GENETIC SURVEY OF *PINUS RADIATA*. 7: VARIATION AND INHERITANCE OF PINENE COMPOSITION IN WOOD OLEORESIN

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ABSTRACT

Oleoresin was sampled from wood in lower boles of trees in a *Pinus radiata* D.Don provenance-progeny trial in Kaingaroa Forest in the central North Island of New Zealand, and the β-pinene/(α-pinene + β-pinene) ratios were determined by gas-liquid chromatography analysis. In one block 379 trees were sampled, representing 50 wind-pollinated progenies from each of two Californian populations (Año Nuevo and Monterey) and two New Zealand ones (Kaingaroa and Nelson); results for 32 and 24 of the progenies from Kaingaroa and Nelson respectively were cross-referenced with determinations on their seed parents. In another block 161 trees were sampled, drawn from 45 Nelson progenies which were all cross-referenced with seed-parent values.

The pinenes were the only major monoterpene components, except in one tree with 22.5% sabinene and 5.6% terpinolene. Populations differed markedly in β-pinene ratio ($p < 0.001$), Año Nuevo averaging ~80% and Monterey ~71%, Kaingaroa and Nelson being intermediate with ~75% and ~73% respectively. Año Nuevo and Kaingaroa were less variable than Monterey and Nelson.

Individual estimates of narrow-sense heritability were imprecise, but clustered around unity. They did not differ clearly between the Californian and New Zealand populations, or according to whether sib-analyses or offspring-parent regressions were used, although the latter gave better precision. The economic significance as a breeding goal, however, seems negligible.

The proportions of β-pinene appeared to rise appreciably as trees got older and taller, raising a caveat for comparing different plantings.

Keywords: monoterpenes; turpentine; oleoresin; variation; provenance; inheritance; heritability; *Pinus radiata*.

INTRODUCTION

Monoterpenes in conifers are of both commercial and scientific interest. They represent the turpentine that can be distilled from chemical pulp digesters or, where labour is cheap, from resin tapped from trees. Turpentine can be used as such, or various monoterpenes can be converted into other, more valuable compounds. For such conversion β-pinene, which predominates in turpentine from *Pinus radiata* wood, is a preferred compound.

Scientifically, monoterpenes are of interest, as indicators of genetic identity, for their roles in metabolic pathways, for their possible fungistatic significance (e.g., Rockwood

1973), and for their ambiguous roles as either toxins or attractants to insect pests (Smith 1972). At the same time they are easy to analyse chemically using gas-liquid chromatography (GLC), although each monoterpene is usually quantified only as a percentage of the turpentine fraction of oleoresin.

The issues of genetic identity include taxonomic status (both within and between species), determination of ancestry, and possible fingerprinting of individual genotypes. For these purposes monoterpene composition must vary, but be phenotypically stable (at least in relation to some sampling protocols) and should preferably show a high narrow-sense heritability (h^2). The additive inheritance and phenotypic stability which are both implied by $h^2 \rightarrow 1$ are important for inferring the status of a hybrid swarm. High h^2 has generally been found in conifer monoterpenes (Squillace 1976) but had not hitherto been confirmed for *P. radiata*.

In *P. radiata* both tree-to-tree variation and population differences in monoterpene composition were found by Bannister *et al.* (1962) and Blight *et al.* (1964) and, although the composition in individual trees proved to be stable in the short term, stability in the long term and across widely different sites was unproven. Moreover, the samples studied were from wood of the lower bole. This is a convenient collection site that gives stable composition, and where in *P. radiata* there are generally only two major components, α-pinene and β-pinene, which provide univariate data that are relatively easy to analyse. This last feature, however, makes comparisons one-dimensional, which is a severe restriction on the information content.

By contrast, the monoterpenes in oleoresin from the crown of the tree represent a far more complex mixture, with several major components that vary widely in their relative amounts. This has been confirmed for *P. radiata* by Zabkiewicz & Allan (1975). Foliage typically contains the most complex mixture, but with the least stable composition. Cortex of twigs offers a good compromise, still containing a fairly complex mixture in *P. radiata*, yet showing reasonable phenotypic stability provided sampling position and shoot ripeness are well standardised (cf. Burdon & Zabkiewicz 1973; Burdon, Gaskin, Low & Zabkiewicz 1992).

This paper is concerned with refining knowledge of variation within and between *P. radiata* populations in the α-pinene/β-pinene mixture in the lower bole, focusing on the two New Zealand populations included in the Genetic Survey experiment (Burdon, Bannister, Madgwick & Low 1992) and their two Californian progenitor populations (Burdon & Bannister 1973). It also covers heritability estimates, using different methods which, since they are subject to different biases from non-random mating (Burdon, Bannister & Low 1992b), provide an additional test of the convenient and often-used assumption of random mating. Furthermore, it addresses the question of long-term phenotypic stability of the composition of the mixture. The next paper in the series (Burdon, Zabkiewicz & Andrew 1992) covers the study of the more complex monoterpene mixture in the cortex of twigs to compare the various populations of *P. radiata*.

MATERIAL AND METHODS

The experiment, a provenance-progeny trial, has been described in detail by Burdon, Bannister, Madgwick & Low (1992). Relevant features for this paper are: the inclusion of

two New Zealand "land-race" populations, Kaingaroa and Nelson, and their Californian progenitor populations, Año Nuevo and Monterey, each sampled genetically in 50 essentially random wind-pollinated progenies (cf. Burdon, Bannister & Low 1992a); subdivision of the experiment into large site/stage blocks; and virtually complete individual randomisation within each block.

The parent stands of the Kaingaroa and Nelson populations have been described by Burdon, Bannister, Madgwick & Low (1992), and the parent-tree ortets were sampled for oleoresin, in addition to oleoresin sampling from offspring in the provenance-progeny trial.

Given the available material, the following procedures were undertaken:

(1) Oleoresin samples from the genetic samples of the Kaingaroa, Nelson, Año Nuevo, and Monterey populations in the Site B, Stage 2 block of the experiment were used for common-garden population comparisons and estimating variances and heritabilities by sib-analysis.

(2) The above oleoresin samples were cross-referenced with oleoresin samples from the seed parents in the Kaingaroa and Nelson populations respectively, for estimating heritability from offspring-parent regressions/correlations.

(3) Oleoresin samples from the Nelson population progeny in the Site A, Stage I block, were used for estimating variances and heritability by sib-analysis, and cross-referencing with oleoresin samples from their seed parents as in (2) to estimate heritability from offspring-parent relationships.

(4) Incidental to (1)–(3), possible shifts in monoterpene composition with increasing age of trees were investigated.

Sampling and Analysis

Samples from all sets of material described below were stored in sealed tubes or phials at around –20°C pending analysis. Delays between collection and refrigeration were inevitably longer in samples collected using the "tube-in-hole" method.

Nelson parents

Procedures were as described by Bannister *et al.* (1962). The trees were $15^1/_2$ years from seed, and around 18 m tall; oleoresin was collected by the tube-in-hole method from around breast height, and was analysed by gas-liquid chromatography (GLC) using the steam distillation technique and a thermistor detector, with the quantities of monoterpenes initially determined as peak areas. Of the trees sampled, 45 could be cross-referenced with their progenies on Site A of the experiment and 24 on Site B.

Kaingaroa parents

Preliminary sampling and GLC analyses were as described by Blight *et al.* (1964) and Blight & McDonald (1964), the methods being similar to those described by Bannister *et al.* (1962). Forty trees were sampled at age 16 years from seed, when the trees were around 21 m tall.

Further sampling was done when the trees were 24 years from seed and around 34 m tall. Microlitre samples of oleoresin were collected from notches in the wood at breast height

(1.4 m), using glass capillary tubes. Thirty-two trees which had progenies included in the experiment were successfully sampled. For GLC analysis c. 200 µl diethyl ether was added to each sample and an aliquot (1–4 µl) injected into the gas chromatograph. Equipment and conditions for analysis were: instrument—Pye 104; detector—flame ionisation detector (FID); automatic injector—S4 Pye Autojector; column—single, metal capillary FFAP SCOT, 50' x 0.02"; column oven—75°C; carrier gas—He, flow 6.7 ml/min; makeup gas—N_2, flow 40 ml/min; injector heater setting—4.5; recorder—HP 3380A.

Supplementary oleoresin samples were taken at the same time from twigs in the crowns of 15 of the trees, the resin being collected from scalpel cuts in the cortex just below the foliage of fully-ripened (well-lignified) first-season shoots (cf. Burdon, Zabkiewicz & Andrew 1992).

Nelson offspring, Site A

Forty-five progenies, whose seed parents had been successfully sampled, were chosen. One individual from each of four "colour replicates" (*see* Burdon, Bannister, Madgwick & Low 1992) was sampled, giving an intended genetic sample of four random trees per progeny. Of the intended 180 trees, 161 were successfully sampled at $10^3/_4$ years from planting, when the trees were about 15 m tall. Sampling was as described for the Kaingaroa parents at 24 years, except that the resin was collected from lower on the bole (40–50 cm height). GLC analysis was as described for the 24-year samples from the Kaingaroa seed parents.

Offspring, four populations, Site B

Oleoresin samples from all 50 progenies of each of the Año Nuevo, Monterey, Kaingaroa, and Nelson populations were collected, the use of one individual per progeny from each of two colour replicates giving essentially random sampling. Of the intended 400 trees, 379 were successfully sampled. Sampling was as described for the Nelson offspring, Site A. GLC analysis was as described for the 24-year samples from the Kaingaroa seed parents and for the Nelson offspring, Site A, except for the following features: column—18' glass/20% FFAP/20% Carbowax on GC-P 100–120 support; column oven—140°C; carrier gas—N_2, flow 60 ml/min. In addition, results were obtained with and without peak areas being corrected for detector response factors.

Data Analysis

All results of GLC analyses were expressed in terms of the ratio (β-pinene)/(α-pinene + β-pinene), henceforth referred to as $\beta/(\alpha + \beta)$ or the pinene ratio. The resulting data were analysed both as untransformed percentages and as arcsin transformations.

For each population, sib-analysis was based on one-way analysis of variance which tested for the significance of progeny differences (and thence heritability) and provided estimates of between-family variance (σ^2_f) and within-family variance (σ^2_w). The standard error of the population mean was calculated on the basis of the progenies mean square. The phenotypic coefficient of variation for the population (CV_P) was estimated as:

$$\widehat{CV}_P = (\hat{\sigma}^2_f + \hat{\sigma}^2_w)^{1/2} / \{x(Q - x)\}^{1/2} \quad (1)$$

where $\sigma^2_f + \sigma^2_w = \sigma^2_P$ = phenotypic variance
x = population sample mean
Q = upper bound of variable = 1 for untransformed values
zero = lower bound.

This expression is independent of whether composition is expressed as $\beta/(\alpha + \beta)$ or $\alpha/(\alpha + \beta)$.

Population differences overall were tested against progenies within populations in nested analysis of variance.

Narrow-sense heritability h^2 was estimated from sib-analysis as

$$\hat{h}^2 = 4\hat{\sigma}^2_f/(\hat{\sigma}^2_f + \hat{\sigma}^2_w) \quad (2)$$

under the provisional assumption that all progenies were half-sib families—in other words, that random mating had occurred in very large undifferentiated populations. Regressions of offspring family means on seed-parent values were used to estimate heritabilities as described by Becker (1984). The corresponding correlations were also used to estimate heritabilities by the method of Franklin (1974), albeit with approximations. Confidence limits were calculated as set out by Becker (1984) for heritability estimates from the sib-analyses and the offspring-parent (O/P) regressions.

Heritability estimates obtained assuming random mating are termed "apparent heritabilities" (Burdon, Bannister & Low 1992b). Departures from random mating have two components, inbreeding (expressed as an equivalent rate of self-fertilisation in non-inbred parents), and "full-sibbing" (expressed as the reciprocal of the effective number of unrelated pollen parents). The biases arising in sib-analysis estimates of $\hat{h}^2$ from non-random mating are addressed by Burdon, Bannister & Low (1992b, c), as are inferences concerning the magnitudes of the non-random components, and appropriate adjustments to apparent heritabilities. The expected bias in apparent heritability from offspring-parent (O/P) regression is a factor of 1 + z, z being the equivalent rate of selfing, which appears to be extremely low (c. 1%) in the New Zealand material.

Assumed mating patterns and appropriate correction factors for sib-analysis estimates based on random mating are listed by Burdon & Low (1992, Table 12).

RESULTS

As expected, the monoterpene fraction in the main batches of samples almost invariably comprised over 95% (and generally >97%) α-pinene and β-pinene. The β-pinene was almost always predominant with only occasional trees containing over 50% α-pinene. An exception was one Nelson offspring tree in Site A which had two other significant components, 22.5% of sabinene and 5.6% terpinolene.

Very highly significant ($p < 0.001$) differences were evident among the four populations sampled in Site B of the experiment (Table 1). Año Nuevo had the highest average level of β-pinene and Monterey the lowest, Kaingaroa being almost exactly intermediate between these two, and Nelson intermediate between Kaingaroa and Monterey. All pair-wise population differences were highly significant ($p < 0.01$) except those between Kaingaroa and Nelson and between Nelson and Monterey, with or without arcsin transformation.

Within populations the values of the pinene ratio were consistently somewhat skewed, the modes being higher than the means. Arcsin transformation removed most of the skewness,

but did not materially affect statistical tests for differences between populations or between families within populations. Variation within populations (Table 2) was consistently less, with and without data transformation, and for both parents and offspring, in Año Nuevo and Kaingaroa than in Monterey and Nelson, although none of the individual pair-wise differences in variances among populations was statistically conclusive. The transformation, however, markedly reduced the coefficients of variation.

Heritability estimates, representing "apparent heritabilities", were all very high (Table 3). Roughly half of them exceeded the theoretical bound of unity, but confidence limits were very wide, particularly with sib-analysis even though more families were involved than with the offspring-parent methods. Data transformation had very little effect on either point estimates or confidence limits, and so results are shown only for untransformed values. With the impreciseness of point estimates there were no clear overall differences in heritability between the natural populations and the New Zealand ones (although the estimate for Año Nuevo was significantly ($p < 0.05$) above the theoretical upper bound), nor between the estimates from sib-analysis and offspring-parent methods respectively although the latter gave marginally lower values overall.

TABLE 1–Population comparisons within a single site/stage block (Site B, Stage 2) for mean pinene ratio variables.

Population	Variable			
	(1)* $\frac{\beta}{\alpha+\beta}$ %	(2)* $\frac{\beta}{\alpha+\beta}$ % ±s.e.	(3) 2 Arcsin (2) ±s.e.	(4) $(\text{Arcsin})^{-1}$ (%)
Año Nuevo	78.8	79.7 ± 0.68 a	2.21 ± 0.017 a	80.0
Kaingaroa	74.2	75.2 ± 0.72 b	2.10 ± 0.017 b	75.5
Nelson	72.2	73,3 ± 0.96 bc	2.06 ± 0.022 bc	73.7
Monterey	70.1	71.2 ± 0.95 cd	2.01 ± 0.021 cd	71.5

Values in a column that are suffixed with a letter in common do not differ significantly ($\alpha = 0.05$, protected t-test).

* Variable 1 calculated on basis of unadjusted peak areas, variable 2 on basis of areas adjusted for detector response factors. Standard errors for variable 1 virtually identical to those for variable 2.

TABLE 2–Population comparisons for phenotypic variances $(\%)^2$ and coefficients of variation (%) (Eqn 1) in pinene composition, in offspring and parent material

Population	Trial site	σ^2_P		Coefficients of variation (%)			
				$\beta/(\alpha+\beta)$		Arcsin $\{\beta/(\alpha+\beta)\}$	
		Offspring	Parents	Offspring	Parents	Offspring	Parents
Año Nuevo	B	36	–	14.8	–	9.7	11.6*
Monterey	B	70	–	18.5	–	12.1	13.9*
Kaingaroa	B	39	55	14.4	18.5	9.7	8.2
Nelson	B†	64	76	18.1	21.2	12.2	12.6
Nelson	A	88	89	20.3	19.5	13.5	13.0

* Inferred from Bannister *et al.* (1962), without correspondence between sample trees and progenies in experiment.

† Parents and progenies represented are subsamples of the genetic samples providing the Site A values.

TABLE 3–Heritability estimates ("apparent heritabilities", based on assumption of random mating) for pinene ratio ($\beta/(\alpha+\beta)$), obtained using alternative methods, for individual populations. Point estimates (bold type) are flanked by 90% confidence limits

Population	Trial site	Method						
		Sib-analysis			Offspring-parent relationships			
					Regression			Correlation*
Año Nuevo	B	1.06	**1.93**	2.59		–		–
Monterey	B	–0.32	**0.77**	1.71		–		–
Kaingaroa	B	0.17	**1.12**	1.94	0.47	**0.93**	1.21	**1.01**
Nelson	B	0.36	**1.33**	2.11	0.73	**1.23**	1.76	**1.14**
	A	0.32	**0.80**	1.40	0.49	**0.86**	1.24	**0.76**

* Using method of Franklin (1974)—estimates necessarily rough approximations for $\hat{h}^2 > 1$.

Adjusting the sib-analysis estimates by a factor of 0.75 to 0.8, to allow for likely non-randomness of mating in native populations (Burdon, Bannister & Low 1992b, c; Burdon & Low 1992, Table 12) brought the lower 90% confidence limit for the Año Nuevo estimates well within bounds, and the average value for the two native populations to around unity. Adjusting the corresponding estimates for New Zealnand material by a factor of 0.9 to 0.95 brings the average value very close to unity, almost exactly into line with the average values from the regression/correlation methods which should be virtually unbiased.

Among trees of different ages the measured levels of β-pinene tended to increase progressively with tree age (Table 4). Some of the age-age comparisons, either within

TABLE 4–Comparisons between mean β-pinene ratios (i.e., $\beta/[\alpha+\beta]\%$), unadjusted for detection response factors, in parents and offspring at different ages (years) from planting and approximate tree heights (m).

Class of material	Comparison (where applicable)	Population					
		Kaingaroa			Nelson		
		Ratio	Age	Height	Ratio	Age	Height
Parent ortets	–	74.00*†	16	21	72.40†‡	$15^1/_2$	18
	–	81.04	25	34	72.52†	$15^1/_2$	18
	Age-age difference	7.04* ($p<0.01$)	9	13	–	–	–
Offspring	–	74.29	$12^1/_2$	18	69.20†	$10^3/_4$	15
	–	–	–	–	71.45	$12^1/_2$	17
	Age-age difference	–	–	–	3.25 ($p<0.02$)	$1^1/_2$	2
Parents-offspring	Difference	–0.29 ($p\sim0.2$)	$3^1/_2$	3	1.07 ($p>0.05$)	3	1
		–	–	–	3.20 ($p\approx0.05$)	$4^3/_4$	3

* Slightly different samples of parents involved at two ages, without pairing of values for parents common to both samples.

† Thermistor detector used, otherwise FID used throughout.

‡ Site A study, based on different sample of families from main Site B study.

parental material or between parents and offspring, were confounded with a difference in detector type, but the broad age-age pattern held up whether the thermistor detector was used on samples from younger trees or vice versa.

In the Kaingaroa population, where 15 parent trees were sampled for cortical oleoresin in the crown, pinene ratio was negligibly correlated between the crown samples and the breast-height wood samples ($r = 0.09$).

DISCUSSION

This study corroborated the higher average proportion of β-pinene in the Año Nuevo population than in Monterey which was observed by Bannister *et al.* (1962), and the tentative earlier results (Bannister *et al.* 1962; Blight *et al.* 1964) concerning the comparative variability of pinene ratio in samples of the four populations when allowance is made for a difference in the basis for calculating coefficients of variation. This study also corroborated the earlier results in showing Kaingaroa to resemble Año Nuevo more closely than did Nelson in both mean and variance. However, results in this study showed less resemblance than the earlier ones between the means of the New Zealand populations and Año Nuevo.

Estimates of the percentage of Año Nuevo genes in the respective New Zealand populations could be made on the basis of pinene ratios using the following equation:

$$\text{Año Nuevo genes (\%)} = [(NZ - M)/(A - M)] \times 100 \quad (3)$$

where NZ, M, and A are the means for the New Zealand population, Monterey, and Año Nuevo respectively. This gave figures of around 47% and 25% of Año Nuevo genes in Kaingaroa and Nelson respectively, regardless of whether arcsin transformation was used or not. The standard errors of the population means could be used to derive standard errors for both the numerator and denominator of Eqn 3, and thence standard errors of the ratio (Kendall & Stuart 1977, Ch. 10) which appear to be around 13% and 15% for the Kaingaroa and Nelson figures respectively. Thus, while the estimated percentages of Año Nuevo genes are lower than those obtained using means for some other traits (Burdon, Bannister & Low 1992a; Burdon, Zabkiewicz & Andrew 1992) they are not actually inconsistent with most of those estimates.

The use of Eqn 3 assumed additive genetic control, which is supported by the narrow-sense heritability being clearly very high. The use of the pinene ratio could generate some non-linearity with respect to variation in absolute amounts of one or the other of the components. That would tend to cause departures from purely additive inheritance of the ratio (even if absolute amounts are under strictly additive genetic control), and thereby erode heritability. No such effects, however, were evident; this does much to allay concerns of the sort of expressed by Birks & Kanowski (1988) over the analysis and interpretation of monoterpene composition data which are necessarily based on proportions.

Comparisons of apparent heritabilities between New Zealand and native populations, and from sib-analysis and O/P regressions/correlations, can indicate departures from random mating. The native populations were expected to show more inbreeding than the New Zealand land-race populations, and evidence reviewed by Burdon, Bannister & Low (1992b) indicated that this is so. In fact, with the limited numbers of imprecise point estimates there was no strong evidence of the higher apparent heritability that might be expected to result

from the inbreeding in natural populations. Similarly, there was no strong evidence of higher apparent heritabilities being obtained from sib-analysis, compared with O/P methods, in New Zealand material, despite the expectation that full-sibbing would bias upwards sib-analysis estimates but not O/P regression/correlation estimates. Nevertheless, assuming likely mating patterns (12% and 1% effective selfing in the native and New Zealand populations respectively, with corresponding rates of full-sibbing of 10–20% and 5–10%), the adjusted $\hat{h}^2$ values averaged around unity, and essentially the same between native and New Zealand populations and between sib-analysis and O/P methods. The results were not sensitive to variations in assumed rate of full-sibbing below 10%. It can thus be concluded with confidence that h^2 is extremely high, while the assumptions stated earlier in this paragraph concerning effective departures from random mating seem basically realistic.

In any event, the study does illustrate the greater power of the O/P regression method for estimating h^2 when family sizes are small, at least with a high-heritability trait (cf. Burdon & Low 1992).

Despite the high heritability of pinene ratio and the preferred status of β-pinene, there are no net economic attractions in breeding for increased β-pinene content. Assuming $h^2 = 0.8$, $\sigma_P = 7\%$, with 1.25 kg turpentine/m^3 wood, the price premium for β-pinene, and 90% culling for β-pinene level, the anticipated value gain per cubic metre of kraft-pulped wood would be barely NZ$0.10. That gain would be reduced by the proportion of the wood that is not kraft pulped, and would be obtained at appreciable cost of potential gain in other traits, notably stem volume production, which cannot be justified.

The level of β-pinene appears to rise as the trees get older and taller, allowing for some reservations about the comparisons between different batches of analyses. The data, however, give no clear indication as to whether age or height represents the more important determinant. Thus, despite the short-term stability of pinene ratio (Bannister *et al.* 1962) comparisons between trees of markedly different ages should be avoided. Differences in stand structure should probably be avoided if possible, too, because the real determinant of the increase in β-pinene level may be distance down the bole from the green crown. This factor may have introduced some variation in the Californian mainland samples reported by Bannister *et al.* (1962). The one other comparison that is available for trees of widely differing ages involved Guadalupe Island trees (Bannister & McDonald 1983), but the population samples were very narrowly based and the old trees on the island often had quite low crowns.

That the single tree with a high sabinene level also had a significant terpinolene peak is very interesting in view of the finding that levels of these two monoterpenes are almost perfectly correlated in cortical oleoresin of *P. radiata* (Burdon, Zabkiewicz & Andrew 1992; Burdon, Gaskin, Low & Zabkiewicz 1992; Burdon *et al.* in prep.), and the co-occurrence of these monoterpenes in the southern populations of the closely-related *P. muricata* D.Don (Forde & Blight 1964; Mirov *et al.* 1966). This suggests a close biosynthetic link between these compounds, which may be common to the two species. The tree in question showed no visual sign of being a hybrid with *P. muricata*, nor has any *P. muricata* from the populations with that feature of bole oleoresin been recorded in New Zealand, except as part of a recent experimental importation.

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