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GENETIC CONTROL OF CONE AND SEED YIELD IN *PINUS TECUNUMANII* EGUILUZ & J. P. PERRY

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ABSTRACT

Genetic control of cone and seed yield was investigated in seven- and eight-year-old combined provenance-progeny tests containing 160 families from 16 wild populations of *Pinus tecunumanii* at four sites in Zimbabwe. Half of the *P. tecunumanii* populations originated from altitudes above 1500 m a.s.l. (High elevation populations) while the other half were from below this altitude (low elevation populations).

Significant differences were detected between the high and low elevation population groups, for cone and seed yield at several of the sites. In the combined analysis, site effect was not significant for both cone and seed yield but its interactions with population and family were significant. Individual site family mean heritabilities for cone yield ranged from 0.20 to 0.75 for high elevation populations and from 0.00 to 0.63 for the low elevation population. The family mean heritabilities for seed yield ranged from 0.03 to 0.78 and 0.00 to 0.62 for the high and low elevation populations, respectively. For the composite population, the individual site population heritabilities for cone and seed yield ranged from 0.16 to 0.82 and 0.18 to 0.90 respectively. The across site unbiased family mean heritability for cone and seed yield ranged from 0.22 to 0.46 in the low and high elevation population groups. The population and family-within-population variance components, and the family heritabilities of the high elevation population sources were consistently larger than those of the low elevation population group. The response to family selection for cone yield ranged from 0.0% to 120.4% in the low elevation group and from 23.1 to 88.2% in the high elevation group. For seed yield, the response to family selection varied from 0.0 to 215.5% and from 2.2 to 111.4% for the low and high elevation populations respectively. The percentage gain in either cone or seed yields was highest at altitudes above 1500 m a.s.l. in the low elevation population group and at altitudes below 1500 m a.s.l. in the high elevation population group. However, the actual gain in cone and seed yield was highest above 1500 m a.s.l. for high elevation population and below 1500 m a.s.l. for low elevation population group. This reversal was due to the low cone and seed yield potential of the low elevation group. The study demonstrated that cone and seed yields are under moderate to strong genetic control and that family selection can substantially improve these two traits.

Key words: *P. tecunumanii*, low and high elevation populations, cone and seed yield, heritability, genetic gain

INTRODUCTION

The study of tropical and subtropical pines has largely been devoted to genetic variation in timber yields and quality, with little attention paid to genetic variation in cone and seed yield. This is so because the major product of the plantation forest is timber and in addition, seed production in many of the planted pines has not been a serious limiting factor to afforestation projects. When it has, foresters have turned to alternative species or seed sources. Some timber companies have resorted to importing seed from those countries or areas with a suitable climate for seed production of their species.

The potential of *P. tecunumanii* as a plantation species in several tropical and subtropical countries has already been demonstrated (HODGE & DVORAK 1999, MOURA & DVORAK 1998, NYOKA & BARNES 1995, CROCKFORD *et al.* 1990, DVORAK *et al.* 1989). The species is however widely known as a shy flowerer and seeder in many countries (DVORAK & LAMBETH 1992). Cone and seed production can have a major impact in the choice of seed sources or parental trees for breeding programmes (GIBSON *et al.* 1983). Whole populations, families or individual trees may be rejected in a breeding programme if they fail to flower, fruit and seed. In the selection of plus trees of the three varieties of *Pinus caribaea* (*hondurensis*, *caribaea* and *bahamensis*) in Zimbabwe, consideration was given to both silvicultural attributes as well as ability to flower and produce seed. In a survey covering 57 sites, DVORAK & LAMBETH (1992) found that seed production potential of *P. tecunumanii* was influenced by latitude of the sites.

There is some limited information on genetic

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variation in flowering, cone and seed production in other related tropical and subtropical pines. In *P. caribaea* var. *hondurensis* for example, SIRIKUL *et al.* (1991) found heritability of provenance means for cone count ranging from 0.69 to 0.91. The heritability for conelet production which was also equally high ranged from 0.68 to 0.95. CROCKFORD *et al.* (1990) found family heritabilities of cone count ranging from 0.11 to 0.42 for *P. oocarpa* and 0.20 to 0.58 for *P. tecunumanii*. Recently, NYOKA & TONGOONA (*in press*) found significant differences among populations and families of *P. tecunumanii* for cone and seed production on a range of sites in Zimbabwe. They suggested a strategy of either selecting provenances and families for their seed production potential, or selecting sites where seed production potential was reasonably high or a combination of both since genotype-environment interaction was evident.

This study was undertaken as a follow up to the recent work by NYOKA & TONGOONA (*in press*), with the specific objectives of determining the magnitude of genetic parameters (variances and heritabilities) for cone and seed yield and to estimate the potential response to family selection for the two traits in *P. tecunumanii*.

MATERIALS AND METHODS

Open pollinated seed was collected from 160 mother trees in 16 geographic populations of *P. tecunumanii* in its natural range which extends from Chiapas in Mexico through Guatemala, Belize, Honduras into central Nicaragua. The seed was collected by the Oxford Forestry Institute, Oxford University, who then distributed it to a number of research organisations in the tropics and subtropics including the Zimbabwe Forestry Commission. Eight of the populations originated from an elevation below 1500 m a.s.l. (low elevation populations) while the other half was from above this altitude (high elevation populations). Each population was represented by 10 mother trees that were selected based on above average bole straightness, fine branching and stem volume. The selected trees were a minimum distance of 100 m apart to minimize relatedness among them. Table 1 shows the geographic details of the different populations used in the study.

The material gave a hierarchically nested structure of two elevation population groups, each with eight populations which in turn had 10 open pollinated families per population. The genetic material was such that it had three important genotypic levels namely elevation population group, population-within-elevation group and family-within-population-within-elevation group. Two other commercially planted species *Pinus patula* and *P. oocarpa*, each represented by 10 families were also included in the tests as controls.

The seed was sown in April 1987 and the field trials established at five sites (Table 2) in December of the same year in the plantation growing areas of the eastern highlands of Zimbabwe. The sites ranged in altitude

Table 1. Location and climatic data of sites from which the populations originated.

Provenance	Group Elevation	Country	Altitudinal range in m	Latitude N	Longitude W	Mean annual rainfall (mm)	Mean annual temperature°C
Yucul	LE	Nicaragua	850–1000	12°55'	85°48'	1394	22.4
Culmi	LE	Honduras	550– 650	15°06'	85°21'	1325	24.3
Villa Santa	LE	Honduras	850– 950	14°11'	86°20'	1348	22.4
Mt. Pine Ridge	LE	Belize	700– 720	17°00'	88°55'	1558	23.9
San Esteban	LE	Honduras	700– 800	15°22'	85°35'	1400	25.0
Jocon	LE	Honduras	850–1100	15°16'	86°55'	1400	21.7
San Francisco	LE	Honduras	870–1100	15°05'	86°20'	1600	20.0
Finca las Victorias	LE	Guatemala	1200–1300	15°12'	89°22'	1700	22.4
Cusuco	HE	Honduras	1500–1650	15°30'	88°10'	2500	17.0
La Paz	HE	Honduras	1750–2000	14°19'	87°45'	1619	20.0
Guajiquiro	HE	Honduras	1835–2250	14°11'	87°50'	2000	15.0
San Jeronimo	HE	Guatemala	1700–2000	15°03'	90°18'	1600	17.0
Montana Sumpul	HE	Honduras	1950–2050	14°24'	89°08'	2200	16.0
Juquila	HE	Mexico	2000–2250	16°15'	97°17'	1400	14.0
La Soledad	HE	Guatemala	2000–2300	14°35'	90°25'	1543	15.0
Las Piedrecitas	HE	Mexico	2300–2600	16°46'	92°35'	1228	14.8

HE – High Elevation population, LE – Low Elevation population

Table 2. Details of climatic and geographic factors of the five test sites in Zimbabwe.

Geographic factors	Site				
	Stapleford	Gungunyana	Cashel	Maswera	Nyangui
Altitude in m	1760	1050	1450	780	1845
Latitude °S	18°41'	20°24'	19°25'	18°41'	18°00'
Longitude °E	32°51'	32°43'	32°45'	32°55'	32°47'
Mean annual rainfall (mm)	2159	1097	891	1498	1572
Mean annual temperature °C	15.1	18.1	19.5	20.7	13.0
Mean max. temperature°C	19.2	24.0	24.4	28.4	17.7
Mean min. temperature °C	11.1	13.9	14.6	13.0	08.3

from about 780 to 1845 m above sea level.

Trial Design

The field design was a randomized complete block arranged as a split-plot, often called compact family design (WRIGHT 1978). The populations were randomized in the main plots and the families were in turn randomized into the subplots. Each trial had five replications with five family tree line plots (subplots). The population main plot had therefore 50 trees. The trees were spaced at the currently recommended spacing in commercial plantations of 3 x 3m.

The trials were assessed for cone and seed yield at seven and eight years by harvesting and weighing the two-year old cones by family subplots. Seed was also extracted and weighed by family subplots. No measurements were done at Cashel at seven years and only four instead of five replications were assessed at eight years.

Statistical Analysis

Although all five tests were completely balanced at establishment, subsequent differential mortality mainly due to drought at Maswera resulted in the loss of 2.1 percent of the family sub plots and deliberate vandalism by squatters at Nyangui resulted in the loss of 16.3 percent of the sub plots. Data from the latter site was therefore excluded in all the analyses. Since this paper looked at genetic parameters only, the two species controls were not included in all the analyses reported in this paper.

The first analysis was for all the 16 geographic populations combined, i.e. the low and high elevation populations which are referred throughout this paper as a composite population. For each of the individual site analyses a mixed model [1] was fitted to the data to test the significance of the elevation population group source. This hypothesis is based on DVORAK (1985, 1986) who suggested the creation of separate breeding populations from selections from the high and low elevation population groups. The analysis of variance was conducted using the GLM Procedure in SAS (SAS®/SAT 1988).

$$Y_{ijkl} = \mu + B_i + A_j + {}_{Baij} + P(A)_{k(j)} + BP(A)_{ik(j)} + F(PA)_{l(jk)} + \epsilon_{ijkl} \qquad [1]$$

where: Y_{ijk} =phenotypic observation of the $ijkl^{th}$ plot, μ = overall trial mean, B_i = random effect of the i^{th} block, A_j = fixed effect of the j^{th} elevation population group, BA_{ij} = interaction effect of the i^{th} block and the j^{th} elevation population group, $P(A)_{k(j)}$ = random effect of the k^{th} population of the j^{th} elevation population group, $BP(A)_{ik(j)}$ = interaction effect of the i^{th} block and the k^{th} population of the j^{th} elevation population group, $F(PA)_{l(jk)}$ = random effect of the l^{th} family of the k^{th} population from the j^{th} elevation population group, ϵ_{ijkl} = plot error.

In view of the suggestion of creating separate breeding populations from the high and low elevation sources (DVORAK 1985, 1986) and also the presence of significant differences between the two elevation population sources after fitting model [1], the second analyses to estimate variance components were done for the low and high elevation population groups separately as well as for the composite population. The appropriate model for analysing data from the low and high elevation population groups was that similar to [1] without the elevation population group effect and its interactions. For the composite population the elevation population group effect and its interactions were deliberately ignored although it had been shown to be significant. The variance components were estimated using the restricted maximum likelihood (REML) method of Varcomp Procedure in SAS rather than equating the mean squares from the traditional analysis of variance to their expectations (SAS®/STAT 1988). The expectation of mean squares for the reduced model [1] are shown in Table 3.

Table 3. Form of analysis of variance and expectation of mean squares for individual sites for each elevation population group.

Source of Variation	DF	Expectation of Mean Square
Block (B)	$b-1$	$\sigma^2_\epsilon + f\sigma^2_{bp} + fp\sigma^2_b$
Population (P)	$p-1$	$\sigma^2_\epsilon + b\sigma^2_{f(p)} + f\sigma^2_{bp} + bf\sigma^2_p$
B × P	$(b-1)(p-1)$	$\sigma^2_\epsilon + f\sigma^2_{bp}$
Family (Population)	$p(f-1)$	$\sigma^2_\epsilon + b\sigma^2_{f(p)}$
Error	$p(f-1)(b-1)$	σ^2_ϵ

b, p, f are number of blocks, populations and families, respectively.

Table 4. Form of analysis of variance and expectation of mean squares for across site analysis.

Source of Variation	DF	Expectation of Mean Square
Sites S	$s-1$	$\sigma^2_\varepsilon + b\sigma^2_{i(p)} + f\sigma^2_{pb(s)} + bf\sigma^2_{sp} + fp\sigma^2_{b(s)} + bfp\sigma^2_s$
Block(Sites) B(S)	$s(b-1)$	$\sigma^2_\varepsilon + f\sigma^2_{pb(s)} + fp\sigma^2_{b(s)}$
Populations P	$p-1$	$\sigma^2_\varepsilon + b\sigma^2_{sf(p)} + bs\sigma^2_{f(p)} + f\sigma^2_{pb(s)} + bf\sigma^2_{sp} + bfs\sigma^2_p$
Site × Population SP	$(s-1)(p-1)$	$\sigma^2_\varepsilon + b\sigma^2_{sf(p)} + f\sigma^2_{pb(s)} + bf\sigma^2_{sp}$
P × B(S)	$s(b-1)(p-1)$	$\sigma^2_\varepsilon + f\sigma^2_{pb(s)}$
Family(Population) F(P)	$p(f-1)$	$\sigma^2_\varepsilon + b\sigma^2_{sf(p)} + bs\sigma^2_{f(p)}$
SF(P)	$sp(f-1)$	$\sigma^2_\varepsilon + b\sigma^2_{sf(p)}$
Error	$ps(f-1)(b-1)$	σ^2_ε

s, b, p are number of sites, blocks, and populations, respectively.

The procedure in the combined site analysis for each of the yearly cone and seed yields was also similar to that for individual sites in that, a full mixed model [2] was first fitted on all the data, i.e. the composite population to test the significance of elevation population group and its interaction with site.

$$Y_{ijklm} = \mu + S_i + B(S)_{j(i)} + A_k + SA_{ik} + BA(S)_{jk(i)} + P(A)_{l(k)} + SP(A)_{il(k)} + BP(SA)_{kl(ik)} + F(PA)_{m(kl)} + SF(PA)_{im(kl)} + \epsilon_{ijklm} \quad [2]$$

where: Y_{ijklm} = phenotypic observation in the *ijklm*th plot, μ = across site mean, S_i = random effect of the *i*th site, $B(S)_{k(i)}$ = random effect of the *j*th block of the *i*th site, A_k = fixed effect of the *k*th altitude or elevation population group, SA_{ik} = interaction effect of the *i*th site and the *k*th elevation population group, $BA(S)_{jk(i)}$ = interaction between the *j*th block of the *i*th site and the *k*th elevation population group, $P(A)_{l(k)}$ = random effect of the *l*th population of the *k*th elevation population group, $SP(A)_{il(k)}$ = interaction between the *i*th site and the *l*th population of the *k*th elevation population group, $BP(SA)_{kl(ik)}$ = interaction between the *j*th block of the *i*th site and the lth population of the *k*th elevation population group, $F(PA)_{m(kl)}$ = random effect of the mth family in the *l*th population of the *k*th elevation population group, $SF(PA)_{im(kl)}$ = interaction between the *i*th site and the *m*th family of the *l*th population of the *k*th elevation population group, ϵ_{ijklmn} = experimental error.

After fitting model [2] separate analyses were done for both the low and high elevation and for the composite populations to estimate the variance components for the combined site analysis. The model used was also a completely random model that was similar to [2] without the elevation population group effect and its interaction effects. Table 4 shows the expectation of mean squares for the reduced model [2] for each of the two elevation sources. Where direct F-tests were not possible, the method of approximation was used to synthesise appropriate mean squares for testing effects in the model (SATTERTHWAITE 1946).

The heritability of family means were estimated at both individual sites and combined sites for the low and high elevation populations as well as the composite population. At individual sites, the family heritabilities

$$h_f^2 = \frac{\sigma^2_{f(p)}}{\frac{\sigma^2_\varepsilon}{b} + \sigma^2_{f(p)}} \quad [3]$$

of cone and seed yield for the three populations, the low and high elevation and composite populations were estimated from [3] and for across sites the heritabilities were calculated from [4] (WRIGHT 1976, FALCONER

1989, NYQUIST 1991).

The parameters in [3] and [4] are defined in Tables 3 and 4 respectively. The denominators in [3] and [4] are the phenotypic variances of family means (σ^2_F) for single site and across sites respectively as in equation

$$h_f^2 = \frac{\sigma^2_{f(p)}}{\frac{\sigma^2_\varepsilon}{bs} + \frac{\sigma^2_{sf(p)}}{s} + \sigma^2_{f(p)}} \qquad [4]$$

26 of NYQUIST (1991). The standard errors of the family heritabilities were estimated as in (BECKER 1984). Because all the analyses were based on plot means, the individual heritabilities were not calculated but they can still be estimated (WRIGHT 1976).

For the composite population, a second heritability namely that for population means was estimated as a ratio of between population variance to the total phenotypic variance of population means (HARVEY & TOWNSEND 1985, LAND *et al.*, 1986). At individual site, this heritability was estimated from [5] and from the combined sites, this was estimated from [6]. The denominators in [5] and [6] are the phenotypic variances of population means (σ^2_P) for single site and across site respectively. The parameters in [5] and [6] are as defined in Table 3 and 4.

$$h_p^2 = \frac{\sigma^2_p}{\frac{\sigma^2_\varepsilon}{bf} + \frac{\sigma^2_{f(p)}}{f} + \frac{\sigma^2_{bp}}{b} + \sigma^2_p} \qquad [5]$$

Genetic gain from family selection was calculated for individual sites for both the high and low elevation populations. The genetic gain, Δ_G expressed as percentage of site cone and seed yield means following family selection were computed from [5] (FALCONER 1989).

$$h_p^2 = \frac{\sigma^2_p}{\frac{\sigma^2_\varepsilon}{bfs} + \frac{\sigma^2_{sf(p)}}{fs} + \frac{\sigma^2_{f(p)}}{f} + \frac{\sigma^2_{pb(s)}}{bs} + \frac{\sigma^2_{sp}}{s} + \sigma^2_p} \qquad [6]$$

$$\Delta_G = \frac{(i h_f^2 \sigma_F)100}{\bar{x}} \qquad [7]$$

where: i is selection intensity (0.790); h^2_f is the family heritability; σ_F is the phenotypic standard deviation of family means, $\bar{x}$ is the mean of the trait (cone or seed) at each site.

RESULTS

Table 5 shows the cone and seed yield means of the two population groups namely the low and high elevation at individual sites. There were significant differences at different probability levels between the two elevation population groups for both cone and seed yield in both years at the other three sites except at Gungunyana. The high elevation population had consistently larger cone and seed yields than the low elevation population at Stapleford and Cashel but was the opposite at Gungunyana and Maswera.

Table 6 shows the variance components of the two genotypic levels, population and family-within-population as percentages of total variance and the family phenotypic variance for cone and seed yield at individual sites. The population variance for cone yield ranged from 0.0 to 8.4 % in the low elevation group while that of the high elevation group ranged from 0.0 to 9.9 %. This population variance was only significant for eight-year cone yield at Stapleford in the low elevation population and at all the other three sites except Gungunyana at eight years in the high elevation population (Table 6). The family-within-population variance which was mostly significant ranged from 0.0 to 22.5 % in the low elevation population and from 5.0 to 36.2 % in the high elevation group.

The population variance for seven-year seed yield was nonsignificant at all the sites in both population groups but that for eight-year seed yield was significant at different probability levels at Stapleford and Cashel in both population groups (Table 6). The significant population variance for seed yield ranged from 9.0 to 10.6 % in the low elevation population and from 4.3 to 12.8 % in the high elevation population. The family-within-population variance for seven-year seed yield was significant at Stapleford and Gungunyana in both the low and high elevation population groups (Table 6). At age eight years, the family variance was only significant ($P < 0.001$) at Stapleford in the low elevation population and at all the other sites except Maswera in the high elevation population. In magnitude, the significant family-within-population variances for seed yield ranged from 8.9 % to 23.6 % in the low elevation population and from 10.6 to 39.8% in the high elevation population. In general the variance components of seed yield followed a similar trend to that of cone yield. The highest percentages of variances were again in the high elevation population group in which the family and population variances respectively accounted for 39.8 % (Maswera) and 12.8 % (Stapleford) of the total variation at eight years.

Table 5. Means for seven- and eight-year cone and seed yield (g/plot) of the low and high elevation populations at individual sites.

Site	Population	Trait			
		Cn7 (g)	Cn8 (g)	Sd7 (g)	Sd8 (g)
Stapleford	Low	79.5	69.2	0.5	1.3
	High	558.2	589.9	8.8	13.0
Gungunyana	Low	49.0a	23.0a	1.8a	3.6a
	High	42.0a	18.9a	1.5a	3.6a
Cashel	Low	–	13.7	–	1.8
	High	–	49.0	–	6.4
Maswera	Low	23.0	309.0	0.0	3.3
	High	11.6	170.3	0.0	1.7

means followed by a common letter for each trait at each site do not differ significantly at 5%
– = not assessed; Cn7, Cn8 cone yield at 7 and 8 years; Sd7 and Sd8 seed yield at 7 and 8 years

Table 6. Population (σ^2_p) and family ($\sigma^2_{f(p)}$) variance components and (percent) of total variance (σ^2_T), family phenotypic variance (σ^2_F) for cone and seed yield in the low and high elevation populations.

Site	Trait	Low Elevation population				High Elevation population			
		σ^2_p	$\sigma^2_{f(p)}$	σ^2_T	σ^2_F	σ^2_p	$\sigma^2_{f(p)}$	σ^2_T	σ^2_F
St	Cn7*	1.16 (1.4)^{ns}	0.0 (0.0)^{ns}	82.9	16.12	12.17 (1.3)^{ns}	108.9 (11.6)^{c}	938.6	259.5
Gu		0.27 (1.1)^{ns}	1.46 (6.0)^{a}	24.2	5.55	0.47 (1.7)^{ns}	3.67 (13.2)^{c}	27.81	8.24
Ma		0.22 (0.9)^{ns}	0.0 (0.0)^{ns}	17.1	3.37	0.0 (0.0)^{ns}	0.46 (5.0)^{ns}	9.31	2.28
St	Cn8*	11.12 (8.4)^{b}	29.93 (22.5)^{c}	132.9	47.52	111.18 (8.5)^{b}	179.4 (13.6)^{c}	1314	366.1
Gu		0.0 (0.0)^{ns}	0.55 (9.7)^{c}	5.60	1.49	0.085 (1.9)^{ns}	0.33 (7.2)^{a}	4.58	1.09
Ca		0.023 (3.1)^{ns}	0.0 (0.0)^{ns}	0.75	0.18	0.55 (9.9)^{a}	1.87 (33.5)^{c}	5.60	2.64
Ma		1.82 (0.7)^{ns}	26.76 (9.8)^{b}	273.0	68.68	12.0 (5.3)^{a}	81.6 (36.2)^{c}	225.3	108.6
St	Sd7	0.61 (2.8)^{ns}	5.15 (23.6)^{c}	21.81	8.23	13.52 (2.0)^{ns}	75.73 (11.3)^{b}	667.1	184.6
Gu		1.07 (3.3)^{ns}	2.78 (8.9)^{b}	32.47	7.92	0.40 (1.0)^{ns}	4.22 (10.6)^{b}	39.89	10.94
Ma		0.0 (0.0)^{ns}	0.0 (0.0)^{ns}	0.49	0.01	0.001 (1.0)^{ns}	0.001 (1.0)^{ns}	0.07	0.02
St	Sd8	2.67 (10.6)^{c}	3.43 (13.7)^{c}	25.11	7.10	78.91 (12.8)^{c}	75.69 (12.3)^{c}	615.0	168.2
Gu		0.68 (0.4)^{ns}	0.0 (0.0)^{ns}	153.8	29.36	8.81 (4.3)^{a}	0.88 (0.4)^{ns}	205.4	44.1
Ca		0.66 (9.0)^{a}	0.07 (0.6)^{ns}	11.11	2.33	10.03 (10.0)^{b}	21.54 (21.5)^{c}	100.2	37.7
Ma		1.16 (1.8)^{ns}	0.17 (0.3)^{ns}	66.18	17.1	1.03 (3.3)^{ns}	12.49 (39.8)^{c}	31.38	16.0

St, Gu, Ca and Ma are sites Stapleford, Gungunyana, Cashel and Maswera.
Cn7, Cn8 cone yield at 7 and 8 years; Sd7 and Sd8 seed yield at 7 and 8 years.
Variances for cone yield are = × 10^3. ns, a, b, c for not significant, significant at 5 %, 1 % and 0.1 % respectively.

Family heritability for cone yield ranged from 0.20 to 0.75 in high elevation population group and from 0.0 to 0.63 in the low elevation population group (Table 7). Family heritabilities of seed yield ranged from 0.0 to 0.62 in the low elevation population group and from 0.02 to 0.78 in the high elevation group (Table 7). Overall, family heritabilities of seed were generally comparable to those of cone yield. The family heritabilities of cone and seed yield of the high elevation population group were generally higher than those of the low elevation group. Excluding the zero estimates, all the family heritabilities of cone were larger than their standard errors.

Table 8 depicts the population and family-within-population variance components for cone and seed

Table 7. Family heritability estimates (±se) for seven- and eight-year cone and seed yield in the low and high elevation populations at individual sites.

Site	Population	Cn7	Cn8	Sd7	Sd8
Stapleford	Low	0.00±0.19	0.63±0.17	0.62±0.17	0.48±0.17
	High	0.42±0.17	0.49±.17	0.41±0.17	0.45±0.17
Gungunyana	Low	0.26±0.17	0.37±0.17	0.35±0.17	0.00±0.16
	High	0.45±0.17	0.30±0.17	0.38±0.17	0.02±0.18
Cashel	Low	–	0.00±0.18	–	0.03±0.21
	High	–	0.71±0.17	–	0.57±0.17
Maswera	Low	0.00±0.16	0.39±0.17	0.00±0.16	0.01±0.14
	High	0.20±0.18	0.75±0.16	0.03±0.13	0.78±0.17

Cn7, Cn8 cone yield at 7 and 8 years; Sd7 and Sd8 seed yield at 7 and 8 years

Table 8. Population, σ^2_p and family, $\sigma^2_{f(p)}$ variance components, their (%) of the total variance, σ^2_T, phenotypic variances of family, σ^2_F and population, σ^2_P for seven and eight-year cone and seed yield of the composite population

Trait	Site	σ^2_p (%)	$\sigma^2_{f(p)}$ (%)	σ^2_T	σ^2_F	σ^2_P	h^2_f±se	h^2_p±se
Cn7*	St	32.46 (6.0)^{b}	54.04 (10.1)^{c})^{a}	536.5	137.5	50.1	0.39±0.12	0.65±0.35
	Gu	312.04 (1.2)^{a}	2566.65 (9.9)^{c}	25.9	6.8	1.2	0.37±0.12	0.26±0.33
	M	121.20 (0.9)^{ns}	67.29 (0.5)^{ns}	13.3	2.7	0.4	0.03±0.12	0.31±0.35
Cn8*	St	126.99 (16.1)^{c}	104.66 (13.3)^{c}	789.7	208.8	154.2	0.50±0.11	0.82±0.33
	Gu	32.2 (0.6)^{ns}	441.67 (8.7)^{c}	5.1	1.3	0.2	0.34±0.12	0.16±0.34
	Ca	589.96 (17.0)^{c}	926.36 (26.6)^{c}	3.5	1.3	0.7	0.71±0.11	0.80±0.34
	Ma	11.22 (4.4)^{a}	53.20 (21.0)^{c}	253.0	87.4	22.3	0.61±0.12	0.50±0.35
Sd7	St	24.01 (6.6)^{b}	40.43 (11.2)^{b}	361.3	95.5	37.2	0.42±0.12	0.65±0.35
	Gu	0.68 (1.9)^{a}	3.50 (9.7)^{c}	36.1	9.4	1.9	0.37±0.13	0.36±0.34
	Ma	0.0 (0.5)^{ns}	0.0 (0.0)^{ns}	0.06	0.01	0.002	0.00±0.13	0.18±0.34
Sd8	St	73.03 (21.2)^{c}	39.31 (11.1)^{c}	354.0	87.0	83.7	0.45±0.12	0.90±0.33
	Gu	4.45 (2.5)^{a}	0.0 (0.0)^{ns}	178.8	34.1	8.0	0.00±0.13	0.56±0.35
	Ca	10.28 (17.0)^{c}	10.81 (17.8)^{c}	61.3	60.6	18.2	0.59±0.12	0.83±0.33
	Ma	1.55 (3.1)^{a}	6.13 (12.4)^{c}	49.3	14.3	3.1	0.43±0.13	0.50±0.34

St, Gu, Ca, and Ma are sites Stapleford, Gungunyana, Cashel, Maswera. Cn7, Cn8 cone yield at 7 and 8 years; Sd7 and Sd8 seed yield at 7 and 8 years. * Variances for cone yield = × 10^3
ns, a, b, c refer to not significant at 5 %, significant at 5 %, 1 % and 0.1 %, respectively.

yield of the composite population i.e. the combined low and high elevation populations. The population variance component which ranged from 1.2 to 17.0 % was significant at all the sites except Maswera and Gungunyana for seven- and eight-year cone yield respectively. The family-within population variance was also significant at most of the sites and ranged from 8.7 to 26.6 %. For seed yield, both the population and family-within population variances were significant in both years at all the sites except Maswera at seven years. The variances ranged from 1.9 to 17.0% and from 9.7 to 17.8 % respectively.

Table 8 also shows heritability estimates of family and population means for cone and seed yield in the composite population. The family heritabilities for cone yield ranged from 0.03 to 0.71 with moderate standard errors while the population heritability ranged from 0.16 to 0.90. The family and population heritabilities for seed yield ranged from 0.00 to 0.59 and from 0.18 to 0.90 respectively.

Table 9. Variance components as percentages of the total variance (σ^2_T), and family and population heritabilities for seven- and eight-year cone and seed yield across sites four for three kinds of populations.

Trait	σ^2_S	$\sigma^2_{B(S)}$	σ^2_P	σ^2_{SP}	$\sigma^2_{PB(S)}$	$\sigma^2_{F(P)}$	$\sigma^2_{SF(P)}$	σ^2_E	σ^2_T	h^2_f ±se	h^2_p ±se
Low elevation											
Cn7	0.0^{ns}	1.6^{a}	0.0^{ns}	1.3^{a}	1.3^{ns}	1.6^{a}	0.0^{ns}	94.2	41.4*	0.31±.18	–
Cn8	14.3^{c}	2.2^{b}	0.3^{ns}	2.2^{a}	6.2^{c}	3.2^{a}	8.2^{c}	63.2	125.7*	0.46±.16	–
Sd7	3.4^{a}	2.3^{b}	0.0^{ns}	3.1^{a}	2.7^{a}	3.1^{ns}	10.9^{c}	74.5	18.8	0.22±.17	–
Sd8	0.9^{ns}	2.6^{c}	0.0^{ns}	2.1^{b}	0.0^{ns}	1.4^{ns}	0.0^{ns}	92.9	67.5	0.26±.16	–
High elevation											
Cn7	8.9^{b}	3.8^{c}	0.2^{ns}	1.0^{ns}	2.3^{ns}	1.0^{ns}	9.4^{c}	73.5	361.7*	0.43±.18	–
Cn8	13.5^{c}	1.1^{a}	1.2^{ns}	5.4^{c}	3.0^{b}	2.2^{ns}	11.6^{c}	62.0	470.2*	0.34±.17	–
Sd7	7.7^{c}	1.1^{ns}	0.1^{ns}	1.7^{ns}	4.6^{c}	1.4^{ns}	8.9^{c}	74.5	258.9	0.35±.18	–
Sd8	7.9^{b}	0.9^{a}	2.5^{ns}	6.9^{c}	0.0^{ns}	4.0^{b}	6.0^{b}	71.8	266.8	0.40±.18	–
Composite											
Cn7	3.4^{a}	2.4^{c}	0.0^{ns}	5.5^{c}	3.4^{c}	1.2^{ns}	8.3^{c}	75.9	200.2*	0.20±.18	0.11±.18
Cn8	6.9^{c}	1.0^{b}	0.0^{ns}	11.8^{c}	4.0^{c}	2.5^{a}	11.0^{c}	62.8	294.6*	0.38±.16	0.27±.17
Sd7	3.2^{a}	0.9^{a}	0.0^{ns}	6.0^{c}	4.7^{c}	1.5^{ns}	9.1^{c}	74.5	191.4	0.27±.17	0.15±.18
Sd8	1.3^{ns}	0.8^{c}	2.6^{ns}	11.2^{c}	0.0^{ns}	3.5^{c}	4.5^{b}	76.1	209.8	0.24±.16	0.44±.18

σ^2_S, $\sigma^2_{B(S)}$, σ^2_P, σ^2_{SP}, $\sigma^2_{PB(S)}$, $\sigma^2_{F(P)}$, $\sigma^2_{SF(P)}$ and σ^2_E are variances of site , block within-site, population, site × population interaction, main plot error, family within-population, site × family interaction and sub plot error, respectively. Cn7, Cn8 cone yield at 7 and 8 years; Sd7 and Sd8 seed yield at 7 and 8 years. ns, a, b and c for not significant, significant at 5, 1 and 0.1%, respectively. * = × 10^3

Table 10. Genetic gain expressed as percentage of site mean yield following family selection.

Site	Population	Trait			
		Cn7	Cn8	Sd7	Sd8
Stapleford	Low	0.0	120.4	215.5	59.7
	High	23.1	30.5	38.5	27.2
Gungunyana	Low	23.9	37.8	33.2	0.0
	High	58.9	32.0	50.8	2.2
Cashel	Low	–	0.0	–	1.5
	High	–	50.2	–	33.2
Maswera	Low	0.0	20.1	0.0	0.8
	High	50.2	88.2	ne	111.4

– = not assessed, ne = not estimable due to a site mean of zero.
Cn7, Cn8 cone yield at 7 and 8 years; Sd7 and Sd8 seed yield at 7 and 8 years

Table 9 shows the variance components as percentage of the total variance and heritabilities of cone and seed yield for the low and high elevation and the composite populations across sites. The site variance component was significant for both seven- and eight-year cone and seed yield in the high elevation population but was only significant for seven-year seed yield and eight-year cone yield in the low elevation population. In the composite population, the site variance was significant for both seven- and eight-year cone yield and only for seven-year seed yield. Although the population variance component for cone and seed yield was non-significant in the three populations, the site*population interaction variance component was significant in the low elevation and composite populations for all the traits and only for eight-year cone and seed yield in the high elevation population. The site*population interaction variance component was consistently larger than both the site and the population variances.

The family-within-population variance component was only significant for cone yield in the low elevation population and for eight-year seed yield in the high elevation population. In the composite population, the family-within-population variance component was only significant for eight-year cone and seed yield. The site*family interaction variance was significant at different probability for both cone and seed yield in the high elevation and composite populations and only for eight-year cone and seven-year seed yield in the low elevation population. In general, the family variance was always larger than the population variance for both traits in the three populations. The site*family interaction variance was also consistently larger than both the family and site variances in the high elevation and composite populations.

The heritability of family means for across site for cone yield ranged from 0.31 to 0.46 while that for seed yield were also moderate and ranged from 0.22 to 0.40 (Table 9). The heritability of population means was up to 0.27 for cone yield and 0.44 for seed yield. The standard errors were in general lower than their estimates. The family heritability estimates of the low elevation population were lower than those of high elevation population while those of the composite population were always intermediate.

Table 10 shows the percentage gain in cone and seed yield following family selection to retain a breeding population of 62.5 % of the families at each of the four sites. Family selection gave gains in cone yield ranging from 0.0 to 120 % and from 0.6 to 88.2 % in the low and high elevation population groups respectively. The response to selection following family selection for seed yield was up to 215.5 % in the low elevation group and up to 111.4 % in the high elevation group. The zero responses in yield were all due to a zero heritability which in turn was due to a zero family variance. The highest response to family selection in the low and high elevation groups for cone yield were at Stapleford and Maswera respectively. Both responses were for eight-year cone yield. This was also the case for seed yield. The low elevation population tended to have higher responses to family selection compared to the high elevation population at Stapleford but the latter had higher responses to selection at the other three sites.

A simple arithmetic average of the gains between the two years indicated that the highest percentage gains from family selection for both cone and seed yield were at Stapleford, for the low elevation population group and at Maswera and Gungunyana for the high elevation population group.

DISCUSSION AND CONCLUSIONS

The results of this study indicated that there is substantial variation in cone and seed yield among and within populations of *P. tecunumanii*. The family heritability estimates of cone count for *P. tecunumanii* reported by CROCKFORD *et al.* (1990) were largely comparable with estimates from the present study which were based on actual cone yields. Also, in *P. oocarpa*, CROCKFORD *et al.* (1990) found family heritability for cone count that ranged from 0.11 to 0.42 which again were comparable to those reported in this study. The population heritabilities for cone yield of the composite population i.e. the combined low and high elevation populations were very large and ranged from 0.18 to 0.82. These estimates are consistent with those reported for *P. caribaea* which ranged between 0.69 and 0.91 (SIRIKUL *et al.* 1991). The family heritabilities at individual sites were variable and often very high mainly due to inflation by the evidently significant genotype-environment interaction which was present at both population and family level. The across site or unbiased family heritabilities were moderate to high but still usable.

The family heritabilities of the high elevation population group were in most cases larger than those of low elevation population group while those of the composite population were always moderate and between the two elevation population groups. The magnitudes of these heritabilities varied from site to site and year to year. The heritabilities were often very low due to low family variances as a result of low cone and seed yields.

Although the site effect was often significant, the site x population and site x family interaction variances were invariably significant and always larger than the population and family variances respectively. Using the rule of thump proposed by SHELBOURNE (1972), the interactions would be described as being of practical importance as they were in most cases more than twice the magnitude of the genotypic variances. The implication of these results is that, if cone and seed yields are included in the selection programme, consideration would need to be given to how best to use these significant interactions which if ignored could impede selection and genetic progress for these traits.

Cone and seed yield can be improved substantially through selection of superior families. From this study, family selection to retain 62.5 % of the families in each elevation population group resulted in percentage gain in seed yield of up to 215 % at individual sites. Although the magnitude was large the actual increase in yield was very low. Such an increase was based on the current site mean seed yield estimate of only 0.5g which would result in just over a gramme of seed yield after selection. Such a response therefore has to be treated with caution as it can easily lead to wrong conclusions. The highest seed yield in the low and high elevation population groups were at Gungunyana and Stapleford at age eight years but had responses to selection of only 0.0 % and 27.2 % respectively. It was also noted that most of the sites with the highest seed yields did not necessarily have the highest responses while some of the highest responses to selection were on sites that had average to very low yields implying that the high responses will not offset the already low yields in such sites. Of the tested sites the ideal site for family selection for seed yield in the high elevation population was Stapleford where yields were already highest coupled with modest responses. An appropriate site for family selection for seed yield in the low elevation population was not obvious as Gungunyana, which had the highest seed yield potential had very low responses to selection.

The magnitude of response to selection estimated in the present study if imposed on the breeding populations of *P. tecunumanii* may result in seed yields of this species being improved significantly particularly in the high elevation population. The high elevation population group appeared to be more variable and had higher family heritabilities together with higher responses to family selection for both cone and seed yields. It was therefore concluded that the low elevation population has inherently lower cone and seed yields compared to the high elevation population group and that the latter has higher genetic parameters compared to the former. Although the low elevation population group had higher percentage response to selection, the actual gain was smaller than that from the high elevation population mainly due to the inherent low seed production potential of the low elevation population.

This study therefore demonstrated that cone and seed yield are under moderate to strong genetic control and that family selection could significantly improve these two traits. The fear of having to abandon this species for timber production because of paucity of seed production may be circumvented by deliberating breeding and selecting for seed yield in this species as well. Although only family selection was investigated in this study, more gains could still be realized through population, individual as well as combination selection. Effect of seasons could be efficiently evaluated in mature stands where yields have stabilized and thus removing age effects. This present study could not evaluate this source of variation as this was likely to be confounded by age as the stands were still young and their yields may not have peaked and stabilized. There is need also to investigate the genetic relationship i.e. correlation between conventionally selected silvicultural traits such as growth rate and seed yield to efficiently design breeding programmes for the simultaneous improvement of both silvicultural and reproductive traits.

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