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Cone and Seed Yield of 16 Populations of *Pinus tecunumanii* at 5 Sites in Zimbabwe

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Summary

Cone and seed yield of 160 families from 16 populations (10 families per population) of *Pinus tecunumanii* were assessed in eight- and nine-year old provenance/progeny tests located at five sites ranging in altitude from 700 m to 1700 m a.s.l. Eight of the 16 *P. tecunumanii* populations came from an altitudinal range of above 1500 m a.s.l. (high elevation population group) while the other eight were from below 1500 m a.s.l. (low elevation population group). *P. patula* and *P. oocarpa*, a high and low elevation species respectively, were also included in the test as controls.

Provenance variation in cone and seed yield was significant at varying probability levels at all sites. Family within-provenance effects were significant at some sites while at other sites they were not ($P < 0.05$). At Nyangui and Stapleford, both high altitude sites, *P. patula* was consistently superior in cone and seed yield to all the populations of *P. tecunumanii* but *Pinus oocarpa* was not significantly different from most of the *P. tecunumanii* populations in the lower altitude sites.

Cone yields for the high elevation population group were highest at Nyangui (13.8 g per tree) while the highest yields for the low elevation population group were at Maswera (6.1 g per tree). The highest seed yields for high elevation population was at Stapleford (0.26 g per tree) and Gungunyana (0.07 g per tree) for the low elevation population. Best locations for seed orchards of *P. tecunumanii* are sites above 1600 m a.s.l. for selections made in high elevation populations and below 1100 m a.s.l. for selections made from low elevation populations.

The highest cone and seed yields were from San Jeronimo, Piedrecitas, La Paz and La Soledad in the high elevation population group and from Jocon, Mountain Pine Ridge and San Francisco in the low elevation group. At family level, some families from populations like Piedrecitas, San Jeronimo and La Paz had seed yields of up to 55 g, 49 g and 48 g per tree respectively. In the low elevation populations the most productive families from Culmi, Mountain Pine Ridge and San

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Estaban, had seed yields of up to 21 g, 21 g and 19 g per tree respectively.

Cone and seed yield differences appeared to be chiefly caused by failure to produce cones or seed by all or some of the families in some populations. Frequency of cone or seed production among families of the different populations ranged from 0% to 100%. Juquila for example, only produced few cones and seed at only site in one year.

In the across site analysis, site, population and their interaction effects were all significant ($P < 0.001$). The family and the family-site interaction effect was only significant for cone yield in one season.

Key words: Pinus tecunumanii, cone and seed yield, high and low elevation populations.

Introduction

Pinus tecunumanii is a Central American and Mexican closed-cone-pine that has been a subject of intense studies on its potential as a plantation species in the tropics and subtropics. In its natural range, the species extends from Oaxaca and Chiapas in Mexico through the central American countries of Guatemala, Belize, El Salvador, Honduras to central Nicaragua in a series of small disjunct populations (BARNES and STYLES, 1983; STYLES and HUGHES, 1983; STYLES, 1985; DVORAK and RAYMOND, 1991). The altitudinal range of distribution spans from 440 m a.s.l. to over 2800 m a.s.l. and the latitudinal range varies from 12 °N to 18 °N.

P. tecunumanii has for long been a subject of intense debate on its taxonomic status. The species was first described and named *P. tecunumanii* in the early 1950s (SCHWERDTFEGER, 1953). STANDLEY and STEYERMARK (1958) regarded SCHWERDTFEGER's pine as a deviant form of *P. oocarpa* or a hybrid between *P. oocarpa* and *Pinus pseudostrobus*. AGUILAR (1962) considered it to be a variety of *P. oocarpa* (*P. oocarpa* var. *tecunumanii*). STYLES (1985) considered SCHWERDTFEGER's pine to be a southern, more tropical variant of *P. patula* to which he accorded a subspecific rank (*P. patula* ssp. *tecunumanii*). The taxon is today, regarded as a distinct species, *P. tecunumanii*, with a slight change in the original spelling of the epithet (EGUILUZ and PERRY, 1983).

Extensive exploration and assemblage of *P. tecunumanii* germplasm by the Central America and Mexico Coniferous Resources cooperative (CAMCORE) and the Oxford Forestry Institute (OFI) began in the early 1980s and continued through to the 1990's (DVORAK and DONAHUE, 1992). The germplasm was evaluated extensively for adaptation and productivity of wood in provenance and progeny tests. Although these studies have been exciting as some of the populations have outperformed some of the traditional species (CROCKFORD *et al.,* 1990; DVORAK and SHAW, 1992; DVORAK and ROSS, 1994), the poor cone and seed production in this species in most of the areas tested has almost killed the enthusiasm originally created by its phenomenal growth.

There is limited information on site requirements of this species for optimum seed production. In its native environment, populations growing at altitudes above 1500 m a.s.l., *P. tecunumanii* trees were found to produce only about 6 filled seeds per cone (DVORAK and LAMBETH, 1992). Trees in populations growing at altitudes lower than 1500 m were found to produce three times that of the high altitude populations. In the many provenance and progeny tests established in many countries, cone production was reported to be low and this was attributed to the age of the tests (5 to 10 years), close commercial spacings used and climatic and soil factors (DVORAK and LAMBETH, 1992). They concluded that *P. tecunumanii* orchards should be sited between latitudes 17 °S and 28 °S in areas with well defined dry seasons.

Seed production is very important for propagation in the absence of cost effective vegetative propagation programmes. Also, early seed production can shorten the breeding cycle thereby improving the economics of breeding of the plantation tree species (GIBSON *et al.,* 1983). The choice of provenances, families or even individuals to use in a breeding programme may necessarily be influenced by variation in cone and seed production. In *Pinus caribaea,* GIBSON *et. al.* (1983) have shown that there is wide provenance variation in cone production and that climate and altitude both influence cone production. Significant genotype-environment interaction in cone production has also been reported in *P. caribaea* (SIRIKUL *et al.,* 1991; GIBSON *et al.,* 1983).

In this study we report on variation in cone and seed yield among 16 populations of *P. tecunumanii* at five sites in Zimbabwe.

Materials and Methods

Open pollinated seed was collected from 160 parent trees comprising 16 wild populations of *P. tecunumanii* from the natural range of the species in southern Mexico and central America. Eight of the populations were from sites above 1500 m a.s.l. while the other half were from sites below this altitude. These two population groups are often referred to as high and low elevation populations respectively. Each population was represented by 10 families. *Table 1* shows the geographic and climatic details of the native environment of the populations used in the study. Two other commercially planted species (*P. patula* and *P. oocarpa*), each represented by 10 families, were included in the tests as control lots. The control species are not only commercially important species in the high and low altitude sites in Zimbabwe but have in the past been taxonomically linked to the different population groups of *P. tecunumanii.*

The seed was sown in April 1987 and the field trials established at five sites in December of the same year as provenance/progeny tests in which families were nested in populations. *Table 2* shows the details of the test sites. The field design was a randomized complete block arranged as a split plot. The populations were randomized into the main plots and the families were in turn randomized into the subplots. Each trial had 5 replications with 5 tree family line plots (subplots). The population main plot had therefore 50 trees at establishment.

The trials were assessed for cone and seed yield at eight and nine year in 1995 and 1996 by harvesting and weighing the two-year-old cones by family (subplot). Seed was then extracted and weighed also by family. No assessments were done at Cashel in 1995 and only four blocks were assessed in 1996.

Although all five tests were completely balanced at establishment, subsequent differential mortality mainly due to drought at Maswera and vandalism at Nyangui resulted in an unbalanced design at family subplot level but not at population main plot level. All analyses were done using generalized linear models to get least squares means. This was done using Procedure GLM in SAS® (SAS Institute Inc., 1988).

For individual sites a full mixed model (1) based on subplot family means was fitted to test significance of the various sources of variation and to estimate population means of cone and seed yield.

$$Y_{ijk} = \mu + B_i + P_j + BP_{ij} + F(P)_{k(j)} + E_{ijkl} \quad \text{.............}(1)$$

Y_{ijk} = is the cone or seed yield of the kth family of the jth population in the ith block;

Table 1. – Locations of origin and climatic data of the *P. tecunumanii* populations used in the test.

Provenance Name (Number)	Code	Altitude Group	Country	Altitude in m	Latitude °N	Longitude °W	Mean rainfall mm	Mean temp. °C
Yucul (1)	Yuc	LE	Nicaragua	850-1000	12°55'	85°48'	1394	22.4
Culmi (2)	Cul	LE	Honduras	550-650	15°06'	85°21'	1325	24.3
Villa Santa (3)	Vil	LE	Honduras	850-950	14°11'	86°20'	1348	22.4
Mt Pine Ridge (4)	Mpr	LE	Belize	700-720	17°00'	88°55'	1558	23.9
San Esteban (5)	Est	LE	Honduras	700-800	15°22'	85°35'	1400	25.0
Jocon (6)	Joc	LE	Honduras	850-1100	15°16'	86°55'	1400	21.7
San Francisco (7)	Fra	LE	Honduras	870-1100	15°05'	86°20'	1600	20.0
Finca las Victorias (8)	Vic	LE	Guatemala	1200-1300	15°12'	89°22'	1700	22.4
Cusuco (9)	Cus	HE	Honduras	1500-1650	15°30'	88°10'	2500	17.0
La Paz (10)	Paz	HE	Honduras	1750-2000	14°19'	87°45'	1619	20.0
Guajiquiro (11)	Gua	HE	Honduras	1835-2250	14°11'	87°50'	2000	15.0
San Jeronimo (12)	Jer	HE	Guatemala	1700-2000	15°03'	90°18'	1600	17.0
Montana Sumpul (13)	Sum	HE	Honduras	1950-2050	14°24'	89°08'	2200	16.0
Juquila (14)	Juq	HE	Mexico	2000-2250	16°15'	97°17'	1400	14.0
La Soledad (15)	Sol	HE	Guatemala	2000-2300	14°35'	90°25'	1543	15.0
Las Piedrecitas (16)	Pie	HE	Mexico	2300-2600	16°46'	92°35'	1228	14.8
P. patula (17)	Pat	HEC	Zimbabwe	Clonal orchard seed controls				
P. oocarpa (18)	Ooc	LEC	Zimbabwe	Clonal orchard seed controls				

HE and LE refers to High and Low Elevation populations,
HEC and LEC refers to High and Low Elevation species controls,
Temp. refers to temperature

μ = is the general trial mean;
B_i = is the fixed effect of the ith block;
P_j = is the fixed effect of the jth population;
BP_{ij} = is the fixed interaction effect of the ith block with the jth population;
$F(P)_{k(j)}$ = is the random effect of the kth family of the jth population in the ith block;
E_{ijkl} = is the random plot error.

Four orthogonal contrasts were tested namely:-

(a) High altitude *P. tecunumanii* populations versus low altitude populations.

(b) *P. tecunumanii* populations versus *P. patula* (at medium and high altitude test sites Cashel, Stapleford and Nyangui) and versus *P. oocarpa* (at low altitude sites, Gungunyana and Maswera).

(c) Low altitude *P. tecunumanii* populations versus the low altitude Belize populations.

(d) All high altitude *P. tecunumanii* populations versus the high altitude Mexican populations.

The last two contrasts were performed to test the validity of the suggestion that Belize and Mexican populations are respectively different from the low and high elevation population groups (DVORAK, 1985, 1986).

For the across site analysis, another mixed model (2) was fitted to the data.

$$Y_{ijkl} = \mu + S_i + B(S)_{j(i)} + P_k + SP_{ik} + PB(S)_{kji(i)} + F(P)_{l(k)} + SF(P)_{il(k)} + E_{ijkl} \quad (2)$$

Y_{ijkl} = is cone or seed yield of the lth family of the kth population in the jth block of the ith site;
μ = is the across site mean;
S_i = is the fixed effect of the ith site;
$B(S)_{j(i)}$ = is the random effect of the jth block of the ith site;
P_k = is the fixed effect of the kth population;
SP_{ik} = is the fixed interaction effect between the ith site and the kth population;
$PB(S)_{kj(i)}$ = is the random interaction effect between the jth block of the ith site and the kth population;

Table 2. – Details of test sites included in this trial series.

Location	Trial Code	Altitude (m)	Lat. °S	Long. °E	Rainfall (mm)	Mean Temperature °C annual	max.	min.
Stapleford	PX125A	1651	18°41'	32°51'	2159	15.1	19.2	11.1
Gungunyana	PX125B	1050	20°24'	32°43'	1097	18.1	24.0	13.9
Cashel	PX125C	1450	19°25'	32°45'	891	19.5	24.4	14.6
Maswera	PX125D	750	18°41'	32°55'	1498	20.7	28.4	13.0
Nyangui	PX125E	1800	18°00'	32°47'	1572	13.0	17.7	08.3

Lat., Long., max. and min. Refer to latitude, longitude, maximum and minimum respectively

$F(P)_{l(k)}$ = is the random effect of the lth family of the kth population;

$SF(P)_{il(k)}$ = is the random interaction between the ith site and the lth family of the kth population;

E_{ijkl} = is the random plot error.

For those effects in the models that did not have exact test statistics, the method of SATTERTHWAITE, (1946) method was used to synthesize the mean square errors and their associated degrees of freedom.

Besides the statistical analyses, the percentage of families with either cones or seed was also derived for each population for all the five sites.

Results

There were significant differences at varying probability levels among the populations and the species controls for cone yield in both years at all five sites (*Table 3* and *4*). Except for Maswera in the 1995 season, there were also significant differences at varying probability levels among populations for seed yield. The contrasts that were consistently significant for both traits at all sites were those of *P. tecunumanii* populations against either of the two species controls and that between the two elevation population groups of *P. tecunumanii*. Mountain Pine Ridge, essentially a low elevation population from Belize was significantly different ($P < 0.05$) from the other low elevation populations for both cone and seed yield at Maswera only. The two Mexican high elevation populations were also significantly different ($P < 0.05$) from the other high elevation populations for both cone and seed yield at Gungunyana, Cashel and Maswera. Family-within-population differences were significant at varying probabilities at Stapleford, Gungunyana and Maswera.

In both the high and medium altitude environments of Nyangui, Stapleford and Cashel, the top-ranked populations were all of high elevation origin namely San Jeronimo, Las Piedrecitas, Montana Sumpul, La Paz and La Soledad (*Table 5* and *6*). The ranking of the populations was completely reversed at Maswera, the lowest altitude of the test sites, where the top ranked populations were mostly from the low elevation group. These were San Francisco, Jocon, Culmi, San Estaban and Mountain Pine Ridge. The mean cone and seed yields of the high elevation population group were consistently higher than that of the low elevation group at Stapleford, Nyangui and Cashel. At Maswera and Gungunyana, the low elevation population group was more productive than the high elevation group (*Tables 5* and *6*).

Montana Sumpul, a high elevation population was however surprisingly ranked consistently in the top five for both cone and seed yield at all the five sites. At Nyangui and Stapleford, both high altitude sites, *P. patula* was always consistently superior to all populations of *P. tecunumanii* in both cone and seed yield. This was also true at Cashel, a site considered marginal for both timber and seed production of *P. patula*. At Nyangui, where there was the highest cone yield of *P. tecunumanii*, the most productive populations, San Jeronimo and Las Piedrecitas had cone yields of about half those of *P. patula* and only about tenth of seed yield. Although most of the high elevation populations were significantly superior to *P. oocarpa* at high altitudes, the low elevation populations were, however not significantly different from *P. oocarpa* at all the five sites.

Although not statistically tested, there was evidence of seasonal variation in cone and seed yield at Nyangui, Stapleford and Maswera with the 1995 year having lower yields than the year later. The differences between years was however confounded by age effects as yields of 1996 are from older trees

Table 3. – Significance of the different sources of variation at individual sites for cone and seed yield in 1995.

Source of Variation	DF‡	Stapleford VR	Nyangui VR	Gungunyana VR	Maswera VR
CONE					
Blocks	4	2.4ns	1.2ns	4.60**	2.84*
Populations	17	4.35***	15.4***	2.53**	3.12***
P. tecunumanii vs Controls§	1	63.0***	ne	24.3***	37.6***
Low alti. vs Low Belize	1	0.01ns	ne	0.58ns	7.94**
High alti. vs High Mexican	1	0.39ns	0.12ns	3.22ns	0.81ns
Low altitude vs High altitude	1	6.24*	ne	0.20ns	1.37ns
Block*Population	68	5.4***	2.04***	1.44*	0.78ns
Family(Population)	161	5.43***	0.82ns	1.54***	1.37**
Error	649				
SEED					
Blocks	4	1.95ns	1.14ns	5.76***	2.60*
Populations	17	11.0***	12.45***	2.18*	1.46ns
P. tecunumanii vs Controls§	1	150.0***	ne	11.65***	21.72***
Low alti. vs Low Belize	1	0.01ns	ne	0.50ns	0.00ns
High alti. vs High Mexican	1	1.62ns	0.01ns	3.65ns	0.12ns
Low altitude vs High altitude	1	18.2***	ne	0.46ns	0.21ns
Block*Population	68	1.60**	2.87***	1.36*	2.93***
Family(Population)	161	1.41**	0.99ns	1.61***	0.83ns
Error	649				

DF = degrees of freedom, VR = variance ratio, ns = not significant at 5%, *,** and *** significant at respectively 5%, 1% and 0.1%; ne = not estimable due unbalancedness at the site. §) Control is *P. patula* at Stapleford and Nyangui, *P. oocarpa* at Gungunyana and Maswera; ‡) DF of Error at Nyangui is 509.

Table 4. – Significance of the different sources of variation at individual sites for cone and seed yield in 1996 season.

Source of Variation	DF ‡	Stapleford VR	Nyangui VR	Cashel VR	Gungunyana VR	Maswera VR
CONE						
Blocks	4	1.11ns	3.58*	0.75ns	5.58***	3.83***
Populations	17	25.8***	11.90***	16.9***	2.03*	3.52***
P. tecunumanii vs Control§	1	373.9***	ne	226.4***	12.85***	31.36***
Low alti. vs Low Belize	1	0.11ns	ne	0.05ns	0.36ns	0.38ns
High alti. vs High Mexican	1	1.69ns	1.56ns	5.21*	5.14*	4.08*
Low altitude vs High altitude	1	30.7***	ne	26.8***	0.41ns	5.71*
Block*Population	68	1.28ns	2.49***	0.98ns	1.43*	1.88***
Family(Population)	161	1.72***	0.91ns	1.50***	1.32*	2.45***
Error	649					
SEED						
Blocks	4	0.53ns	1.25ns	1.45ns	4.82**	1.44ns
Populations	17	36.0***	13.1***	19.0***	2.47**	2.94***
P. tecunumanii vs Control§	1	556.4***	ne	257.9***	2.36ns	22.65***
Low alti. vs Low Belize	1	0.07ns	ne	0.18ns	1.09ns	5.10*
High alti. vs High Mexican	1	1.72ns	0.01ns	5.92*	6.89*	3.49ns
Low altitude vs High altitude	1	23.6***	ne	28.7***	0.00ns	4.46*
Block*Population	68	1.42*	6.48***	0.83ns	1.02ns	1.24ns
Family(Population)	161	1.32*	1.12ns	0.98ns	0.97ns	1.67***
Error	649					

DF = degrees of freedom, VR = variance ratio, ns = not significant at 5%, *,** and *** significant at respectively 5%, 1% and 0.1%; ne = not estimable due unbalancedness at this site. §) Control is *P. patula* at Stapleford, Cashel and Nyangui, *P. oocarpa* at Gungunyana and Maswera; ‡) DF of Error at Nyangui and Cashel are 509 and 487 respectively. DF for Block is 3 at Cashel.

Table 5. – Cone yield in grams per plot (g/plot) of 16 populations of *P. tecunumanii* at all five sites in the 1995 and 1996 seasons.

Stapleford						Gungunyana						Cashel			Maswera						Nyangui					
1995			1996			1995			1996			1996			1995			1996			1995			1996		
Pop	yld g/plot		Pop	yld g/plot		Pop	yld g/plot		Pop	yld g/plot		Pop	yld g/plot		Pop	yld g/plot		Pop	yld g/plot		Pop	Yld g/plot		Pop	yld g/plot	
Jer	977.6	a	Jer	1166	a	Fra	116.6	a	Fra	43.6	a	Jer	83.5	a	Mpr	74.8	a	Sum	463.4	a	Jer	1190	a	Pie	1445	a
Paz	884.6	ab	Paz	964.0	ab	Cus	107.0	a	Jer	33.6	a	Sum	76.0	ab	Sum	40.0	a	Est	400.2	ab	Pie	892.2	ab	Jer	1030	ab
Pie	845.0	abc	Pie	877.2	abc	Mpr	72.4	a	Est	33.2	a	Paz	71.0	abc	Fra	32.6	a	Joc	399.2	abc	Sum	577.6	abc	Sum	895.8	abc
Sole	684.8	abcd	Sum	688.4	abcd	Paz	68.8	a	Cus	33.0	a	Pie	55.8	abcd	Cul	26.0	a	Fra	376.6	abcd	Paz	326.6	abc	Sol	755.0	abcd
Sum	629.4	abcd	Sol	449.6	bcde	Sum	63.7	a	Cul	32.6	a	Sol	54.5	abcde	Joc	23.6	a	Mpr	375.8	abcd	Sol	305.0	bc	Paz	628.8	bcde
Vic	452.6	abcd	Vic	381.4	bcde	Cul	54.4	a	Sol	31.8	a	Cus	33.3	cdef	Cus	21.2	a	Vic	365.6	abcd	Gua	160.6	bc	Gua	399.2	bcde
Cus	238.6	bcd	Cus	311.8	bcde	Vic	47.4	a	Sum	30.6	a	Vic	28.5	def	Sol	14.6	a	Cus	258.6	abcd	Vic	118.1	bc	Juq	214.2	cde
Gua	205.2	bcd	Gua	258.6	cde	Sol	43.6	a	Mpr	30.2	a	Est	15.0	def	Est	13.4	a	Cul	252.2	abcd	Juq	48.8	bc	Cus	156.0	cde
Est	112.0	d	Fra	57.8	e	Joc	41.4	a	Paz	19.8	a	Yuc	14.0	ef	Jer	8.6	a	Jer	249.6	abcd	Cus	19.2	bc	Vic	103.2	de
Mpr	40.0	d	Est	55.0	e	Jer	40.8	a	Yuc	18.8	a	Gua	14.0	ef	Yuc	6.4	a	Vil	238.4	abcd	Cul	13.0	c	Est	44.4	de
Fra	20.0	d	Joc	20.0	e	Est	32.2	a	Vil	9.6	a	Cul	12.8	f	Paz	6.2	a	Paz	157.0	abcd	Joc	5.8	c	Yuc	20.0	de
Joc	11.4	d	Yuc	14.0	e	Yuc	16.8	a	Vic	9.4	a	Fra	12.3	f	Vil	3.6	a	Sol	119.2	abcd	Fra	4.6	c	Fra	17.2	de
Vil	0.0	d	Cul	13.6	e	Vil	11.0	a	Joc	6.8	a	Vil	11.5	f	Vict	3.2	a	Yuc	64.0		Yuc	3.8	c	Joc	15.4	de
Cul	0.0	d	Mpr	12.0	e	Pie	10.8	a	Pie	2.0	a	Mpr	10.8	f	Gua	1.6	a	Gua	56.8	bcd	Vil	3.8	c	Vil	7.0	de
Yuc	0.0	d	Juq	3.8	e	Gua	0.0	a	Gua	0.0	a	Joc	4.8	f	Pie	0.6	a	Pie	47.6		Est	3.2	c	Mpr	0.0	c
Juq	0.0	d	Vil	0.0	e	Juq	0.0	a	Juq	0.0	a	Juq	4.0	f	Juq	0.0	a	Juq	10.2	bcd	Mpr	2.4	c	Cul	0.0	c
$\bar{x}_{low}$	**79.5**		$\bar{x}_{low}$	**69.2**		$\bar{x}_{low}$	**49.0**		$\bar{x}_{low}$	**23.0**		$\bar{x}_{low}$	**13.7**		$\bar{x}_{low}$	**23.0**		$\bar{x}_{low}$	**309.0**		$\bar{x}_{low}$	**19.3**		$\bar{x}_{low}$	**25.0**	
$\bar{x}_{high}$	**558.2**		$\bar{x}_{high}$	**589.9**		$\bar{x}_{high}$	**42.0**		$\bar{x}_{high}$	**18.9**		$\bar{x}_{high}$	**49.0**		$\bar{x}_{high}$	**11.6**		$\bar{x}_{high}$	**170.3**	bcd	$\bar{x}_{high}$	**440.0**		$\bar{x}_{high}$	**690.6**	
Pat	**3703**		**Pat**	**4068**		**Pat**	**4.1**		**Pat**	**0.0**		**Pat**	**243**		**Pat**	**0.0**		**Pat**	**17.1**	d	**Pat**	**2818**		**Pat**	**3288**	
Ooc	**270.8**		**Ooc**	**313.5**		**Ooc**	**216.3**		**Ooc**	**69.6**		**Ooc**	**38.9**		**Ooc**	**146**		**Ooc**	**981**		**Ooc**	**68.8**		**Ooc**	**287.1**	

Means followed by the same letter do not differ significantly at 5%. $\bar{x}_{low}$ and $\bar{x}_{high}$ are respectively means of low and high elevation population groups; Pat and Ooc is *P. patula* and *P. oocarpa* controls.

Table 6. – Seed yield in grams per plot (g/plot) of 16 populations of *P. tecunumanii* at all five sites in the 1995 and 1996 seasons.

Stapleford						Gungunyana						Cashel			Maswera						Nyangui					
1995			1996			1995			1996			1996			1995			1996			1995			1996		
Pop	yld g/plot		Pop	yld g/plot		Pop	yld g/plot		Pop	yld g/plot		Pop	yld g/plot		Pop	yld g/plot		Pop	yld g/plot		Pop	Yld g/plot		Pop	yld g/plot	
Jer	17.2	a	Jer	29.2	b	Fra	5.0	a	Cus	10.2	a	Paz	10.5	a	Sum	0.2	a	Mpr	6.2	a	Jer	18.0	a	Pie	20.6	a
Paz	15.2	ab	Paz	21.8	b	Cus	3.6	ab	Jer	6.8	ab	Sum	10.5	a	Fra	0.0	a	Joc	5.2	ab	Pie	16.8	a	Paz	16.8	ab
Sol	13.2	abc	Pie	18.0	b	Mpr	2.6	ab	Fra	5.8	ab	Jer	8.5	ab	Joc	0.0	a	Sum	5.0	abc	Sum	11.8	a	Sum	15.4	abc
Pie	10.0	abc	Sum	14.4	b	Sum	2.6	ab	Est	5.6	ab	Pie	7.3	abc	Yuc	0.0	a	Est	3.8	abc	Paz	5.0	a	Jer	14.4	abcd
Sum	9.2	abc	Sol	11.0	b	Sol	2.4	ab	Cul	5.2	ab	Sol	7.0	abcd	Mpr	0.0	a	Vic	3.0	abc	Sol	4.2	a	Sol	12.2	abcde
Vic	3.4	abc	Vic	5.8	b	Cul	2.2	ab	Sol	5.0	ab	Cus	5.0	abcde	Esta	0.0	a	Fra	2.6	abc	Gua	1.8	a	Gua	5.4	bcde
Cus	3.2	abc	Gua	5.6	b	Paz	1.8	ab	Joc	4.8	ab	Vic	4.3	bcde	Vic	0.0	a	Vil	2.6	abc	Cus	1.6	a	Juq	1.8	cde
Gua	2.4	bc	Cus	4.0	b	Vic	1.6	ab	Sum	4.4	ab	Yuc	2.3	cde	Paz	0.0	a	Cul	2.4	abc	Vic	1.0	a	Cus	1.4	cde
Fra	0.4	c	Fra	1.8	b	Est	1.4	ab	Yuc	2.2	ab	Gua	1.8	cde	Cul	0.0	a	Cus	2.4	abc	Juq	0.6	a	Vic	0.8	de
Est	0.0	c	Est	1.2	b	Joc	1.2	ab	Mpr	1.8	ab	Est	1.8	cde	Vil	0.0	a	Jer	2.0	abc	Vil	0.2	a	Est	0.2	e
Mpr	0.0	c	Yuc	0.6	b	Jer	1.2	ab	Vic	1.8	ab	Fra	1.8	cde	Gua	0.0	a	Sol	2.0	abc	Cul	0.1	a	Fra	0.2	e
Joc	0.0	c	Joc	0.4	b	Yuc	0.6	ab	Vil	1.2	ab	Cul	1.5	e	Jer	0.0	a	Paz	1.4	abc	Jon	0.0	a	Joc	0.2	e
Vil	0.0	c	Cul	0.4	b	Pie	0.4	ab	Pie	1.2	ab	Mpr	1.0	e	Cus	0.0	a	Yuc	0.8	bc	Fra	0.0	a	Yuc	0.0	e
Cul	0.0	c	Juq	0.2	b	Vil	0.0	b	Paz	1.0	b	Vil	1.0	e	Sol	0.0	a	Gua	0.6	bc	Yuc	0.0	a	Vil	0.0	e
Yuc	0.0	c	Mpr	0.0	b	Gua	0.0	b	Gua	0.0	b	Joc	0.8	e	Pie	0.0	a	Pie	0.4	bc	Est	0.0	a	Mpr	0.0	e
Juq	0.0	c	Vil	0.0	b	Juq	0.0	b	Juq	0.0	b	Juq	0.8	e	Juq	0.0	a	Juq	0.0	c	Mpr	0.0	a	Cul	0.0	e
$\bar{x}_{low}$	**0.5**		$\bar{x}_{low}$	**1.3**		$\bar{x}_{low}$	**1.8**		$\bar{x}_{low}$	**3.6**		$\bar{x}_{low}$	**1.8**		$\bar{x}_{low}$	**0.0**		$\bar{x}_{low}$	**3.3**		$\bar{x}_{low}$	**0.2**		$\bar{x}_{low}$	**0.2**	
$\bar{x}_{high}$	**8.8**		$\bar{x}_{high}$	**13.0**		$\bar{x}_{high}$	**1.5**		$\bar{x}_{high}$	**3.6**		$\bar{x}_{high}$	**6.4**		$\bar{x}_{high}$	**0.0**		$\bar{x}_{high}$	**1.7**		$\bar{x}_{high}$	**7.5**		$\bar{x}_{high}$	**11.0**	
Pat	**53.5**		**Pat**	**126**		**Pat**	**0.2**		**Pat**	**0.0**		**Pat**	**32.3**		**Pat**	**0.0**		**Pat**	**0.1**		**Pat**	**171**		**Pat**	**231**	
Ooc	**2.3**		**Ooc**	**4.9**		**Ooc**	**5.6**		**Ooc**	**6.5**		**Ooc**	**3.4**		**Ooc**	**0.5**		**Ooc**	**9.4**		**Ooc**	**1.1**		**Ooc**	**4.2**	

Means followed by the same letter do not differ significantly at 5%. $\bar{x}_{low}$ and $\bar{x}_{high}$ are respectively means of low and high elevation population groups; Pat and Ooc is *P. patula* and *P. oocarpa* controls.

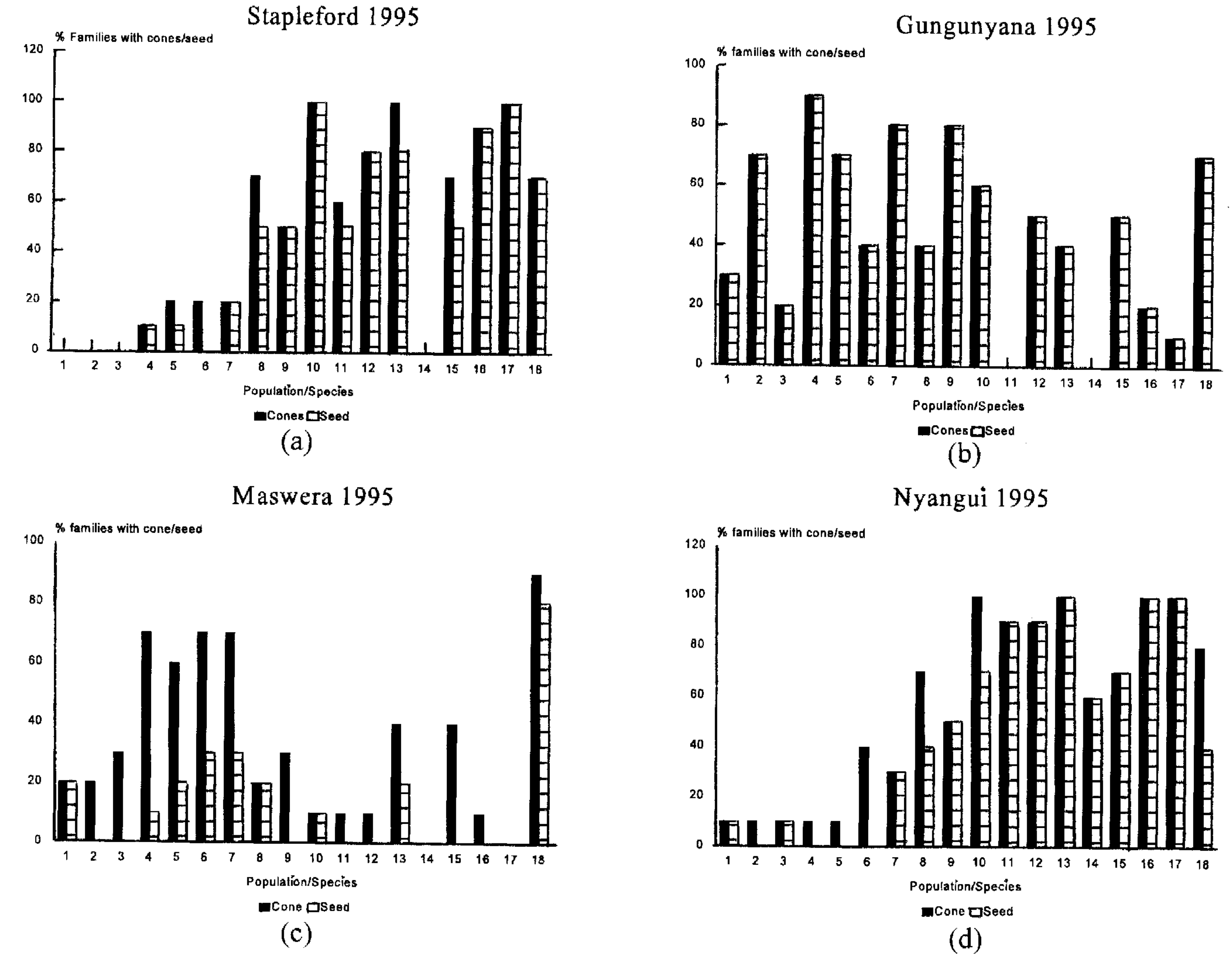

Fig. 1. – Frequency of cone and seed production at four sites in the 1995 season. 1 to 8 low elevation populations, 9 to 16 high elevation populations, 17 *P. patula*, 18 *P. oocarpa*.

than those of 1995. There was however an unexpected trend at Gungunyana where yields were higher in 1995 than in 1996.

The family ranges in cone and seed yield ranged from 0 g to 8600 g of cones and 276 g of seed per five tree plot. The highest yielding families in Las Piedrecitas, San Jeronimo and La Paz, the most productive high elevation populations had seed yields of 276 g, 243 g and 242 g per plot (55 g, 49 g and 48 g per tree) respectively. The most productive families in the low elevation populations were from Culmi, Mountain Pine Ridge and San Estaban and had yields of 107 g, 104 g and 94 g per plot (approximately 21, 21 and 20 seeds per tree) respectively. In general, the cone and seed yield ranges of the *P. tecunumanii* populations were very much comparable to those of the controls particularly that of *P. oocarpa*.

The percentage of families with either cones or seed also followed the same trends as actual yields. The percentage of families with either cones or seed in the high elevation population group ranged from 60% to 100% at Stapleford, Nyangui and Cashel in both years (*Fig. 1a* and *d*, *Fig. 2a*, *d* and *e*). At these same sites, the percentage of families from the low elevation populations with cones and seed were all below 60%. At Gungunyana and Maswera, both low altitude sites the trend was reversed, with low elevation populations having a higher frequency of cone and seed production than the high elevation populations (*Fig. 1b* and *c*, *Fig. 2b* and *c*).

Site and population effects were both significant ($P < 0.001$) in both years for the two traits (*Table 7*). Family effects were significant at all three probability levels ($P < 0.001$, 0.01 and 0.05) tested. Genotype-environment interaction was present and significant ($P < 0.001$) at population level but was not consistently significant at family level (*Table 7*). A plot of the population means against the site means although not shown, indicated that this interaction was mainly due to rank changes. Most of the populations from the high elevation group gave high cone and seed yields in the high altitude sites while populations from low elevation group were more productive in low altitude sites.

Discussion and Conclusions

The two population groups of *P. tecunumanii* are different in their cone and seed production as evidenced by the significant contrasts tested. The differences between the isolated Mountain Pine Ridge population and other low elevation populations although significant, may be of limited practical relevance to breeding as the differences were only significant at one site. The differences between the Mexican high elevations popula-

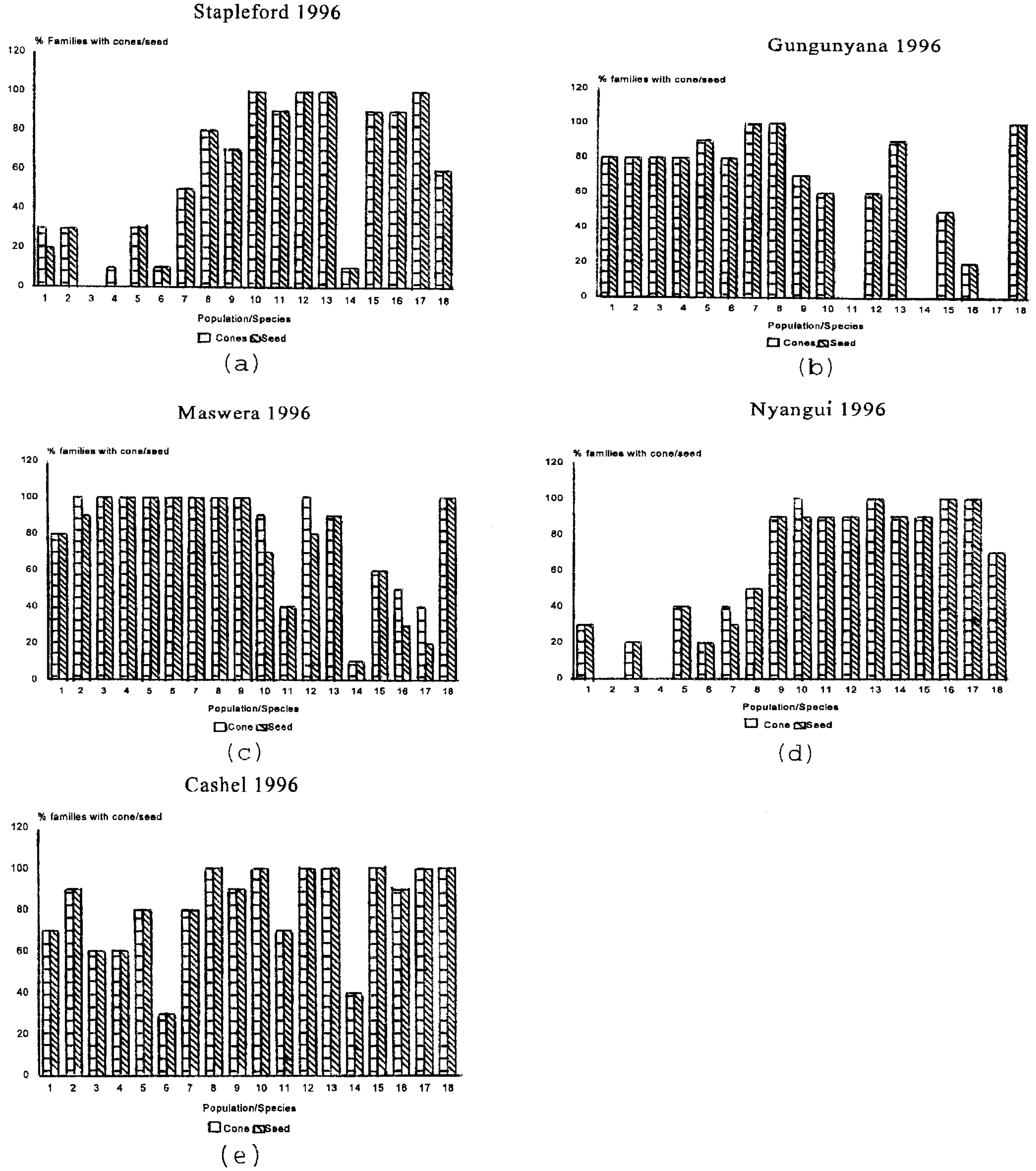

Fig. 2. – Frequency of cone and seed production at five sites in 1996. 1 to 8 low elevation populations, 9 to 16 high elevation populations, 17 *P. patula*, 18 *P. oocarpa*.

tions and the other high elevation populations were consistent at medium and low altitude sites and this was attributed to Juquila, a Mexican high elevation population which sometimes failed to produce cones and seed. The differences between the population groups largely agree with suggestions made by DVORAK (1985, 1986), although then this was largely based on less substantial evidence.

Seed orchards of the selections made in the high elevation populations group will produce more seed if sited in equally high altitude environments while the reverse is true of selections made in populations from low elevation environments. Only one population namely Montana Sumpul, a high elevation source, was consistently ranked in the top five at all sites and years. Despite this stability or consistency in ranking across sites, selections from this population should ideally be planted in higher elevation sites where yields were higher.

Cone and seed yields of the high elevation populations were lower than that of *P. patula* in the high altitude sites while the

Table 7. – Variance ratios of the various sources of variation for across site analysis of cone and seed yield, and significance of the differences between means.

Source	1995 Season			1996 Season		
	DF	Cone	Seed	DF	Cone	Seed
Site S	3	68.8***	39.3***	4	86.5***	59.0***
Block/Site B/S	16	7.1***	3.5***	19	5.7***	5.6***
Population P	17	27.2***	36.1***	17	37.9***	83.8***
Site*Population	51	17.5***	26.4***	68	20.6***	45.7***
Block/Site*Popn	270	3.6***	3.0***	321	2.0***	4.9***
Family/Population	161	1.7***	1.3*	161	1.3*	1.5***
Site*Family/Popn	483	1.0ns	1.1ns	644	1.3***	1.1ns
Error	2419			2910		

DF = degrees of freedom, VR = variance ratio, ns = not significant at 5%, *,** and *** significant at respectively 5%, 1% and 0.1%.

low elevation populations were comparable to those of *P. oocarpa* in the lower altitudes. The low yields may mean that the cost of seed production will be much higher for selections from high elevation populations of *P. tecunumanii* than for *P. patula* due in part to a large land area required to get reasonable quantities of seed. The other option available to plantation developers will be to bulk seedlings by vegetative propagation provided the timber yield potential of the species is high enough to justify such a strategy.

There could be an argument that the low yields reported in this study could be influenced by the genetics of the species, spacings in the tests and the age of the trees (DVORAK and LAMBETH, 1992). Considering that the results here are contrasted with those of *P. patula* and *P. oocarpa* of the same age and spacing, they can be taken to be absolute. It can be inferred from the evidently wide provenance and family variation in frequency as well as actual yields of cone and seed that it is both genetics of the species as well as environmental factors that affect seed production. HALL, (1985) came to the same conclusions regarding seed yield in clones of European Larch (*Larix decidua* MILL.).

In this study with trees of about eight years old, the highest seed yield in the most productive family from an equally productive high elevation population was 276 g per plot of 5 trees or 55 g per tree. The highest yielding family in the low elevation population Culmi, had seed yield of 107 g of seed per plot or (21 g per tree). Observations made in 60-year old trees of populations growing above 1500 m a.s.l. in the natural range of the species indicated that trees averaged only 10 to 15 filled seeds per cone or 10 to 20 grammes per tree and three times this figure for trees in populations growing at an elevation below 1500 m a.s.l. (DVORAK and LAMBETH, 1992). The yields from this present study are obviously higher than those reported by DVORAK and LAMBETH (1992) for this species. This therefore means that some sites in Zimbabwe are even more favourable for cone and seed yields than the sites in the species native range. Also in this study, the seed yields of the low altitude populations in their best sites were always lower than those of high altitude populations also in their best sites. This finding is not consistent with observations made in the wild in which low altitude populations were found to produce three times the amount of seed produced from high elevation populations (DVORAK and LAMBETH, 1992).

Although DVORAK and LAMBETH (1992) studied the number of filled seeds per cone as opposed to absolute yield quantities, their conclusions largely agree with our findings in that the seed orchards of selections from the two elevation population groups of *P. tecunumanii* will have to be sited in different localities. In a related study with seed from this series of tests, MANHANDO (1995) reported germination percentages ranging from 12% to 82% at Stapleford, 6% to 84% at Maswera and 34% to 88% at Nyangui with the highest proportion of empty seeds coming from Maswera.

The best sites for siting seed orchards of *P. tecunumanii* for optimum seed production in Zimbabwe are Stapleford and Nyangui for selections made from high elevation sources. This represents an altitudinal range >1600 m a.s.l. Selections from low altitude sources can be planted at Gungunyana and Maswera representing an altitudinal range of between 700 m and 1100 m a.s.l. An analysis of percentage of families with cones and seed showed that this ranged from 0% to 100% and this appeared to be the major source of differences between populations.

This study also found evidence of significant population variation as well as *genotype x environment* interaction for both cone and seed yield. This is consistent with results reported for other pines (*Pinus caribaea* var *hondurensis* by SIRIKUL *et al.*, 1991; *P. caribaea* by GIBSON *et al.*, 1983; *P. tecunumanii* by DVORAK and LAMBETH, 1992). Effect of seasons, although evident from the data, was difficult to quantify due to confounding effect of age. This could be resolved by assessing mature tests where flowering and seed production has peaked and stabilized.

In Malawi, *P. tecunumanii,* has been reported to flower much more profusely (Dr. R. D. BARNES, pers. comm.)[3]). This observation indicates that seed production could be higher in the lower latitudes.

Even in the high altitude sites, considered potentially prime environments for it, Juquila, a high elevation population, consistently produced fewer cones and seed than any other population of the same group. On the other hand, Montana

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Sumpul, also a high elevation population was consistently ranked in the top five across all five sites. Juquila is isolated from any other known stands of this taxon in its natural range of occurrence. This high degree of dissimilarity from other populations confirms the results from molecular studies indicating that it may be a natural interspecific hybrid of *Pinus herrerai* and *P. patula.* (Dr. W. S. DVORAK, pers. comm.)[4]. In the natural range, trees of Montana Sumpul were reported to exhibit characteristics intermediate between *P. oocarpa* and *P. patula* suggesting a possibility of hybridization. These natural hybrids, being a result of a cross between high and low altitude species would obviously show the typical stability found in this study.

Except probably for the stable Montana Sumpul population, it is recommended to create two breeding populations namely high and low elevation group as originally proposed by DVORAK (1985, 1986). The population and within-population variation in cone and seed yield in *P. tecunumanii* is substantially high enough to warrant selection. This finding has significant bearing in the future breeding of this species, which was nearly abandoned because of its poor seed set. In view of the evidently wide between population and within-population variation in cone and seed production in *P. tecunumanii*, it is recommended to include these as additional traits in the selection of superior trees for further breeding. Before this is done, information on genetic control of these traits must be investigated so as to design an efficient selection method. This additional information forms part of our second paper. Methods of inducing flowering could also be investigated otherwise superior individuals from populations such as Juquila will not be very useful in the breeding programme.

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[4]) CAMCORE director, North Carolina State University, Raleigh, USA.