PROVENANCE PERFORMANCE AND GENETIC PARAMETER ESTIMATES FOR *PINUS CARIBAEA* VAR. *HONDURENSIS* PLANTED AT THREE SITES IN ZIMBABWE

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ABSTRACT

Three provenance trials of *Pinus caribaea* var. *hondurensis* were established at three locations in Zimbabwe between 700 m to 1052 m altitude and included 16 populations. The trials were assessed at ages 8 and 15 years for height, diameter at breast height (dbh), stem straightness and foxtailing. Genetic and phenotypic parameters for growth and quality traits were estimated. Mean tree height was approximately 20 m while mean dbh was approximately 21 cm at 15 years. Significant differences between provenances were detected for height, dbh, and volume but not for stem straightness at both ages. Mean single-site provenance repeatability estimates for height, dbh and volume were approximately 0.15 ± 0.05, 0.15 ± 0.08, and 0.14 ± 0.06, respectively, at age 8 years and peaked at 15 years to 0.22 ± 0.03, 0.16 ± 0.07, and 0.17 ± 0.09, respectively. Repeatability for stem straightness was low at both ages (0.02 ± 0.01 and 0.03 ± 0.02). The most productive provenances were Potosi, Rio Coco, Santa Clara, Mt. Pine Ridge and Melinda and these were relatively stable across sites. Genotype *x* environment interaction was due mainly to change in ranks of some of the provenances across sites and was considered biologically important.

Keywords: *Pinus caribaea*, provenance, provenance repeatability, provenance × environment interaction.

INTRODUCTION

Pinus caribaea Morelet was first planted in Zimbabwe in 1954 when the variety *hondurensis* was introduced at Mtao Forest (BARNES *et al.* 1977). The first introductory plot was a failure because of low rainfall. Subsequent provenance tests that included var. *bahamensis* and var. *caribaea* were established in 1968 in the Eastern Highland areas of Zimbabwe and early results indicated that var. *hondurensis* had greater potential as a plantation species than the other varieties (BARNES *et al.* 1977). This stimulated the introduction of more material of var. *hondurensis* from the species' range through the acquisition of material from the Oxford Forestry Institute (OFI) for the establishment of further provenance trials. The objectives of the trials were to determine the differences in provenance performance across a complete range of climatic environments, estimate the relative importance of genetic and environmental influences in the control of economically important traits, and to investigate the significance of provenance by environment interaction.

Results from the initial provenance tests indicated that *P. caribaea* var. *hondurensis* (PCH) had the ability to yield more than the three accepted commercial species, *Pinus patula* Schiede and Deppe, *P. taeda* L. and *P. elliottii* Engelm at low altitude high rainfall areas (BARNES *et al.* 1977). PCH was also observed to be resistant to black aphid, leaf aphid and the woolly aphid. However, PCH had low wood density and associated defects that created problems with utilization both for sawn timber and pulp (BARNES *et al.* 1977). Furthermore, PCH neither produced many strobili nor seed at high elevations in Zimbabwe. In consequence, PCH has remained a minor exotic species in Zimbabwe.

The distribution and potential of *P. caribaea* var. *hondurensis* (Sénécl) Barr. et Golf. as an exotic plantation species have been noted by several authors (GREAVES 1978; BIRKS & BARNES 1990; DIETERS & NIKLES 1997; HODGE & DVORAK 2001). Approximately 1.0 million ha have been planted in the tropical and subtropical regions (DIETERS & NIKLES 1997). PCH is native to Belize, Guatemala, Honduras, Nicaragua, and Mexico (PERRY 1991). New areas of PCH have also been recently located in El Salvador by the CAMCORE Cooperative (DVORAK *et al.* 2000). PCH grows in frost-free areas, primarily from sea level to 500 m elevation with outlier populations extending to 1000 m elevation. Much good work with PCH was carried out in the 1970s and coordinated by the Oxford Forestry Institute (OFI), with provenance tests established in over 50 countries in the tropics and subtropics (BIRKS & BARNES 1990). To date, the Queensland Forest Research Institute (Australia) and CAMCORE (USA) are two of the leading organizations for large scale work on testing of PCH as an exotic plantation species. For example, CAMCORE has sampled 1400 trees in 29 populations in Central America and its members in Brazil and Venezuela have made over 200 selections in first generation tests (HODGE & DVORAK 2001).

In the last decade, significant opportunities have arisen to hybridize PCH with other species. In particular, PCH has been gaining increasing commercial importance as a hybrid parent with *Pinus elliottii*, *P. tecunumanni* and *P. oocarpa* (NYOKA 2000). The PCH × *P. tecunumanni* cross is predicted to have high productivity, drought tolerance, wind firmness, good stem straightness, fine branching, dense crown and resistance to stem breakage (NYOKA 2000). Early performance of interspecific hybrids between PCH and *P. tecunumanni* in Zimbabwe produced twice as much volume as *P. elliottii* (GWAZE 1999). The efficacy of parental selection to increase productivity in hybrids have been demonstrated in several studies. For example, natural hybrids of eucalypts were outperformed by the pure species while hybrids of selected parents were not, thus indicating the benefits of selecting within pure species prior to crossing (GWAZE *et al.* 2000). In addition, Zimbabwe intends to run a joint program with Mozambique to establish composite breeding seedling orchards (CBSO) of PCH in low elevation areas of Mozambique to produce seeds for both Zimbabwe and Mozambique. This emphasizes the importance of identifying the most productive individuals from several provenances on which to base future breeding work and selection of hybrid parents. This paper reports 8 and 15-year results for three provenance tests of *P. caribaea* var. *hondurensis* established at three sites in Zimbabwe.

MATERIALS AND METHODS

Plant material, field establishment and test design

Sixteen provenances of *Pinus caribaea* var. *hondurensis* were established at Gungunyana, Muchakata and Chiwengwa in the Eastern Highlands of Zimbabwe (Table 1). The provenances were comprised of bulked seedlots from at least 25 to 100 trees per location, so individual family identities were not maintained. The trees from which seed was collected were at least 50 metres apart. Seedlings were grown in black polythene sleeves measuring 10 cm × 15 cm in dimensions with 1178 cm^3 of inoculated top soil from pine plantations as the growing media. The 3 test sites ranged in altitude from 700 to 1052 m (Table 2). The experimental design at each location was a randomized complete block with three blocks per test with 9 × 9 tree square plots. Each site had an exterior border row. The measurement plot had a border row and was not included for analysis because of unequal competition by adjoining, different provenances. Spacing was approximately 2 × 2 m in all tests.

Data Collection

Survival, height, diameter, stem form and foxtailing were assessed at ages 8 and 15 years as follows (scale listed in parentheses): *HT* = height (m), *DBH* = diameter at breast height, i.e., 1.3 m (cm), *STR* = stem straightness (1 = very crooked, 7 = very straight), FOXT = foxtailing (0 = no foxtail, 1 = foxtail, i.e., presence of an internode > 3 m long), and a volume index for juvenile trees was calculated using height and *DBH* using a formula for juvenile pines proposed by LADRACH (1986):

$$\text{Volume Index} = 0.00003\ (DBH^2 \times HT) \qquad [1]$$

As part of the data preparation, a plot of height ×*DBH* was inspected visually. Trees that had abnormal height-diameter ratios were deleted from the data set by visual examination of a plot of height by *DBH*.

Statistical Analyses

In the first stage, the total variance in each of the three tests was partitioned into provenance, plot and within plot components. The single-site analysis was based on the following additive model:

$$y_{jkl} = \mu + B_j + P_k + PB_{jk} + e_{jkl} \qquad [2]$$

where: y_{jkl} = overall mean of the l^{th} tree in the j^{th} block and the k^{th} provenance, $E(y_{jkl}) = \mu + B_j + P_k$; $Var(y_{jkl}) = \sigma^2_{P(1)} + \sigma^2_{BP(1)} + \sigma^2_{e(1)}$; μ = a general mean; B_j = the effect of the j^{th} block; P_k = random effect of the k^{th} provenance; $E(P_k) = 0$, $Var(P_k) = \sigma^2_{P(1)}$; PB_{jk} = random plot error due to interaction between j^{th} block and k^{th} provenance; $E(PB_{jk}) = 0$, $Var(PB_{jk}) = \sigma^2_{PB(1)}$; e_{jkl} = random tree error of the l^{th} tree in the jk^{th} plot; $E(e_{jkl}) = 0$, $Var(e_{jkl}) = \sigma^2_{e(1)}$.

The variance components were estimated using the method of restricted maximum likelihood (REML), available in the MIXED procedure of SAS/STAT

Table 1. Summary information for *P. caribaea* provenances tested in Zimbabwe.

Provenance	Code	Country	Latitude	Longitude	Elevation m	Precipitation
Slilma Sia	4470	Nicaragua	14	83	70	2863
Karawala	4471	Nicaragua	12	83	10	3897
Rio Coco	4486	Nicaragua	14	83	20	3208
Santa Clara	4491	Nicaragua	13	86	700	1818
Poptun	4472	Guatemala	16	89	470–580	1688
Poptun*	6175	Guatemala	16	89	470–580	1688
Gracias a Dios	4473	Honduras	15	84	10	2840
Guanaja Island	4474	Honduras	16	85	50–100	2308
Guanaja Island - 2	4487	Honduras	16	85	60–165	2447
El Paraiso	4488	Honduras	14	86	700	663
Olanchito	4489	Honduras	15	86	600	912
Potosi	4490	Honduras	15	88	650	1205
Mt. Pine Ridge	4475	Belize	17	88	400	1558
Melinda	4484	Belize	17	88	10–20	2144
Santos	4492	Belize	17	88	20–30	1818
Queensland**	4493	Australia	22	150	5–15	1820

Provenance	Code	Country	Mean annual temperature	Provenance gain (% volume, age 15)		
				Gungunzana	Muchakata	Chiwengwa
Slilma Sia	4470	Nicaragua	30.4	+5	–2	–4
Karawala	4471	Nicaragua	26.4	–4	+1	–2
Rio Coco	4486	Nicaragua	26.5	–1	+12	
Santa Clara	4491	Nicaragua	23.4	0	+3	+9
Poptun	4472	Guatemala	24.2	–3	–4	+9
Poptun*	6175	Guatemala	24.2	–4	+4	
Gracias a Dios	4473	Honduras	26.5	–2	0	–7
Guanaja Island	4474	Honduras	27.1	+1	–19	–24
Guanaja Island - 2	4487	Honduras	26.8	–2	+2	
El Paraiso	4488	Honduras	22.2	–1	0	–3
Olanchito	4489	Honduras	24.0	+2	+5	–12
Potosi	4490	Honduras	23.7	+3	+7	+17
Mt. Pine Ridge	4475	Belize	23.9	+3	–1	
Melinda	4484	Belize	26.9	+3	+1	+4
Santos	4492	Belize	26.2	+2	+1	+3
Quensland**	4493	Australia	21.6	+5	–6	

Table 2. Details of test sites, number of blocks and provenances and climatic conditions for three provenance tests of *Pinus caribaea* var. *hondurensis* in Zimbabwe.

Test Site	Latitude	Longitude	Altitude (m)	Mean annual rainfall (mm)	Mean annual temperature (°C)	Soils	Blocks (No)	No. of provenances
Gungunyana	20°24′ S	32°43′ E	1050	1711	18.1	Clay loam	3	16
Muchakata	18°42′ S	32°53′ E	1052	1516	19.6	Clay loam	3	16
Chiwengwa	18°41′ S	32°55′ E	700	1380	20.6	Clay loam	3	16

package (SAS 1992, LITTELL *et al.* 1996). The single-site estimates of provenance variance ($\sigma^2_{P(1)}$) were biased upwards, by the variance component that estimates the varying relative performance of provenances from one site to another. To obtain unbiased estimates of genetic variance, data from multiple environments are mandatory (ZOBEL & TALBERT 1984).

Data from all tests were standardized prior to analysis to eliminate scale effects from the G × E interaction variances by multiplying all observations by a factor $\sigma^2_{Pn} / \sigma^2_{Pi}$, where σ^2_{Pi} denotes a single-site estimate of the provenance variance standard deviation for the i^{th} test and σ^2_{Pn} is some constant (SONESSON & ERIKSSON 2000). In this study, σ^2_{Pn} was set equal to the mean of the provenance variance standard deviations for the three tests included in the analysis. The model used to estimate variance components across tests was:

$$y_{ijkl} = \mu + S_i + B_{ij} + P_k + PS_{jk} + PB_{ijk} + e_{ijkl} \quad [3]$$

where: y_{ijkl} = overall mean of the lth tree in the kth provenance and jth block in the ith site; $E(g_{ijkl}) = \mu + S_i + B_{ij} + P_k$; Var $(g_{ijkl}) = \sigma^2_P + \sigma^2_{PS} + \sigma^2_{PB} + \sigma^2_e$; μ = a general mean; S_i = random effect of the ith site; B_j = random effect of the jth block 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 effect of the kth provenance in the ith site; $E(PS_{ik}) = 0$, $Var(PS) = \sigma^2_{PS}$; PB_{jk} = random plot effect due to interaction between kth provenance and jth block in the ith site; $E(PB_{ijk}) = 0$, Var $(PB_{ijk}) = \sigma^2_{PB}$; e_{ijkl} = random tree error of the lth tree in the ijkth plot; $E(e_{ijkl}) = 0$, Var $(e_{ijkl}) = \sigma^2_e$.

Estimation of genetic parameters

Repeatability estimates (t^2) give an upper limit of heritability in the broad or narrow sense. Repeatability in the genetic context is the proportion of phenotypic variance of a trait that is due to permanent effects, both genetic and environmental (FALCONER & MACKAY 1996). Examples of repeatability estimates include milk yield in cattle and litter size in mice. In this study, we cannot estimate the family variance but only provenance variance, hence we prefer to use the term "provenance repeatability" as a measure of heritability.

Single-site [4] provenance repeatability estimate denoted ($t^2_{b(l)}$), across-site [5] provenance repeatability denoted (t^2), provenance mean repeatability [6] estimate denoted (t^2bar) (this is similar in concept to the family heritability) were calculated from the equations:

$$t^2_{b(l)} = \sigma^2_{P(l)} / (\sigma^2_{P(l)} + \sigma^2_{PB(l)} + \sigma^2_{e(l)}) \quad [4]$$

$$t^2 = \sigma^2_P / (\sigma^2_P + \sigma^2_{PS} + \sigma^2_{PB} + \sigma^2_e) \quad [5]$$

$$t^2_{ba} = \sigma^2_P / \sigma^2_P + ((\sigma^2_{PS}/s) + (\sigma^2_{PB}/b) + (\sigma^2_e/sbn)) \quad [6]$$

The terms s, b and n in Equation [6] refer to the number of sites, replications per test and number of trees per plot, respectively, and all other terms as defined in Equations [2] and [3]. The subscript "b" in Equation [4] indicates that the estimate is biased upwards.

Standard errors of the provenance repeatability estimates were calculated according to an approximation given by DICKERSON (1969).

Least square means were estimated using the procedure GLM (SAS 1992). Provenance effects were predicted for volume at age 15 years. SAS PROC-MIXED was utilized to predict provenance effects for each site (SAS Institute Inc. 1992). Least square provenance means for volume were used as units of observation.

RESULTS AND DISCUSSION

Provenance Productivity

The best provenances overall were Potosi from Honduras; Rio Coco and Santa Clara from Nicaragua; Mt. Pine Ridge, Melinda and Santos from Belize (Table 1). These populations averaged approximately 7 % better than the mean of all Caribbean pine populations tested. The difference between the most productive and least productive provenance was 36 %. Three populations are wetland coastal or insular sources (Rio Coco, Santos and Melinda) and the remaining three (Mt. Pine Ridge, Potosi and Santa Clara) are inland provenances. There was a significant correlation, $r = 0.83$ ($p < 0.05$) between productivity in Zimbabwe and elevation at the collection site. For example, Rio Coco, Melinda and Santos are low elevation provenances and were some of the best performing provenances in Zimbabwe (Table 1). Two inland provenances, El Paraiso and Olanchito from high elevation and driest areas performed very poorly. HODGE & DVORAK (2001) reported that many of the inland PCH sources have been subjected to high-grading (harvesting of largest and best quality stems). Although there was no significant correlation ($r = 0.16$) between provenance productivity in Zimbabwe and rainfall, generally, provenances with greater than 1200 mm rainfall were above average performers.

HODGE and DVORAK (2001) report on the results of 48 international trials of PCH established by members of the CAMCORE Cooperative in Brazil, Colombia and South Africa. There are five provenances represented in both of these data sets that were also included in the Zimbabwe trials (Melinda, Queensland, Guanaja Island, Poptun and Karawala). There was reasonable agreement between the provenance rankings from the two data sets. Comparing the predictions from Gungunyana in Zimbabwe (Table 1) and predictions from Brazil reported in HODGE & DVORAK (2001), data from the Gungunyana trial indicate that Queensland (+5 %) and Melinda (+3 %) had the best growth of these five provenances, followed by Guanaja Island (+1 %), Poptun (–3 %), and Karawaka (–4 %). Melinda and Guanaja Island were some of the best provenances tested by CAMCORE in Brazil (HODGE & DVORAK 2001).

One improved source of PCH from Queensland, Australia and the first generation selection source from Zimbabwe were included in two of the trials and thus have predicted provenance effects. Both sources had somewhat similar predictions, similar to some of the best performing provenances like Melinda and Santos. The selection of the improved source in Zimbabwe was done in one environment and did in fact perform better (+4 %) in the environment in which it was selected (Muchakata). The Queensland source was one of the best performing provenances at one site in Zimbabwe (Gungunyaya). However, the magnitude of predicted effects for both the improved source from Queensland and first generation selection in Zimbabwe was less than the predicted gains often cited from one generation of selection (HODGE *et al.* 1989).

Provenance variation Across Planting Sites

Provenances differed significantly in growth traits at all sites ($p < 0.05$), but stem straightness did not. All growth traits and stem straightness had a similar pattern at both ages 8 and 15 years, with better growth rates at Gungunyana and Muchakata than at Chiwengwa (Table 3). For example, at Gungunyana and Muchakata, overall height growth at age 15 was 20.9 m and 20.0 m, respectively, whereas at Chiwengwa, height growth was 18.4 m (Table 3).

Mean tree volume at age 8 was highest at Gungunyana (0.05 m^3) while at Chiwengwa, it was 0.03 m^3, a difference of 40 %. PCH grows best in areas receiving more than 1500 mm of annual precipitation with loamy clay soils that are at least 1 m deep (DVORAK *et al.* 2000). It appears that the relatively better growth rates at Gungunyana and Muchakata were attributable to high altitude and high rainfall (Table 2). BARNES *et al.* (1977) reported similar conditions as being favorable for continuous growth of PCH.

The overall growth of unimproved PCH in Zimbabwe at both ages was less encouraging. Mean tree volume at ages 8 and 15 years were 0.04 m^3 and 0.30 m^3, respectively (Table 3). Assuming 1372 stems/ha with 90 % survival, these growth rates correspond to volumes of 6.2 $m^3 \cdot ha^{-1} \cdot yr^{-1}$ and 24.7 $ha^{-1} \cdot yr^{-1}$ at ages 8 and 15 years, respectively. These growth rates were considerably lower than most estimates of productivity of other unimproved pine species in Zimbabwe. For example, unimproved *P. oocarpa* achieved individual tree volume of 0.11 m^3 and mean annual increment of 17 $m^3 \cdot ha^{-1} \cdot yr^{-1}$ at 8 years (NYOKA & BARNES 1995). Similarly, unimproved *P. tecunumanii* achieved individual tree volume of 0.16 m^3 and mean annual increment of 19 $m^3 \cdot ha^{-1} \cdot yr^{-1}$ at 8 years (NYOKA & BARNES 1995).

Provenance × environment interaction

Provenance × environment interaction was present in all traits, except for stem straightness. Provenance × environment interaction was due mainly to change in ranks of the provenances across sites and therefore are important (Table1). For example, Mt. Pine Ridge, # 4475 ranked second at Gungunyana, eleventh at Muchakata and second at Chiwengwa for height at age 15 years. The Queensland source, # 4493 ranked first at Gungunyana and 15th at Muchakata. Santa Clara, # 4491, Potosi, # 4490, and Melinda, # 4484 were relatively stable across sites and were the best source of PCH at all three sites.

Provenance repeatability

Variance components were used to estimate single-site provenance repeatability estimates (t^2_b) (Table 4). The estimates for growth traits and stem straightness were generally low. The incidence of foxtailing was less than 5 % in all the three tests and therefore no further analysis was carried out on foxtailing.

Estimates of t^2_b for both growth traits within a location were generally higher at Gungunyana than at Muchakata and Chiwengwa at both ages 8 and 15. For

Table 3. Least squares means ± standard errors for height, diameter, volume and stem straightness for *Pinus caribaea* var *hondurensis* at 8 and 15 years in Zimbabwe.

Location	HT8 (m)	HT15 (m)	DBH8 (cm)	DBH15 (cm)	VOL8 m³)	VOL15 (m³)	STR8 (1-7)	STR15 (1-7)
Gungunyana	8.2 ± 0.02	20.9 ± 1.09	11.8 ± 1.03	23.3 ± 1.45	0.05 ± 0.01	0.36 ± 0.07	3.2 ± 0.44	3.8 ± 0.34
Muchakata	7.8 ± 1.18	20.0 ± 1.55	9.3 ± 1.07	20.9 ± 1.56	0.03 ± 0.01	0.30 ± 0.08	3.1 ± 0.67	3.6 ± 0.25
Chiwengwa	7.6 ± 0.74	18.4 ± 1.15	9.3 ± 0.82	19.2 ± 1.75	0.03 ± 0.01	0.25 ± 0.07	3.0 ± 0.37	3.6 ± 0.32
Overall mean	7.9 ± 0.65	19.8 ± 1.26	10.1 ± 0.97	21.2 ± 1.59	0.04 ± 0.01	0.30 ± 0.07	3.1 ± 0.49	3.5 ± 0.30

example, t_b^2 for HT8 at Gungunyana was 0.17 ± 0.03, Muchakata was 0.15 ± 0.04 and Chiwengwa was 0.12 ± 0.06. Similar trends were observed at age 15 although there was a slight increase in the repeatability estimates for HT15. Estimates of t_b^2 for height at age 15 at Gungunyana, Muchakata and Chiwengwa were 0.24 ± 0.05, 0.21 ± 0.06 and 0.19 ± 0.04 respectively (Table 4). The moderately high t^2_b estimates for growth traits at Gungunyana and Muchakata was probably related to greater growth rates observed in these high altitude sites (Table 2). Across all sites, mean t^2 for height was 0.15 ± 0.05 and 0.24 ± 0.04 respectively at ages 8 and 15, respectively. Similar trends were observed in mean t^2 for volume that was 0.12 ± 0.03 and 0.18 ± 0.05 at ages 8 and 15, respectively.

These repeatability values obtained for PCH are lower than heritability values reported for most pine species. For example, WOOLASTON *et al* (1991) report higher estimates of single-site heritability for age 5 height (h_b^2 = 0.20) and diameter (h_b^2 = 0.30) than were observed in this study. Similarly, DEAN *et al.* (1986) report higher estimates for age–7½ height (h_b^2 = 0.29) and diameter (h_b^2 = 0.48) than observed here. The estimates from both WOOLASTON *et al* (1991) and DEAN *et al.* (1986) studies should be regarded as reasonably precise as they were based on 19 and 5 trials, respectively. However, such genetic parameter estimates are always specific for the populations and the environments examined (HODGE & DVORAK 2001). As might be expected, the across-site provenance repeatability estimates were generally lower than the single-site estimates. For example, across-site estimate for HT8 was 0.11 ± 0.05, a value lower than any of the single-site.

CONCLUSION

Growth rates for PCH in Zimbabwe are unimpressive when compared to other unimproved pine species like *P. oocarpa* or *P. tecunumanii.* Repeatability estimates for growth traits were moderate and those for stem straightness were relatively low. The tests have demonstrated significant differences among provenances, and suggest where further provenance collections should be carried out in Central America. Genetic gains in excess of 20 % are possible if family and within family selections could be made within the best provenance. PCH generally remains a minor exotic species in Zimbabwe but may be important if hybrid crosses are ever considered. The results of this study give useful insights for planning selection of breeding material for both CBSOs and hybrid parents. The selections in Zimbabwe may serve as *ex-situ* reserves for some of the most threatened provenances like Melinda and Guanaja Island.

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