Variation Among Natural And Domesticated Populations of *Pinus caribaea* Var. Bahamensis When Grown In Queensland And South China

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ABSTRACT

Family-in-provenance tests of *Pinus caribaea* var. *bahamensis* were established on two sites, one in south China and the other in south-east Queensland, in the early 1990s using seeds that had been collected by the Oxford Forestry Institute from the islands of Abaco, Grand Bahama, Andros and New Providence in the Bahamas. The Queensland trial also included open-pollinated progeny of first-generation plus-trees that had been selected in Queensland. Investigations of provenance variation (at 6 and 7 years of age in the China and Queensland trials respectively) suggested that there is substantial variation among these four island groups. Provenances from the northern part of the distribution of var. *bahamensis* (ie. Abaco and Grand Bahama) generally performed better in both Queensland and China than the southern sources – faster growth, higher wood density, and thinner bark, but longer foxtails. The latitude of origin appeared to be strongly related to the performance of var. *bahamensis* as an exotic in both countries.

Canonical analysis of data from the trial in Queensland clearly delineates the provenances into their island groups, and distinguished the domesticated and natural populations. The patterns identified through the canonical analysis of data from trials in both Queensland and China, indicated a strong relationship between the geographic origin of provenances and their performance in the provenance tests.

Components of variance estimated using Restricted Maximum Likelihood (REML), indicated that there was substantial variation among the islands and individual trees within provenances; however, relatively little variation was found among provenances within island groups for the traits investigated (height, diameter, and volume in both trials; bark thickness, pilodyn penetration, and length of the longest internode in the Queensland trial; crown width, height to first branch, and wood density in the China trial). Heritabilites for growth traits were around 0.2- 0.3 in the Queensland trial, but higher in the China trial (around 0.4). Internode length and bark thickness had heritabilities between 0.3 and 0.4, while the heritability of wood traits (density and pilodyn penetration) exceeded 0.4.

This information is being used for in the selection of future breeding populations in Queensland and China, and for the development of breeding strategies for the continued genetic improvement of this species.

INTRODUCTION

Pinus caribaea has been divided into three taxonomic varieties: var. *bahamensis*, var. *caribaea* and var. *hondurensis*. Var. *hondurensis* has been the most widely used of the three varieties in commercial plantations (Dieters and Nikles, 1997); however var. *bahamensis* is showing considerable potential as a pure species or in hybrids, where greater resistance to tip moth attack, wind-damage, or frost is required (Baylis and Barnes 1989, Dieters 2000, Zheng et al. 2000). The natural distribution of var. *bahamensis* is restricted to the Bahama and Caicos Islands (Baylis and Barnes 1989), and at 27°N latitude in Grand Bahama and Great Abaco it has the most northerly distribution of the three varieties.

In the late 1980s the Oxford Forestry Institute (OFI) initiated a project to collect and distribute seed of var. *bahamensis* following recognition of the possible value of this variety. Seeds were collected from up to 10 individual trees in each of 14 provenances throughout the four main island groups of the Bahamas (Baylis and Barnes 1989). This paper summaries results of measurements and assessments conducted in the two family-in-provenance tests (one in Queensland, the other in China) established with seed collected by OFI from the natural range of var. *bahamensis* and aims to: (1) investigate patterns of natural variation with this variety, and (2) determine the genetic control of traits of economic importance.

MATERIALS AND METHODS

Genetic material

Open-pollinated seeds of *P. caribaea* var. *bahamensis* that was collected from individual mother trees in the Bahamas was distributed from OFI to Queensland and China in the late 1980s, and used to independently establish one family-in-provenance trial in each country (Table 1). The approximate locations of the seed collection sites in the Bahamas are indicated in Figure 1.

Table 1. Provenance origin and composition of *P. caribaea* var. *bahamensis* family-in-provenance trials established in Queensland and China.

Provenance	Oxford Seed ID Number	Latitude (ºN)	Longitude (ºW)	Altitude (m a.s.l.)	Number Families QLD	Number Families China
Abaco						
1. Cedar Harbour	658/1-10	26º53'	77º39'	10	10	10
2. Norman Castle	668/1-10	26º45'	77º26'	5	10	10
3. Central Abaco	678/1-10	26º26'	77º05'	5	8	5
4. Sandy Point	688/1-10	26º02'	77º12'	10	10	10
Andros						
5. San Andros	698/1-10	24º57'	78º01'	5	10	10
6. Staniard Creek	708/1-10	24º50'	77º55'	5	10	10
7. Roker Cay	718/1-10	24º07'	77º44'	2	8	8
8. Kemps Bay	728/1-10	24º06'	77º36'	5	10	9
Grand Bahama						
9. Freeport	738/1-10	26º32'	78º45'	5	6	3
10. South Riding	748/1-10	26º40'	78º13'	10	10	9
11. Maclean's Town Cay	758/1-10	26º34'	77º55'	2	9	7
12. Little Harbour Cay	768/1-10	26º33'	77º53'	2	10	10
New Providence						
13. Adelaide	778/1-10	25º00'	77º26'	10	10	10
14 East New Providence	788/1-10	25º01'	77º24'	5	10	10
Queensland						
15. Open-pollinated ortets	–	–	–	–	9	–
16. Open-pollinated ramets	–	–	–	–	10	–

Note: The provenance origins of the Queensland parents in this study are: 6 parents from Abaco, 1 from Grand Bahama, and 8 most probably originate from Grand Bahama or New Providence.

Figure 1. Approximate location of sites from which *P. caribaea* var. *bahamensis* seed was collected by the Oxford Forestry Institute. (Provenance numbers correspond to those in Table 1.)

In addition to the seeds collected in the natural stands, the Queensland trial also included open-pollinated seed of first-generation plus-trees that was collected from the ortets, or from ramets in the clone banks of var. *bahamensis* (Table 1). There were four Queensland-bred parents in the trial that were represented by both open-pollinated ortet and ramet families.

Experimental design and site details

The Queensland test included a total of 150 open-pollinated families (Table 1), and was planted in May 1990 at a spacing of 4.5 x 1.5 m, on a coastal site in south-east Queensland (25º S, 152º 47'E) with a mean annual rainfall of 1370 mm/yr, and yellow podzolic or yellow earth soil types. The test was established in a randomised complete block design, with 2 disconnected sets, and up to 50 replicates of each family, in single tree plots (ie. one tree per family per replicate). All surviving trees were measured and assessed in 1997 at 7 years of age.

The test in China included a total of 121 open-pollinated families (Table 1), and was planted in May 1991 at a spacing of 3 x 3 m, in Hepu County (Guangxi Province, 21º 41'N, 109º 11'E) with a mean annual rainfall of 1650 mm/yr, and a lateritic red-yellow sandy soil. The test was established using a resolvable incomplete block design, with six replicates of 4-tree square plots of each family. However, so that the same statistically models could be applied to data from China and Queensland, the incomplete block structure was ignored. All surviving trees were measured and assessed in 1997 at 6 years of age.

Traits Measured and Assessed

In the Queensland test the following traits were measured or assessed: diameter (over-bark) at breast height (cm); total tree height (m); length of longest internode (derived from heights of whorls at top and bottom of longest internode); pilodyn penetration (mm) – two measurements in each of two bark-windows on opposite sides of each tree; and, bark thickness (mm) – mean from two bark-windows on opposite sides of each tree. Conical volume under- and over-bark was calculated from these measurement. (*Note: pilodyn, bark thickness and internode length assessed only on 41 of the 50 replicates.)*

In the China test the following traits were measured or assessed: diameter (over-bark) at breast height (cm); total tree height (m); height to first branch (cm); crown width (cm), and wood density – one bark to bark core, taken from the "average" tree in each family plot, in each replicate.

Statistical analyses

Two separate analyses were conducted on the data collected in the var. *bahamensis* provenance trials. The first analysis aimed to investigate patterns of provenance variation amongst the natural populations, and the relationship of the natural populations to domesticated populations from Queensland. The second analysis aimed to investigate the variance within and between provenances in order to estimate the heritability and genetic correlations of the traits.

The significance of variation due to provenance effects were first tested at each site using PROC GLM of the SAS system (SAS 1989), using a model that fitted effects due to blocks, provenance and family within provenance. All effects in the model were considered to be fixed with the exception of the residual error term, and least squares means were estimated for each provenance and family as part of this analysis. The least squares family means for all traits were then used in a canonical discriminant analysis using PROC CANDISC in the SAS System (SAS 1989). Separate analyses were performed using data from sites in China and Queensland, since a different set of families were included in the two countries and the procedure can not use unbalanced data.

Variance components were then estimated from univariate analyses for each trait with ASREML (Gilmour et al. 1999). Preliminary analyses indicated that the domesticated populations of *Pinus caribaea* var. *bahamensis* probably had a different variance structure to the natural populations, therefore the Queensland-bred families were excluded from the analyses. A model that fitted an additive genetic (ie. individual tree model), block, island, provenance within island and residual effects was used for the univariate analyses in ASREML. All effects other than μ were assumed to be random, approximately normally distributed with means of zero, and variances σ^2_A, σ^2_b, σ^2_i, σ^2_p, and σ^2_e for effects of additive genetic variance, blocks, islands, provenances within islands, and residual respectively. Multivariate analyses were then performed to estimate genetic correlations between the traits measured/assessed at each site. A simpler model (excluding effects of island and provenance) was used, as it was not possible to achieve convergence of all parameters using the full model. The post-processing options in ASREML were used to estimate heritabilities (h^2) and genetic correlations (r_g) between traits at each site. The phenotypic variance for the estimation of h^2 was calculated as the sum of σ^2_A, σ^2_b, σ^2_i, σ^2_p, and σ^2_e.

RESULTS AND DISCUSSION

Provenance Means

Preliminary analysis of data in SAS PROC GLM indicated that the effects of provenance and family within provenance were highly significant ($p < 0.01$) for all traits in the two tests. From the least squares provenance means (Tables 2 and 3) the following general trends can be observed at the provenance level:

- The natural provenances from the northern part of the distribution of var. *bahamensis* (ie. Abaco and Grand Bahama, Figure 1) appeared to have the fastest early growth when planted in south-east Queensland (Table 2) and southern China (Table 3). These provenances also appeared to have increased wood density and reduced pilodyn penetration (Tables 2 and 3).
- The families that were from first-generation plus-trees selected in Queensland were clearly superior to those from the natural stands in growth.
- Although genetic gains have been achieved in growth traits and the length of the longest internodes had been reduced through selection in Queensland, there appeared to have been a negative impact on wood density (increased pilodyn penetration) and bark thickness (Table 2).
- The provenance means were correlated with the latitude of origin in both tests (Tables 2 and 3). This indicated that there was a strong positive relationship between latitude and growth traits, length of the longest internode, and wood density (negative with pilodyn penetration), but a slight negative correlation with bark thickness.

The combination of faster growth and higher wood density suggests that provenances from Abaco and Grand Bahama may be more suitable for use in plantation establishment than those from the southern part of the distribution of var. *bahamensis*. The two most southerly provenances tested in this study (Roker Cay and Kemps Bay from Andros) tended to be amongst the poorest in terms of average growth in both Queensland and China (Tables 2 and 3).

Canonical Analysis

The squared distances between the Queensland domesticated populations and the natural populations (Table 4) suggests that the Queensland material is most closely related to that from New Providence and Abaco. This corresponds with the provenance origin of the Queensland-bred families in this experiment (refer to note at bottom of Table 1). The statistical significance of squared distances within island sources (in analyses of data from both Queensland and China) indicates that while the squared distances between provenances from different island groups were usually highly significant ($p < 0.01$), the distances between provenances from the same island group were also often significant ($p < 0.1$). This tends to suggest that the four island groups in the Bahamas are a logical grouping for the individual provenance collections, but that there is still substantial variation within island groups. Further, all multivariate test statistics

Table 2. Least squares provenance means at 7 years of age (standard errors in parentheses) for a *P. caribaea* var. *bahamensis* family-in-provenance test established in Queensland (Exp. 686 TBS), and correlations between provenance means and latitude of provenance origin in natural stands.

Provenance	Diameter (cm)		Diameter Under Bark (cm)		Height (m)		Volume (dm^3)		Volume Under Bark (dm^3)		Longest Internode (m)		Pilodyn 1 (mm)		Pilodyn 2 (mm)		Bark Thickness (mm)	
Abaco																		
1. Cedar Harbour	14.41	(0.10)	11.23	(0.09)	9.78	(0.05)	55.36	(0.85)	33.88	(0.62)	1.54	(0.05)	18.38	(0.12)	17.08	(0.11)	16.32	(0.15)
2. Norman Castle	14.73	(0.11)	11.59	(0.10)	10.02	(0.06)	59.51	(0.93)	37.05	(0.66)	1.37	(0.05)	18.71	(0.12)	17.15	(0.12)	16.77	(0.16)
3. Central Abaco	13.91	(0.12)	11.01	(0.10)	9.84	(0.06)	52.17	(1.00)	32.98	(0.71)	1.85	(0.06)	18.26	(0.13)	16.66	(0.13)	15.57	(0.18)
4. Sandy Point	14.16	(0.11)	11.08	(0.09)	9.86	(0.05)	53.86	(0.89)	33.50	(0.64)	1.50	(0.05)	18.31	(0.12)	16.94	(0.11)	16.52	(0.16)
Andros																		
5. San Andros	13.71	(0.11)	10.73	(0.10)	9.50	(0.05)	49.01	(0.92)	30.36	(0.65)	1.20	(0.05)	19.44	(0.12)	18.08	(0.12)	16.20	(0.16)
6. Staniard Creek	13.60	(0.11)	10.45	(0.09)	9.50	(0.05)	48.19	(0.87)	28.79	(0.62)	1.25	(0.05)	19.49	(0.12)	17.68	(0.11)	16.49	(0.15)
7. Roker Cay	12.91	(0.12)	9.98	(0.10)	9.24	(0.06)	43.53	(0.96)	26.14	(0.68)	1.12	(0.06)	19.61	(0.13)	18.17	(0.12)	16.02	(0.17)
8. Kemps Bay	13.43	(0.11)	10.41	(0.10)	9.35	(0.05)	46.92	(0.88)	28.50	(0.65)	1.26	(0.05)	19.55	(0.12)	17.85	(0.12)	16.22	(0.16)
Grand Bahama																		
9. Freeport	13.53	(0.14)	10.64	(0.12)	9.54	(0.07)	48.29	(1.18)	29.87	(0.84)	1.40	(0.07)	19.28	(0.16)	17.92	(0.15)	15.98	(0.21)
10. South Riding	13.19	(0.11)	10.44	(0.09)	9.56	(0.05)	45.83	(0.87)	28.86	(0.64)	1.35	(0.05)	18.19	(0.12)	17.01	(0.12)	15.08	(0.16)
11. Maclean's Town Cay	13.39	(0.12)	10.58	(0.10)	9.65	(0.06)	47.60	(0.98)	30.10	(0.70)	1.34	(0.06)	17.90	(0.13)	16.67	(0.13)	15.04	(0.17)
12. Little Harbour Cay	13.67	(0.11)	10.71	(0.09)	9.69	(0.05)	49.85	(0.88)	30.69	(0.64)	1.20	(0.05)	17.79	(0.12)	16.55	(0.12)	16.19	(0.16)
New Providence																		
13. Adelaide	13.81	(0.11)	10.71	(0.10)	9.81	(0.05)	51.09	(0.88)	31.06	(0.65)	1.22	(0.05)	19.24	(0.12)	17.81	(0.12)	15.88	(0.16)
14 East New Providence	13.83	(0.10)	10.57	(0.09)	9.60	(0.05)	50.66	(0.85)	29.68	(0.62)	1.16	(0.05)	18.84	(0.12)	17.49	(0.11)	16.93	(0.15)
Queensland																		
15. Open-pollinated ortets	14.77	(0.11)	11.60	(0.09)	10.02	(0.05)	61.00	(0.88)	37.92	(0.64)	1.11	(0.05)	19.41	(0.12)	18.00	(0.12)	17.28	(0.16)
16. Open-pollinated ramets	15.11	(0.10)	11.80	(0.09)	10.12	(0.05)	64.18	(0.87)	39.53	(0.63)	1.02	(0.05)	19.40	(0.12)	18.15	(0.11)	17.45	(0.16)
Correlation with latitude	0.45		0.64		0.67		0.50		0.63		0.59		-0.80		-0.76		-0.28	

Table 3. Least squares provenance means at 6 years of age (standard errors in parentheses) for a *P. caribaea* var. *bahamensis* family-in-provenance test established in China, and correlations between provenance means and latitude of provenance origin in natural stands.

Provenance	Diameter (cm)		Height (m)		Volume (dm^3)		Crown Diameter (m)		Height to 1st branch (m)		Density (kg/m^3)	
Abaco												
1. Cedar Harbour	11.61	(0.12)	6.66	(0.06)	24.79	(0.61)	3.07	(0.03)	1.39	(0.04)	0.435	(.005)
2. Norman Castle	11.83	(0.13)	6.96	(0.07)	26.71	(0.65)	3.17	(0.03)	1.46	(0.05)	0.437	(.006)
3. Central Abaco	11.30	(0.18)	6.74	(0.09)	23.82	(0.87)	3.17	(0.04)	1.26	(0.06)	0.436	(.007)
4. Sandy Point	11.61	(0.12)	6.98	(0.06)	25.96	(0.61)	3.14	(0.03)	1.45	(0.04)	0.444	(.005)
Andros												
5. San Andros	11.24	(0.13)	6.52	(0.07)	23.15	(0.65)	3.09	(0.03)	1.21	(0.05)	0.427	(.005)
6. Staniard Creek	10.93	(0.12)	6.52	(0.06)	21.79	(0.61)	3.10	(0.03)	1.13	(0.04)	0.417	(.005)
7. Roker Cay	10.71	(0.14)	6.16	(0.07)	20.28	(0.68)	2.99	(0.03)	0.94	(0.05)	0.420	(.005)
8. Kemps Bay	10.38	(0.14)	6.04	(0.07)	18.61	(0.68)	2.90	(0.03)	1.20	(0.05)	0.420	(.005)
Grand Bahama												
9. Freeport	10.60	(0.23)	6.14	(0.11)	19.43	(1.11)	2.97	(0.06)	1.38	(0.08)	0.437	(.009)
10. South Riding	10.69	(0.13)	6.57	(0.07)	21.21	(0.65)	2.99	(0.03)	1.42	(0.05)	0.448	(.005)
11. Maclean's Town Cay	10.84	(0.15)	6.71	(0.07)	21.84	(0.73)	3.06	(0.04)	1.31	(0.05)	0.419	(.006)
12. Little Harbour Cay	11.79	(0.12)	6.80	(0.06)	25.94	(0.61)	3.16	(0.03)	1.24	(0.04)	0.442	(.005)
New Providence												
13. Adelaide	11.42	(0.12)	6.87	(0.06)	24.72	(0.61)	3.08	(0.03)	1.34	(0.04)	0.428	(.005)
14. East New Providence	11.71	(0.12)	6.56	(0.06)	24.92	(0.62)	3.23	(0.03)	1.17	(0.04)	0.428	(.005)
Correlation with latitude	0.36		0.53		0.41		0.29		0.76		0.72	

Table 4. Average squared distances of Queensland open-pollinated families from natural stands of *P. caribaea* var. *bahamensis*.

Provenance	Open-pollinated ortet families	Open-pollinated ramet families
Abaco	9.8	14.8
Andros	11.0	17.4
Grand Bahama	10.3	16.2
New Providence	6.6	11.0

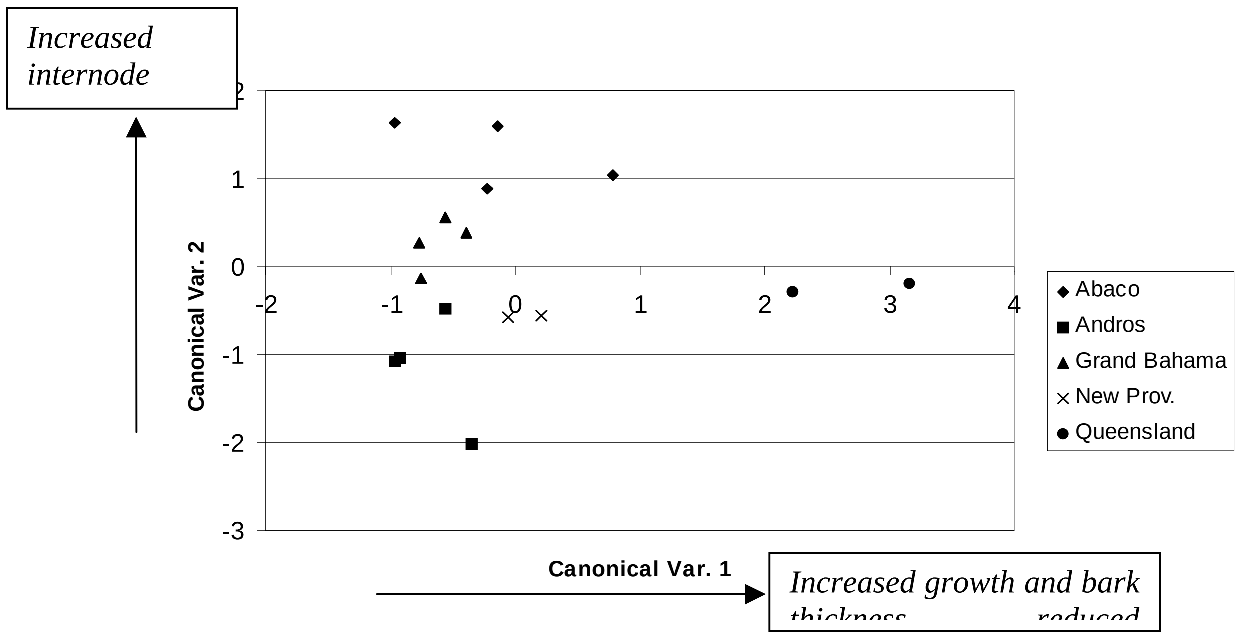

Figure 2. Plot of provenance means for canonical variables 1 and 2 for data from the Queensland trial of *P. caribaea* var. *bahamensis*.

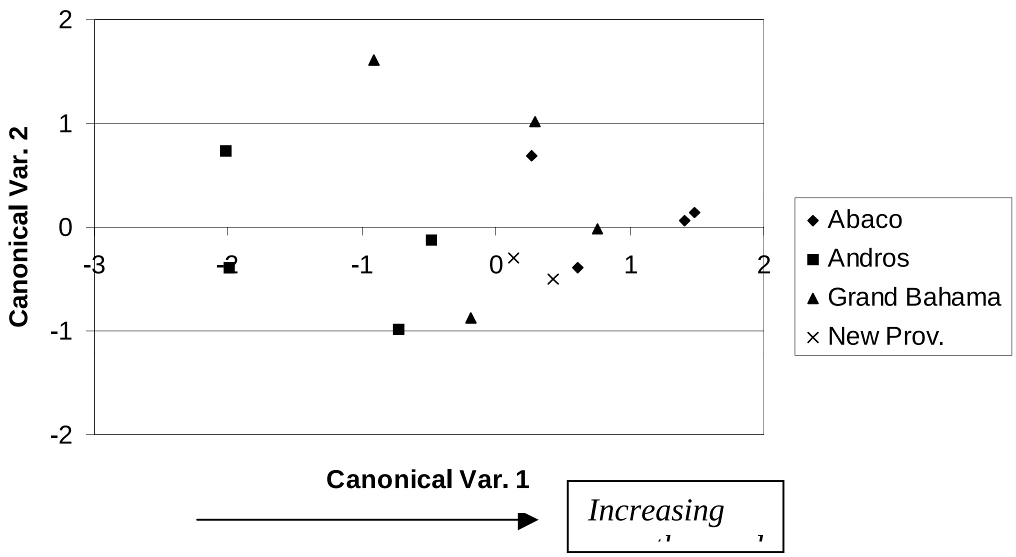

Figure 3. Plot of provenance means for canonical variables 1 and 2 for data from the China trial of *P. caribaea* var. *bahamensis*. (Note: the two points on the far left of the graph are from provenances 7 & 8 on the southern part of Andros, Figure 1.)

indicate that the provenance means were not all equal (all tests were highly significant, $p < 0.01$) in either the China or the Queensland tests, which substantiates results from the preliminary analyses which found significant differences between provenances.

The first canonical variable explained between 55% and 60% of the variation in the data from the Queensland and China tests; however, the second variable explained 50% of the variation in the Queensland test, but only just over 30% of the variation in the China test. This may reflect the fact that traits measured in the China test were mostly correlated at the provenance mean level, so that there is relatively little variation left in the data that can be explained by a second, uncorrelated canonical variable. Relationships between the first and second canonical variable variables are represented in Figures 2 and 3.

Based on seedling traits to one year of age (height, diameter, autumn height increment, cold hardiness, number of needles per fascicle, and needle length) Nikles (1966) was able to identify similar patterns in the natural variation of var. *bahamensis*. Two clusters were identified in var. *bahamensis*: the first comprised Grand Bahama, Abaco and New Providence, and the second Andros and the Caicos Islands (Nikles 1966, page 124). Studies of natural variation patterns in var. *bahamensis* using isozymes (Zheng and Ennos 1999) also produced similar results based on estimates of genetic distance between the populations: two populations from New Providence formed one group, three populations from Abaco, Grand Bahama and Byfield (Queensland) formed a second group, and one population form Andros was intermediate between these two groups.

The pattern of variation among natural populations of var. *bahamensis* report in this paper (ie. from north to south) provides additional support to the work of Schmidtling and Hipkins (2000) who have suggested that there is continuous variation from var. *hondurensis* to var. *caribaea* to var. *bahamensis* to *P. elliottii*, and that Dvorak et al. (2000) who suggest that "an ancestral form of *P. caribaea* var. *caribaea* was the founder species for the Florida/Caribbean taxa".

Quantitative Genetics

The variance components estimated using restricted maximum likelihood for traits measured in the two tests (excluding the families of Queensland origin) indicate that there was considerable variance between families within provenances and between the islands, but relatively little variation between provenances within islands (Table 5). Nikles (1966) and Zheng et al. (1994) found similar patterns of variation in var. *bahamensis*. This suggests that significant gains can be achieved through selection of the best island groups, and the best individuals; however, there is less to be gained through testing of different sources within the island populations.

The heritabilities for growth traits in the Queensland test (Table 5) were of a magnitude commonly reported for forest trees (ie. 0.2 to 0.3); however, heritability of diameter and volume were substantially higher in China than Queensland (0.4 vs. 0.25). The heritability of over- and under-bark assessments of diameter and volume were very similar. Bark thickness and internode length had slightly higher heritabilities (0.3 – 0.4), while wood traits had the highest heritabilities (over 0.4).

The heritability of pilodyn penetration assessed in the Queensland test (0.6) was considerably higher than that for wood density assessed from cores sampled in the China test (0.45), and had lower standard errors. This suggests that pilodyn penetration may be a better method of assessing wood density because the lower assessment cost allows a much larger number of trees to be measured, leading to greater precision and avoiding sampling bias.

Genetic correlations (Table 6) indicate that all growth traits are strongly correlated, particularly diameters (over- and under-bark) with volume, as would normally be expected. However, the genetic correlations between under-bark and over-bark diameters/volumes (around 0.8) were poorer than anticipated. This combined with the positive correlation between diameter and bark thickness suggests that selection on over-bark diameters will result in an indirect increase in bark thickness, but will not necessarily maximise gain in under-bark volume.

The length of the longest internode (ie. the propensity of trees to produce foxtails) was negatively correlated with diameter (and volume) but positively correlated with height. This suggests that trees with long internodes (foxtails) tend to be taller and with a smaller diameter. The negative correlation between internode length and diameter is in fact favourable, as selection for increased diameter will lead to an indirect reduction in internode length; however, this correlation is not strong (-0.35) so indirect selection will not be an effective means of reducing the incidence of foxtails.

The correlations between Pilodyn 1 and Pilodyn 2 (assessed on opposite sides of the tree) were very high (0.98, Table 6) suggesting that only one bark window assessment is required. Further, pilodyn penetration was essentially uncorrelated with all other traits (ie. all correlations were not significantly different from zero), which suggests that this trait can be improved independently of all other traits.

CONCLUSIONS

Performance of var. *bahamensis* as an exotic plantation species was strongly related to provenance origin, with those provenances from the northern part of the distribution (ie. Abaco and Grand Bahama) being the most promising, with a strong relationship to latitude of origin. Estimates of variance between and within provenance, and of heritability and genetic correlations, indicate that there are good prospects for the genetic improvement of both growth and wood density in this species.

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REFERENCES

Baylis, W.B.H., and Barnes, R.D. 1989. International provenance trial of *Pinus caribaea* var. *bahamensis*. *In* Breeding topical tees: Population structure and genetic improvement strategies in clonal and seedling forestry. Proc. IUFRO Conf., Pattaya, Thailand, November 1988 (*Edited by* G. L. Gibson, A. R. Griffin, and A. C. Matheson). Oxford Forestry Institute/Winrock International, Oxford/Arlington Virginia. pp. 283-290.

Dieters, M.J. 2000. Performance of *Pinus caribaea* hybrids in north and central Queensland and on dry sites in south-east Queensland. *In* Hybrid Breeding and Genetics of Forest Trees. Dungey, H.S., Dieters, M.J. and Nikles, D.G. (*Compilers*). Proceedings of QFRI/CRC-SPF Symposium, 9-14 April 2000, Noosa, Queensland, Australia. (Department of Primary Industries, Brisbane). pp.404-412.

Dieters, M. J., and Nikles, D. G. 1997. The genetic improvement of Caribbean pine (*Pinus caribaea* Morelet) - building on a firm foundation. *In* Proc. 24th Southern Forest Tree Improvement Conference, Orlando, FL., June 10 - June 12, 1997, pp. 33-52.

Dvorak, W.S., Jordan, A.P., Hodge, G.R., Romero, J.L. 2000. Assessing evolutionary relationships of pines in the *Oocarpae* and *Australes* subsections using RAPD markers. New Forests 20: 163-192.

Gilmour, A.R., Cullis, B.R., Welham, S.J. and Thompson, R. 1999. ASREML Reference Manual. NSW Agriculture Biometric Bulletin No. 3. NSW Agriculture, Orange, NSW. 210p.

Lamb, A.F.A. 1973. Fast growing timber trees of the tropics. No. 6. *Pinus caribaea*. Vol. 1. Commonwealth Forestry Institute, Department of Forestry, University of Oxford. 254 p.

Nikles, D.G. 1966. Comparative variability and relationship of Caribbean pine (*Pinus caribaea* Mor.) and slash pine (*Pinus elliottii* Engelm.). Ph.D. Thesis, Department of Forest Management, North Carolina State University, 201p.SAS Institute Inc. 1989. SAS/STAT® User's Guide, Fourth Ed., Volumes 1 and 2, Cary, NC.

Schmidtling, R.C. and Hipkins, V. 2000. Evolutionary relationships of slash pine (*Pinus elliottii*) with its temperate and tropical relatives. *In* Forest Genetics for the Next Millennium. Proc. IUFRO Conf., Durban, South Africa, 8-13 October, pp. 53-57.

Zheng, Y., Ennos, R. and Wang H. 1994. Provenance variation and genetic parameters in a trial of *Pinus caribaea* Morelet var. *bahamensis* Barr. and Golf. Forest Genetics 1 (3): 165-174.

Zheng, Y., and Ennos, R. 1999. Genetic variability and structure of natural and domesticated populations of Caribbean pine (*Pinus caribaea* Morelet). Theoretical and Applied Genetics 98: 765 -771.

Zheng, Y., Wang, H., Qi, W. 2000. Conserving and breeding of *Pinus caribaea* for China. *In* Forest Genetics for the Next Millennium. Proc. IUFRO Conf., Durban, South Africa, 8-13 October, pp. 244-248.