Provenance Variation in Pinus radiata at Six Sites in South Africa

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Summary

Genetic variation in height, diameter at breast height, volume per tree, stem-form, crown-form, resistance to *Pineus pini* and in defects between 16 provenances and two genetic controls of *Pinus radiata* were analysed at age four and eight years. Six trials were planted in the constant, winter and summer rainfall areas of South Africa. The 16 provenances originated from the international collection made by K.G. ELDRIDGE and A. FIRTH in 1978.

Volume growth at eight years was the fastest at Hogsback where annual precipitation was the highest for constant effective soil depth. It was the lowest at Witfontein where effective soil depth was the smallest although annual precipitation was 995 mm.

Only the Kluitjieskraal I trial did not show any significant differences among seedlots for the growth traits studied at both ages. At the four remaining sites the genetic controls did not differ from the best provenances and no genetic gain could be expected by selecting among the new provenances except for crown-form at Witfontein.

Provenance means heritabilities varied from 0.00 to 0.82 depending on trait and trial.

In height, volume growth and stem-form the seed orchard control was not better than the commercial control in most trials studied.

Irrespective of differences with the genetic controls, the pattern of provenance variation varied widely from site to site. Not a single provenance was best for all traits at all sites. The pattern of provenance variation could not be related to ecological characteristics of the trials although site effects were undeniable.

There were no significant differences for any trait between provenances within population except for aphid resistance at Kruisfontein. In practice thus any provenance within a population could be used once the superiority of a population had been shown.

Across-site analyses of variance showed small provenance-by-site interaction for height and aphid resistance at eight years. The study of provenance stability by use of regression analysis showed that most provenances and genetic controls were stable over the five sites for height and tree volume but not so for aphid resistance at eight years.

Mortality was high (38%) at Witfontein but lower at the other trials. Mortality increased in all trials from four to eight years because of hail damage and drought periods. No provenance variation in defects was detected although site seemed to influence the occurrence of some defects such as terminal leader dieback and forks at eight years.

Individual tree selection irrespective of population within trials and propagation of the trees selected for their volume, stem-form, crown-form and aphid resistance should be the best approach to improve radiata pine in South Africa.

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Key words: Pinus radiata, provenance variation, 1978 International Collections, four and eight years.

Introduction

Pinus radiata D. DON or Monterey pine is an important commercial species in the winter and uniform rainfall areas of South Africa. In 1987, it covered 54 896 ha (Anon., 1987). The origin of the seed used for commercial planting in South Africa is unknown. A tree breeding programme was initiated in 1961 by the then Department of Forestry (POYNTON, 1977).

Monterey pine is a most successful exotic species in the southern hemisphere although it has a very restricted natural area of distribution which only covers 7000 ha (ELDRIDGE, 1983). The area consists of five main disjunct populations: Año Nuevo, Monterey, Cambria, Guadalupe Island and Cedros Island. These five populations consist of three varieties: the first three populations belong to the variety *radiata*, the fourth one to the variety *binata* and the last one to the variety *cedrosensis* (LAVERY, 1986). The autecology and distribution of Monterey pine have been summarised by ELDRIDGE (1978 and 1983). GREY and TAYLOR (1983) and GREY (1989) have summarised the site requirements of radiata pine for South African conditions.

Young trials of the natural populations planted on five sites in New Zealand showed that the New Zealand population outgrew the natural populations by about 20% in volume per tree on two sites but on the other sites the Monterey population was sligthly better than the New Zealand population. The need for further testing was emphasised (SHELBOURNE *et al.*, 1979). In provenance trials in New Zealand the two island populations (Cedros and Guadalupe Islands) were inferior in growth rate to those of the mainland (ELDRIDGE, 1983). In Australia, on five sites, the Guadalupe and Cedros populations had much thinner bark and somewhat denser wood than those from the mainland of California, and the population from Monterey had denser wood than that of the other mainland populations (NICHOLLS and ELDRIDGE, 1980). In Turkey, six-year old trials of *Pinus radiata* provenances planted on five sites showed no significant differences between provenances for growth and stem traits (SIMSEK and TULUKCU, 1983). In France, at two years there were no differences in growth rate between the main populations tested but frost resistance varied clinally with the northern population of Año Nuevo the least affected by frost (ALAZARD and DESTREMAU, 1981). In general however the genetic variation within the natural populations of Monterey pine has not been adequately assessed in field trials (ELDRIDGE, 1983) except in New Zealand (SHELBOURNE et al., 1979). The choice of the right provenance is a most important step to obtain well adapted, fast growing stands and can save decades of tree breeding (WRIGHT, 1976). It is therefore most important to compare the progeny of the trees selected in the South African breeding programme of Mon-

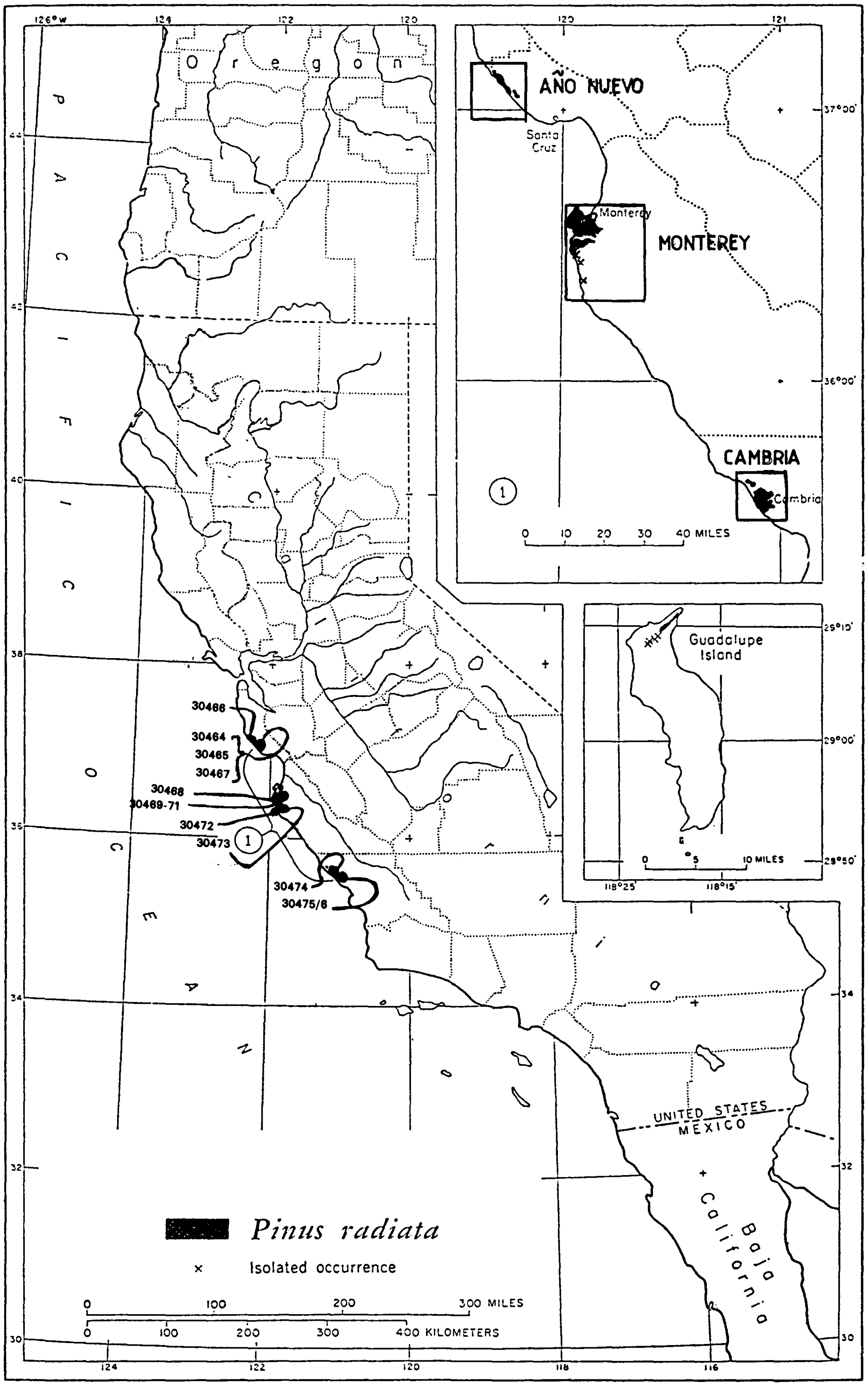

Figure 1. — Location of the *P. radiata* provenances studied in the natural distribution area. Area of distribution according to CRITCHFIELD and LITTLE (1966).

terey pine or used as seed source for reforestation with a large sample of provenances of that pine, in order to enable the choice and use of the best genetic material, be it local or exotic.

In 1978 an international expedition was mounted to collect seed from stands in the five natural populations of *Pinus radiata* in California (ELDRIDGE, 1978). Seed from that collection was received by the South African For-

Table 1. — Name and geographical coordinations ofthe *Pinus radiata* proventnces studied. (According to Eldridge, 1978).

Australian stock numbers	South African stock numbers	Population	Subpopulation	Latitude (degrees, hundredth)	Longitude (degrees, hundredth)	Altitude (m)	Number of trees collected
S 12586	30464	Año Nuevo	Coastal strip	37.10	122.28	20	70
S 12585	30465	Año Nuevo	Inland Central	37.10	122.25	200	40
S 12587	30466	Año Nuevo	Inland Swanton	37.07	122.23	150	40
S 12588	30467	Año Nuevo	Inland Northern	37.13	122.30	140	20
S 12590	30468	Monterey	Coastal sand dunes	36.62	121.95	30	55
S 12589	30469	Monterey	Monterey-Delmonte	36.58	121.87	45	37
S 12592	30470	Monterey	Huckleberry Hill	36.58	121.92	135	35
S 12591	30471	Monterey	Jacks Peak Park	36.55	121.87	200	61
S 12593	30472	Monterey	Point Lobos-Yankee Pt	36.50	121.95	50	22
S 12594	30473	Monterey	Carmel Highlands	36.50	121.92	330	34
S 12596	30474	Cambria	Pico Creek	35.62	121.15	75	26
S 12597	30475	Cambria	Cambria Town	35.57	121.10	75	49
S 12595	30476	Cambria	Scott Rock Inland	35.58	121.07	192	24
S 12657	30477	Canberra,	Guadalupe Hybrid	.	.	.	.

estry Research Institute and six trials were planted in 1980 and 1981 mainly in the winter and constant rainfall areas of South Africa.

In this article the pattern of genetic variation within and between the main populations is discussed with reference to commonly assessed silvicultural traits at age four and eight years. Finally the best provenances or local genetic controls are selected.

Materials and Methods

The three main populations of Monterey pine were sampled : Population 01 : Año Nuevo and Swanton, population 02: Monterey and Carmel and population 03: Cambria. Stands called subpopulations were collected within each population: four at Año Nuevo, six at Monterey and three at Cambria. Seed from 22 to 70 parent trees was collected within each subpopulation. Furthermore seed from 48 and 51 parent trees was collected on the islands of Guadalupe and Cedros respectively (Eldridge, 1978).

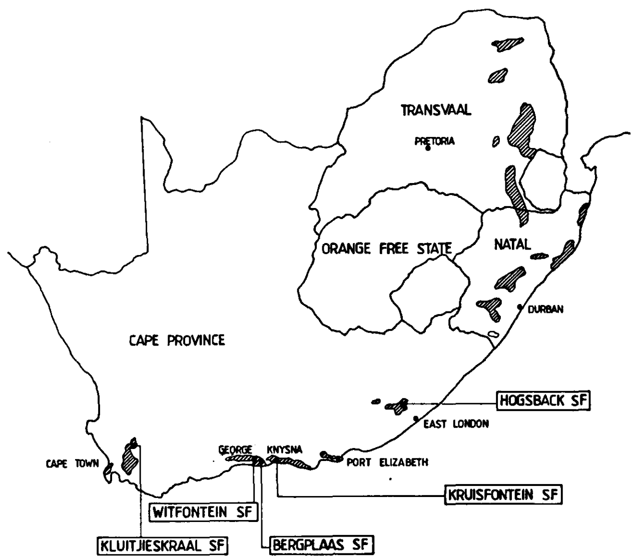

Figure 2. — Location of the *P. radiata* provenance trials in South Africa. Shaded areas are forest areas.

Table 2. — Details on the *Pinus radiata* provenance trials analysed.

Name	Location	Latitude (degrees, minutes)	Longitude (degrees, minutes)	Altitude (m)	Silvi-cultural zone	Annual rainfall (mm)	Soil	Effective soil depth (mm)	Date planted	Provenances tested	Design	Plot Size	Number of replications	Remarks
Bergplaas	Bergplaas State Forest (SF)(S.Cape)	33°52	22°38	1850	Bu4	862	Sandy loam to loamy sand (Longland and Wasbank forms)	600	8/80	All	Randomized complete block design (RCB)	10 trees row	10	Upper and mid-slope of a low mountain ridge. Slope:12°, aspect:east
Hogsback	Hogsback SF (E Cape)	32°36	26°53	1400	Bs5	1252	Sandy to clay sandy loam (Oakleaf and Glenrosa forms)	500 to 1000	3/81	All except 30472	RCB	10 trees row	9	Upper midslope. Slope:7°,aspect: east. Two major soil types exist. Many replications incomlete.
Kluitjies-kraal (I)	Kluitjieskraal SF (SW Cape)	33°26	19°10	800	Bw4	650	Loamy to coarse sands (Avalon, Longlands and Fernwood forms)	600 to 1000	9/80	All	RCB	10 tree row	10	Alluvial plain with three different types of soil. Many replications incomplete.
Kluitjies-kraal (II)	Kluitjieskraal SF (SW Cape)	33°25	19°07	460	Bw4	650(?)	Sand (Longlands and Clovelly forms)	800 to 1200	8/80	All	RCB	4x4 trees plot	5	Flootslope of intermontane basin. Destroyed by fire in 1986.
Kruisfon-tein	Kruisfontein SF (S Cape)	34°04	23°11	650	Bu3	906	Sandy to sandy loam (Constantia form)	800	8/80	All	RCB	4x4 trees plot	5	Upper and middle slope of dune ridge.Slope:11° aspect:south east. Wet, poorly drained soil.
Witfontein	Witfontein SF (S Cape)	33°58	22°31	215	Bu4	995	Loamy sand (Estcourt)	300	7/80	All except 30466 30472 30473	RCB	10 trees row	10	Moderately, poorly drained soil. Slope:1°, aspect:east.

Table 1 and *Figure 1* indicate the geographical coordinates and the location in California of the provenances studied respectively. Each subpopulation is considered as a provenance in this article. The three main populations are well delineated in the right corner of *Figure 1.* All provenances tested belong to one of the three mainland populations except the Canberra provenance whose seed was collected in a small Canberra (Australia) trial plantation established with Guadalupe Island seed. Seed collected in this trial is probably a hybrid with the pollen from surrounding plantations, which are largely of Monterey origin (personal communication of K. G. ELDRIDGE).

Figure 2 shows the location of the trials in South Africa. *Table 2* indicates the location, silvicultural zone, soil characteristics and design of the trials. The design in the field was a randomized complete block (RCB). Planting espacement was 3x3 m. Soil classification was done according to MACVICAR *et al.* (1977). All the trials contained the same genetic controls: a *Pinus radiata* commercial collection (29925) and a *Pinus radiata* seed orchard seedlot (25133). Two trials also contained controlled crosses.

In all trials, except at Hogsback, the following traits were measured at age four years: total height (HT) in m to the nearest 100 mm using a graduated staff; stem-form (STEM) according to a discrete, subjective eight-class scale (1:very poor - 8:excellent) and degree of infestation by the pine woolly aphid (*Pineus pini* MACQUART) (ARES) according to a discrete five-class scale (1:very heavy infestation - 5:no infestation). The Hogsback trial was measured at age five years six months and the following traits were measured: HT; diameter at breast height (DBH) to the nearest 5 mm; STEM according to the subjective scale and crown-form (CROWN) according to a subjective scale with eight classes (1:very poor - 8:excellent). At age eight years, the following traits were assessed on all trees in the five trials still surviving, the Kluitjieskraal II trial having been destroyed by fire in 1986: total height (HT) in m to the nearest 500 mm using a graduated staff; diameter at breast height (DBH) in mm to the nearest 10 mm; stem-form (STEM) and crown-form (CROWN) according to a discrete five class scale (1:very poor - 5: very good); aphid infestation (ARES) according to a discrete five class scale (1:very heavy infestation - 5:no infestation). Single tree volume (VOL) was calculated using the equation used by the Forestry and Environmental Conservation Branch of the Department of Environment Affairs. Beside these traits a number of defects such as foxtails, forks and epicormic branching were also assessed at both ages. For each trial a two-way frequency table was constructed and visually analysed for these defects.

All trials were analysed as RCB using the plot means. Nested analyses of variance were also calculated in order to compare provenances-within-population variability with between-populations variability. A nested model crossed with the replications was used. Non-orthogonal contrasts were calculated to compare two by two the three main populations. In all cases, the plot means were used. The procedure GLM (SAS, 1985) was used throughout. The procedure VARCOMP with the MIVQUEO method was used to estimate the variance components corresponding to the different effects (provenance, population, block and error) (SAS, 1985). Subset selection was used to select the best provenances (GIBBONS *et al.*, 1977).

In order to study provenance-by-site interaction the following approaches were used. (1) Across-sites analyses of variance were calculated for all traits and a completely random model was used to test the effects. (2) The regression of the mean of each provenance on the trial average for each trait was calculated in order to study the genotypic stability of the provenances. Stable provenances should have a regression coefficient equal to one. The coefficient of regression of each provenance was tested for equality with one. The dispersion of the provenance means around the regression lines was looked at visually. (3) Average for each provenance at each trial was plotted against the rank of the provenances at one trial for each trait. This allows a visual representation of provenance-by-site interaction.

We can accept that the genetic composition of a provenance can be re-constituted indefinitely by collecting seed from the same parents in the same seed stand pooling the seed for a number of years. Therefore the repeatability can be used to estimate the expected genotypic

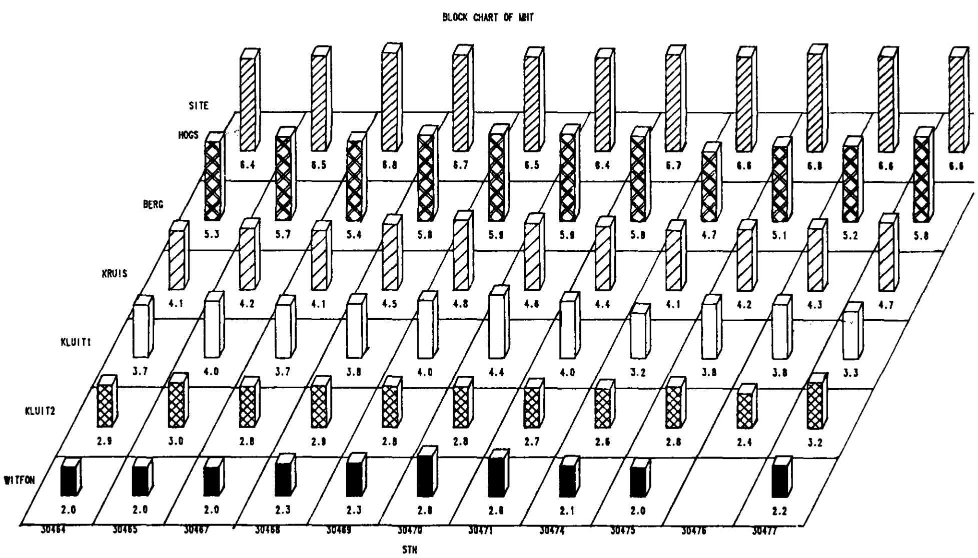

Figure 3. — Block chart of the mean height of 11 provenances common to the six sites. The name of the sites have been abbreviated. The mean heights have also been indicated. Age: 4 years.

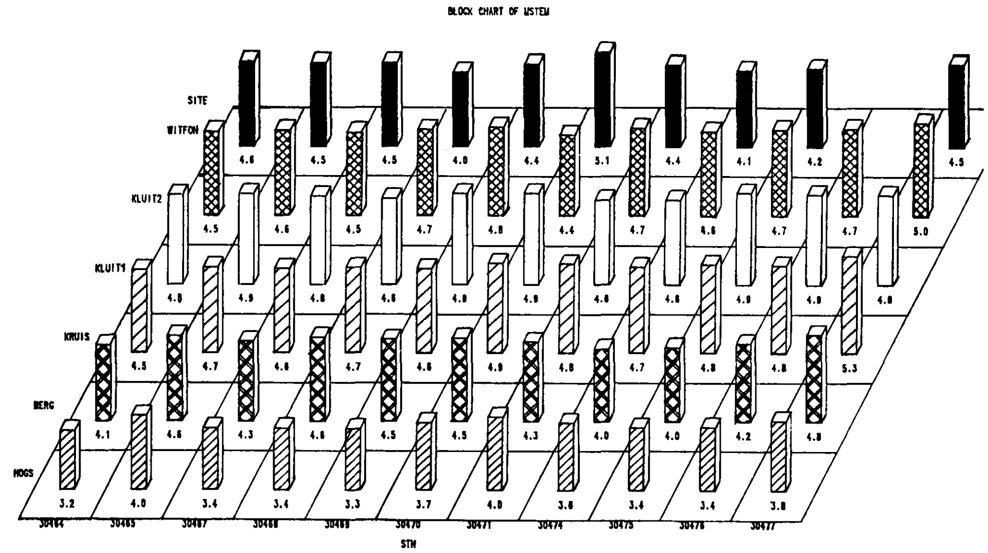

Figure 4. — Block chart of the mean stem-form of 11 provenances common to the six sites. Legend: see *Figure 3.*

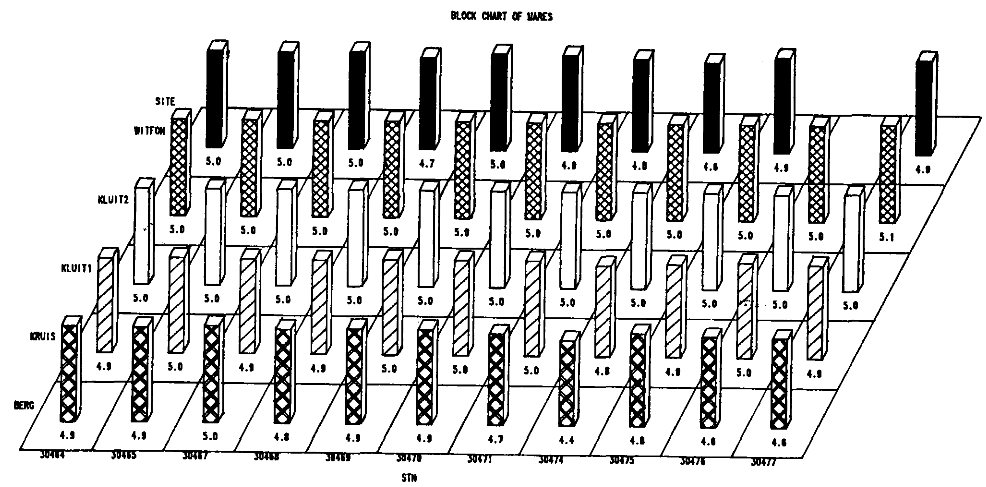

Figure 5. — Block chart of the mean aphid resistance of 11 provenances common to five sites. Legend: see *Figure 3.*

gain obtained by selecting the best provenance(s) if we disregard:

1) the fact that we do not know the exact ranking of the provenances,
2) the large sampling error affecting the estimation of that repeatability and of the genetic gains.

The repeatability in the broad sense was calculated in such a way as to allow the selection of the provenances on the basis of their averages (NANSON, 1970).

That repeatability or heritability of provenance means is:

$$h^2 = s^2_{prov}/s^2_{total}$$

s^2_{prov} = component of variance for provenance effect

s^2_{total} = $s^2_{prov} + s^2_{error}/r$

s^2_{error} = component of variance for the error term

r = number of replications (blocks) (NANSON, 1970).

The expected genotypic gain is:

$$R = h^2.S$$

h^2 = the coefficient of regression of the genotypic value of the provenance on its phenotype.

S = the selection differential is the difference between the mean of the provenance(s) selected and the mean of the trial.

Test significance was presented in the usual way: *** significant at a probability level of 0.001, ** at 0.01, * at 0.05 and NS: not significant.

Results

Provenance averages for mean height, stem-form and aphid resistance at four years for the six sites studied are shown in *table 3*. Provenance averages for height and tree volume at eight years for the five sites studied are shown in *table 4*.

3.1. Analyses of variance on a trial basis

The heritability applicable to provenance mean selection, the best provenances and genetic controls contained in the best subset identified with a probability of correct selection of 95% and the expected genetic gain in absolute value and as a percentage of the trial mean for the traits and trials where significant differences existed are shown

Table 3. — Average height (m), stem-form and aphid resistance (classes) of 11 provenances and two controls common to the six sites at age four years. The sites are ranked as much as possible from smallest to largest values of the traits. The standard deviation of the mean of the trial (SD) and the population mean (PM) are also indicated.

Population		Ano Nuevo				Monterey					Cambria				Canberra	Controls	
Provenance stock number		30464	30465	30467		30468	30469	30470	30471		30474	30475	30476		30477	29925	25133
Trait							Height										
Sites	SD				PM					PM				PM			
Witfontein	0.3	2.0	2.0	2.0	2.0	2.3	2.3	2.8	2.6	2.5	2.1	2.0	-	2.0	2.2	2.7	2.4
Kluitjieskraal I	0.3	2.9	3.0	2.8	2.9	2.9	2.8	2.8	2.7	2.8	2.6	2.8	2.4	2.6	3.2	3.6	4.2
Kluitjieskraal I	0.2	3.7	4.0	3.7	3.8	3.8	4.0	4.4	4.0	4.0	3.2	3.8	3.8	3.6	3.3	2.7	3.1
Kruisfontein	0.2	4.1	4.2	4.1	4.1	4.5	4.8	4.6	4.4	4.6	4.1	4.2	4.3	4.2	4.7	4.6	4.4
Bergplaas	0.2	5.3	5.7	5.4	5.5	5.8	5.9	5.9	5.8	5.8	4.7	5.1	5.2	5.0	5.8	5.8	5.6
Hogsback	0.2	6.4	6.5	6.8	6.6	6.7	6.5	6.4	6.7	6.6	6.6	6.8	6.6	6.7	6.6	7.0	6.8
							Stem-form										
Sites	SD				PM					PM				PM			
Hogsback	0.2	3.2	4.0	3.5	3.6	3.4	3.3	3.7	4.0	3.5	3.6	3.4	3.4	3.5	3.8	3.2	3.6
Bergplaas	0.2	4.1	4.6	4.3	4.5	4.6	4.5	4.5	4.3	4.1	4.0	4.0	4.2	4.1	4.8	4.5	4.4
Kruisfontein	0.2	4.5	4.7	4.6	4.8	4.7	4.6	4.9	4.8	4.8	4.7	4.8	4.8	4.8	5.3	5.1	5.1
Kluitjieskraal I	0.2	4.8	4.9	4.8	4.8	4.6	4.9	4.9	4.6	4.7	4.6	4.9	4.9	4.7	4.8	4.8	5.2
Kluitjieskraal I	0.2	4.5	4.6	4.5	4.6	4.7	4.8	4.4	4.7	4.7	4.6	4.7	4.7	4.7	5.0	4.5	5.4
Witfontein	0.2	4.6	4.5	4.5	4.0	4.4	4.4	5.1	4.4	4.1	4.1	4.2	-	4.1	4.5	4.4	4.4
							Aphid Resistance										
Sites	SD				PM					PM				PM			
Bergplaas	0.2	4.9	4.9	5.0	4.9	4.8	4.9	4.9	4.7	4.8	4.4	4.8	4.6	4.6	4.6	4.8	4.9
Kruisfontein	0.06	4.9	5.0	4.9	4.9	4.9	5.0	5.0	5.0	5.0	4.8	4.9	5.0	4.9	4.9	5.0	5.0
Kluitjieskraal I	0.01	5.0	5.0	5.0	5.0	5.0	5.0	5.0	5.0	5.0	5.0	5.0	5.0	5.0	5.0	5.0	5.0
Kluitjieskraal I	0.01	5.0	5.0	5.0	5.0	5.0	5.0	5.0	5.0	5.0	5.0	5.0	5.0	5.0	5.0	5.0	5.0
Witfontein	0.09	5.0	5.0	5.0	5.0	4.7	5.0	4.9	4.8	4.8	4.6	4.9	-	4.8	4.9	4.9	4.9

Table 4. — Average height (m) and tree volume (m^3) of 11 provenances and two controls common to the five sites at age eight years. The sites are ranked as much as possible from smallest to largest values of the traits. The standard deviation of the trial (SD) and population means (PM) are also indicated.

Population		Ano Nuevo				Monterey					Cambria				Canberra	Controls	
Stock number		30464	30465	30467		30468	30469	30470	30471		30474	30475	30476		30477	29925	25133
Trait							Height										
Sites	SD				PM					PM				PM			
Witfontein	0.7	5.9	5.9	5.7	5.8	6.5	6.7	7.5	6.8	6.9	6.3	5.8	-	6.0	6.1	7.6	6.7
Kluitjieskraal I	0.4	8.5	8.6	8.2	8.4	8.3	8.0	7.5	8.1	8.0	7.8	7.8	7.5	7.7	8.9	8.0	8.8
Kruisfontein	0.7	8.3	8.8	7.8	8.3	9.8	9.6	9.7	8.7	9.4	8.9	9.9	9.6	9.5	10.2	9.6	9.9
Bergplaas	0.4	10.3	10.1	9.2	9.9	10.5	10.4	10.5	10.9	10.6	9.7	10.1	9.6	9.8	10.6	11.2	11.4
Hogsback	0.4	11.2	10.9	11.0	11.0	11.2	10.5	10.5	11.1	10.8	10.6	11.2	11.0	10.9	11.4	11.5	11.4
							Tree Volume										
Sites	SD				PM					PM				PM			
Witfontein	0,007	0,02	0.0	0.0	0,02	0.03	0.03	0.04	0.03	0.03	0.02	0.02		0.02	0.02	0.04	0.03
Kluitjieskraal I	0,004	0.05	0.05	0.05	0,05	0.06	0.04	0.05	0.05	0.05	0.05	0.05	0.04	0.05	0.06	0.05	0.06
Kruisfontein	0,009	0.04	0.05	0.04	0,04	0.06	0.06	0.06	0.05	0.06	0.05	0.06	0.06	0.06	0.06	0.06	0.06
Bergplaas	0,008	0.06	0.06	0.06	0,06	0.08	0.07	0.08	0.07	0.08	0.06	0.07	0.06	0.06	0.08	0.09	0.09
Hogsback	0,02	0.11	0.10	0.11	0,11	0.11	0.11	0.10	0.12	0.11	0.10	0.12	0.11	0.11	0.11	0.14	0.14

in *Table 5*. However the genetic gain was considered as nil if the best subset contained a genetic control.

The F-tests (not shown) at eight years yielded similar results as at four years except that at Bergplaas, stem-form did not show any significant differences between the provenances or genetic controls at eight years and that at Kruisfontein at least significant differences existed for all traits while at four years some differences were significant at the 7% level. At Kluitjieskraal I there were no significant differences between provenances or genetic controls at both ages for growth traits but the other traits showed significant differences at eight years. At four years there were no significant differences between treatments for any traits at Kluitjieskraal II.

The pattern of differences remained fairly constant with the genetic controls the best at both ages. At Witfontein the Monterey provenance 30470 was the only best treatment for height at four years but it was not different from the commercial control for growth traits at eight years. Thus even at Witfontein selection of the best provenance would bring no genetic gain in growth. Note that at Hogsback the controlled cross was the best for growth traits but the two genetic controls ranked immediately below the controlled cross. At eight years all the traits

Table 5. — Heritability in the broad sense applicable to provenance selection (h^2), expected genotypic gain in absolute value (GG) and as a percentage of trial mean (%) if what seems to be best provenance is selected and reproduced totally and best subset of provenances (BS) for the traits and trials where significance was detected at age eight years. The stock numbers are ranked in decreasing order of mean values.

TRIALS	HT			DBH			VOL			STEM			CROWN			ARES		
	h^2	GG	BS	h^2	GG	BS	h^2	GG	BS	h^2	GG	BS	h^2	GG	BS	h^2	GG	BS
Bergplaas	0,68	Nil	25133* 29925*	0,75	Nil	25133* 29925*	0,73	Nil	25133* 29925*	0,00	Nil	-	0,67	Nil	30477 30464 29925*	0,82	Nil	30467 30464 30465 30469 25133*
Hogsback	0,74	Nil	20X32**	0,82	Nil	20X32**	0,84	Nil	20X32**	0,39	Nil	30477 20X32** 25133*	0,73	Nil	29925* 20X32** 30477 25133* 30464	0,78	Nil	20X32** 30467 30465 30464 29925* 30469 30473 30466 30470 25133* 30471
Kruisfontein	0,70	Nil	30477 25133* 30475	0,63	Nil	29925* 30469 30470 25133*	0,60	Nil	30470 25133* 29925* 30469 30475 30477	0,67	Nil	25133* 30477	0,50	Nil	30477 25133*	0,37	Nil	30466 30465 30470 30472 30469 25133* 30464 30471 30476 30467
Kluitjeskraal (I)	0,19	Nil	-	0,00	Nil	-	0,00	Nil	-	0,68	Nil	10X43**	0,56	Nil	10X43** 30477 25133* 29925*	0,58	Nil	30476 30475 30473 30471 30470 30469 30468 30467 30464 29925* 25133*
Witfontein	0,75	Nil	29925* 30470	0,57	Nil	30470 29925*	0,64	Nil	30470 29925*	0,32	Nil	30477 30474 30468 25133*	0,45	0,14 (5%)	30465 30464	0,79	Nil	30465 30464 30467 30470 30471 29925*

*) Genetic control
**) Controlled cross

Table 6. — Component of variance of the different sources of variation studied expressed as percentages of total variability and significance of these sources of variation for the study of the relative importance of population versus provenances within population effects for five sites at eight years and for average volume per tree. The order of the sites is that of *Table 4.*

Sources of Variation	Degrees (*) of Freedom	SITES: Witfontein	Kluitjieskraal I	Kruisfontein	Bergplaas	Hogsback
Population	2	16,60 *	0,00 NS	11,55 *	7,93 **	0,00 NS
Provenances Within Population	10	0,39 NS	0,00 NS	7,42 NS	2,40 NS	12,11 NS
Replication	4	5,39 NS	51,14 ***	27,41 ***	20,44 **	24,73 **
Error	48	77,62	48,86	53,62	69,23	63,14
TOTAL	64	100,00	100,00	100,00	100,00	100,00

(*) The degrees of freedom are given as an example and depend on trials.

showed significant differences while at four years height did not show any significant differences between treatments.

At both ages the heritabilities were similar at all trials. A look at *table 5* shows clearly that at age eight years no genetic gain could be expected by selecting imported provenances, except perhaps at Witfontein for crownform by using two Año Nuevo provenances. Still the expected genetic gain was small (5% of the trial average).

3.2. Differences between the three main Pinus radiata populations

Nested analyses of variance showed that there were no significant differences between provenances within population for any traits and trials except for aphid resistance at Kruisfontein. As an example the results of the analyses of variance performed for volume per tree are shown in *table 6.*

The comparisons of the three populations two by two by means of contrasts resulted in the following.

At Bergplaas, the Monterey population was significantly superior to the Año Nuevo population in growth traits as was the case at four years, but it was not dif-

Table 7. — Component of variance of the different sources of variation studied expressed as percentages of total variability and significance of the sources of variation for across-site analyses at age eight years.

		Traits					
Sources of variation	Degrees of freedom	Height	Diameter at breast height	Volume	Stemform	Crownform	Aphid resistance
Site (S)	4	73,19 ***	72,51***	76,66***	50,87***	38,40***	51,03 ***
Provenance (P)	10	1,12 ***	1,89*	1,37*	2,90*	9,87***	7,54 ***
Replications within site	20	5,55 ***	4,08***	4,20***	6,21***	19,36***	1,33 NS
SxP interaction	39	4,18 *	0,00NS	0,48 NS	0,00 NS	0,43 NS	5,53 ***
Error	189	15,96	21,52	15,29	40,02	35,94	34,57
Total	262	100,00	100,00	100,00	100,00	100,00	100,00

ferent from the Cambria population. For stem-form, crown-form and above all, aphid resistance, the Año Nuevo population was significantly the best.

At Hogsback at eight years, contrary to four years, there was no significant difference between the three populations in any traits except in aphid resistance with the Año Nuevo population showing the highest aphid resistance.

At Kluitjieskraal I as at four years, there was no difference between the three populations for growth traits. However small significant differences existed in stem-form and crown-form with the Monterey population sligthly better and in aphid resistance with the Año Nuevo population presenting sligthly better resistance.

At Kruisfontein at eight years, contrary to four years, for growth traits the Monterey population was significantly better than the other two populations. In stem-form and crown-form and in aphid resistance there was no significant difference between the three populations.

At Witfontein the Monterey population tended to grow the best, being significantly different from the Año Nuevo population but not from the Cambria population. In stem-form there were hardly any significant differences and none in crown-form. In aphid resistance the Año Nuevo population was significantly better.

3.3 Genotype-by-environment interaction

3.3.1. Across-sites analyses

Table 7 summarises the analyses of variance performed. There was a small site-by-provenance interaction for height and for aphid resistance at eight years. However for DBH and volume there was no significant interaction. Thus only the interaction for aphid resistance should concern us. Plotting of mean aphid resistance of the provenances over the rank of the same provenance at Kluitjeskraal I shows that the Hogsback site was responsible for that interaction, with the Año Nuevo population showing better resistance while at the other sites very little differences between provenances were expressed. Aphid infestation was at its worst at Hogsback (average score:4.35) as opposed to Kluitjieskraal I (4.99). However average infestation was low at all trials.

3.3.2. Provenance stability

The results of regressing each provenance mean on the trial mean for all the traits studied at eight years, in order to study provenance stability over the ecological range of five trials, are as follows. Height and DBH did not show any regression line which had a regression coefficient significantly different from one, partly because of the small number of sites which could be used (five) and thus the small number of degrees of freedom available. For height the two controls were stable and two provenances had regression coefficient nearly significantly different from one. For average volume per tree, most provenances and the two controls showed stability. However one provenance (30476) from Cambria had a regression coefficient highly significantly different from one ($b = +0.78$). Stem-form and crown-form were stable characters over the five sites studied. Aphid resistance showed great instability with many provenances having a regression coefficient significantly different from one. The commercial control had a highly significantly smaller regression coefficient of $+0.68$, indicating that that control was under-reacting to higher level of aphid infestation. The seed orchard control appeared to be stable.

Thus for aphid resistance the regression analyses confirmed the across-sites analyses of variance and indicated clearly what provenances were unstable. For height, no significant instability was detected. For volume per tree, some significant instability was detected although the analyses of variance did not detect any provenance-by-site interaction.

It seems that a variety of statistical techniques must be used to study a phenomenon like provenance-by-site interaction because of the notorious inability of the analysis of variance to detect "swamped" differences or interactions in treatment effects.

In practical terms, most provenances and controls appeared stable for the growth traits studied however.

3.4. Correlations between four-and eight-year measurements

At Bergplaas, correlations between four- and eight-year measurements using provenance means and plot means were moderate (r = + 0.58* to 0.62*) except for aphid resistance (r = + 0.93***). At Hogsback, very strong correlations existed between growth traits at four and eight years (r = +0.86*** to 0.94***). Stem-form at eight and four years was not correlated (r = 0.09 NS). At Kluitjieskraal I strong correlations (r = +0.92*** and higher) existed between four-and eight-year measurements except fcr aphid resistance which was not correlated. At Kruisfontein, all traits at four and eight years were moderately correlated (r = + 0.66** to 0.73**). At Witfontein, all traits at four and eight years were strongly correlated (r = +0.93***) except stem-form which was not correlated.

3.5. Variation in defects

Average natural mortality increased in all trials from four to eight years: at Bergplaas from 4.4% to 6.7%, at Hogsback from 8.5% to 16.0%, at Kluitjieskraal I from 9.7% to 11.9%, at Kruisfontein from 3.0% to 8.0% and at Witfontein from 30.6% to 38.8%. The percentage of living trees with defects increased substantially from 37.0% to 48.8% at Bergplaas. In the other trials it remained the same as at four years. In all trials, at eight years, the number of foxtail trees was negligible probably through natural elimination of the foxtails present at four years.

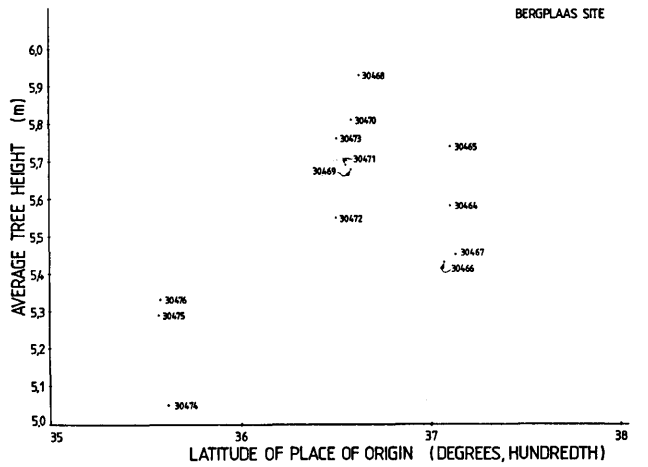

Figure 6. — Plotting of the average provenance height against latitude of place of origin at Bergplaas. Age : 4 years.

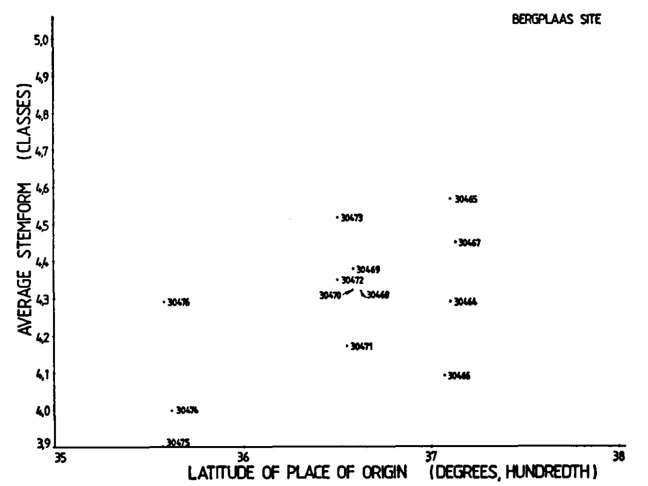

Figure 7. — Plotting of the average provenance stem-form against latitude of place of origin at Bergplaas. Age : 4 years.

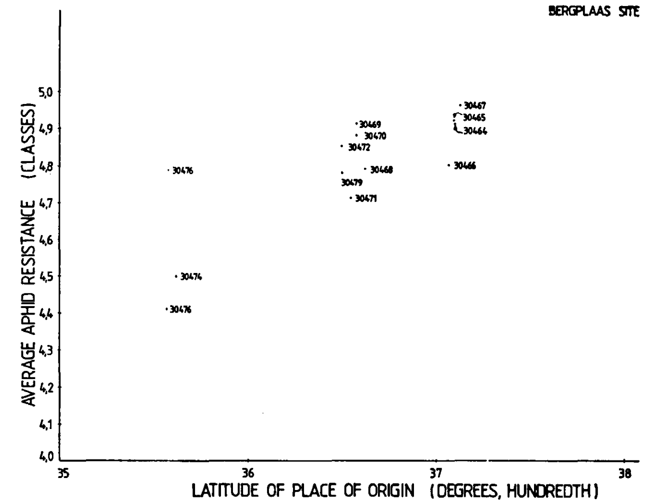

Figure 8. — Plotting of the average aphid resistance against latitude of place of origin at Bergplaas. Age : 4 years.

There was no evidence of provenance variation in rate of defects at any trial.

At Bergplaas forty nine percent of the living trees presented some defects. The most common defects were terminal leader dieback and forks (24.0% and 20.0% of the living trees). At Hogsback thirty two percent of the trees presented some defects. As at Bergplaas, the most common defects were terminal leader dieback (19.0%) and forks (9.0%). At Kluitjieskraal I, seventeen percent of the trees presented some defects. The most common defects were epicormic branching (9.0%), terminal leader dieback (4.6%) and forks (3.0%). At Kruisfontein thirty five percent of the trees presented some defects. The most common defects were terminal leader dieback (26.0%) and forks (9.0%). At Witfontein seventeen percent of the trees presented some defects. The most common defects were epicormic branching (7.0%), terminal leader dieback (5.0%) and forks (3.0%).

Discussion and Conclusions

The eight-year results showed that no introduced provenance performed better than the South African controls and that any gain should be sought from single tree selection and/or vegetative propagation. At Witfontein, while at four years large gain could be expected in height, at eight years, the South African commercial collection grew faster. At that site, small gain could be expected only in crown-form by selecting two Año Nuevo provenances at the expense of growth. Overall the error made by selecting the best genetic material at four years seemed to be acceptably small. It is recommended to survey the trials for outstanding individual trees to be grafted in a seed orchard or a clone bank especially if they are immune to aphid attack.

Irrespective of differences with the genetic controls the pattern of variation of the provenances varied widely from trial to trial. At Kluitjieskraal I there were no provenance differences for growth traits but elsewhere there was one different provenance outstanding for each trait at each site probably because of weak provenance correlations between the traits studied. Variation in provenance differences could not be related to design defects and soil heterogeneity because trials with more uniform soil did not show any more significant differences than other trials which contained three different soil types. The pattern of variation expressed by the provenances could not be related to silvicultural zones or other ecological characteristics although the average productivity level of the sites could. The change of pattern of variation at Bergplaas from four to eight years might be due to the number of trees with terminal leader dieback and forks which might have affected the measurements of height at eight years.

Most important was the fact that there was no significant difference for any trait between provenances within population except for aphid resistance at Kruisfontein. In other words, any provenance within a population could be used once the superiority of a population had been shown.

The frequency of forks and terminal leader dieback were attributed to hail damage and subsequent *Sphaeropsis sapinea* (FR.) DYKO and SUTTON localised infection (personal communication of Dr. D. GREY). That frequency varied from site to site. Hail damage was reported at Bergplaas and could be responsible for increased defects at that site. Increased mortality from four to eight years at all other trials could be due to hail damage and drought which affected the Southern Cape in the recent past. Poor growth and increasing average mortality at Witfontein was due to water logging.

The ranking of the sites in decreasing order of productivity is as follows at eight years: Hogsback, Bergplaas, Kruisfontein, Kluitjieskraal I and Witfontein. Volume growth at eight years was the fastest at Hogsback where annual precipitation was the highest for constant effective soil depth and it was the lowest at Witfontein where effective soil depth was the smallest although annual precipitation was sufficient (995 mm). Stem-form tended on average to deteriorate where height growth was the highest although within trial stem-form and height were generally positively correlated.

In growth traits, stem-form and crown-form the seed orchard seedlot was generally not significantly different from the commercial control, a fact which warrants further research in seed orchard management and the establishment of genetic gain trials. LAVERY (1986) contends that high humidity during summer is a limiting factor for Monterey pine as it results in building up of disease. The highest growth rate was experienced at Hogsback in an area with summer rainfall. It remains to be seen whether LAVERY's (1986) contentions will be true at Hogsback in the future.

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Provenance Variation in Pinus muricata in South Africa

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Summary

Genetic variation in height, diameter at breast height, stemform, crownform, resistance to *Pineus pini* and form defects, between six provenances of the "blue" and one of the "green" strain of *Pinus muricata* D. DON, have been analysed at the age of four and eight years, in four trials established in the constant, winter and summer rainfall areas of South Africa.

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