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Performance of Pinus patula Genotypes Selected in South Africa and Growing in Their Native Mexican Environment

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Abstract

Two tests of *Pinus patula* SCHIEDE and DEPPE half-sib progenies from South African seed orchards and superior tree selections were planted in Veracruz, Mexico. Measurements made during the first 3 years after planting included height, diameter, crown with, total number of whorls, branch angle, stem straightness, phenology of leader growth and frost damage.

South African families differed in all traits from the unimproved local controls except branch angle. They were taller, had larger diameters and initiated growth earlier. The precocious growth, however, made them more susceptible to frost damage.

Development differed greatly at the two test sites. At one site family variances were nonsignificant, thus improvement was possible only through selection of the South African population over the control. In contrast, selection of the best individuals of the best South African families would result in substantial gains at the other site.

Phenotypic correlations at the two sites were similar and followed a regular pattern. Age-age genetic correlations (determined only at one site), however, were erratic. With non significant family variances and erratic genetic correlations, the results of early selection are unpredictable.

Key words: Pinus patula, progeny test, heritability, selection response, genetic and phenotypic correlations.

FDC: 232.11; 165.3; 165.4; 174.7 *Pinus patula;* (68); (72).

Introduction

Pinus patula SCHIEDE and DEPPE, is one of the most promising plantation species in Mexico, with a natural range from 18⁰ latitude N in the state of Oaxaca to 24⁰ N in Tamaulipas. It grows in dense, pure stands or in mixtures with *Pinus pseudostrobus* LINDL., *Pinus teocote* SCHIEDE and DEPPE, *Pinus ayacahuite* EHRENB. and *Abies religiosa* (H.B.K), CHAM. and SCHL. at altitudes from 2000 m to 3000 m. The discontinous distribution forms a narrow belt on the eastern slope of Sierra Madre Oriental, in the mountains in central Mexico (Eje Neovolcanico) and in Oaxaca. In these regions climate is characterized by average annual temperatures from 10⁰ C to 16⁰ C with 1000 mm to 2000 mm y^{-1} precipitation (MADRIGAL, 1967; WORMALD, 1975; VELA, 1980). Light frost occurs at higher elevations.

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The species has been planted extensively in Africa particularly in South Africa, Zimbabwe and Malawi (Wormald, 1975; Barnes, 1977; Barnes and Schweppenhauser, 1978, 1979; Zobel et al., 1987). Per hectare yields are high (Vela, 1980); in natural stands near Tlaxco, Tlaxcala, growth of 14.7 m^3 Ha^{-1} y^{-1} has been reported (Flores, 1986) and a plantation from unimproved seed near Las Vigas, Veracruz, achieved an average annual yield of 21. 8 m^3 Ha^{-1} y^{-1} (Valenzuela, 1980). Comparable yields were reported in Malawi, but these were far exceeded on a good site in Tanzania with 40 m^3 Ha^{-1} y^{-1} (Wormald, 1975).

Breeding programs are in progress in Africa and results of progeny tests with *Pinus patula* have been reported by several authors (Vaclav, 1972; Kageyama et al., 1977; Barnes, 1977; Barnes and Schweppenhauser, 1978, 1979, Falkenhagen, 1979; Ladrach, 1987; Barnes et al., 1987; Birks and Barnes, 1991; Barnes et al., 1992a and b); these studies have demonstrated the feasibility of selection and breeding to improve growth rate and stem and crown characteristics.

In contrast, intensive tree improvement in Mexico has hardly begun; a few *Pinus patula* seed production areas have been established (Saenz and Nepamuceno, 1989). However, improved genotypes are urgently needed for a growing forest plantation program. In this paper we present results from the initial phases of a genetic improvement program i. e. the early field evaluation of two tests of half-sib progenies from South African seed orchards and superior tree selections planted in Veracruz, Mexico.

Assuming that genotypes selected in exotic environments may be reintroduced into native environments without loss of genetic improvement, we tested two hypotheses: (1) are populations of *P. patula* from South African sources detectably different in measured traits from local populations of the same species ?; and (2) do the South African populations of *P. patula,* as represented in the tests, contain sufficient genetic variation to justify additional selective breeding? In addition, age-age trends of genetic parameters were evaluated in one of the tests.

Materials and Methods

Twenty-two families from second generation selections from a Rietfontein (South Africa) seedling seed orchard are being tested at "Huayacocotla" in the Canalejas communal farm forest near Huayacocotla, Veracruz (20^0 25'N, 98^0 23'W) at an elevation of 2250 m, with an average precipitation of 2000 mm and an average annual temperature of 13 °C.

The test "Oxtlapa" is located on the Oxtlapa communal farm forest, Veracruz (19^0 25'N, 97^0 06'W) at 2360 m, and 2600 mm of precipitation. The test evaluates 47 families of first generation selections from South Africa. Six are from Spitzkop clonal seed orchard. The remaining families come from superior trees selected in plantations at the following locations (number of families in parenthesis): Olifantsgeraamte (1), Sabie (3), Hendriksdal (4), Elandsdrift (7), London (1), Doornhoek (7), Hebron (1), Peak Timbers (1) and Driekop (6). The original seed sources in Mexico are not known (personal communication Kietzka, 1991).

The Huayacocotla test was sown on January 28 to 31, 1986 in a forest soil in 6.5 cm x 22 cm black plastic containers in the experimental nursery of Centro de Genetica Forestal, A.C., Chapingo, located near Texcoco about 40 km east of Mexico City. Field planting was December 9 to 13, 1986 on a newly cleared site within a natural *Pinus patula* stand of good quality. The Oxtlapa test was similarly sown on May 5 to 13 and June 4 to 5 1986 and planted in the field during September 1987, on a site that had been clearcut 1985 and converted into pasture.

The control plots (2 per block in Huayacocotla and 1 in Oxtlapa) were seedlings taken at random from local nurseries. They came from unselected local provenances.

Plantations at Huayacocotla and Oxtlapa were established in a randomized complete blocks experimental design with 12 and 9 replications, respectively. Both plantings had 2 m x 2 m spacing and were surrounded by two exterior isolation rows. Families were planted in 4-tree linear plots.

At Huayacocotla height was measured at ages 3, 10, 17, and 23 months from planting. At age 26 months height, diameter, total number of whorls, crown width, stem straightness, branch angle, phenology of current leader growth (Jan. 21st) and frost damage (Feb. 21st) were also measured. At age 38 months height, diameter, number of whorls and phenology (Feb. 7th) were evaluated again. At Oxtlapa height, diameter, crown width, stem straightness, branch angle and phenology (Feb. 23rd 1990) were measured approximately 28 months after planting. Height, diameter and number of whorls were determined again at 38 months of age. Measurements units and scales of indices are given in *table 1.*

Crown widths were not measured at age 38 months because by then crowns were clearly competing in both tests. Branch angles were similarly dropped, because they had changed little in the intermeasuring period. Frost damage was present only in February, 1989, at Huayacocotla.

Table 1. — Variables measured at the Huayacocotla and Oxtlapa test.

VARIABLE	UNITS
HEIGHT total to the tip of the leader.	cm
DIAMETER at 8 cm above the soil.	mm
WHORLS total number of.	number
CROWN WIDTH at the widest point.	cm
STEM STRAIGHTNESS. Scale from 1 to 5. 1 = very much curved or forked with very open angle of forking. 5 = completely straight.	indices
BRANCH ANGLE. Largest branch angle in the 4 th whorl from above in 10 classes of 9 °.	degrees
PHENOLOGY of current leader growth. Scale from 1 to 5. 1 = no elongation; 5 = elongation with fascicles well developed and separated from the stem.	indices
FROST DAMAGE. Scale from 1 to 5. 1 = no damage; 5 = very severe damage.	indices

Table 2. — Expected mean squares from the ANOVA for the traits measured at both test plantations.

SOURCE OF VARIATION	DEGREES OF FREEDOM	a/	b/	ESPECTED MEAN SQUARES c/
BLOCKS (B)	b-1	7	5	$S^2_{W/k} + S^2_E + fS^2_B$
FAMILIES (F)	f-1	21	46	$S^2_{W/k} + S^2_E + bS^2_F$
PLOT ERROR (E)	(b-1) (f-1)	147	229d/	$S^2_{W/k} + S^2_E$
WITHIN PLOT (W)	$\sum_{i=1}^{t} (n_i-1)$	488	714	S^2_W

b = number of blocks; f = number of families; k = harmonic mean of trees per plot; n_i = number of trees in plot i, t = total number of plots in the test; S^2_W = within-plot variance; S^2_E = among-plot variance; S^2_B = variance among blocks; S^2_F = variance among families.

a/ = at Huayacocotla test.

b/ = at Oxtlapa test.

c/ = For covariance analyses, cross products are used instead of mean squares.

d/ Corrected by one plot estimated.

Mortality was low (9% at Huayacocotla and 14% at Oxtlapa) and concentrated in poorly drained blocks; therefore, the analyses were done on the 8 and 6 blocks with least mortality at Huayacocotla and Oxtlapa respectively.

Statistical analyses were done separately for each test and include the following steps: (a) An analysis of means, using the student "t" test (SAS, 1987) to evaluate differences between the South African progenies and the local controls; (b) variance analysis to estimate narrow-sense heritabilities and potential responses to selection for each trait; and (c) covariance analyses (SAS, 1987) to estimate phenotypic and genetic correlations among traits.

Variance and covariance analyses excluded the local controls and were performed in 2 stages. First, family and among-plot variances were estimated using plot-mean values. Second, within-plot variances and covariances, and the harmonic mean of trees per plot, were estimated separately by pooling individual plot values. Components of variance and covariance were estimated using the appropriate mean squares and cross products according to the random-effects model (*Table 2*). Only one missing plot was estimated and the bias of sum of squares corrected according to STEEL and TORRIE (1988) for the Oxtlapa test.

Narrow-sense heritabilities for each trait, assuming complete outcrossing, were estimated on the basis of individual trees (h^2_I), families (h^2_F) and individuals within family (h^2_{IF}), using the following equations (NAMKOONG et al., 1966; ZOBEL and TALBERT, 1984; KLEIN, 1989):

$$h^2_I = 4S^2_F \;/\; (S^2_W + S^2_E + S^2_F) \qquad (1)$$

$$h^2_F = S^2_F \;/\; (\,(S^2_W \;/\; kb) + (S^2_E \;/\; b) + S^2_F) \qquad (2)$$

$$h^2_{IF} = 3S^2_F \;/\; S^2_W \qquad (3)$$

Symbols are as defined in *table 2*.

Response to selection was estimated using 2 different selection levels (NAMKOONG, 1979; NAMKOONG et al., 1966, 1988): Level I: Selection of the South African "population" over the local control. Level II: Selecting the best individual in each plot of the 12.5 % best families of the South African population. The Level I was used when the variances among families were nonsignificant and the Level II when variances were significant.

The formulas for the selection differentials were:

$$s_1 = X_{SA} - X_C \qquad (4)$$

$$s_2 = X_F - X_{SA} \qquad (5)$$

$$s_3 = X_{I(F)} - X_F \qquad (6)$$

Where: s_1, s_2 and s_3 are the selection differentials. X_{SA} = the average of the South African families; X_C = the average of the controls; X_F = the average of the best families; $X_{I(F)}$ = the average of the best individuals within the best families, one per plot.

Formulas for the responses to selection were:

Level I:

$$G_1 = (s_1 \;/\; X_C) \times 100 \qquad (7)$$

Level II:

$$G_2 = (\,(\,s_1 + s_2\,h^2_F + s_3\,h^2_{IF}\,) \;/\; X_C\,) \times 100 \qquad (8)$$

Where: G_1 and G_2 are the expected response to selection as compared to the controls (expressed as percentage), of each level of selection. In formulas (4), (7) and (8), we assumed that we were comparing 2 "populations" and that X_{SA} and X_C represented the appropiate estimate for the means of these populations. In other words, that s_1 is equal to the realized gain.

Table 3. — Averages of: the control (X_C), the South African families (X_{SA}), the 12.5 % best families (X_F) and the best individuals within the best families, one per plot ($X_{I(F)}$).

	AGE$^{a/}$	X_C	X_{SA}	X_F	$X_{I(F)}$
HUAYACOCOTLA TEST					
HEIGHT (cm)	3	26*	22	25	30
	10	51	53	59	73
	17	85	97**	107	129
	23	134	150**	167	198
	26	151	177**	196	229
	38	278	301**	323	375
DIAMETER (mm)	26	33	39**	43	52
	38	62	69**	76	86
WHORLS (number)	26	7.1	8.1**	8.9	10.3
	38	9.7	11.0**	12.1	13.8
CROWN WIDTH (cm)	26	105	115*	129	152
STEM STRAIGHTNESS (indices)	26	3.9	3.8	4.0	4.7
BRANCH ANGLE (degrees)	26	60.3	60.3	65.2	71.3
PHENOLOGY (indices)	26	2.1	3.4**	3.7	4.6
	38	2.6	3.0**	3.5	4.2
FROST DAMAGE (indices)	26	1.4	1.8**	1.4	1.0
OXTLAPA TEST					
HEIGHT (cm)	28	178	209**	239	279
	38	302	345**	392	442
DIAMETER (mm)	28	31	40**	48	54
	38	62	78**	90	103
WHORLS (number)	28	6.2	7.5**	8.5	9.8
	38	9.4	11.3**	12.5	14.4
CROWN WIDTH (cm)	28	124	149**	173	196
STEM STRAIGHTNESS (indices)	28	3.2	3.8**	4.2	4.8
BRANCH ANGLE (degrees)	28	63.0	63.9	69.2	78.2
PHENOLOGY (indices)	28	1.9	2.4**	2.9	3.5

a/ In months after field planting. *, **, Student t-Test significance between X_C and X_{SA}, at the 0.05 and 0.01 level of significance, respectively. ns = not significant.

Genetic correlations between traits "x" and "y" (R_{gxy}) were estimated as:

$$R_{gxy} = COV_{Fxy} / SQRT(S^2_{Fx}S^2_{Fy}) \qquad (9)$$

Where: COV_{Fxy} = family covariance component between variables "x" and "y". SQRT = square root, S^2_{Fx} = family variance component of the variable "x"; S^2_{Fy} = family variance component of the variable "y".

Phenotypic correlations between traits were estimated in a similar way, but using phenotypic variances and covariance components instead. Standard errors of correlations were estimated using the methodology proposed by MODE and ROBINSON (1959).

The trend of the age-age correlations for height in the Huayacocotla test was evaluated using the regression analysis of the age-age phenotypic correlation coefficient (r) and the log of the ratio of the ages involved (LAR) developed by LAMBETH (1980):

$$r = B_0 + B_1 \ (LAR) \qquad (10)$$

Results and Discussion

Comparison of South African Families with the Controls

The South African families, treated as a single population or provenance, differed significantly from the local controls. Except for heights after 3 and 10 months at Huayacocotla the heights are superior at all ages in both tests (*Table 3*). At Huayacocotla, control seedlings were taller at the time of planting, perhaps as a results of an age difference, but subsequently they grew slower than the

South African progenies. With the exception of stem straightness and branch angle in both plantings all other traits showed significant differences between the two populations.

Phenology of the leader shoot at age 26 months showed the greatest difference between the 2 populations at Huayacocotla (an index of 2.1 versus 3.4, *Table 3*). South African families initiated growth earlier than the controls. This factor may partially explain the superior heights shown by these families, although superior growth rate may also have contributed.

Even though early shoot elongation may be a desirable trait, it might increase the risk of frost injury. Temperatures as low as —4 °C were reported at the nearby village of Huayacocotla and undoubtedly were lower at the test site. As a result, the South African families showed typical frost injury, while the controls with less developed shoots showed less damage (*Table 3*). A similar phenomenon has been observed in *Picea glauca* (MOENCH) VOSS; individuals with early flushing buds were more susceptible to frost injury and showed severe reduction of current growth (NIENSTAEDT, 1985). The effects of the damage, however, are not permanent, since examinations made later in the year and again in February 1990 showed that the South African families had recovered. In *Picea glauca* the effects were also insignificant 7 years after the damage took place (NIENSTAEDT, 1985).

Differences between the South African progenies and the controls may be explained either as a provenance effect or as a result of the selection pressure that the South African populations were exposed to before the reintroduction in Mexico. LADRACH (1987) reported similar results in a Columbian test comparing progeny of South African seed orchards with progeny of trees selected from Columbian plantations. He attributed the superiority of the South African progenies to the fact that in the orchard the pollen also came from superior trees. In our study the controls do not represent genetically improved genotypes. Therefore, it is not possible to know if the South African progenies would be superior to progenies from selected trees from native stands.

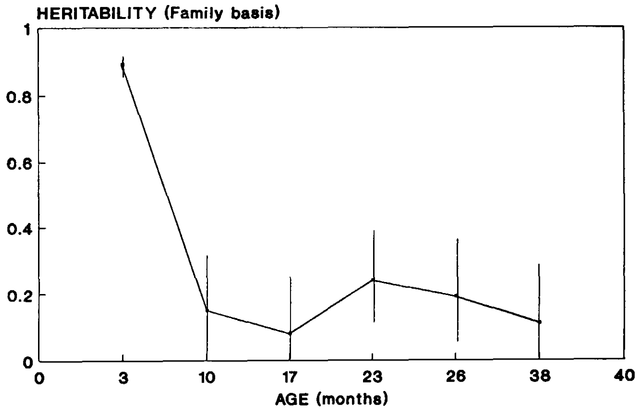

Figure 1. — Estimated heritabilities for height at different ages at the Huayacocotla test. Vertical lines represent Standard Errors.

Genetic Variances and Responses to Selection

The Huayacocotla Test

For heights the among family variance was very high at 3 months of age (*Table 4*), but not significant from 10 months to 38 months. The very high h² estimated at the first evaluation may reflect the uniform growing conditions in the nursery. The error variance would be reduced and the differences among families more readily distinguished. The values of h^2_I at 3 months >1 (which theoretically are impossible) may be due to an over-estimation

Table 4. — Variance components derived from ANOVA, heritabilities and responses to selection for all variables at different ages at the Huayacocotla test.

VARIABLE	AGE	S^2_F	S^2_E	S^2_W	h^2_f	$h^2_{i(f)}$	I	II
HEIGHT	3	6.59**	2.10	16.12	0.89	1.23		18.5
	10	2.06ns	16.64	222.34	0.18	0.03	3.9	
	17	1.96ns	94.36	552.42	0.06	0.01	14.1	
	23	19.78ns	253.23	1088.59	0.22	0.05	11.9	
	26	16.55ns	310.98	1463.28	0.16	0.03	17.2	
	38	15.94ns	606.84	3367.51	0.08	0.01	8.3	
DIAMETER	26	3.18ns	23.67	85.28	0.35	0.11	18.2	
	38	4.88ns	62.74	229.40	0.24	0.06	11.3	
WHORLS	26	0.18**	0.30	2.41	0.60	0.22		25.0
	38	0.21**	0.43	3.79	0.54	0.17		22.4
CROWN WIDTH	26	38.13**	29.98	565.80	0.52	0.20		20.9
STEM STRAIGHTNESS	26	0.01ns	-0.01	0.70	0.31	0.04	-2.6	
BRANCH ANGLE	26	0.07**	0.03	0.79	0.70	0.27		8.4
PHENOLOGY	26	0.02*	0.07	0.46	0.39	0.10		71.9
	38	0.02ns	0.16	0.72	0.34	0.10	15.4	
FROST DAMAGE	26	0.04*	0.15	0.58	0.52	0.21		7.7

Age in months after field planting. S^2_F = Variance component among families. S^2_E = Variance component among-plots. S^2_W = Variance component within-plot. h^2_f = heritability on the basis of families. $h^2_{i(f)}$ = heritability on the basis of individuals within families. I, II, responses to selection as percentage of the control mean, using the formulas (7) and (8), respectively. *, **, F-Test significance at the 0.05 and 0.01 level of significance, respectively. ns = not significant.

of the additive variances perhaps because: (a) in some families not all individuals are half sibs — some may be full sibs; (b) random sampling error included in the variance among families; and (c) confounded maternal effects (Lowe *et al.*, 1983).

The absence of significant height differences among families between 10 months and 38 months has no clear explanation. Heritabilities computed on the basis of the measurements show a decreasing trend (*Figure 1*) and, although this might be spurious, it is similar to the trend reported for the species between the ages of 1.5 and 8 years by Barnes et al. (1992b). It is possible that this will change and that heritabilities will increase at later age as reported for some species by Namkoong and Conkle (1976), Nienstaedt and Riemenschneider (1985) and Riemenschneider (1988).

Differences among families for diameter, stem straightness and phenology of shoot growth at 38 months of age, were also nonsignificant (*Table 4*); consequently, their heritabilities are meaningless. In the case of stem straightness, the absence of significant differences should be taken with caution, since the stems were evaluated at a very early age using a coarse scale. Stem straightness could be better assessed over intervals of one meter, as proposed by Barnes and Gibson (1986).

In contrast to the differences among families in the characteristics mentioned above, the number of whorls, crown width, branch angle, frost injury and phenology at 26 months differed significantly among families (*Table 4*). The heritabilities for these characteristics were correspondingly important.

The response to independent selection for any one of the characteristics would be very variable. Considering that the family variances for heights — excepting measurements at 3 months — diameter, stem straightness and phenology at 38 months, are nonsignificant, early selection based on the selection of best families and best individuals within these would be meaningless. An alternative is selecting only the South African "population" over the local control with the expected response indicated for Level I in *table 4*.

Table 6. — Genetic (above diagonal) and phenotypic (below diagonal) correlations between heights at different ages in the Huayacocotla test.

AGE months	3	10	17	23	26	38
3		1.12 (.75)	.57 1.51)	.36 (.46)	.69 (.68)	.40 (1.01)
10	.33 **		-.14 (3.06)	.38 (.88)	.76 (.62)	.11 1.97)
17	.22 **	.83 **		1.02 (.93)	1.09 (.94)	-.17 (4.7)
23	.20 **	.71 **	.89 **		.75 (.40)	.45 (1.12)
26	.21 **	.70 **	.88 **	.96 **		.97 (.49)
38	.17 **	.61 **	.78 **	.85 **	.88 **	

( ) = Standard Error. Significance: *: $P < 0.05$; **: $P < 0.01$.

Using Level II selection on the other characteristics, selecting the South African "population" over the local control, the 12.5% of the best families and within these the best individual in each plot, the greatest responses would be achieved selecting for phenology of leader growth at 26 months, crown width or number of whorls, with 71.9%, 20.9% and 22.4% over the controls, respectively (*Table 4*). However, selecting for early leader growth would tend to make young tree more susceptible to frost damage, and it is questionable whether broad crowns or many whorls are desirable.

The Oxtlapa Test

At Oxtlapa family differences were much larger than at Huayacocotla and with the exception of stem straightness, they are statistically significant for both sets of measurements of all variables. Heritabilities are also larger than at Huayacocotla; this is particularly the case for height and diameter at both dates for which h^2_F ranged from 0.52 to 0.64. h^2_F values for the other traits with significant family variances, ranged from 0.47 to 0.70. The variables closely related to growth rate i.e. height, diameter, the total number of whorls and crown width, all have high heritabilities.

Table 5. — Variance components derived from ANOVA, heritabilities and response to selection for all variables at 2 ages at Oxtlapa test.

VARIABLE	AGE	S^2_F	S^2_E	S^2_W	h^2_f	$h^2_{i(f)}$	I	II
HEIGHT	26	214.87**	332.64	1712.56	0.61	0.38		36.1
	38	442.91**	826.82	3752.19	0.58	0.35		26.5
DIAMETER	26	12.39**	15.18	87.92	0.64	0.42		53.8
	38	25.49**	53.39	292.78	0.52	0.26		44.0
WHORLS	26	0.28**	0.09	2.16	0.70	0.39		42.5
	38	0.47**	0.22	3.96	0.67	0.36		32.1
CROWN WIDTH	26	119.02**	153.46	852.05	0.64	0.42		40.9
STEM STRAIGHTNESS	26	0.01ns	0.03	0.63	0.22	0.05	18.7	
BRANCH ANGLE	26	0.06**	0.10	1.06	0.47	0.17		4.0
PHENOLOGY	26	0.05**	0.09	0.57	0.52	0.25		44.2

Age in months after field planting. S^2_F = Variance component among families. S^2_E = Variance component among-plots. S^2_W = Variance component within-plot. h^2_f = heritability on the basis of families. $h^2_{i(f)}$ = heritability on the basis of individuals within families. I, II, Response to selection as percentage of the control mean, using the formulas (7) and (8), respectively. *, **, F-Test significance at the 0.05 and 0.01 level of significance, respectively. ns = not significant.

Table 6a. — Genetic (above diagonal) and phenotypic (below diagonal) correlations. Huayacocotla test at 26 months.

	HEIGHT	DIAMETER	WHORL	CROWN	STEM	BRANCH	PHENOLOGY	FROST
HEIGHT		.46 (.62)	.95 (.53)	.45 (.52)	- .26	-.35 (.63)	-.91 (1.14)	.11 (.79)
DIAMETER	.82 **		.30 (.40)	.54 (.32)	-.31	-.57 (.36)	.25 (.56)	.21 (.53)
WHORL	.66 **	.59 **		-.02 (.39)	.40	-.69 .23)	-.36 (.41)	.04 (.38)
CROWN	.76 **	.79 **	.54 **		-.87	.46 (.32)	-.37 (.46)	.25 (.43)
STEM	.36 **	.30 **	.20 **	.21 **		-.66	1.2	-.01
BRANCH	-.09 *	-.12 **	-.09 *	.05	-.03		-.34 (.38)	-.11 (.35)
PHENOLOGY	.02	.02	-.08 *	.01	.01	-.002		.15 (.47)
FROST	-.22 **	-.18 **	-.11 **	-.19 **	-.14 **	.01	-.08 *	

( ) = Standard Error. Significance: *: $P < 0.05$; **: $P < 0.01$.

Predicted responses to Level II selection, independently for each trait, are very promising, particularly for the characteristics of greatest economic value (height 36.1%; diameter 53.8% (*Table 5*). Selection for a greater number of whorls (42.5%) and crown width (40.9%) would also be very effective, but, as mentioned, a larger number of whorls and wide crowns are of questionable value from a commercial point of view. The response to selection for branch angle (4.0%) would be much smaller.

Correlations

Phenotypic and genetic correlations among all the height measurements in the Huayacocotla test are in *table 6*. Phenotypic correlations between height at age 3 months and all later measurements are low, but among the remaining measurements they are high with values between 0.61 and 0.96.

Similarly, Barnes et al., (1992a and b) found low correlations between 12 months nursery heights and heights at 5 and 8 years in the field. Correlations among heights at 2, 5 and 8 years were high.

Studies with other species have also shown that early height in plantations is a poor indication of subsequent growth (Namkoong and Conkle, 1976; Lambeth, 1980; Riemenschneider, 1988), probably because the plants are suffering from transplanting shock and are in a period of adaptation to the new site (Lambeth, 1980). Once through this period, correlations show a regular pattern and decrease, as the period between measurements increases. A similar pattern has been shown for *Pinus resinosa* Ait. (Lester and Barr, 1966), *Pinus ponderosa* Laws. (Lambeth, 1980) and *Pinus banksiana* Lamb. (Riemenschneider, 1988).

Table 6b. — Genetic (above diagonal) and phenotypic (below diagonal) correlations between different traits measured at 38 months in the Huayacocotla test.

	HEIGHT	DIAMETER	WHORL	PHENOLOGY
HEIGHT		-.00 (1.9)	.70 (.83)	-1.9 (4.1)
DIAMETER	.79 **		-.02 (.67)	-.73 (.92)
WHORL	.74 **	.64 **		-.09 (.53)
PHENOLOGY	.04	.02	.02	

( )= Standard Error. Significance: *: $P < 0.05$; **: $P < 0.01$.

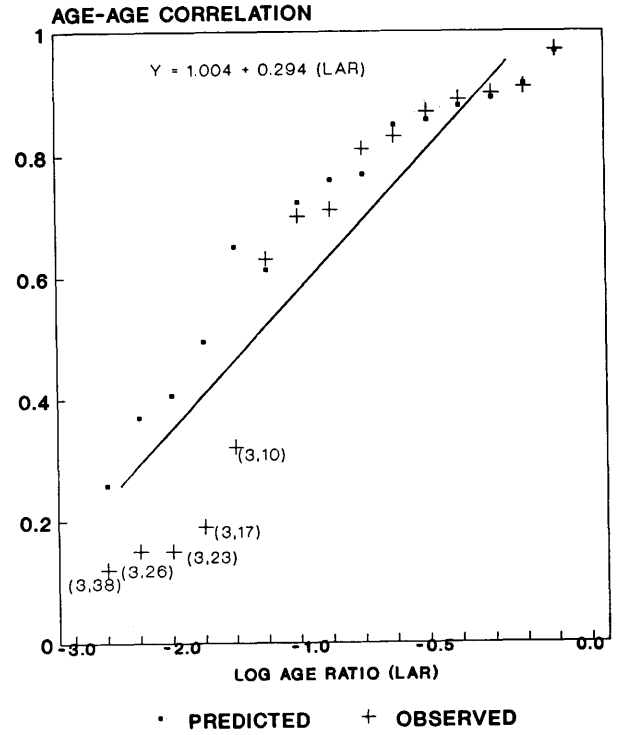

Figure 2. — Regression of phenotypic age-age correlations vs. log age ratio at Huayacocotla Test. Correlations involving age 3 months were not used to estimated the regression equation.

Disregarding the heights at 3 months it is possible to predict the phenotypic correlations between heights at different ages using the formula:

$$Y = 1.004 + 0.294 X \qquad (11)$$

Where Y = correlation between heights at 2 ages, and X = natural logarithm of the ratio of the younger to the older ages at which the measurements were made (*Figure 2*). The estimated regression coefficient was similar to the one found by Lambeth (1980) and Riemenschneider (1988). Our results, however, are based on only 3 years of measurements. Additional years of measurements will have to be made to establish whether this trend will continue.

Table 7. — Genetic (above diagonal) and phenotypic (below diagonal) correlations at 28 months at Oxtlapa test.

	HEIGHT	DIAMETER	WHORL	CROWN	STEM	BRANCH	PHENOLOGY
HEIGHT		.80 (.08)	.54 (.16)	.83 (.07)	-.05 (.41)	.05 (.28)	.45 (.22)
DIAMETER	.86 **		.76 (.10)	.83 (.07)	.13 (.39)	-.14 (.26)	.36 (.22)
WHORL	.57 **	.61 **		.58 (.15)	.35 (.36)	.18 (.25)	.20 (.23)
CROWN	.82 **	.85 **	.51 **		.00 (.39)	-.01 (.27)	.35 (.23)
STEM	.11 **	.05	.16 **	-.02		-.39 (.50)	-.87 (.49)
BRANCH	-.06 *	-.13 **	.01	-.02	.03		.00 (.29)
PHENOLOGY	.32 **	.33 **	.26 **	.29 **	-.002	-.05	

( )= Standard Error. Significance: *: $P < 0.05$; **: $P < 0.01$.

Table 7a. — Genetic (above diagonal) and phenotypic (below diagonal) correlations at 38 months at Oxtlapa test.

	HEIGHT	DIAMETER	WHORL
HEIGHT		.86 (.07)	.31 (.21)
DIAMETER	.83 **		.60 (.16)
WHORL	.49 **	.51 **	

( ) = Standard Error
Significance: *: $P < 0.05$; **: $P < 0.01$.

Of the characteristics measured at 26 months and 38 months height, diameter, and crown width were highly correlated phenotypically with r values between 0.76 and 0.82 (*Tables 6a* and *b*), whereas the number of whorls was less correlated with these characteristics.

Frost damage was negatively correlated with the above 4 characteristics, indicating that larger trees may be more susceptible to damage. However, the phenotypic correlation was low (—0.22**), perhaps due to partial recovery. The same response was found in *Picea glauca* in which the effects of the initial damage from frost was minimal seven years later (NIENSTAEDT, 1985). Phenology of leader growth was not correlated with any other characteristics.

The high positive correlations among height, diameter and crown width, and their negative correlations with frost damage indicates that selection for fast growth i.e. height and diameter would result in simultaneous selection for wide crowns and susceptibility to frost injury — both undesirable characteristics. Negative selection for crown width and the number of whorls would probably result in less height growth because the three characters are highly correlated (*Table 6a*). An alternative could be to develop a restricted selection index, selecting for increased height and diameter, while trying to avoid any change in crown width and susceptibility to frost damage.

In contrast to phenotypic correlations, age-age genetic correlations among heights at Huayacocotla (*Table 6*) are not different from zero. This is also the case for the correlation among other variables measured at 26 months and 38 months, and with nonsignificant variances (*Tables 6a* and *b*).

With the exception of growth phenology, phenotypic correlations at Oxtlapa (*Tables 7* and *7a*) are similar to those observed at Huayacocotla. Height, diameter and crown width are positively correlated; and the number of whorls is also positively correlated with the above 3 characteristics with r values between 0.51 and 0.61. Correlation coefficients are low for stem straightness and branch angles; correlations too low to be of practical value. In contrast to Huayacocotla, growth phenology is significantly correlated with height and diameter ($r = 0.32$ and 0.33 respectively). This may support the hypothesis that the early shoot elongation of the South African families, in part, explains their superior growth.

Conclusions

As a group, the South African families differed from the local controls in all measured traits except branch angle. They were taller and had greater diameters than the control populations. This superiority is partially explained by early elongation of the leader shoot. However, the precocious growth pattern could make the trees susceptible to frost damage.

Because genetically unimproved controls were used it is not possible to determine if the South African progenies would be better than progenies from local superior trees. Nevertheless, since selection of superior trees in natural stands is costly and probably relatively ineffective in Mexico, where most stands are unevenaged and grow on highly variable sites, early phases of tree improvement programs in Mexico might take advantage of the selections already available in South Africa. The results suggest this as a practical for *Pinus patula,* additional testing of other species would of course be necessary for broader application of the approach.

Family variances at Huayacocotla, apart from the height differences resulting from growth in the uniform nursery environment, were nonsignificant. Selection for height or diameter would, therefore be ineffective on a family basis at these early ages. In contrast, heritabilities at Oxtlapa are high and responses to selection for height and diameter are promising. Both tests would respond to selection for the number of whorls and crown width.

The Huayacocotla test could be converted to a seedling seed orchard cutting the control plots and thinning from below to achieve spacing. The gain would derive from the selection of the South African "population" over the local control.

The Oxtlapa test could be converted to a seedling seed orchard cutting the control and selecting the best families and the best individuals within these, one per plot. Long-term breeding, however, require a much larger genetic base (Kang and Nienstaedt, 1987); population size must therefore be increased. Because the test does not compare the South African families with progenies from Mexican superior trees, progenies should be added from both Mexican and South African selections.

The phenotypic age-age correlations for height show a regular trend at Huayacocotla. Genetic correlations, on the other hand, are erratic. With the erratic genetic correlations and because heritabilities for height were low, it was not possible to predict whether early selection is feasible. More detailed phenological studies of shoot growth are needed to explain growth differences and the lack of genetic age-age correlations. Measurements should be made on the same dates from year to year.

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