8	BD5	BD8
Brazil	1.4 ± 0.01	2.1 ± 0.01	2.0 ± 0.01	1.7 ± 0.01
Colombia	1.7 ± 0.01	1.1 ± 0.00	1.7 ± 0.01	1.4 ± 0.00
South Africa	1.5 ± 0.00	1.4 ± 0.00	2.1 ± 0.02	1.7 ± 0.00
Overall Mean	1.5 ± 0.01	1.5 ± 0.01	1.9 ± 0.01	1.6 ± 0.01

served in survival differences among provenances. Survival of *P. tecunumanii* planted at the same site but 10 months earlier than the *P. maximinoi* was 88 % at 8 years of age. The Paraná sites are subtropical with zero to six frosts per year and annual rainfall of approximately 1400 mm distributed evenly throughout the year (DVORAK *et al.* 2000). Mean survival of *P. maximinoi* at the subtropical sites was 83 % vs. 92 % for the *P. taeda* controls at 8 years of age. In South Africa, survival of provenances from Mexico, Guatemala, and Honduras was 79 %, 64 %, and 58 %, respectively. The more southerly and easterly the collection site in Central America, the poorer the adaptability in South Africa. The poor survival in South Africa may be attributed to a combination of several factors. The tests suffered hailstorm damage in their early growth stages. However, there may also be an adaptability problem with some of the provenances. For example, survival was as low as 43 %, 53 % and 56 % for Valle de Angeles #14, Tapiquil #6 and El Portillo #19, respectively. KIETZKA (1988) also found that the Nicaraguan sources had poorer survival (60 %) than the Guatemalan and Honduran sources (67 %) in Oxford Forestry Institute studies planted six years earlier than the CAMCORE progeny trials in South Africa. The general conclusion is that survival can be maintained around 85 % in areas with good soils and well-distributed rainfall, as in Colombia and southern Brazil.

Generally, the best growth rates for all traits were observed in Colombia, with means in Brazil and Colombia relatively similar (Table 3). Substantial improvements could be made in *P. maximinoi* through selection of an adapted "landrace". Mean productivity for *P. maximinoi* in CAMCORE tests (all provenances included) was estimated at 18 $m^3 \cdot ha^{-1} \cdot yr^{-1}$, 25 $m^3 \cdot ha^{-1} \cdot yr^{-1}$ and 11 $m^3 \cdot ha^{-1} \cdot yr^{-1}$, for Brazil, Colombia and South Africa, respectively. Average productivity values varied greatly between the tropical (9 $m^3 \cdot ha^{-1} \cdot yr^{-1}$) and subtropical regions (28 $m^3 \cdot ha^{-1} \cdot yr^{-1}$) of Brazil. Productivity values for *P. maximinoi* in South Africa are somewhat biased (downward) because of the low (68 %) survival rates. Considering only the best one-third of the families, and assuming an average of 85 % survival, productivity estimates become 11 m^3/ha/yr in tropical Brazil, 32 $m^3 \cdot ha^{-1} \cdot yr^{-1}$ in subtropical Brazil, 41 $m^3 \cdot ha^{-1} \cdot yr^{-1}$ in Colombia and 17 $m^3 \cdot ha^{-1} \cdot yr^{-1}$ in South Africa, respectively. The productivity values of unimproved *P. maximinoi* are approximately twice that of improved *P. taeda* in subtropical Brazil and *P. patula* in Colombia and 17 % better than improved *P. patula* in South Africa.

Quality traits

Stem straightness and branch diameter means by country are given in Table 4.

The quality traits in Brazil and South Africa were consistently better than in Colombia. Although the assessment procedures for such quality traits are uniform across countries, they still remain somewhat subjective because of the human aspect element. In that respect, it may be difficult to make a meaningful comparison between countries. As would be expected, the commercial controls were superior in both stem straightness and branch diameter. There were higher percentages of fox-tailing in tests in Colombia (>20 %)

Table 5. Mean single-site estimates of individual tree heritability (h^2_b), within-family heritability (h^2_w), family heritability (h^2_f) and coefficient of variation (CV) for growth and quality traits by country from single-site analyses for CAMCORE tests for *Pinus maximinoi*.

Trait	Country	#Tests	h^2_b ± s.e.	h^2_w ± s.e.	h^2_f ± s.e.	CV± s.e.
DBH3	Brazil	5	0.15 ± 0.03	0.12 ± 0.01	0.53 ± 0.31	0.26 ± 0.04
	Colombia	8	0.16 ± 0.05	0.13 ± 0.04	0.65 ± 0.07	0.22 ± 0.05
	South Africa	15	0.10 ± 0.07	0.07 ± 0.05	0.49 ± 0.23	0.31 ± 0.04
	Overall	28	0.13 ± 0.08	0.10 ± 0.03	0.55 ± 0.05	0.26 ± 0.04
DBH5	Brazil	4	0.24 ± 0.09	0.16 ± 0.16	0.71 ± 0.20	0.24 ± 0.05
	Colombia	7	0.22 ± 0.07	0.16 ± 0.05	0.79 ± 0.05	0.21 ± 0.02
	South Africa	18	0.16 ± 0.13	0.12 ± 0.05	0.62 ± 0.22	0.25 ± 0.03
	Overall	29	0.19 ± 0.09	0.14 ± 0.03	0.71 ± 0.04	0.23 ± 0.03
DBH8	Brazil	4	0.25 ± 0.08	0.15 ± 0.18	0.75 ± 0.04	0.25 ± 0.04
	Colombia	7	0.19 ± 0.07	0.14 ± 0.05	0.71 ± 0.07	0.26 ± 0.03
	South Africa	16	0.18 ± 0.09	0.13 ± 0.15	0.60 ± 0.18	0.26 ± 0.01
	Overall	27	0.21 ± 0.08	0.14 ± 0.03	0.68 ± 0.06	0.26 ± 0.03
BD5	Brazil	4	0.08 ± 0.05	0.06 ± 0.03	0.53 ± 0.15	0.27 ± 0.13
	Colombia	7	0.11 ± 0.08	0.08 ± 0.06	0.54 ± 0.26	0.35 ± 0.05
	South Africa	14	0.07 ± 0.02	0.04 ± 0.02	0.49 ± 0.07	0.28 ± 0.03
	Overall	25	0.08 ± 0.07	0.11 ± 0.01	0.52 ± 0.16	0.30 ± 0.07
BD8	Brazil	4	0.17 ± 0.24	0.19 ± 0.21	0.64 ± 0.19	0.31 ± 0.17
	Colombia	7	0.11 ± 0.08	0.09 ± 0.06	0.63 ± 0.19	0.36 ± 0.09
	South Africa	16	0.07 ± 0.05	0.05 ± 0.04	0.47 ± 0.22	0.35 ± 0.04
	Overall	27	0.11 ± 0.05	0.11 ± 0.01	0.58 ± 0.06	0.34 ± 0.10
ST5	Brazil	4	0.14 ± 0.08	0.10 ± 0.06	0.64 ± 0.16	0.29 ± 0.04
	Colombia	7	0.17 ± 0.07	0.15 ± 0.06	0.69 ± 0.10	0.36 ± 0.06
	South Africa	16	0.18 ± 0.11	0.13 ± 0.08	0.68 ± 0.13	0.32 ± 0.03
	Overall	27	0.17 ± 0.05	0.12 ± 0.01	0.67 ± 0.06	0.32 ± 0.04
ST8	Brazil	4	0.29 ± 0.15	0.23 ± 0.12	0.78 ± 0.12	0.31 ± 0.04
	Colombia	7	0.07 ± 0.09	0.05 ± 0.06	0.37 ± 0.32	0.21 ± 0.12
	South Africa	16	0.17 ± 0.11	0.12 ± 0.09	0.67 ± 0.17	0.35 ± 0.02
	Overall	27	0.17 ± 0.05	0.12 ± 0.01	0.60 ± 0.06	0.29 ± 0.06
FX5	Colombia	5	0.21 ± 0.08	0.15 ± 0.09	0.76 ± 0.08	0.28 ± 0.07
FX8	Colombia	5	0.19 ± 0.09	0.14 ± 0.10	0.74 ± 0.07	0.26 ± 0.06

than in Brazil and South Africa (< 10 %). This may be due to latitudinal and elevational differences. This is consistent with results reported by WRIGHT *et al.* (1993), where they found that the proportion of foxtailed trees in plantations and tests in Colombia was higher at altitudes between 1400 and 2000 m. The high incidence of foxtailing in Colombia, with up to 60 % of the stems with foxtails on some sites, may be a serious limitation of *P. maximinoi* in Colombia. There is a tendency for trees with foxtails to die back from the terminal bud (URREGO & LAMBETH 1988, WRIGHT *et al.* 1993). Planting the species at altitudes above 2000 m in Colombia may significantly reduce foxtailing. Encouraging results were seen in one test planted at elevation above 2000 m in Colombia where less than one percent foxtailing was observed.

Heritability estimates

Values of heritability for growth and quality traits were moderate, ranging from 0.13 to 0.21. Single-site estimates of individual tree heritability (h^2_b), within-family heritability (h^2_w) and family heritability (h^2_f) within a country and the overall estimates for the *P. maximinoi* population are summarized in Table 5.

Estimates of h^2_b for both growth and quality traits within a country were generally higher in Brazil than in Colombia and South Africa. For example, h^2_b for dbh8 in Brazil was 0.25 ± 0.08, Colombia was 0.19 ± 0.07 and South Africa was 0.18 ± 0.09.

Table 6. Mean age-age genetic correlation estimates for selected pairs of traits of *P. maximinoi* measured at ages 3, 5, and 8 years in the same tests.[a]

Trait 1	Trait 2	N	r_g	SE(r_g)
DBH3	DBH5	25	0.86	0.09
DBH3	DBH8	27	0.76	0.06
DBH5	DBH8	26	0.93	0.04
BD5	DBH3	23	0.19	0.13
BD5	DBH5	23	0.28	0.16
BD5	DBH8	22	0.39	0.12
ST5	DBH3	25	–0.19	0.07
ST5	DBH5	26	0.23	0.09
ST5	DBH8	27	0.41	0.10
ST5	BD5	25	0.47	0.06
ST5	BD8	25	0.43	0.09
ST5	ST8	23	0.67	0.07
ST8	BD5	26	0.49	0.05
BD5	ST8	23	0.53	0.09
BD8	ST8	23	0.46	0.10

N = number of tests

[a] Genetic correlation estimated only if $h^2_b > 0.05$ for both traits. Estimates of $r_g > 1.00$ from individual tests were set equal to 1.00 when calculating means.

There are no published estimates of heritability for stem straightness and branch diameter for *P. maximinoi*. However, in comparison to other pine species, similar trends in low heritability estimates for branch diameter and stem straightness were observed in *P. tecunumanii* by HODGE & DVORAK (1999) and in *P. taeda* by GWAZE *et al.* (1997). COTTERILL *et al.* (1987) report a heritability of 0.15 ± 0.09 at age 8 years for *P. elliottii* in South Africa. NYOKA *et al.* (1994) report a heritability of 0.29 ± 0.11 and 0.32 ± 0.09 for stem straightness at 5 and 8 years, respectively, for *P. patula* grown in Zimbabwe.

Age-age genetic correlations

Age-age correlations (r_g) were estimated for dbh, branch diameter and stem straightness (Table 6). Age-age correlations for dbh growth averaged 0.86 ± 0.11 across 25 tests for ages 3–5, 0.76 ± 0.06 across 27 tests for ages 3–8, and 0.91 ± 0.03 across 26 tests for ages 5–8.

These correlations are large and positive, above 0.76 at all ages. These results are very encouraging. Additive genetic correlations for dbh increased between the ages of 5 and 8 years. The age 5 -age 8 correlation indicates that the diameter at two ages is likely controlled by the same set of genes. Estimates of the same magnitude for volume correlations have been noted (CAMCORE 1996) for *P. patula*, (r_g (3–5) = 0.75, r_g (3–8) = 0.70, and r_g (5–8) = 0.87) and also by HODGE & DVORAK (1999) for *P. tecunumanii*, r_g (3–5) = 0.74± 0.03, r_g (3–8) = 0.74±0.03, and r_g (5–8) = 0.89±0.03. Similar age-age correlations for volume growth estimates for *P. caribaea* averaged 0.88 ± 0.05 across 21 tests for ages 3–5, 0.53 ± 0.11 across 5 tests for ages 3–8, and 0.93 ± 0.04 across 4 tests for ages 5–8 (HODGE & DVORAK 2001). The magnitude of genetic correlations found in this study are generally similar to those reported in the literature for other pine species, e.g. *P. patula* (BARNES *et al.* 1992a and 1992b), *P. caribaea* (WOOLASTON *et al.* 1990), *P. elliottii* (COTTERILL *et al.* 1987; PSWARAYI *et al.* 1996), *P. taeda* (FOSTER 1986; GWAZE *et al.* 1997) and *P. radiata* (COTTERILL & DEAN 1988).

The age-age genetic correlations for dbh at all ages and the quality traits (see Table 6) were low to high. Generally, genetic correlations between age 5 and age 8 DBH and BD ranged from 0.28 to 0.39. These indicate large diameters are associated with large branches, which is undesirable. Genetic correlation among age 5 and age 8 DBH and straightness were of similar magnitude, ranging from 0.23 to 0.41, however this correlation is a favorable one indicating larger diameter associated with straight stems. Favorable genetic correlations between stem straightness and dbh was also reported for *P. elliottii* (COTTERILL *et al.* 1987).

Genotype × environment Interaction

Provenance × site interaction effects for dbh were significant in 30 % of the test pairs ($p < 0.05$) at ages 3 and 5, and in even fewer pairs of tests at age 8. For pairs of tests within a country, provenance × site effect was not significant. Generally, 10 % of the pairs of tests in different countries had statistically significant provenance × site interaction as would be expected. The site details within a country were almost uniform as opposed to sites between countries (Table 2). CROCKFORD *et al.* (1991) found provenance × site interaction to be significant in *P. maximinoi* in southern Africa on a broader range of sites than in this study. Family × site interaction effects for dbh were significant in 60 % of the test pairs ($p < 0.05$) at ages 3, 5, and 8. For pairs of tests within a country, family × site effect was significant ($p < 0.05$) but in only 10 % of the test pairs. High productivity with this species is thus realized with correct matching of site.

Summary statistics from the paired-site analysis for Type B genetic correlations and Type B provenance correlations for dbh are presented in Table 7.

As might be expected, Type B provenance correlations were always higher than the Type B genetic correlations. This trend is in accordance with results reported by DVORAK & SHAW (1992) based on 18 five-

Table 7. Type B genetic and provenance correlation estimates for DBH growth at 5 & 8 years in pairs of *P. maximinoi* tests.

Country 1	Country 2	Trait	*N*	Type B Genetic Corr $r_{Bg} \pm$ SE	N	Type B Prov Corr $r_{Bprov} \pm$ SE
Same Country						
Brazil	Brazil	DBH5	2	0.91 ± 0.01	2	0.96 ± 0.02
		DBH8	3	0.95 ± 0.04	2	0.97 ± 0.05
Mean			5	0.95 ± 0.04	4	0.97 ± 0.04
Colombia	Colombia	DBH5	3	0.97 ± 0.04	3	0.98 ± 0.06
		DBH8	3	0.96 ± 0.03	3	0.98 ± 0.07
Mean			6	0.95 ± 0.03	6	0.97 ± 0.06
South Africa	South Africa	DBH5	11	0.92 ± 0.05	15	0.96 ± 0.09
		DBH8	15	0.95 ± 0.04	15	1.00
Mean			26	0.93 ± 0.03	30	0.98 ± 0.09
Different Country						
Brazil	Colombia	DBH5	5	0.53 ± 0.07	5	0.68 ± 0.14
		DBH8	1	0.73	1	0.72
Mean			6	0.64 ± 0.07	6	0.70 ± 0.14
Brazil	South Africa	DBH5	6	0.68 ± 0.08	6	0.69 ± 0.14
		DBH8	6	0.74 ± 0.09	6	0.74 ± 0.12
Mean			12	0.71 ± 0.08	12	0.72 ± 0.13
Colombia	South Africa	DBH5	11	0.66 ± 0.05	6	0.69 ± 0.08
		DBH8	9	0.73 ± 0.04	5	0.78 ± 0.09
Mean			20	0.69 ± 0.05	11	0.73 ± 0.09

Abbreviations are as follows:

N = number of test pairs
r_{Bg} = mean of ratios (negative variance components set to zero)
SE (r_{Bg}) = empirical standard error of the mean of the ratios
r_{Bprov} = mean of ratios for provenances (negative variance components set to zero)
SE (r_{Bprov}) = empirical standard error of the mean of the ratios for provenances

year-old *P. tecunumanii* trials, where there was little provenance × site interaction in comparison to the family × site interaction. There is a very low level of ***gei*** within a country at both the provenance and family level for dbh at both ages 5 and 8 years. The Type B genetic correlations for the same age test pairs within a country increased slightly from age 5 to age 8; i.e. ***gei*** declined with age and appeared to be relatively unimportant at age 8 years (Type B not significantly differently from 1.0).

For pairs of tests in Brazil, as age increased there was a slight but not statistically significant increase in both the Type B genetic correlations and Type B provenance correlations. For example, for pairs of tests in Brazil, the Type B genetic correlations increased from 0.91 ± 0.01 at age 5 to 0.95 ±0.04 at age 8 and Type B provenance correlations increased from 0.96 ±0.02 at age 5 to 0.97 ±0.04 at age 8. For pairs of tests in South Africa, there was also increase in the Type B genetic correlations and Type B provenance correlations with age.

For *P. maximinoi*, almost all ***gei*** was restricted to pairs of tests in different countries, with mean Type B genetic correlation equal to 0.68 ±0.07, and mean Type B provenance correlation equal to 0.72 ±0.12. For example, for pairs of tests between Brazil and Colombia, mean Type B genetic correlation was 0.53 ±0.07 at age 5 years and 0.73 ±0.08 at age 8 years and mean Type B provenance correlation was 0.68 ±0.14 and 0.72 ±0.15 at 5 and 8 years, respectively. Similar correlation coefficients were also observed in pairs of tests between Brazil and South Africa and Colombia and South Africa (Table 7).

Our genetic correlation estimates are much higher (i.e. less ***gei***) than the range of Type B genetic correlations shown in other pine studies. DIETERS *et al.* (1995) reported an increase trend in *P. elliottii*. Average Type B genetic correlations for height in slash pine ranged from 0.59 to 0.82 (DIETERS *et al.* 1995; HODGE & WHITE 1992). HODGE & DVORAK (1999) report ***gei*** for *P. tecunumanii* volume growth to be stronger at the family level than at the provenance level, and higher for tests located in different countries than in the same countries. For example, age 8 r_{Bg} for volume for test pairs within a country was 0.74, and for different countries was 0.38. In contrast, *P. patula* has shown much lower r_{Bg} (in the range of 0.38 to 0.45) across countries for tests in Brazil, Colombia and South Africa (CAMCORE 1998). These data indicate that in *P. maximinoi* there is very low *gei* among families and provenances within a country and relatively low *gei* at both the family and provenance level across countries.

Estimated effects for some provenances

Although type B provenance correlations from country to country were moderately high (r_{Bg} = 0.72, Table 7), an estimate of provenance basal area gain (i.e., the percent superiority above the overall unimproved provenance mean) was calculated for each country (Table 1). La Cañada, #12 and San Jeronimo, #2 were relatively stable across countries and were the best source of *P. maximinoi* in all three countries. As would be expected, a provenance that was predicted to grow poorly in one country was also predicted to be rather poor in other countries. For example, Valle de Angeles, (#14, –8 %), Tapiquil (#6, –8 %), and Coapilla (#11, –5 %) were consistently poor in all three countries. However, there was some rank change of provenances across countries. This is clearly seen in the BLUP of the provenance effects (Table 1). To illustrate this, Tatumbla, #7 was in the top five best provenances in Colombia (+4.6 %), and one of the worst in South Africa (–2.7 %). Similarly, San Juan Sacaptepequez, #3 was in the top five best provenances in South Africa (+4.6 %), and one of the worst in Colombia (–5.4 %).

The provenance BLUP effects indicated that there was only a 15 % maximum difference between the best and worst provenance depending on the country where it was tested (Table 1). This is in contrast to other pine species tested by CAMCORE in similar countries. For example, in *P. tecunumanii* tested in Brazil, Colombia, South Africa and Venezuela, there was a substantial variation among provenances. The difference between the best and worst provenance was 35 % in volume growth (HODGE & DVORAK 1999). Similar volume growth differences were observed in P. *caribaea* tested in Brazil, Colombia and Venezuela (HODGE & DVORAK 2001).

Efficiency of early selection

Since mean single-site heritability for volume at age 5 and age 8 are nearly identical (Table 5), the age 5–8 genetic correlation of 0.91 indicates that selection for age 8 dbh using age 5 data would be essentially as effective as selection at age 8. Early selection at age 5 years on dbh appears to yield nearly as much genetic gain (E = 83 %) as selection for dbh at 8 years in *P. maximinoi*. However, when expressed on a time efficiency basis, selection at age 5 is more efficient than selection at age 8. Some breeders may feel uncomfortable making early selection decisions, however many decisions are not irrevocable. For example, selection of offspring, scion collection and grafting into a clone bank or orchard can be done at age 5. Selected trees can be re-inspected at age 8 for confirmation. For all candidates still acceptable (which should be most of the selections), the breeder has gained three years.

Potential for genetic gain

Genetic gains in basal area growth can be made simply by selection of the best provenances. Depending on country, use of the best provenance will result in basal area gains of 6 to 8 % above the species mean, while the difference between the best and worst provenances can exceed 10 % (Table 1). Genetic gain from within-provenance selection and breeding for basal area growth is also expected to be substantial. The mean basal area breeding value of the selected 10 % would exceed the population mean by approximately $2\sigma_A$ (specifically 1.755 σ_A where σ_A = additive genetic variance and assuming a normal distribution). For age-8 basal area growth in *P. maximinoi* the following within-provenance genetic parameter estimates are appropriate: $\bar{x}$ = 18.40 cm (Table 3) which when converted to basal area equals 0.027 m^2·ha–1, CV = 0.26, $h^2_b = 0.21$ (Table 5), and $r_{Bg} = 0.95$ for tests in the same country (Table 7). One can then calculate the gain from selection of the top 10 % of the population in a particular country (i.e., breeding region) as follows:

$$\Delta G_{10} = 100\ \% \times 1.755\ \sigma_A/\bar{x} = 100\ \% \times 1.755\ (h^2{}_b\ r_{Bg})^{½}$$
$$CV = 100\ \% \times 1.755 \times (0.21 \times 0.95)^{½} \times 0.26 = 20\ \%$$

A gain of 20 % in 8-year basal area growth would obviously be of very high economic value. This potential gain is intended only to provide a rough indication of the level of genetic gain that is possible in an improvement program for a single trait.

A total of 422 *P. maximinoi* families were ranked for GCA. In Brazil, a total of 80 individual tree selections were made from the highest ranked 62 families from 12 provenances. In Colombia, a total of 85 individual tree selections were made from the highest ranked 65 families from 12 provenances. In South Africa, a total of 111 individual tree selections were made from the highest ranked 84 families from 19 provenances. No more than 3 individual trees were selected in any one family, and in the highest ranked families more selections were made as suggested above. For example, in Brazil families ranked 1–10 contributed an average of 2 selections, while all other families contributed an average of 1.15 selections.

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LITERATURE CITED

BARNES, R. D., MULLIN, L. J. & BATTLE, G. 1992a: Genetic control of fifth year traits in *Pinus patula* Schiede and Deppe. *Silvae Genetica* **41**: 242–248.

BARNES, R. D., MULLIN, L. J. & BATTLE, G. 1992b: Genetic control of eight year traits in *Pinus patula* Schiede and Deppe. *Silvae Genetica* **41**: 318–325.

BECKER, W. R. 1985: Manual of Quantitative Genetics. Washington State University Press, Washington 170 pp.

BURDON, R. D. 1977: Genetic correlation as a concept for studying genotype-environment interaction in forest tree breeding. *Silvae Genetica* **26**: 168–175.

CAMCORE. 1996: Annual Report. Dept. of Forestry, College of Forest Resources, North Carolina State University, Raleigh. USA. 29 pp.

CAMCORE. 1998: Annual Report. Dept. of Forestry, College of Forest Resources, North Carolina State University, Raleigh. USA. 28 pp.

COMSTOCK, R. E. & MOLL, R. H. 1963: Genotype-environment interactions. *In*: Hanson R. Robinson, H. F. (eds) Statistical genetics and plant breeding. NAS-NRC Pub. 982, Washington D.C., pp 164–194.

COTTERILL, P. P. & DEAN, C. A. 1988: Changes in the genetic control of growth of radiata pine to 16 years and efficiencies of early selection. *Silvae Genetica* **37**: 138–146.

COTTERILL, P. P., DEAN, C. A. & VAN WYK, G. 1987: Additive and dominance genetic effects in *Pinus pinaster*, *P. radiata* and *P. elliottii* and some implications for breeding strategy. *Silvae Genetica* **36** (5–6): 221–232.

CROCKFORD, K. L., BAYLIS, W. B., DUNSDON. A. J., WANYACHA, J. M. & WRIGHT, J. A. 1991: Provenance productivity of *Pinus maximinoi* in Southern Africa. *Commonwealth Forestry Review* 70 (**4**): 213–236.

DIETERS, M. J., WHITE, T. L., & HODGE, G. R. 1995: Genetic parameter estimates for volume from full-sib tests of slash pine (*Pinus elliottii*). *Canadian Journal of Forest Research* **25**: 1397–1408.

DVORAK, W. S. & DONAHUE, J. K. 1988: *Pinus maximinoi* seed collections in Mexico and Central America. CAMCORE Bulletin on Tropical Forestry No **4**: 47p.

DVORAK, W. S., GUTIERREZ, E. A. & GAPARE, W. J. 2000: *Pinus maximinoi*. *In*: Conservation and Testing of Tropical and Subtropical Species by the CAMCORE Cooperative. pp: 107–127.

DVORAK, W. S. & SHAW, E. A. 1992: Five year results for growth and stem form of *Pinus tecunumanii* in Brazil, Colombia and South Africa. CAMCORE Bulletin on Tropical Forestry. No. **10**. 22pp.

EISEN, E. & SAXTON, A. 1983: Genotype by environment and genetic correlations involving two environment factors. *Theoretical and Applied Genetics* **67**: 75–86.

FALCONER, D. S. & MACKAY, T. F. C 1996: Introduction to Quantitative Genetics. 4th edition. Longman Scientific and Technical, London, 464p.

FOSTER, G. S. 1986: Trends in genetic parameters with stand development and their influence on early selection for volume growth in loblolly pine. *Forest Science* **32**: 944 –958.

GWAZE, D. P., WOOLLIAMS, J. A. & KANOWSKI, P. J. 1997: Genetic parameters for height and stem straightness in *Pinus taeda* Linnaeus in Zimbabwe. *Forest Genetics* **3**(3): 159 –169.

HILL, W. G. 1984: On selection among groups with heterogeneous variance. *Animal Prod.* **39**: 473–477.

HODGE, G. R. & DVORAK, W. S. 1999: Genetic parameters and provenance variation of *Pinus tecunumanii* in 78 international trials. *Forest Genetics* **6**(3): 157–180.

HODGE, G. R. & DVORAK, W. S. 2001: Genetic parameters and provenance variation of *Pinus caribaea* var. *hondurensis* in 48 international trials. *Canadian Journal of Forest Research* **31**: 496–511.

HODGE, G. R. & WHITE T. L. 1992: Genetic parameter estimates for growth traits at different ages in slash pine and some implications for breeding. *Silvae Genetica* **41**: 252–262.

KIETZKA, J. E. 1988: *Pinus maximinoi*. A promising species in South Africa. *South African Forestry Journal* **145**: 33–38.

LADRACH, W. E. 1984: Growth of *Pinus pseudostrobus* Lind., *Pinus maximinoi* H.E. Moore after 5 years. Carton de Colombia Research Report, No. **94**.

NYOKA, B. I. 1994: Provenance variation in *Pinus maximinoi*: a promising species for commercial afforestation in Zimbabwe. *Commonwealth Forestry Review* **73** (**1**): 47–53.

NYOKA, B. I., BIRKS, J. S., & GUMBIE, C. M. 1994: *Pinus patula* progeny test: Heritability estimates and genetic correlations between fifth- and eighty-year traits. *Southern African Forestry Journal* **168**: 23–26.

PSWARAYI, I. Z., BARNES, R. D., BIRKS, J. S. & KANOWSKI, P. J. 1996: Genetic parameter estimates for Production and Quality Traits of *Pinus elliottii* ENGLM. var. *elliottii* in Zimbabwe. *Silvae Genetica* **45** (4): 216–222.

SAS INSTITUTE INC. 1990: SAS/STAT User's Guide, Version 6. 4th edn. Vol 2. SAS Institute Inc., Cary, NC. USA.

SEARLE, S. R., CASELLA, G. & MCCULLOCH, C. E. 1992: Variance Components. JohnWiley and Sons, Inc. New York. 501 p.

SQUILLACE, A. E. 1974: Average genetic correlations among offspring from open-pollinated forest trees. *Silvae Genetica* **23**: 149–156.

UREGGO, J. B. & LAMBETH, C. C. 1988: Provenance and family foxtailing of *Pinus maximinoi* H. E. Moore in the Andes Mountains of Colombia. Smurfit Carton de Colombia Research Report No. 121. 4 p.

WOOLASTON, R. R., KANOWSKI, P. J., & NIKLES, D. G. 1990: Genetic parameter estimates for *Pinus caribaea* var *hondurensis* in coastal Queensland, Australia. *Silvae Genetica* **39**: 21–28.

WRIGHT, J. E., OSORIO, L. F., & LAMBETH, C. C. 1993: Development of a tree improvement program with *Pinus maximinoi* in Colombia. *Forest Ecology and Management* **62**: 313 -322.

YAMADA, Y. 1962: Genotype by environment interaction and genetic correlation of the same trait under different environments. *Japanese Journal of Genetics* **37**: 498–509.