PROVENANCE VARIATION IN WOOD PROPERTIES OF *PINUS CARIBAEA* VAR. *HONDURENSIS*

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(Received for publication 20 March 1989; revision 9 August 1989)

ABSTRACT

Variation in the densitometric traits of wood density (DEN) and within-sample density variation (VAR) of 11 provenances of *Pinus caribaea* var. *hondurensis* Barr. and Golf. at 11 sites was studied. The analysis of variance revealed significant differences (p 0.001) between sites and provenances for DEN and VAR, with site accounting for more of the variance than provenance. The site × provenance interaction term was not statistically significant and accounted for none of the variance. Thus, provenances were consistently ranked for DEN and VAR regardless of site. The lowest values for DEN and VAR were at sites with higher altitude (1000 m). Coastal provenances were generally lower for DEN and VAR than inland provenances but these differences were not significant.

Keywords: wood density; within-sample density variation; genotype × environment interaction; climatic and geographic parameters; *Pinus caribaea* var. *hondurensis*.

INTRODUCTION

International provenance trials of *Pinus caribaea* Morelet, co-ordinated by the Oxford Forestry Institute (OFI) and funded principally by the Overseas Development Administration of the British Government, have been established in more than 400 locations in 49 countries. Previous assessments of these trials with respect to survival, growth, yield, and form traits have resulted in an increased awareness of the afforestation potential of this species and many countries have established breeding programmes. Variation in many of the external morphological characteristics due to provenance and/or site have been well documented (Barnes *et al.* 1983; Gibson *et al.* 1983; Gibson 1982) but the wood properties have been studied less intensively (Cown *et al.* 1983; Plumptre 1984). These properties are of critical importance since the wood from fast-grown plantations of exotic conifers may not satisfy the product standards of domestic or international markets.

In 1983, an intensive assessment of wood properties of *P. caribaea* var. *hondurensis* was begun using the Joyce-Loebl micro-densitometer at the OFI. The purpose of this work was to determine the following.

(1) Variation in densitometric density (DEN) and within-sample density variation (VAR) due to site and provenance;

(2) Extent and nature of genotype × environment interaction in DEN and VAR from an orthogonal set of sites and provenances.

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Provenance differences in DEN and VAR from certain sites of these trials have been discussed previously (Wright 1987; Wright *et al.* 1986a,b, 1987, 1988) as has variation in gravimetric density (Barnes *et al.* 1983; Ladrach 1986; Woessner 1983). This paper reports the variation in DEN and VAR of 11 provenances of *P. caribaea* var. *hondurensis* at 11 sites in eight countries.

Literature Review

Provenance variation in wood density of temperate pines has been studied in, for example, *P. sylvestris* L. (Echols 1958), *P. strobus* L. and *P. resinosa* Ait. (Gilmore 1968), *P. banksiana* Lamb. (Kennedy 1971), and *P. echinata* Mill. (Posey *et al.* 1970). These and other studies suggest that temperate pines, whether grown within the native range or as exotics, show clinal variation in wood density. This pattern of clinal variation can, in certain instances, be used to predict wood density when provenances are planted in new environments.

There have been few documented studies of variation in wood density across sites for provenances of tropical pines grown as exotics. Garcia de Leon (1982) evaluated the wood density of seven provenances of *P. caribaea* var. *hondurensis* at two sites in Australia and one in Brazil and found that the only significant differences in density were due to site ($p < 0.01$). The provenance × site interaction term was not statistically significant in that study and accounted for only 2.78% of the observed variation. In a study of eight provenances of *P. caribaea* at five sites in Zimbabwe, no significant differences between provenance mean densities were detected using the F test but provenances were significantly different at the 5% level according to Duncan's multiple range test (Barnes *et al.* 1977). The authors found sites to be significantly different ($p < 0.01$) but the interaction between site and provenance was not significant. Five provenances of *P. caribaea* var. *hondurensis*, common to eight of the trials co-ordinated by the OFI, were evaluated for gravimetric density (Barnes *et al.* 1983). As in the previously cited studies, no significant differences were attributable to provenance or to the interaction of provenance and site, but sites were significantly different ($p < 0.01$). Though not statistically significant, there were large differences between provenances at a given site with the coastal provenances being generally lower in density than the inland sources and the insular source, Guanaja.

Values of DEN and VAR can be useful when selecting environments and genotypes for afforestation. For example, Burley & Palmer (1979) found that DEN was significantly ($p < 0.05$) and positively ($r = 0.65$) correlated with total pulp yield in a study on 20 trees of *P. caribaea* from Fiji. Tear factor was significantly ($p < 0.01$) and positively ($r = 0.778$) correlated with the VAR of 15 trees of *Pinus* sp. in the Eastern Transvaal, South Africa (Wright 1987) and in trials of *P. caribaea* var. *hondurensis* in Fiji and Uganda (Wright & Burley 1990). In other words, high tear factor will result from pulping wood of low uniformity (i.e., high variability) in the pith to bark density gradient.

MATERIAL AND METHODS

The trials included in the analysis were selected to represent a range of environments. The experimental details of the trials are listed in Table 1 and

TABLE 1–Experimental design of *Pinus caribaea* var. *hondurensis* trials

Location	No. of blocks	Over-all plot size (trees)	Measured plot size (trees)	Trees sampled per measured plot	Spacing (m)
Anasco-A, Puerto Rico	5	7 × 1	7 × 1	2	2.7 × 2.7
Anasco-B, Puerto Rico	5	7 × 1	7 × 1	1	2.7 × 2.7
Chati, Zambia	4	10 × 10	4 × 4	3	3.0 × 3.0
Loudima, Congo	5	6 × 6	4 × 4	3	2.5 × 2.5
San Pedro, Ivory Coast	5	10 × 6	4 × 4	3	4.0 × 2.0
Mariti, South Africa	5	6 × 6	4 × 4	3	2.7 × 2.7
Bukit Tapah, Malaysia	3	6 × 6	4 × 4	3	2.5 × 2.5
Drasa, Fiji	10	5 × 1	5 × 1	1	3.0 × 3.0
Nanuku, Fiji	10	5 × 1	5 × 1	1	3.0 × 3.0
Beerburrum, Australia	5	10 × 1	10 × 1	3	3.0 × 3.0
Byfield, Australia	5	7 × 7	4 × 4	3	2.4 × 2.7

environmental details are summarised in Table 2. The provenances were selected so that the most orthogonal set of provenances across sites would be included in the analysis (Table 3). Further discussion of the site and the provenance selection process have been given by Gibson (1982).

TABLE 2–Environmental conditions of *Pinus caribaea* var. *hondurensis* trials

Location	Lat. (°)	Alt. (m)	Mean annual precipitation (mm)	Mean annual temperature (°C)	Age (months)
Anasco-A, Puerto Rico	18.33 N	175	2090	25.3	69
Anasco-B, Puerto Rico	18.33 N	175	2090	25.3	69
Chati, Zambia	13.00 S	1300	1273	20.5	86
Loudima, Congo	4.21 S	150	882	24.6	100
San Pedro, Ivory Coast	4.75 N	20	1900	26.0	105
Mariti, South Africa	24.90 S	1000	1556	17.3	75
Bukit Tapah, Malaysia	4.33 N	549	3334	24.3	66
Drasa, Fiji	17.58 S	35	2335	25.5	84
Nanuku, Fiji	17.98 S	230	3119	22.0	86
Beerburrum, Australia	27.00 S	12	1546	20.8	72
Byfield, Australia	22.83 S	30	1745	21.8	73

The trials were evaluated in 1979, 1980, or 1981. The number of trees sampled for density varies from one to three per measurement plot. This sub-sample is likely to contain the final-crop trees and those most likely to be included in any future breeding population. At the time of measurement, increment cores of 8 mm diameter were removed bark to bark at breast height (1.3 m) from the largest diameter tree(s) in the measurement plot. After shipment to the OFI, the cores were oven-dried to 12% moisture content, weighed, and the gravimetric density was determined using dry weight and wet volume calculated from nominal 8-mm increment core diameter and fresh core length (Barnes *et al.* 1983). The cores were then machined to 5 mm thickness in both axial and radial planes and the resin was extracted.

TABLE 3–*Pinus caribaea* var. *hondurensis* provenances (after Greaves 1978)

Source	Provenance	Code	Lat. (°)	Alt. (m)	Mean annual precipitation (mm)	Mean annual temperature (°C)
Coastal	Alamicamba	ALA	13.57 N	20	2610	27.3
	Brus Lagoon	BRU	15.75 N	10	2840	26.5
	Guanaja	GUA	16.47 N	50	2308	27.1
	Karawala	KAR	12.97 N	10	3897	26.4
	Río Coco	RIO	14.75 N	50	2863	25.8
Inland	Byfield*	BYF	22.83 S	10	1820	21.6
	Culmi	CUL	15.10 N	600	1325	24.3
	Mountain Pine Ridge	MPR	17.00 N	400	1558	23.9
	Poptun	POP	16.33 N	500	1688	24.2
	Potosí	POT	15.33 N	600	1205	23.7
	Santa Clara	STA	13.92 N	700	1818	23.4

* Supplied by the Queensland Forestry Department from the 127B clone bank at Byfield, Queensland, Australia. The original selections were from the Mountain Pine Ridge provenance.

Hughes & Sardinha (1975) and Kanowski (1985) have described in detail the equipment and procedures used at the OFI with respect to densitometry. The machined increment cores were X-rayed and the resulting radiographs were scanned using the Joyce-Loebl MDM6 optical densitometer. The resulting data were used to calculate the mean densitometric density (DEN) as well as the within-sample density variation (VAR). The VAR term is derived identically to the standard deviation but does not have its statistical connotations. A lower value of VAR implies greater wood uniformilty. High VAR is likely to be the result of an increased amount of wood with higher density (Echols 1972; Wright 1987).

Bartlett's Test (Snedecor & Cochran 1980) was used before the analysis to determine if the residual variances of the individual trials were sufficiently homogeneous. If the residual variances are heterogeneous, significant treatment effects could occur with greater frequency than would be expected. Gibson (1982) found that for *P. caribaea* "Virtually all traits analysed show significant differences in error variance between experiments". The Bartlett's Test on the residual variances of DEN and VAR from the trials indicated that these variances were significantly different (Table 4). This indicates that treatment effects tested against the pooled residual variance in the F test may be in doubt if they are slightly above the tabular statistical levels (Cochran & Cox 1957).

For the selected provenances and sites, provenance plot means for DEN and VAR were analysed using the analysis of variance (ANOVA). The model used was:

TABLE 4–Bartlett's Test for homogeneity of the residual variance for DEN and VAR

Trait	df	Chi square	Probability
DEN	10	190.6	$p<0.001$
VAR	10	248.3	$p<0.001$

$$DEN_{spb} \text{ or } VAR_{spb} = \mu + \alpha_{b(s)} + \alpha_s + \alpha_p + \alpha_{sp} + \varepsilon_{spb}$$

where DEN_{spb} or VAR_{spb} is the value of the s^{th} site and the p^{th} provenance, μ is the population mean, $\alpha_{b(s)}$ is the effect of the b^{th} block in the s^{th} site, α_s is the effect of the s^{th} site, α_p is the effect of the p^{th} provenance, α_{sp} is the interaction of the s^{th} site and the p^{th} provenance, and ε_{spb} is the residual. A mixed model was used with blocks as random effects and with sites and provenances as fixed effects. The expected mean squares are given in Table 5. Scheffés test (Snedecor & Cochran 1980) was used to determine if there were significant differences for DEN and VAR between the inland and coastal groups of *P. caribaea* var. *hondurensis*. The correlation of geographic and climatic parameters of experimental site and provenance origin on plot means of DEN and VAR was also calculated.

The unequal number of blocks (b) between locations (Table 1) had no effect on the calculation of the degrees of freedom since this term was derived by summation. For the calculation of the variance components, however, a "corrected" value of b was derived using the method of Ganguli (1941). The formula used to derive b was:

$$b = \frac{1}{a-1}\left[N - (\sum_{i=1}^{n} n_i^2)/N\right]$$

where a is the number of sites, N is the total number of blocks, and n_i is the number of blocks at the i^{th} site. For *P. caribaea,* the value of b was calculated to be 5.55.

TABLE 5–Analysis of variance and expectation of mean squares for the GEI assessment

Source	df	Expectation of mean squares
Sites	s–1	$\sigma^2_e + ps\sigma^2_{b(s)} + pb\sigma^2_s$
Blocks in sites	s(b–1)	$\sigma^2_e + ps\sigma^2_{b(s)}$
Provenances	p–1	$\sigma^2_e + sb\sigma^2_p$
Site × provenance	(s–1) (p–1)	$\sigma^2_e + b\sigma^2_{sp}$
Residual	s(b–1) (p–1)	σ^2_e
Total	sbp–1	

RESULTS

The results of the ANOVA are summarised in Table 6 and provenance mean values for DEN and VAR at the 11 sites are presented in Fig. 1 and 2, respectively. The correlations of DEN and VAR with the climatic and geographic parameters are given in Table 7.

There were significant differences ($p<0.001$) between sites and provenances for both DEN and VAR and these two terms accounted for most of the variance due to treatments. The site × provenance interaction term was not significant and accounted for none of the variance, suggesting that the provenance means are valid. Despite the significant differences between the residual variances in DEN and VAR as indicated by the Bartlett's Test, the low F ratio for site × provenance interaction and the high F ratio for provenances suggest that the pooled residual variances were acceptable for testing these sources. Sites accounted for more of the variance in DEN and VAR than did provenances; Gibson (1982) also observed this for certain traits in *P. caribaea*. The low variance accounted for by provenance would be due to large within-provenance

TABLE 6–Analysis of variance of plot means from 11 provenances of *Pinus caribaea* var. *hondurensis* at 11 sites for DEN and VAR

Source	df	MS		VC (%)		F	
		DEN	VAR	DEN	VAR	DEN	VAR
Site	10	0.0662	0.0777	28.9	57.7	24.1***	82.9***
Blocks in sites	51	0.0028	0.0009	0.1	0.1	1.1	1.2
Provenance	10	0.0107	0.0130	4.2	5.5	4.5***	16.7***
Site × provenance	87(13)	0.0016	0.0008	0.0	0.0	0.7	1.0
Residual	463(47)	0.0024	0.0008	66.8	36.7		
Total	621						

TABLE 7–Correlation coefficients (r) of geographic and climatic parameters of experimental site and provenance origin on plot means of DEN and VAR of *Pinus caribaea* var. *hondurensis* (df=620)

Trait	DEN	VAR
VAR	0.701*	
Site latitude (SL)	–0.206	–0.568
Site altitude (SA)	–0.872**	–0.751**
Site rainfall (SR)	0.451	0.044
Site temperature (ST)	0.716*	0.795**
Site age (SA)	–0.028	0.600
Provenance latitude (PL)	0.328	0.362
Provenance altitude (PA)	0.421	0.833**
Provenance rainfall (PR)	–0.436	–0.748*
Provenance temperature (PT)	–0.417	–0.863**

differences. In DEN, the largest part of the variance was accounted for by the residual (66.8%) but for VAR the largest part of the variance was accounted for by sites (57.7%).

The significant differences in DEN and VAR between sites could be the result of differences in age, rainfall, temperature, or their interaction. For example, Cown *et al.* (1983) found density to be correlated with both age and altitude for *P. caribaea* var. *hondurensis* grown in Fiji. The Byfield, San Pedro, Bukit Tapah, Anasco-A, and Drasa trials were clearly higher for DEN; the lowest values for DEN and VAR were at Chati and Mariti which were the sites with the highest altitude. For VAR, the highest trial means were observed at Loudima and San Pedro which were the oldest trials and it is likely that the transition from juvenile to mature wood had occurred in many of the trees. The higher VAR would thus be due to a greater percentage of higher density latewood (Echols 1972).

Scheffés test revealed no significant differences in DEN or Var between the inland and coastal groups of *P. caribaea* var. *hondurensis*. However, the coastal provenances Alamicamba, Brus Lagoon, Karawala, and Rio Coco were generally ranked below the trial mean for DEN and VAR while the inland provenances Potosi and Santa Clara were generally ranked above the trial mean for these traits. The insular provenance

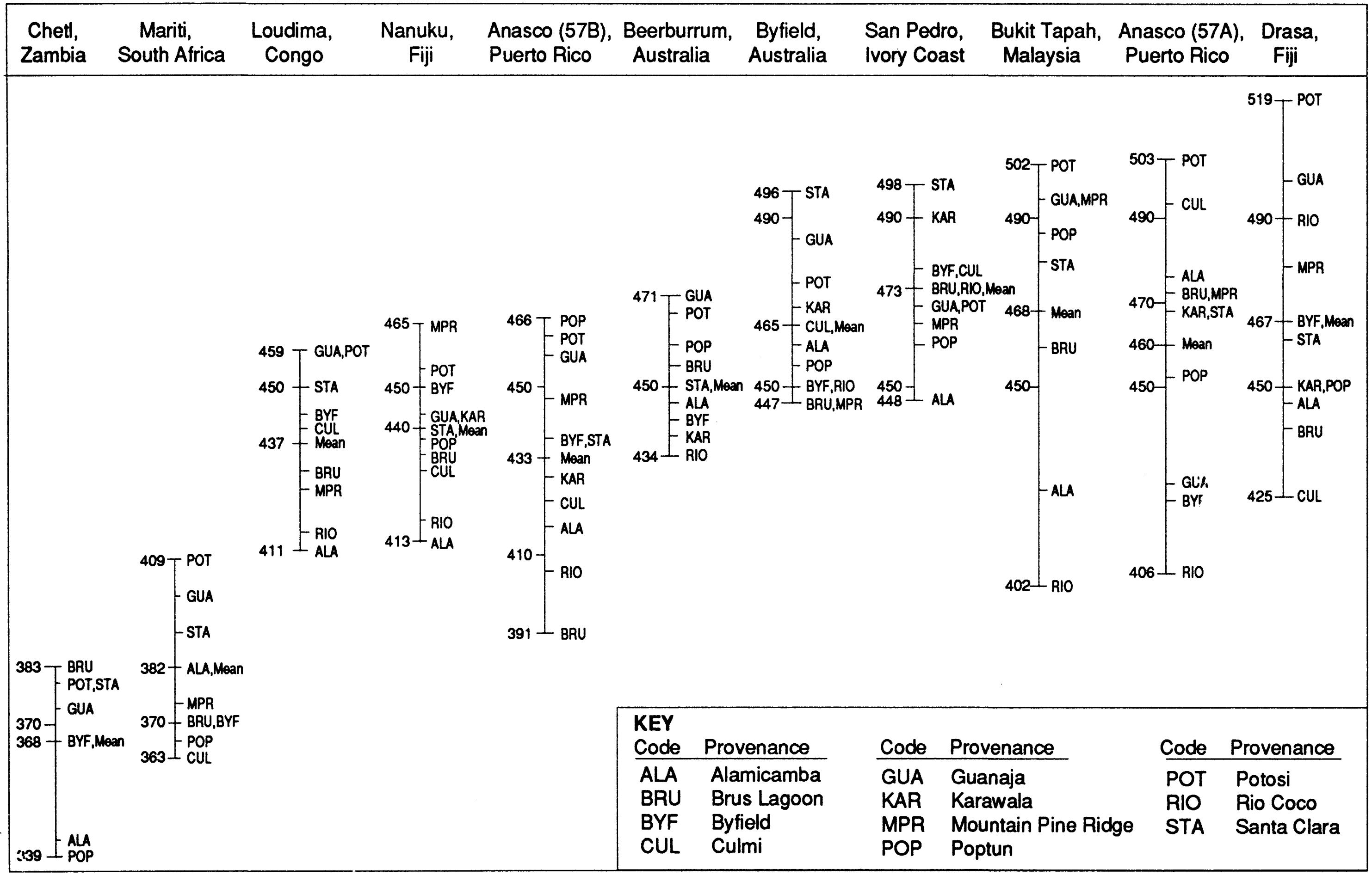

FIG. 1 — Density (kg/m³) of 11 provenances of *Pinus caribaea* var. *hondurensis* at 11 sites.

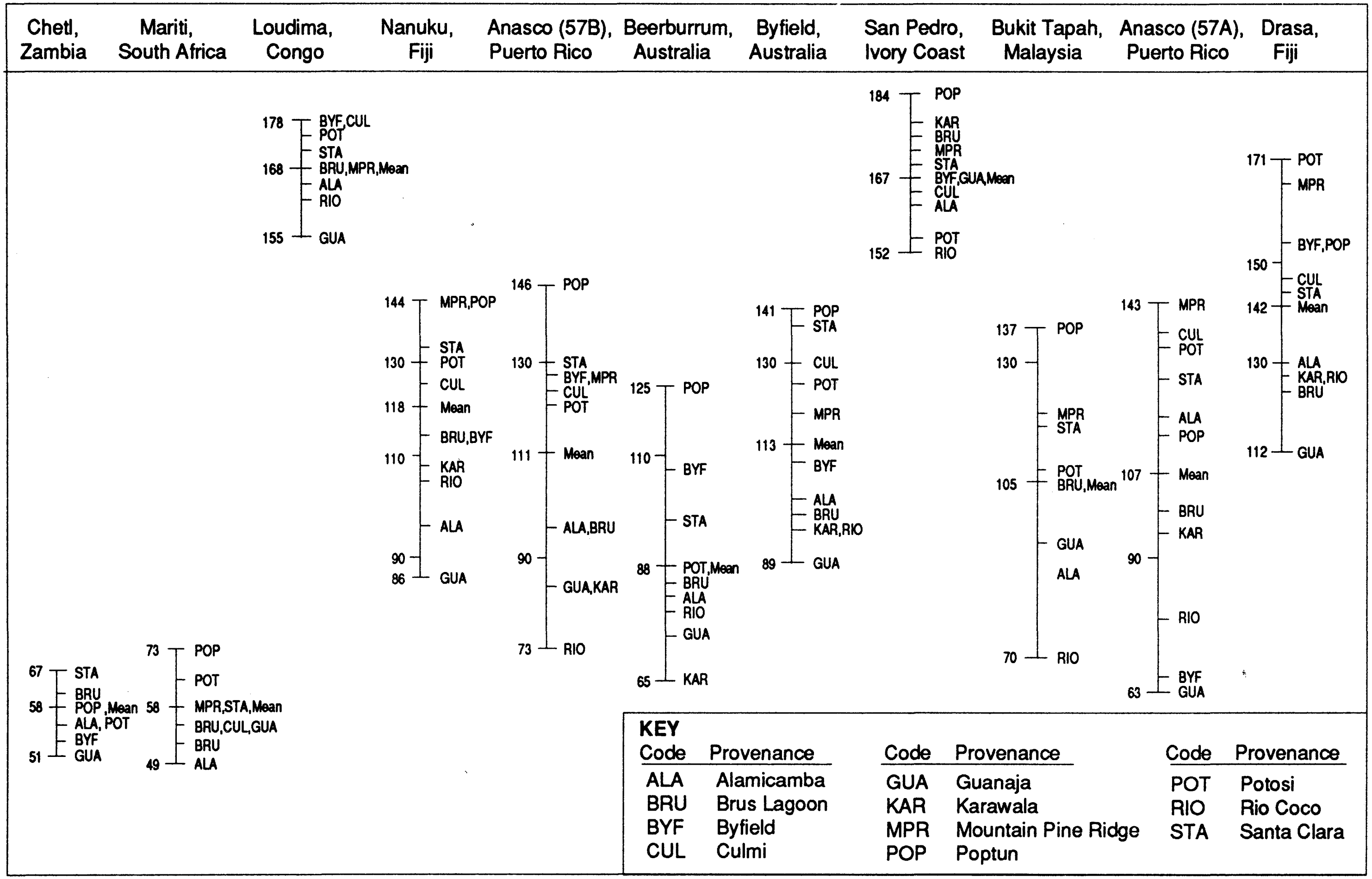

FIG. 2 — Within-sample density variation (kg/m³) of 11 provenances of *Pinus caribaea* var. *hondurensis* at 11 sites.

Guanaja was ranked among the highest for DEN and the lowest for VAR across the 11 sites while the Poptun provenance was ranked the highest for VAR at seven of the 10 sites in which it was planted.

The site means of DEN and VAR were positively and significantly correlatd with site temperature. DEN and VAR were negatively and significantly correlated with site altitude. VAR was found to be positively and significantly correlated with provenance altitude. Provenance rainfall and temperature were negatively and significantly correlated with the mean VAR of a provenance.

The correlation between DEN and VAR was significant and positive (r = 0.701) for provenances of *P. caribaea* var. *hondurensis* (Table 6). Kanowski (1986) found the genotypic correlation between DEN and VAR in a *P. caribaea* var. *hondurensis* progency test to be 0.65 at age 10 years. DEN and VAR were significantly and negatively correlated with site altitude while the correlation with site temperature was significant and positive. VAR was significantly and negatively correlated with the provenance origin characteristics of rainfall and temperature while the correlation with provenance altitude was positive and significant.

CONCLUSION

The large variance accounted for by site would suggest that tree breeders and forest managers should be very concerned with sites chosen for afforestation with *P. caribaea* var. *hondurensis* if wood density is important for the intended end-product. At a given site, there would probably be numerous provenances which would have acceptable mean density values. Within a provenance, there would normally be large tree-to-tree differences for wood density as well as for volume and form. Individual trees within "superior" provenances could therefore be chosen which were superior for DEN, VAR, volume, and form. The fact that provenance × site interaction was not significant for DEN and VAR indicates that provenances would be ranked consistently across sites for these traits.

For DEN, the significant and negative correlation with site altitude supports previous findings (Barnes *et al.* 1977; Cown *et al.* 1983). It can thus be said with some certainty that DEN and VAR of *P. caribaea* var. *hondurensis* will be lower at sites of higher altitude though the data here were insufficient to develop predictive equations. This lower wood density would be caused partly by the lower temperature at these higher altitudes as evidenced by the positive and significant correlation of DEN with site temperature (r = 0.716*). The correlations of VAR with site parameters followed the same pattern as DEN. Planting areas at low altitude with higher mean annual temperatures should result in trees of *P. caribaea* var. *hondurensis* with higher mean DEN and VAR.

ACKNOWLEDGMENTS

Seeds for these trials were collected and distributed under Research Schemes at the Oxford Forestry Institute (OFI), University of Oxford, England, funded by the Overseas Development Administration of the British Government and with the co-operation of the forest authorities in the various countries of Central America where *P. caribaea* var. *hondurensis* is indigenous. The trials were established and maintained by forest research institutes and their help with these assessments is gratefully acknowledged. I would also like to thank Mr Tony Quilter of the OFI for his assistance in preparing the wood samples for densitometry. Dr

Jeff Burley, Dr Richard Barnes, and Dr Peter Kanowski as well as Mrs Jacqui Birks of the OFI kindly read the manuscript and made useful comments.

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