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Heritabilities and Correlations of the Cortical Monoterpenes of Virginia Pine (*Pinus virginiana* Mill.)

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Summary

Cortical oleoresin samples were collected from 840 trees. The sample trees were from 70 families that are part of an 8-year-old half-sib progeny test. Monoterpene analysis was done by gas liquid chromatography and the results were presented in microliters of monoterpene per standard sample.

Heritabilities of individual monoterpenes suggest that changes in concentration can be made through selection breeding. Delta-3-carene concentration appeared to be simply inherited with high concentration dominant over low. Other monoterpenes appeared to be quantitatively inherited. Correlations between the cortical monoterpenes and commercial characteristics indicate that monoterpenes would probably not be valuable as an indirect selection tool.

Key words: Heritabilities, Correlations, Monoterpenes, Inheritance.

Zusammenfassung

Es wurden Monoterpene aus der Rinde von 840 Einzelbäumen aus 70 Familien (8 Jahre alte Halbgeschwister) von *Pinus virginiana* MILL. gaschromatographisch untersucht. Die in Mikroliter angegebenen Mengen an Monoterpenen der standardisierten Proben erlauben die Schlußfolgerung, daß die Konzentrationen erblich sind. Die Delta-3-Konzentration wird direkt vererbt, wobei hohe Konzentrationen dominieren. Andere Monoterpene scheinen quantitativ vererbt zu werden. Nach den Untersuchungen ist es wenig wahrscheinlich, daß Rückschlüsse auf wirtschaftlich wichtige Eigenschaften zu ziehen sind.

Introduction

There are large variations in the monoterpene composition of the cortical oleoresin in pine species. Longleaf pine (*Pinus palustris* MILL.) usually has a 2 component system consisting of alpha- and beta-pinene (FRANKLIN and SNYDER, 1971). Monterey pine (*Pinus radiata* D. DON) represents the other extreme with a complex system of 12 monoterpenes in consistently measurable quantities and 2 more

that occur occasionally in trace amounts (ZABKIEWICZ and ALLEN, 1975).

Cortical monoterpene sampling is a relatively easy method of determining variability within a species and testing differences among populations within a species. If some of the monoterpenes are simply inherited, as indicated in other studies (HANOVER 1966; SQUILLACE 1971), they can be useful as genetic markers in genetic studies. They have also been investigated for possible correlations with growth.

This study was designed to (1) determine the heritabilities of individual monoterpenes and their total, (2) determine the correlations between the various cortical monoterpenes, (3) test previously hypothesized single gene inheritance of individual cortical monoterpenes, and (4) test correlations between the cortical monoterpenes and growth.

Materials and Methods

Experimental Planting

Selection of parents and stands from which open-pollinated progeny tests were derived was described by THOR (1964). The experimental material was a sample of the Vina, Alabama test. Locations of parental stands used in this study are given in Figure 1. The design is a randomized complete block with families randomized within blocks without regard to originating stands.

Statistics

The sample consisted of 4 replications of 10 stands with 7 families per stand and 3 sample progeny per family per replication for a total of 840 sample trees. The analysis of variance and expected mean squares used for determination of variance components are given in Table 1.

Heritability estimates derived from the analysis of variance were calculated from the following formula:

$$h^2 = \frac{4\sigma^2_{F(S)}}{\sigma^2_W + \sigma^2_E + \sigma^2_{F(S)} + \sigma^2_S}$$

Standard errors of heritability estimates were obtained by the method described by KEMPTHORNE (1957).

Genetic correlations were calculated using the formula:

$$gr = \frac{\sigma_{fxy}}{\sqrt{\sigma^2_{fx} \sigma^2_{fy}}}$$

where-

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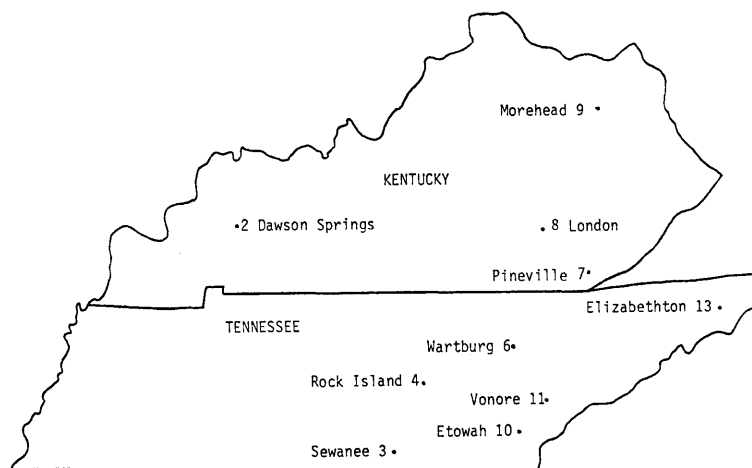


Fig. 1. — Location of parental stands for the Vina, Alabama, test planting.

Table 1. — Analysis of variance and expected mean squares for a randomized complete block with families randomized within blocks without regard to stand.

Source of variation	df	Mean square	Expected mean squares
Replications	$r - 1$		
Stands	$s - 1$	MS 1	$\sigma^2_W + n\sigma^2_E + nr\sigma^2_{F(S)} + pnr\sigma^2_S$
Families/stands	$s(p - 1)$	MS 2	$\sigma^2_W + n\sigma^2_E + nr\sigma^2_{F(S)}$
Among plot error	$r - 1 (sp - 1)$	MS 3	$\sigma^2_W + n\sigma^2_E$
Progeny trees/plots	$rsp(n - 1)$	MS 4	σ^2_W

$$\sigma^2_S = \frac{MS1 - MS2}{pnr}$$

$$\sigma^2_{F(S)} = \frac{MS2 - MS3}{nr}$$

$$\sigma^2_E = \frac{MS3 - MS4}{n}$$

$$\sigma^2_W = MS4$$

$\sigma_{f_{xy}}$ = the family covariance component of two characteristics derived from cross product analyses.

$\sigma^2_{f_x}$ = the family variance component of characteristic x

$\sigma^2_{f_y}$ = the family variance component of characteristic y

Simple correlations are phenotypic correlations calculated from individual tree data.

Sample Collection and Analysis

Cortical oleoresin samples were collected between the first week in October and mid-November when the monoterpene composition is stable. These samples were composited from subsamples taken from 6 to 20 buds in the middle to upper portion of the crown. At least 6 buds were sampled, to get a representative sample of the tree. Except where trees were overtopped, all buds sampled were exposed to full sunlight for a least a portion of the day.

Oleoresin samples were obtained by excising the tips of the buds. Samples were taken about 5 minutes after excision of the bud. A 50-microliter sample was obtained by drawing the resin up into a 100 microliter capillary tube. About 12 percent of the sample trees produced only enough resin for a 25 microliter sample. Immediately after sampling, the capillary tube containing the resin was broken into pieces inside a 3 dram vial, capped with a plastic cap containing a Teflon liner, and placed on ice.

A solvent containing 99 percent hexane and 1 percent paracymene standard was added at the end of the day. A full resin sample received 400 microliters of the mixture and a one-half sample 200 microliters. The vials were

sealed and refrigerated until analysis.

Monoterpene analyses were performed on a Beckman GC-4 gas liquid chromatograph with 20 foot long, 3/16-inch diameter stainless steel columns. These columns were packed with a liquid phase of 20 percent carbowax 20M on a solid phase of 60/80 mesh non-acid washed Chromosorb W. The chromatograph was equipped with flame ionization detectors and a Beckman Model 1005 recorder with a disc integrator. Helium was used as the carrier gas. Injection size was normally 0.7 microliter, but smaller injections were used when alpha-pinene was a large component.

Monoterpene identification was made by comparison of retention times between the samples and commercial monoterpenes and a standard mixture obtained from the USDA Naval Stores Laboratory at Olustee, Florida.

The paracymene added with the solvent was used as an internal standard for quantitative analysis as recommended by HANOVER (1966 c). The integrator value for paracymene represented 4 microliters of standard per 50 microliters of sample. The integrator values of each monoterpene and the sum of all monoterpenes were divided by the integrator value of the standard (paracymene) and multiplied by 4. This put all monoterpenes on a microliter per 50 microliter sample basis for statistical analyses.

Results and Discussion

Means and CV's

The monoterpenes of Virginia pine (*Pinus virginiana* MILL.) cortical bud resin can be divided into 2 groups for

Table 2. — Means and coefficients of variation for the various monoterpenes and total monoterpene content*).

Stand	Location	alpha-pinene	camphene	beta-pinene	myrcene	limonene	delta-3-carene	alpha-phellandrene	phellandrene	terpinolene	total monoterpenes
2	Dawson Springs, Ky.	3.84	.10 BCD**)	1.85 E	.40	.19 BC	.24	.01 BC	4.13 ABCD	.03	10.79 C
3	Sewanee, Tenn.	4.02	.15 A	2.89 BCD	.47	.25 ABC	.17	.03 B	4.85 AB	.01	12.84 A
4	Rock Island, Tenn.	3.05	.09 BCD	2.36 DE	.52	.29 A	.05	.05 A	5.24 A	.04	11.69 BC
6	Warburg, Tenn.	4.25	.11 ABC	2.70 CD	.51	.17 C	.24	.01 BC	3.03 DE	.03	11.05 BC
7	Pineville, Ky.	3.27	.07 CD	2.65 CDE	.60	.23 ABC	.13	.02 BC	4.32 ABC	.03	11.32 BC
8	London, Ky.	3.88	.12 AB	2.90 BCD	.52	.26 AB	.06	.02 BC	4.02 BCD	.03	11.81 BC
9	Morehead, Ky.	3.74	.12 AB	2.63 CDE	.58	.25 ABC	.10	.03 B	4.41 ABC	.00	11.86 B
10	Etowah, Tenn.	4.40	.06 D	3.67 AB	.47	.25 ABC	.00	.01 BC	3.05 DE	.03	11.94 B
11	Vonore, Tenn.	4.94	.08 BCD	3.89 A	.44	.13 C	.06	.00 C	2.08 E	.12	11.74 BC
13	Elizabethton, Tenn.	3.42	.06 D	3.36 ABC	.54	.24 ABC	.06	.01 BC	3.63 CD	.06	11.38 BC
Overall mean		3.86	.10	2.89	.51	.23	.11	.02	3.88	.04	11.63
Coefficient of variation (%)		49	82	41	49	58	586	235	48	440	14

*) Means given in microliters per 50 microliter sample.

***) Means followed by the same letter do not differ at the .05 level of probability.

the purpose of examination of volume differences. These groups were major components that occur all or most of the time in large quantities and minor components that occur irregularly and usually in small quantities. The 3 components which occur regularly in large quantities are alpha-pinene, beta-pinene, and beta-phellandrene, Table 2. Of these both alpha- and beta-pinene occurred in all 840 individual tree samples, but beta-phellandrene was absent in 95 (11%) of the samples.

The minor components occurred with less consistency than the major components. Three of them, however, camphene, myrcene, and limonene, had coefficients of variation that were not too different from those of the major components. The remaining 3 components, delta-3-carene, alpha-phellandrene, and terpinolene varied drastically and all had coefficients of variation greater than 200. The reason for the extremely large coefficients of variation for some of the components is obvious when the ranges in their concentrations and the frequency of their nonoccurrence are examined. The minimum individual sample values for all minor components was zero, which occurred frequently. Maximum sample values were 0.48 microliters for camphene, 2.15 microliters for myrcene, 5.82 microliters for delta-3-carene, 0.23 microliters for alpha-phellandrene, 1.40 microliters for limonene, and 1.85 microliters for terpinolene. The data for these components did not follow the normal distribution because of the large numbers of zero values.

Clinal variations are difficult to detect with only 10 stands sampled in a relatively small area. The data does suggest, however; that the amounts of alpha- and beta-pinene decrease from southeast to northwest. The inverse is true for beta-phellandrene. Delta-3-carene appears to increase from southeast to northwest. This is more evident if the number of trees with high delta-3-carene from Table 5 are plotted on the map.

The least variable of the monoterpene data was that of total monoterpenes. The coefficient of variation of 14 percent indicates very little variability when compared to the means of the individual monoterpenes. This coefficient of variation would be considerably lower if it were not for stands 2 and 3. Stand 2, the isolated stand in western Kentucky, was the only stand to average less than 11 microliters of total monoterpenes. Stand 3, the southern most stand sampled, represents the other extreme and was the only stand to average more than 12 microliters of total monoterpenes which is significantly higher than all the other stands. Although there was considerable variability from stand to stand in the individual monoterpenes, it appears that their total was relatively stable.

Analyses of Variance, Variance Components, and Heritabilities

The analyses of variance indicate that the monoterpenes are under rather strong genetic control, Table 3.

Stand effects were significant for beta-pinene, camphene, alpha-phellandrene, limonene, beta-phellandrene, and total monoterpenes, but they were nonsignificant for the remaining monoterpenes. The stand effect was nonsignificant for alpha-pinene but was significant for beta-pinene. These 2 terpenes are closely related, isomers of each other, and beta-pinene converts to alpha-pinene when subjected to mild heat. In this system of many components, however, they appeared to be independent.

The families within stands effect is significant for all monoterpenes analyzed and for total monoterpenes. This

Table 3. — Variance components and heritabilities for the various monoterpenes and total mono terpene content

	Alpha-pinene	Beta-pinene	Camphene	Myrcene	Delta-3-carene	Limonene	Beta-phellandrene	Alpha-phellandrene	Terpinolene	Total Monoterpenes
Stands	.092468 (2) ¹⁾	.300253* (14)	.000591* (8)	.001817 (2)	—	.001776* (8)	.750952* (15)	.000157* (6)	.000169 (1)	.211413* (6)
Families/stands	1.092550* (22)	.392592* (19)	.000663* (9)	.006927* (10)	.022862* (5)	.002932* (13)	.717518* (14)	.000118* (5)	.004608* (13)	.431950* (12)
Among plot error	.117961 (2)	—	.000261 (3)	.001739 (2)	.000230 (1)	.000536 (2)	—	—	—	.168185 (5)
Progeny trees/plots	3.625420 (74)	1.428710 (67)	.006233 (80)	.061982 (86)	.421422 (94)	.017315 (77)	3.506990 (71)	.002272 (89)	.030075 (86)	2.690980 (77)
Heritability	.89 (.18)**	.75 (.16)	.34 (.11)	.38 (.12)	.21 (.10)	.52 (.14)	.59 (.14)	.19 (.09)	.55 (.13)	.49 (.14)

¹⁾ 0 Percent of positive components.

*) Mean Square of ANOV significant at the .05 level.

**) Number in () is standard error of heritability estimate.

again points to strong genetic control of monoterpene composition of cortical resin. The families within stands effect was the only significant effect in the delta-3-carene analysis of variance. This could indicate that delta-3-carene concentrations may be controlled by one or very few genes as hypothesized by HANOVER (1966 b).

The variance components for alpha- and beta-pinene show a difference in stand effects. The components for the remaining effects for these two terpenes are similar in percentages of total variance components; but their heritabilities, 0.89 for alpha-pinene and 0.75 for beta-pinene, were somewhat different. The heritability for alpha-pinene was the same as that obtained by SQUILLACE (1971) in slash pine, but he obtained a heritability of 0.56 for beta-pinene, considerably lower than that obtained here. His values, however, were based on parent progeny regressions from selfed parents, which may account for some of the difference. The third major component, beta-phellandrene, had a variance component distribution similar to that of beta-pinene. The heritability was also lower than the 0.71 obtained by SQUILLACE (1971) in slash pine.

Alpha-phellandrene had the lowest heritability of all the monoterpenes. Delta-3-carene also had a relatively low heritability, 0.21. Delta-3-carene is thought to be conditioned by a single or only a few genes (HANOVER, 1966 b). If this compound is under strong genetic control, dominance gene action must be involved.

Almost all of the variation was concentrated in the trees-within-plots term, which suggests that selection should be made on an individual tree basis from progeny of selected parents. The heritabilities of all the monoterpenes, except the two mentioned above, were high enough to insure that progress could be made through selection if desired.

The heritability of 0.49 for total monoterpenes was also high enough to suggest that changes could be made through selection. The variance component distribution for total monoterpene was similar to that of the individual monoterpenes.

Correlations Among Monoterpenes

The simple correlation between alpha-pinene and beta-pinene was highly significant and positive, Table 4. If the postulated relationships, that positive simple correlations mean common precursors or biosynthetic pathways and negative correlations mean uncommon precursors or biosynthetic pathways (HANOVER, 1966 a) are valid, alpha-pinene and beta-pinene appear to be biosynthetically related. This is probably true because the two compounds are isomers, and it is reasonable to assume that they arise from a common system. ZAVARIN and COBB (1970) concurred with HANOVER's hypothesis and also found a positive relationship ($r = .65$) between alpha-pinene and beta-pinene in ponderosa pine (*Pinus ponderosa* LAWS.). Alpha-phellandrene and beta-phellandrene also have a positive highly significant simple correlation that is even higher than that of the two pinenes. This may mean either that the two phellandrenes are more closely related biosynthetically than the two pinenes or that the relatively unstable beta-phellandrene is converted to alpha-phellandrene. Both of these simple correlations are supported by even higher genetic correlations.

The cortical resin monoterpenes appear to be made up of two groups of related compounds that encompass seven of the nine analyzed monoterpenes. The first group comprises the two pinenes. They are positively correlated with one another and the correlation is highly significant, but

Table 4. — Simple and genetic correlations among the monoterpenes and total monoterpene content¹⁾

	Beta-pinene	Camphene	Myrcene	Delta-3-carene	Alpha-phellandrene	Limonene	Beta-phellandrene	Terpinolene	Total monoterpenes
Alpha-pinene	.15**) .19	.24**) .56	— .17**) — .03	— .12**) — .11	— .17**) — .42	— .41**) — .60	— .60 — .74	— .08*) — .22	.50**) .73
Beta-pinene		— .09**) — .22	— .10**) — .37	— .16**) .32'	— .27**) — .77	— .11**) — .22	— .49**) — .60	.16**) .16	.30**) .44
Camphene	— .09*) — .22		.17**) .38	— .14**) — 1.02	.15**) .05	.15**) — .15'	.11**) — .21''	— .16**) — .26	.38**) .38
Myrcene	— .10**) — .37	.17**) .38		— .13**) — 1.60	.18**) .59	.30**) .28	.34**) .32	— .06NS .05	.25**) .06
Delta-3-carene	— .16**) .32'	— .14**) — 1.02	— .13**) — 1.60		— .07NS — 1.64	— .16**) — .96	— .15**) — .68	.30**) 1.09	— .10**) — .69
Alpha-phellandrene	— .27**) — .77	.15**) .05	.18**) .59	— .07NS — 1.64		.23**) .91	.50**) .84	— .08*) .07	.21**) — .30''
Limonene	— .11**) — .22	.15**) — .15'	.30**) .28	— .16**) — .96	.23**) .91		.55**) .69	— .11**) — .07	.13**) — .24''
Beta-phellandrene	— .49**) — .60	.11**) — .21	.34**) .32	— .15**) — .68	.50**) .84	.55**) .69		— .17**) .02''	.12**) — .41''
Terpinolene	.16**) .16''	— .16**) — .26	— .06NS .05	.30**) 1.09	— .08*) .07	— .11**) — .07	— .17**) .02''		.01NS .00
Total monoterpenes	.30**) .44	.38**) .38	.25**) .06	— .10**) .69	.21**) — .30	.13**) — .24''	.12**) — .41''	.01NS .00	

NS Not significant at the 0.05 level of testing

*) Significant at the 0.05 level of testing

**) Significant at the 0.01 level of testing

¹⁾ Top number is simple correlation, bottom number is genetic correlation

Negative family covariance component, changes sign of correlation

Family and error covariance of opposite sign, error larger

Family and error covariance of opposite sign, family larger

their simple correlations with other monoterpenes, except camphene and terpinolene, are negative. Camphene has a highly significant positive correlation of 0.24 with alpha-pinene and a significant negative correlation of —0.09 with beta-pinene, while terpinolene has a significant negative correlation of —0.08 with alpha-pinene and a highly significant positive correlation of 0.16 with beta-pinene.

The second group is composed of beta-phellandrene, myrcene, alpha-phellandrene, limonene and camphene. All of these monoterpenes have positive simple correlations with one another and are negatively correlated with alpha- and beta-pinene. All the positive correlations are highly significant. These relationships are reasonable from the biosynthetic standpoint, since they are all acyclic or monocyclic monoterpenes except for camphene which is bicyclic. The pinenes are also bicyclic.

These positive simple correlations within groups and negative simple correlations between groups are generally supported by their genetic correlations. This indicates that at least two precursors, or biosynthetic pathways, are present in the cortical monoterpene resin system of Virginia pine.

The two remaining monoterpenes, delta-3-carene and terpinolene, do not appear to be associated with either group. Delta-3-carene was present in only 34 of the 840 samples and terpinolene in only 55. In both cases, many parents produced progeny without either or both of these monoterpenes. Their highly significant positive simple correlation of 0.30 and the genetic correlation of more than 1 suggest that they may be related. The correlations of these 2 monoterpenes with the others are of the same sign except beta-pinene, which is negatively correlated with delta-3-carene and correlated positively with terpinolene. The individual correlations of delta-3-carene and terpinolene with the other monoterpenes were approximately the same

magnitude, which is another indicator that these two monoterpenes may be related through a common precursor or biosynthetic pathway. Their genetic correlations, however, were quite erratic, had very high values, and did not always have the same sign as the corresponding simple correlations. This, along with their erratic occurrence, could mean that they are simply inherited and have a low frequency gene. Another explanation for the inconsistent genetic correlations may be the different structures of these two monoterpenes. Terpinolene is monocyclic and very similar structurally to limonene, while delta-3-carene is bicyclic and has a structure similar to the pinenes.

Total monoterpenes have a highly significant positive simple correlation with each individual monoterpene except for delta-3-carene and terpinolene. Delta-3-carene is significantly negatively correlated with the total monoterpenes and terpinolene is not significantly correlated. This is reasonable because the two systems of seemingly associated monoterpenes add to total monoterpenes and are significantly correlated, while the two which occur erratically generally contribute little to the total.

Inheritance

Single gene inheritance has been hypothesized and supported by data for beta-pinene and myrcene in slash pine (SQUILLACE, 1971) and for delta-3-carene in western white pine (HANOVER, 1966 b). Examination of the raw Virginia pine data does not indicate that beta-pinene levels are controlled by a single gene. SQUILLACE's data were based on percentages which had a bimodal distribution with a gap between 8 and 20 percent where no sample values occurred. In the present study, the data of beta-pinene approximated a normal curve with no gaps, but this data was in actual volumes and not percentages. Although no plot was made of beta-pinene divided by total monoterpenes, it is doubtful

Table 5. — Number of trees by parent where delta-3-carene makes up more than 2.41 percent of the total monoterpenes

Parent	Stand									
	2	3	4	6	7	8	9	10	11	13
1	1		0		0		0			0
2			1					0	0	0
3	0			0		0		0	0	1
4			0		1		1	0		0
5					0	0	0		0	
6		1			0	1	5			0
7	0	2		0			0			
8			0	0						
9	5	0	0	2		0	0	0	0	0
10	1	0	1	3		0	0	0	0	
11	0			0					0	0
12		0								
13					0	0				
14	1	0	0	0	1	0		0		
15		0			0			0	1	
Total	8	3	2	5	2	1	6	0	1	1

Table 6. — Correlations of Monoterpenes with height and diameter

	Correlation	
	Simple	Genetic
Eight-year-height × myrcene	.24**)	— .03'
Eight-year-height × limonene	.11**)	— .13'
Eight-year-diameter × myrcene	.17**)	— .13'
Eight-year-diameter × camphene	— .13**)	— .27

**) Significant at the .01 level.

Negative family covariance component, changes sign of correlation.

Family and error covariance of opposite sign, error larger.

that a bimodal distribution would develop because total values are relatively stable and beta pinene values are approximately normal; therefore, the results would approximate a normal curve. It appears then, that the beta-pinene component of cortical oleoresin is quantitatively inherited in Virginia pine. Myrcene, which also had bimodal distribution in slash pine, approximates a normal distribution in the present study and appears to be quantitatively inherited.

Using the same criterion as HANOVER, that is, less than 2.41 percent of total monoterpenes being a low concentration of delta-3-carene and more a high concentration, single gene inheritance of delta-3-carene is plausible. Most parent trees produced progeny with no measurable delta-3-carene component in the cortical resin, Table 5. Of the families that had progeny with delta-3-carene concentrations of more than 2.41 percent of total cortical monoterpenes, 5 had more than one progeny tree with high concentrations, 2 families had 2 trees, and 1 family had 3 progeny. The highest number of progeny from a family with a high delta-3-carene concentration was 5, and this number occurred in 2 families. From these data, simple inheritance could be inferred under the assumption that high concentration is dominant and the frequency of the dominant gene is low. Following this assumption, all parent trees were homozygous recessive except parent 9 in stand 2 and parent 6 in stand 9. These 2 parents are assumed to be heterozygous and their 5 high delta-3-carene progeny approximate the expected value of six if all matings were with homozygous recessive males. All other high delta-3-carene progeny would result from pollination by a dominant gene, which

would be a low frequency occurrence, and therefore mostly single progeny with high delta-3-carene were produced as would be expected. This is a relatively uncommon occurrence.

All other cortical monoterpenes are assumed to be quantitatively inherited. Though no distinct inheritance patterns appeared in this study, it is difficult to draw inferences of this type from open-pollinated material except to support or provide evidence against the hypotheses drawn in others studies.

Correlations of Cortical Monoterpenes with Height and Diameter

Simple correlations of total height at age 8 with myrcene and limonene were 0.24 and 0.11, respectively, Table 6. The genetic correlations were negative in both cases. The simple correlation between myrcene and 8-year diameter supports the correlation of myrcene and height, but again the genetic correlation was negative. Further testing of these unrealistic genetic correlations would be required to determine if they were caused by coincidence or a biological reality.

The simple correlation between camphene and 8-year diameter is highly significant (—0.13), and the genetic correlation was —.27. From this relationship and the relationship of myrcene with diameter, it appears that it may be possible, but probably not practical, to increase diameter growth by selecting trees with cortical resins that are high in myrcene and low in camphene.

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