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, Kruistontein. 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.

#### Acknowledgements

I gratefully acknowledge the collection of seed by Dr. K. Eldridge, CSIRO, Australia and M. A. Firth, FRI, New Zealand. I wish to thank Messrs. R. G. Slabbert, J. Mather, B. Sesink and P. J. Lourens who planted and measured the trials studied here. Help from Mrs. R. Falkenhagen in data editing and processing is gratefully acknowledged. I am grateful to Mr. H. A. van der Suidb and Dr. G. van Wyk who commented on this paper.

#### References

ALAZARD, P. and DESTREMAU, D. X.: De l'expérimentation en France de Pinus radiata. Annale de recherches sylvicoles 1981. AFOCEL, 5-33 (1981). - Anon.: Commercial timber resources and roundwood processing in South Africa. Department of Environment Affairs. Forestry and environmental Conservation Branch, Pretoria. 131 pp. (1987). —— CRITCHFIELD, W. B. and LITTLE, Jr, E.L.: Geographic distribution of the Pines of the world. USDA F. S. Miscellaneous publication 991. 97pp. (1966). ELDRIDGE, K. G.: Refreshing the genetic resources of radiata pine plantations. Genetics Section Report No. 7. CSIRO, Division of Forest Research. Canberra, Autralia. 119 pp. (1978). — ELDRIDGE, K. G.: Genetic resources available. In: A. C. MATHESON and A. G. Brown, ed. Radiata pine breeding manual. Division of Forest Research, CSIRO. Canberra. Chapter 3. (1983). - FALKENHAGEN, E. R.: A framework for research on provenances of pine species for South African forestry. Report no P.3/87. South African Forestry Research Institute. Pretoria.92 pp.34 fig. (1987). — GIBBONS. J. D., OLKIN, I. and Zobel, M.: Selecting and ordering populations: a new statistical methodology. J. Wiley and Sons. New York. 569 pp. (1977). - GREY, D. C.: Site requirements of Pinus radiata: a review. South African Forestry Journal 148: 23-27 (1989). -GREY, D. C. and TAYLOR, G. I.: Site requirements for commercial afforestation in the Cape. South African Forestry Journal 127: 35-38 (1983). - LAVERY, P. B.: Plantation forestry with Pinus radiata. Review papers. Paper No. 12. School of Forestry. University of Canterbury, Christchurch, N.Z. 255 pp. (1986). -MACVICAR, C. N., LOXTON, R. F., LAMBRECHTS, J. J. N., LE ROUX, J., DE VILLIERS, J. M., VERSTER, E., MERRYWEATHER, F. R., VAN ROOYEN, T. H. and von M. HARMSE, H. J.: Soil classification. A Binomial system of South Africa. Dept. of Agricultural technical services. 150pp. (1977). - Nanson, A.: L'héritabilité et le gain d'origine génétique dans quelques types d'expériences. Silvae Genetica 19: - Nicholls, J. W. P. and Eldrige, K. G.: Variation 113-121 (1970). in some wood and bark characteristics in provenances of Pinus radiata D. Don. Australian Forest Research 10: 321-35 (1980). POYNTON, R. J.: Tree Planting in Southern Africa. Vol. 1. The Pines. Department of Environmental Affairs. 576pp. (1977). SAS Institute Inc.: SAS Users's guide: Statistics, version 5 edition. Cary, N. C.: SAS Institute. 956 pp. (1985). - Shelbourne, C. J. A., Burdon, R. D., Bannister, M. H. and Thulin, I.J.: Choosing the best provenances of radiata pine for different sites in New Zealand, New Zealand Journal of Forestry 24: 288-301 (1979). -SIMSEK, Y. and TULUKCU, M.: Growth and stem quality in Pinus radiata provenance trials established in the Marmara and Black Sea regions. Doga Bilim Bergisi, 71-77 (1983). - WRIGHT, J. W.: Introduction to forest genetics. Academic Press. New York. 463 pp. (1976).

# Provenance Variation in Pinus muricata in South Africa

By E. R. Falkenhagen\*)

South African Forestry Research Institute, Department of Environment Affairs, Pretoria, South Africa

(Received 17th April 1989)

# 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.

<sup>\*)</sup> Present address: School of Agriculture, University of Bophuthatswana, Private Bag X 2046, Mafikeng, 8670 South Africa.

The Sonoma provenance of the "green" strain was the best provenance in growth and stemform, often identified by subset selection as the sole outstanding treatment.

Strong clinal decline at all sites in growth and stemform with latitude or longitude of place of origin indicated that the most southerly populations of the "green" strain would be optimum for South Africa. Altitude of place of origin had no influence on provenance variation.

There was no evidence of provenance variation in rate of defects.

There was little or no evidence of provenance-by-site interaction for any of the traits studied.

Selection of the best provenance was possible at age four years.

Use of the Sonoma provenance at all sites suitable for Bishop pine was recommended as well as further testing of provenances of the "green" strain.

At four and eight years the growth rate of Bishop pine was inferior to that of *Pinus radiata*.

Key words: Pinus muricata, provenance variation, "green" and "blue" strains.

#### Introduction

Pinus muricata D. Don or Bishop pine is a member of the subsection oocarpae, section Pinus, subgenus Pinus of the genus Pinus and is closely related to Pinus attenuata and Pinus radiata with which it hybridises. It is a very variable maritime species occurring in seven disjunct populations on the coast of California and Northern Baja California and on islands close to the coast (Critchfield and Little, 1966).

In South Africa, *Pinus muricata* has been mainly planted in small trial plantings and is considered as having little or no future as timber tree since it is outclassed by *Pinus radiata* (Poynton, 1977).

However the origin of the seed used to test *Pinus muricata* in South Africa is unknown (Poynton, 1977) and it was decided to test the provenances of the blue strain of Bishop pine collected by the same team which extensively collected *Pinus radiata* in 1978. Eldridge (1979) has given details on the *Pinus muricata* seed collections. Provenance collections were mostly limited to the northern "blue" strain of muricata pine, the "green" strain from the central and southern coast of California having been considered as much less valuable (Eldridge, 1979). The northern part of the range of Bishop pine has a cool, cloudy and equable climate with winter rainfall of about 1000 mm supplemented by fog drip. The species is found on both very poor and very rich soils (Eldridge, 1979).

A very steep cline on less than three kilometer between the blue and green strains has been studied by MILLAR

(1983) using isozyme frequencies and attributed to pollen flow between formerly isolated populations. Differences in stomatal anatomy, monoterpene composition, growth and form, cone shape and resin canal numbers between 11 "green" and "blue" populations of muricata pine have been summarized by MILLAR and CRITCHFIELD (1988) who have also studied crossability between the same populations using viable seed production as criterion. Three isolated breeding units were distinguished. Shelbourne et al (1983) have studied three series of trials of Pinus muricata in New Zealand at age five to six years and concluded that on most sites the Sonoma "green" provenance was growing the fastest but they gave also preference to the Mendocino "blue' provenance. Schniewind and Gammon (1986) mentioned that there was no difference between the four races of Bishop pine (southern, central, northern and island) in wood density and strength properties.

Thus little is known about the genecology of Bishop pine. Therefore the trials of that pine established in South Africa were studied in detail.

#### Materials and Methods

Seed collection was to sub-population (=stand) and not to individual tree level. Between 20 and 40 trees at least 100 m apart were sampled and all cones bulked for each sub-population (Eldridge, 1979). Table 1 and figure 1 give details on the sub-populations collected and their geographical coordinations and ecological characteristics of their place of origin. Each subpopulation is called a provenance in this study.

The South African trials of Bishop pine were planted adjacent to some of the Pinus radiata trials which have been reported on elsewhere (FALKENHAGEN, 1991). The geographical coordinates and ecological characteristics of the trials are shown in Table 2. The trials were planted at Bergplaas State Forest (SF), Hogsback SF, Kluitjieskraal (II) SF and Witfontein SF and were planted in July to August 1980 except the Hogsback trial which was planted in February 1981. The soils were the same as in the Pinus radiata trials except at Kluitjieskraal II where soils of the Cartref, Fernwood and Longlands forms were present with effective soil depth ranging from 600 mm to 1200 mm. Soil classification was done according to Macvicar et al (1977). The design was a randomised complete block (RCB) with five to 10 replications with sometimes missing plots for some provenances. Planting espacement was 3 m  $\times$  3 m. Ten-tree row plots were used throughout except at Kluitjieskraal II where 4 × 4 tree plots were used. A commercial collection of Pinus muricata from a 75-year old-

Table 1. — Name and geographical coordinations of the Pinus muricata provenances studied.

Australian stock number	South African stock number	Name	Race	Latitude (degrees hundredth)	Longitude (degrees hundredth)	Altitude (m)	Number o trees bulked
12602	30457	Humboldt Trinidad Head	Blue	41.10	124.12	275	41
12600	30458	Mendocino coastal, Fort Bragg-Albion	Blue	39.33	123.77	65	21
12599	30459	Mendocino inland, Mendocino-Navarro	Blue	39.25	123.72	250	30
12601	30460	Mendocino Pygmy forest, Albion Ridge	Blue	39.23	123.72	160	20
12598	30461	Mendocino coastal, Pt Árena-Gualala	Blue	38.88	123.62	55	24
12603	30462	Mendocino inland, Pt Arena-Gualala	Blue	38.83	123.58	275	25
12604	30463	Sonoma coastal, Stewart Pt	Green	38.63	123.38	50	30

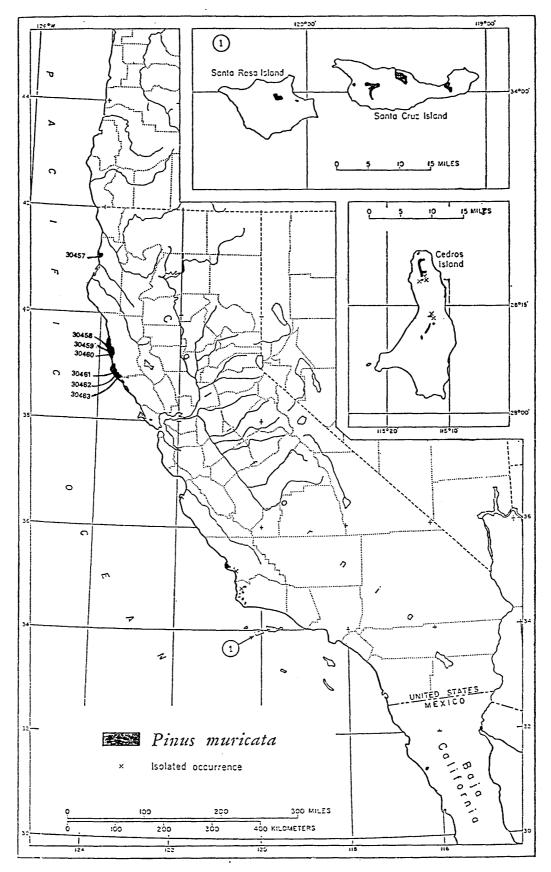


Figure 1. — Geographical distribution of Pinus muricata (after Critchfield and Little, 1966) and location of the provenances tested in South Africa. Other authors consider the Cedros island population as a Pinus radiata population. (See for instance Griffin and Critchfield, 1976).

Table 2. — Details on Pinus muricata provenance trials analysed.

N ame	Location	(degrees,	Longitude (degrees, minutes)		Silvicul- tural zone	Annual rainfall (mm)	<b>\$oil</b>	Effec- tive soil depth (mm)	Date planted	Provenances tested	Design	Plot size	Number of replica- tions	Remerks
Bergplaas	Bergplaas State Forest (SF) (S. Cape)	33*52	22*38	1850	Bu4	862	Sandy loam to loamy sand (Longlands and Wasbank forms)	600	8/80	ALL	Randomized complete block design (RCB)	i 10 trees row	10	Upper and midslope 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 form)	1200	3/81	All except 30460	RCB	10 trees	9	Upper midslope. Slope:3°, aspect: north East. Many replications incom- plete. Destroyed by fire in 1986.
Kluitjies- kraal (II)	Kluitjies- kraal SF (SW Cape)	33*25	19*07	460	Bw4	650(?)	Sand (Cartref, Fernwood and Longlands forms)	600 to 1200	8/80	All except 30460	RCB	4x4 trees plot	5	Footslope of intermontane basin. Destroyed by fire in 1986.
Witfontein	Witfontein SF (S. Cape)	33*58	22*31	215	Bu4	995	Loamy sand (Estcourt form)	300	7/80	All except 30460	RCB	10 trees	10	Moderately, poorly drained soil.

stand in the Tokai SF was used as a control throughout.

The following traits were measured at age four years seven months: total height (HT) in m to the nearest 100 mm using a graduated staff, stemform (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) according to a discrete five class scale (1:very heavy infestation — 5:no infestation). The Hogsback trial was measured at age five years seven months and the following traits were measured: HT, diameter at breast height (DBH) to the nearest 5 mm, STEM according to the subjective scale, crownform (CROWN) according to a subjective scale with eight classes (1: very poor - 8:excellent). In 1986 the Hogsback and Kluitjieskraal trials were destroyed by fire and the two remaining trials were measured at an age of about eight years using the same methods of measurements except that the scale of stem and crown had five instead of eight classes. Beside these traits a number of defects were also assessed such as foxtail, forks and epicormic branching.

The procedure GLM was used for analyses of variance and the procedure VARCOMP was used to estimate the variance components corresponding to the different effects (provenance, block and error) (SAS, 1985). A RCB model without interaction was used. Subset selection was used to select the best provenances (Gibbons et al., 1977).

The correlation matrix between the traits studied and latitude, longitude and altitude of place of origin was calculated for each trial, Multiple regression equations using these three characteristics of place of origin as independent variables were also calculated in order to try and predict the variation detected in each trait.

Provenance-by-site interaction was studied in three ways: (1) Combined analyses of variance were calculated for each trait and a mixed model with site fixed was used to test the effects. (2) The regression of the mean value of each provenance on the trial average 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 prove-

nance was tested for equality with one. Dispersion of the actual means around the regression lines was looked at visually. (3) Average trait values for each provenance at each trial was plotted against the rank of the provenances at one trial. This allows a visual representation of provenance-by-site interaction.

For each trial a two-way frequency table was constructed and analysed visually for the defects studied.

We can accept that the genetic composition of a provenance can be reconstituted indefinitely by collecting seed from the same parents in the same seed stand pooling the seed for a number of years. Therefore the heritability in the broad sense can be used to estimate the expected genotypic gain obtained by selecting the best provenance(s) if we disregard:

- the fact that we do not know the exact ranking of the provenances;
- the large sampling error affecting the estimation of that heritability and of the genetic gains.

The heritability 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 heritability is:

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

 $s_{prov}^2$  = component of variance for provenance effect

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

 $s_{error}^2 = component of variance for the error term$ 

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

The expected genotypic gain is:

$$R = h^2_{BS} \cdot S$$

 ${
m h^2_{BS}}=$  the heritability in the broad sense is 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 or of the control.

Test of significance was presented in the usual way: \*\*\* significant at a probability level of 0.001, etc.

Table 3. — Average height (m) and average stemform (classes) of the six provenances common to the four sites studied at four years. The sites have been ordered as much as possible according to increasing trial average.

Sites	Provenance stock number								
	30457	30458	30459	30461	30462	30463			
			Average hei	ght					
Witfontein Kluitjieskraal Bergplaas Hogsback	1,1 1,7 2,7 4,5	1,4 2,4 3,8 5,8	1,6 2,4 3,7 5,3	1,7 2,5 3,9 5,7	1,6 2,6 3,9 5,8	1,7 2,8 4,2 5,8			
		A	verage stemf	orm					
Hogsback Bergplaas Kluitjieskraal Witfontein	3,4 3,8 3,6	3,5 4,2 3,8 4,1	3,6 4,1 4,3 4,6	3,4 4,2 4,3 4,4	3,5 4,2 4,3 4,5	3,4 4,0 4,4 4,6			

Table 4. — Average height (m) and average stemform (classes) of the six provenances common to the sites studied at age eight years.

Sites	Provenance stock number								
	30457	30458	30459	30461	30462	30463			
	·		Average hei	ght					
Witfontein Bergplaas	2,9 5,2	3,5 6,9	3,9 7,1	4;1 7;5	3,6 7,4	4,7 7,9			
		А	verage stemf	orm					
Witfontein Bergplaas	1,9 2,3	2; <u>2</u> 2;5	2,5 2,6	2,6 2,6	2,5 2,6	2,6 2,4			

#### Results

Tables 3 and 4 show the average provenance height and stemform for the sites studied at age four and eight years respectively.

# 3.1. Four-year-results

# 3.1.1. Analyses of variance on a trial basis

Table 5 shows the broad-sense heritability, the expected genotypic gain in absolute and relative value as a

percentage of the control and the best subset of provenances delineated for each trait and trial where significant differences were detected with a probability of correct selection of  $95^{\circ}/_{\circ}$ .

#### 3.1.1.1. Bergplaas trial

There were at least significant differences between all traits studied at four years except for aphid resistance. The best provenance for height was the Sonoma coastal provenance 30463. For stemform, the best treatment was the control.

#### 3.1.1.2. Hogsback trial

All the traits studied presented at least significant differences except stemform. For height and DBH, the Sonoma provenance 30463 was the best. The expected gain in DBH was 20% of the control. The provenance Humboldt Trinidad Head had the best crownform. No gain could be expected in stemform or height because of lack of genetic variation and of differences with the control respectively.

# 3.1.1.3. Kluitjieskraal II trial

All traits presented at least significant differences except aphid resistance. The Sonoma provenance 30463 was again best in height and stemform with expected gain in height of 14% of the control mean.

#### 3.1.1.4. Witfontein trial

The picture was the same as at Kluitjieskraal with an expected genetic gain of nine percent in height by selecting the Sonoma provenance. In stemform no gain could be expected although the Sonoma provenance had the best stemform, because statistically it was not different from the control.

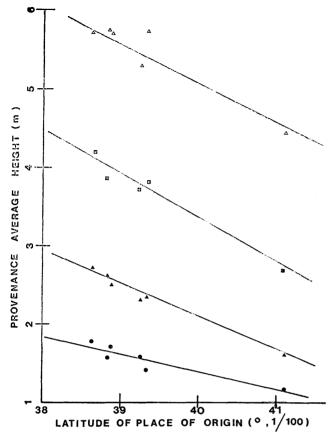
# 3.1.2. Correlation with place of origin

There was a strong correlation between latitude and longitude of place of origin ( $r=+0.92^{***}$ ) and any rela-

Table 5. — Heritability in the broad sense applicable to provenance selection (h²), expected genotypic gain in absolute (GG) and as percentage of the control 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 four years. The stock numbers are ranked in decreasing order of mean values.

Name of trials			Traits												
	нт			STEM			Aphid	resi	stance	DBH			CROWN	)	
	h <sup>2</sup>	GG (m)	BS	h²	GG	BS	h <sup>2</sup>	GG	BS	h <sup>2</sup>	GG	BS	h <sup>2</sup>	GG	BS
Bergplaas	0,96	0,40 (11%)	30463	0,72	nil	30559*	0,31	nil	nil	-	•	-	-	-	-
Hogsback	0,96	nil	30462 30458 30559* 30463 30461	0,06	nil	nil	-	-	-	0,97	19 (20%)	30463	0,70	0,25 (6%)	30457 30462 30458
Kluitjieskraal II	0,91		30463 30462	0,30	0,30 (7%)	30463	0,00	nil	nil	-	-	-	-	-	-
Witfontein	0,75	0,14 (9%)	30463 30461	0,78	nil	30463 30459 30559* 30462 30461	0,19			• 1 2	•	•	• • . •	•	•
	• .			**	• 6.										v.,

<sup>\*)</sup> Genetic control.



The correlation coefficients are all above -0.92\*\*\*

- $\Delta$  = Hogsback site
- Bergplaas site
- = Kluitjieskraal site
- = Witfontein site

Figure 2. — Plotting of the average height of the provenances common to the four sites studied against latitude of place of origin at age four years. The real regression lines are indicated.

tion with latitude holds true for longitude. Remarkably at the four sites there was a strong negative correlation ( $r=-0.92^{***}$  and higher) between height (and DBH) and stemform with latitude of place of origin except at Hogsback where stemform was not correlated with place of origin. Figure 2 shows the relationships of average height with latitude of place of origin. Nowhere altitude of place of origin had any influence. Multiple regression on place of origin did not improve prediction. Thus at all sites the lower the latitude of the place of origin of the provenance the better the height and stemform except at Hogsback where there was no significant difference between provenances for stemform.

# 3.1.3. Correlations between traits

At Bergplaas, Kluitjieskraal and Witfontein, there was a positive (favourable) correlation between height and stemform (r = 0.64\*\* to 0.92\*\*\*). At Hogsback there was none.

# 3.1.4. Provenance by-site-interaction

Table 6 shows the components of variance for the different factors tested as percentages of total variance and their significance. For all traits site effects were most important explaining from 20% to 76% of the total variance. Provenance effect was negligible for aphid resistance confirming the individual analyses. There was

a slight provenance-by-site interaction for height and stemform which explained three and six percent respectively of the total variance. Graphical representation of height and stemform provenance-by-site interaction showed that there was little instability for height, but more for stemform, the Bergplaas and especially the Hogsback trial presenting the greater changes in ranking. Regression analysis of provenance means on trial averages for height showed all provenances stable over the range of trials, particularly the genetic control 30559. This was clear in spite of only two degrees of freedom available to test the regression coefficients. In stemform, there was some wider variation in regression coefficients and dispersion around the regression lines but none statistically significant.

#### 3.1.5. Variation in defects

At four years, average mortality at Bergplaas was 2.2%, at Hogsback: 1.6%, at Kluitjieskraal: 10.4% and at Witfontein: 59.7%. At Bergplaas 20% of the living trees had defects with terminal leader dieback (5% of the living trees), forks (7%) and multiple stems (4%) the most frequent defects. At Hogsback eight percent of the living trees had defects with forks the most frequent defects (4%). At Kluitjieskraal 19% of the living trees had defects with forks (12%) and terminal leader dieback (3%) the most common defects. At Witfontein 17% of the living trees had defects with epicormic branching (4%), forks (4%) and terminal leader dieback (2%) the most frequent defects. There was no provenance variation in rate of defects.

#### 3.2. Eight-year results

The Kluitjieskraal and Hogsback trials were lost through fire in 1986 and only two trials could be analysed.

Table 4 shows the average provenance height and stemform at age eight years.

# 3.2.1. Bergplaas trial

The results were essentially the same as at four years. Correlations between four and eight year measurements were very strong (r=0.88\*\*\* to 0.98\*\*\*). Table 7 shows the eight-year results corresponding to Table 5. All the traits presented at least significant differences between

Table 6. — Component of variance of the different sources of variation studied expressed as percentages of total variance and significance of the sources of variation for across site analysis at four years.

			Traits			
Sources of variation	Degrees of freedom	HT (%)	Degrees of freedom	f STEM (%)	Degrees of freedom	Aphid resistance
Sites(S)	3	76,58***	3	22,03***	2	20,34**
Provenances (P)	5	2,70**	5	15,12***	5	0,00 NS
Replications within sites	33	9,93***	33	14,09**	27	14,90**
SXP interaction	15	2,95*	15	6,42***	10	5,91 NS
Error	148	7,84	146	42,34	124	58,85
Total	204	100,00	202	100,00	168	100,00

<sup>\*\*\*</sup> Significant at p=0,001; \*\* p=0,01 \* p=0,05; NS=not significant.

Table 7. — Heritability in the broad sense applicable to provenance selection (h²), expected genotypic gain in absolute (GG) and as percentage of the control if what seems to be the 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.

Name of trial	s						Traits	:							
	нт			DBH			STEM			CROWN	ı		Aphid	lresis	tance
	h <sup>2</sup>	GG (m)	BS	h <sup>2</sup>	GG (mm)	BS	h <sup>2</sup>	GG	BS	h <sup>2</sup>	GG	BS	h²	GG	BS
Bergplaas	0,98	1,09 (16%)	30463	0,97	201 (19%)	30463	0,81	nil	30559* 30460	0,51	nil	30559* 30463	0,52	nil	ni
Witfontein	0,84	0,63 (16%)	30463	0,67	80 (12%)	30463	0,67	0,11 (4%)	30461 30463 30459 30462	0,00	nil	nil	0,00	nil	nil

<sup>\*)</sup> Genetic control.

Table 8. — Component of variance of the different sources of variation studied expressed as percentage of total variance and significance of the sources of variation for across site analysis at eight years.

Sources of variation	Degrees of freedom		DBH	STEM	CROWN	Aphid resistance	
Sites(S)	1	84,00***	78,56***	0,00 NS	29,35**	0,13 NS	
Provenances(P)	5	4,56**	5,24**	16,46**	2,86 NS	5,65**	
Replications within sites	18	1,00 NS	1,00 NS	5,48**	8,11**	8,12**	
SXP interaction	5	4,11**	3,39 NS	2,54 NS	0,00 NS	0,00 NS	
Error	81	6,33	11,81	75,53	59,68	86,10 NS	
Total	110	100,00	100,00	100,00	100,00	100,00	

<sup>\*\*\*</sup> Significant at p=0,001; \*\* p=0,01; \* p=0,05; NS=not significant.

provenances except for aphid resistance. The Sonoma provenance was best in height and DBH but the genetic control was best in stemform while for crownform, both were best. There was a strong negative correlation between height, DBH and stemform and latitude (r = -0.98\*\*\*) or longitude of place of origin and nearly so for crownform. Average trial mortality was 4.5% at eight years with 46% of the living trees affected by defects with forks (25%) and terminal leader dieback (19%) the most frequent defects. Thus trees with defects had increased substantially at Bergplaas. Growth of the muricata pine was acceptable although slower than of the radiata pine. Average height varied from 5.2 m to 7.9 m, DBH from 84 mm to 126 mm at Bergplaas.

# 3.2.2. Witfontein trial

Again the results were similar to the four-year results with large gain possible in height and DBH (16% and 12% of the control), small gain in stemform and no genetic gain in crownform and aphid resistance. The Sonoma provenance could provide gain both in growth and stemform. Unfortunately at eight years, the average trial mortality reached 74.5%. Of the trees remaining, 27%

had defects with forks (9%), epicormic branching (8%) and terminal leader dieback (8%) the most frequent defects. Growth was very poor, average height varying from 3.0 m to 4.6 m and DBH from 52 mm to 72 mm.

#### 3.2.3. Provenance by-site-interaction

Table 6 shows the results of the across-site analyses done. For growth traits, site effect was predominant explaining  $78^{\circ}/_{\circ}$  to  $84^{\circ}/_{\circ}$  of total variability. There was a small provenance-by-site interaction for height but not for DBH. For the other traits no provenance-by-site interaction was significant. Thus the Sonoma provenance was best in growth at both sites. It is quite remarkable that in spite of a mortality of  $74^{\circ}/_{\circ}$  at Witfontein the pattern of provenance variation was the same as before.

# Discussion and Conclusions

The Sonoma provenance 30463, from Stewart Point, was at four and eight years the best provenance in growth and stemform, often identified by the subset selection test as the sole outstanding treatment. Comparable results were found in New Zealand (Shelbourne et al., 1982). The trees from that provenance were selected within 1.5 km of the coast on a very narrow strip 15 km long. However the trees were not checked for their needle color but reliance was made on geographical position (ELDRIDGE, 1979). Thus the exact taxonomical position of the Sonoma provenance should be checked. Nevertheless, the strong clinal decline in growth and stemform with increasing latitude or longitude of place of origin, clearly suggested that the most southerly of these populations, possibly of the "green" variety would be optimum for South Africa.

The absence of variation in aphid resistance between provenances could be attributed to the low level of infestation: 4.9 on average at both ages.

There was little or no evidence of provenance-by-site interaction in any of the traits studied. The increase in number of trees with defects at eight years at Bergplaas might be due to hail damage and/or drought stress.

At eight years, average height of muricata pine was less by two to three meters compared to the adjacent radiata pine provenance trials. However Pinus muricata

should be compared with *Pinus pinaster* and tested on leached, acid and well drained soils not on sites suitable for *Pinus radiata* (Personal communication by Dr. R. POYNTON). It was also clear that *Pinus muricata* suffered heavier mortality than *Pinus radiata* on waterlogged sites like at Witfontein.

At Bergplaas and Witfontein very strong positive correlations existed between the four and eight year measurements and selection at age four years was perfectly possible if we accept that the relative position of the provenances remains constant from the age of eight years. This was the case in provenance trials of *Pinus caribaea*, *Pinus elliottii* and *Pinus taeda* in South Africa (Falkenhagen, 1978, 1979).

It is recommended that more seed should be obtained from the Sonoma provenance. Further testing of provenances of the green variety should also be contemplated.

#### Acknowledgements

I wish to thank Messrs. R. G. Slabbert, J. Mather, B. Sesink and P. J. Lourens who planted and measured the four trials studied here. Help from Mrs. R. Falkenhagen in data editing and processing is gratefully acknowledged. I am grateful to Dr. P. Robbertse, Mr. H. van der Side and Dr. G. van Wyk for commenting on this paper.

#### References

CRITCHFIELD, W. B. and LITTLE, JR., E. L.: Geographic distribution of the pines of the world. USDA Forest Service. Mis-

cellaneous publication 991. 97pp. (1966). - ELDRIDGE, K. G.: Pinus muricata seed collections, 1978. Genetic section report number 8. CSIRO Division of forest Research, Canberra, Australia. 55pp. FALKENHAGEN, E. R.: Thirty-five years results of Pinus elliottii (Engelman) and Pinus taeda (L.) provenance research in South Africa. South African Forestry Journal 107: 22-36 (1978). FALKENHAGEN, E. R.: Provenance variation in growth, timber and pulp properties of Pinus caribaea Morelet in South Africa. Bulletin 59. South African Department of Forestry. Pretoria. - FALKENHAGEN, E. R.: Provenance variation in Pinus radiata at six sites in South Africa. Four year results. Silvae Genetica 40: (1991) - GIBBONS, J. D., OLKIN, I. and ZOBEL, M.: Selecting and ordering populations: A new statistical methodology. J. Wiley and Sons. New York. 569 pp. (1977). -J. R. and CRITCHPIELD, W. B.: The distribution of forest trees in California. U.S.D.A. Forest Service research paper PSW-82. 114pp. - Macvicar, C. N., Loxton, R. F., Lambrechts, J. J. N., Le ROUX, J., DE VILLIERS, J. M., VERSTER, E., MERRYWEATHER, F. R., VAN ROOYEN, T. H. and Von M. HARMSE, H. J.: Soil classification. A Binomial system for South Africa. Dept. of Agricultural technical services. 150 pp. (1977). — MILLAR, C. I.: A steep cline in *Pinus muricata*. Evolution 37: 311—319 (1983). — MILLAR, C. I. and CRITCHFIELD, W. B.: Crossability and relationships of Pinus muricata (Pinaceae). Mandroño 35: 39-53 (1988). -L'héritabilité et le gain d'origine génétique dans quelques types d'expériences. Silvae Genetica 19: 113-121 (1970). -J.: Tree planting in Southern Africa. Vol. 1. The Pines. Department of Environmental Affairs. 576pp. (1977). -- SAS Institute Inc.: SAS User's guide: Statistics, version 5 Edition. Cary, N. C. SAS Institute. 956pp. (1985). -- Schniewind, A. P. and GAMMON, B.: Strength and related properties of bishop pine. II. Properties of juvenile wood from young stems of various provenances. Wood and Fiber Science 18: 361-368 (1986). - Shelbourne. C. J. A., BANNISTER, M. H., and WILCOX, M. D.: Early results of provenance studies of Pinus muricata in New Zealand. New Zealand Journal of Forestry 27: 50-66 (1982),

# Inheritance Pattern of the Flavonic Compounds in Scots Pine (Pinus sylvestris L.)

By R. Yazdani<sup>1</sup>) and Ph. Lebreton<sup>2</sup>)

(Received 15th August 1989)

## Abstract

A genetic experiment of variation of the flavonic pattern in different crosses of *Pinus sylvestris* is presented. Variations fall in distinct categories in crosses between two clones. Some individuals show high prodelphinidin content (> 85%) and lack taxifolin; they are regared as homozygotes tt, or  $T^-$ . Clones with low prodelphinidin content and presence of taxifolin are all regarded as heterozygotes  $T_t$ , or  $T^+$ . We found no clone homozygote for  $T_t^+$  genotype, which is probably rare in the population.

Crossing experiments between heterozygote Tt and homozygote tt clones give offsprings compatible with 50: 50 segregation, whereas crosses between two heterozygotic clones give offsprings compatible with 75: 25 segregation. Thus it is suggested that one simple locus is responsible for most of the differences seen in the flavonoid patterns in Scots pine.

Key words: inheritance flavonoid Pinus sylvestris.

## Introduction

Laracine (1984), Laracine and Lebreton (1988), reported

the occurrence of two chemotypes within the Scots pine, *Pinus sylvestris*: the first contains prodelphinidin as major flavonic component of the needles. In the second chemomorph, phenyl-trihydroxylation decreases in favour of dihydroxylation of the lateral ring; prodelphinidin is rivalled by procyanidin whereas quercetin increases and taxifolin (= dihydro-quercetin) appears (see biochemical scheme). This taxifolin dimorphism has been more recently confirmed by Lundgren and Theander (1988).

Thus, the first chemomorph was called  $T^-$  (taxifolin absent) and the second  $T^+$  (taxifolin present). In the natural range of Scots pine, covering the whole of Europe, two modes of distribution of these morphs are observed: the first is located at high elevations (over 800 m) and/or latitudes (above Polar circle); the  $T^-$ -morph is largely predominant there, even exclusive in most of the cases (Alps, Pyrenees,..).

The second group of populations with taxifolin present is located at low elevations (from Eastern Europe to Southern France; Central and Southern Sweden is also covered). In these populations, the occurrence of individuals with taxifolin present represents 32% to 62%; however none of these populations differs significantly from the proportion 50%:50%.

Department of Forest Genetics, Faculty of Forestry, Swedish University of Agriculture Sciences, S-75007 Uppsala

<sup>&</sup>lt;sup>2</sup>) Laboratoire de Biochemie Végétale, Université Lyon-I., F-696 22 Villeurbanne