PACIFIC SOUTHWEST Forest and Range Experiment Station

FOREST SERVICE
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LOCAL AND REGIONAL VARIATION IN THE MONOTERPENES OF PONDEROSA PINE WOOD OLEORESIN

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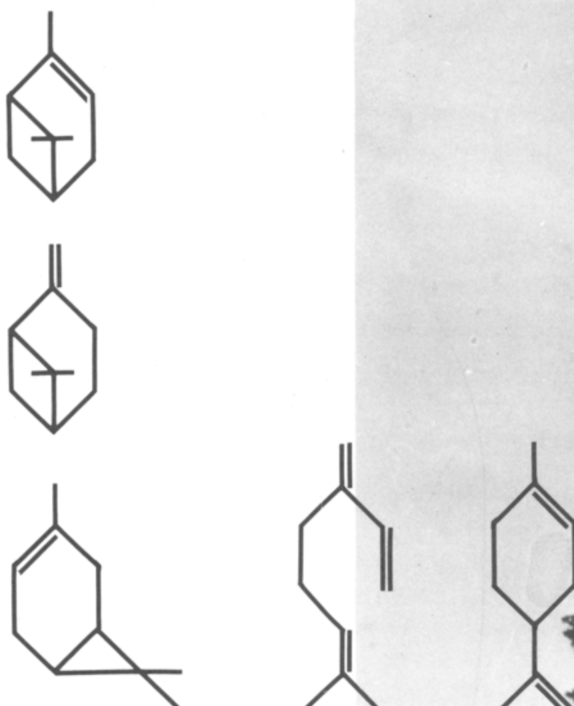

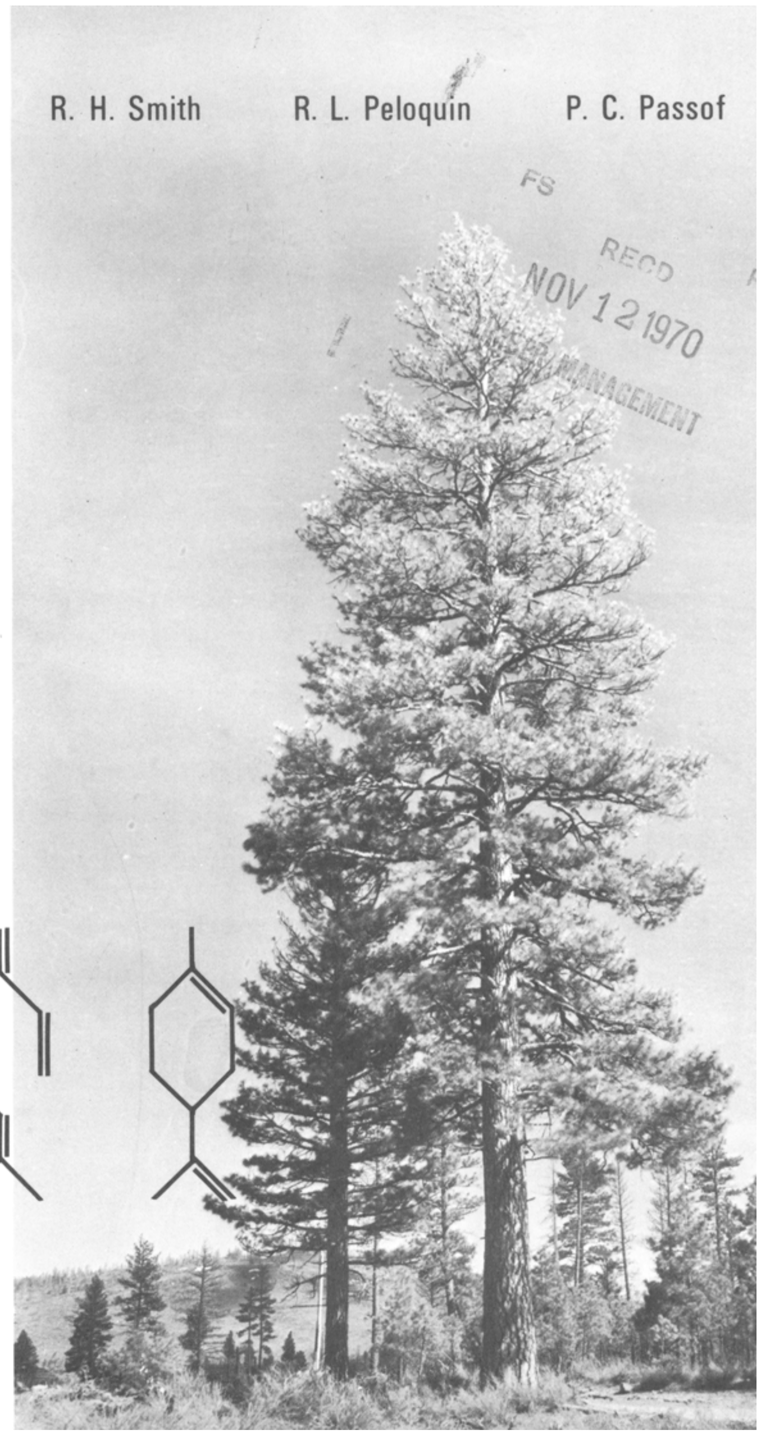

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OXFORD: 174.7 *Pinus ponderosa*–U581.192.1[–U547.596.7–019 + 165.53] .

RETRIEVAL TERMS: Pinus ponderosa; xylem monoterpene analysis; intertree diversity; geographic types.

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CONTENTS

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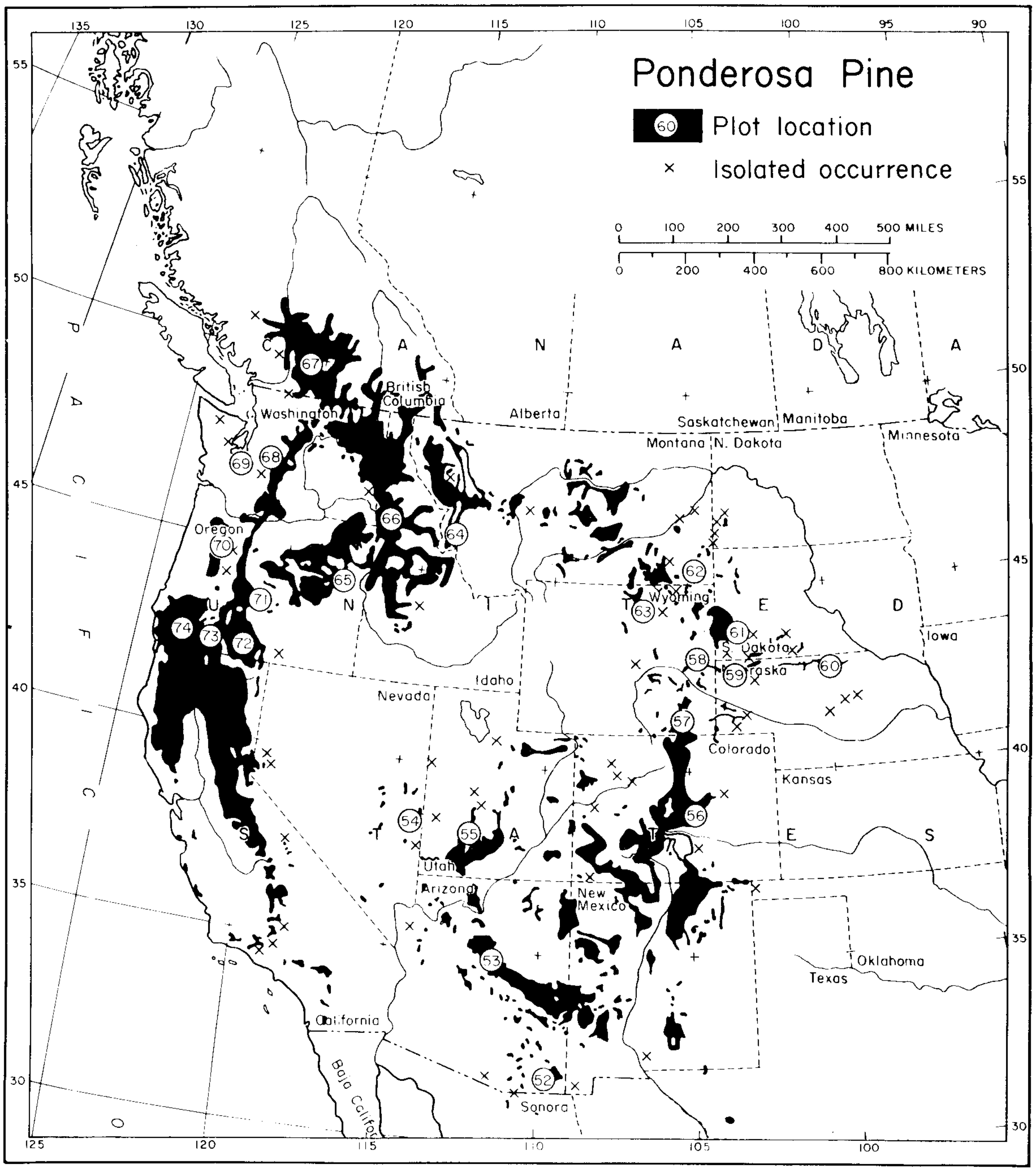

Figure 1.—*Distribution of Pinus ponderosa Laws. (from Critchfield and Little 1966) and location outside California of source used in monoterpene studies.*

Ponderosa pine *(Pinus ponderosa* Laws.*)* is one of the most abundant, economically important, and widely distributed pines in North America. Its range extends from British Columbia to Mexico and from Nebraska to the Pacific Ocean *(fig. 1)*. Quite variable, it is often subdivided into var. *scopulorum,* found on the east side of the northern Rocky Mountains and throughout the central and southern Rockies; var. *arizonica,* found only in southern Arizona and northern Mexico; and var. *ponderosa,* found on the remainder of the range. Var. *ponderosa* generally grows west of a line from the southeastern tip of Alberta to the southwestern tip of California; the other two varieties grow east of that line. But neither the existing definition nor distribution of these varieties is fully satisfactory.

Mirov (1961) found considerable regional variation in the turpentine composition of the wood oleoresin of ponderosa pine. His data were limited to small numbers of trees. And he had to combine resin from several trees to obtain the quantity needed for chemical analysis. Individual tree variation was obscured by the combining process, and he was unable to detect trace amounts of constituents.

Two recent studies have been made of ponderosa pine xylem monoterpene variation. Smith (1964) found large variations in the monoterpene composition within local populations of trees. Peloquin[1] found large regional variations, as did Mirov, and proposed eight types. He also found considerable variation within local populations in a region. Within a tree Smith (1964, 1968) found no variation due to season, method and place of sampling, and time and method of analysis.

This paper reports much of the data in the papers by Peloquin[1] and Smith (1964) and enlarges the scope of the study to include 927 trees. These data were gathered over a period of 3 years from samples taken in natural stands and from trees growing in plantations at the Institute of Forest Genetics (IFG), Placerville, Calif., from seed collected at the designated sites shown in figures 1 and 2. Much of the seed was collected from only a few trees—often less than three—at a locality. Variation could be reduced by this limited parentage. However, Peloquin[2] found nearly as much variation among siblings as among nonsiblings. We assumed that the place of germination of the seed and growth of the tree had no major effect on the monoterpene composition of ponderosa pine.

This study was made for three reasons: (1) Trees of varying composition were needed for further study and testing of the resistance of ponderosa pine to the western pine beetle *(Dendroctonus brevicomis* LeConte*)*; (2) the range of ponderosa pine is much greater than that of the beetle; studies of regional variation of monoterpenes might shed some light on this noncoincidence of ranges; and (3) the definition and distribution of ponderosa pine and its varieties could be clarified by data on monoterpenes.

PROCEDURES

The procedure used to collect and process the samples has been previously described (Peloquin[3]; Smith 1964). Essentially, a pentane preparation was made by adding an approximately equal volume of pentane to a sample of the freshly collected resin; in some cases a molecular distillate of the fresh resin was obtained at 40°C. The analysis of both kinds of preparation of the sample gave identical results. All preparations were held in tightly sealed vials at 35°F.

[1]Peloquin, R. L. *Geographic variations of the monoterpenes of Pinus ponderosa.* 1964. (Unpubl. master's thesis on file Stanford Univ., Palo Alto, Calif.)
[2]*Op. cit.*
[3]*Op. cit.*

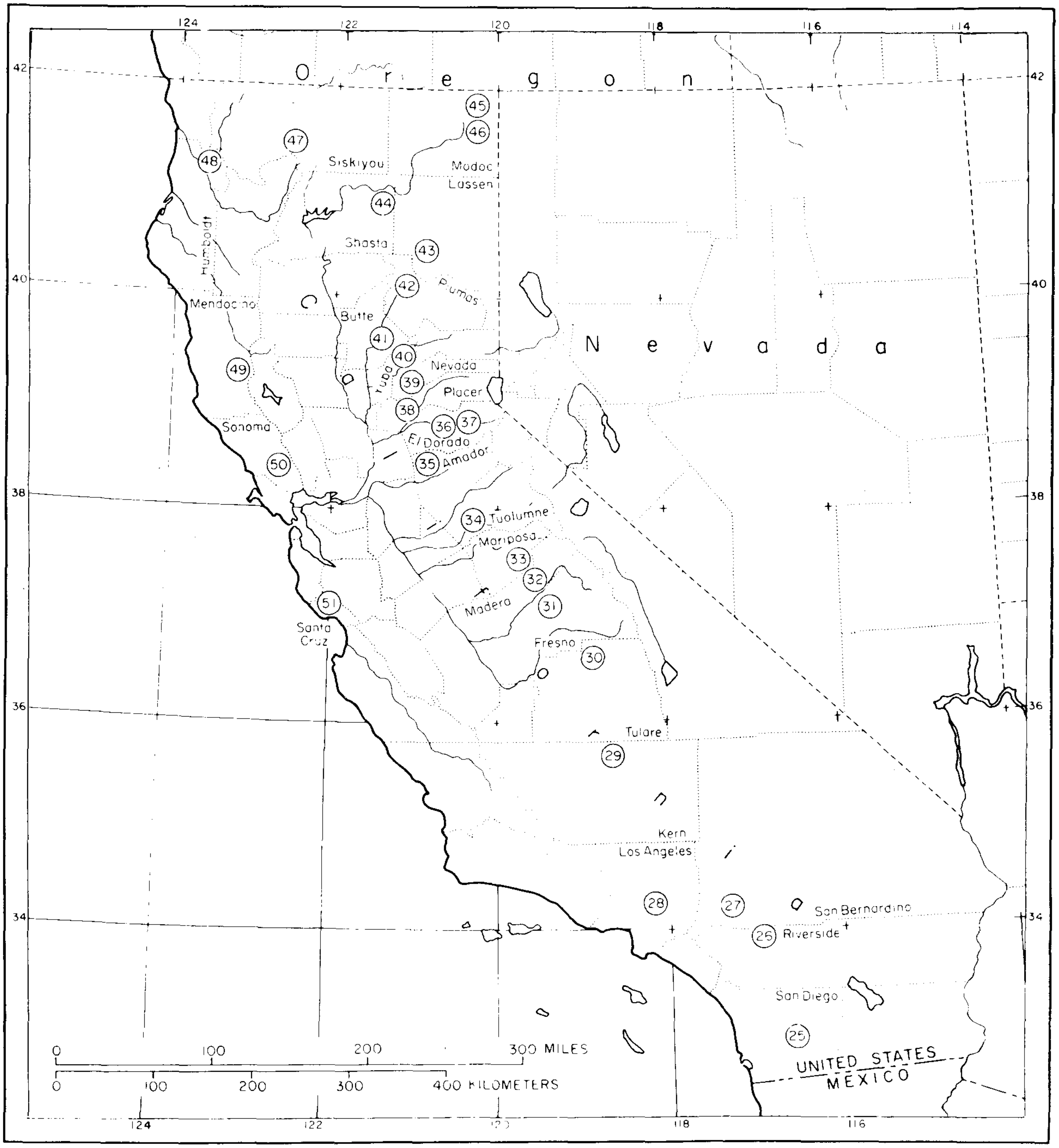

Figure 2.—*Location of sources in California of trees used in the study of the monoterpenes of ponderosa pine wood oleoresin.*

Samples were analyzed on the same gas chromatograph, using a thermal conductivity detector. The column was 8 feet by 1/8-inch stainless steel. The solid support was Chromosorb W A/W at 60/80 or 80/100 mesh; the liquid support was 7-1/2 or 10 percent β,β' oxydipropionitrile. Operational conditions were 130 to 140°C. on the injector, 55 to 65°C. on the column, and 145 to 155°C. on the detector. There were 200 ma. on the detector and 30 to 60 ml. of helium per minute. Sample size varied from 0.2 to 1.0 μ 1. Variations in these working parameters did not affect the analyses.

Qualitative determinations were made by comparing relative retention times with known chemicals and mixtures of known chemicals and by introducing these standards into the sample. These determinations were checked on two alternate columns: LAC-446 at 90°C. and Apiezon L at 110°C. Quantitative determinations were based on normalization of peak areas, as measured by a disc integrator.

Six limitations of the data should be emphasized: (1) All data apply to trees greater than 35 years old; (2) all resin was from the xylem; therefore, the data probably do not apply to other resin systems, such as needle, cortex, etc.; (3) all data apply only to normalized monoterpene components; (4) the data do not consider differences which might exist between trees in the proportion of the monoterpenes to the total resin; (5) the number of trees from a source varied considerably; some sources are represented by as few as two trees; (6) very small amounts of heptane might be masked by the solvent peak; however, measurable amounts can be found with the columns used.

RESULTS

Variations in Major Components

The five major monoterpene components in this analysis were: α -pinene, β-pinene, 3-carene, myrcene, and limonene. The minor components were considered separately.

Elevation

Ponderosa pine grows from near sea level to about 6,500 feet elevation in the central Sierra Nevada. The effect of elevation was studied by using 10 sources in the plantations at IFG and three sources from field locations which together comprise a transect. This transect extended from 1,800 to 6,700 feet. All sources except the one at 6,700 feet were within 10 miles of the South Fork of the American River in El Dorado County, Calif.; the 6,700-foot source was northeast of Lake Tahoe, about 30 miles from the transect line.

The mean and range for the five major monoterpene components varied considerably *(fig. 3A).* No apparent elevational trend was evident. There appeared to be no greater difference among the three field sources (Nos. 1, 5, 8) than there was among the 10 plantation sources. The three plots (Nos. 8, 9, 10) at the same elevation (2,700 feet) showed as much variation and range as did the plots at different elevations.

Eleven field plots were set up at 3,500 ± 300 feet elevation, all within a radius of 3 miles. The site lies near the midelevation of ponderosa pine in this region, near plot 36 *(fig. 2).* Again, there was nearly as much range and variation among single-elevation plots *(fig. 3B)* as among those at differing elevations.

Thus, elevation appears to have little or no effect on monoterpene composition—at least in the central Sierra Nevada. Any variation attributable to elevation appears to be masked by much larger local variations.

California

All but seven counties in California with ponderosa pine were sampled either by plantation plots at IFG or by natural plots *(fig. 2)*. The mean and range for all sources *(fig. 4)* are arranged in the numerical sequence used in figure 2. The trees in plot No. 36 were 30 to 40 years old; those in plot No. 37 were 200 to 400 years. The two plots differed only slightly in their monoterpene composition. Plots Nos. 45 and 46 represented natural and plantation plots; the first was a plantation plot of eight trees, the second a natural plot of 72 trees.

Neither the kind nor size of plot changed the average values appreciably, though an increase in the number of trees increased the minimum-maximum range. With more intensive sampling, all localities might be found to have a greater range of values.

California appears to have at least two types of ponderosa pine — southern California and Sierra Nevada-Cascades — and possibly even a third—northern Coast Ranges. And there may be a difference between the trees found in the central Sierra Nevada and in the Cascades.

Trees in the southern California mountains typically lack 3-carene and have large amounts of β-pinene. However, 3-carene begins to appear more often in trees and in increasing amounts as a northward direction is pursued in the southern California mountains and into the southern end of the Sierra Nevada.

In the Sierra Nevada-Cascades, trees have much less β-pinene and much more 3-carene than those from the southern California mountains. It is not

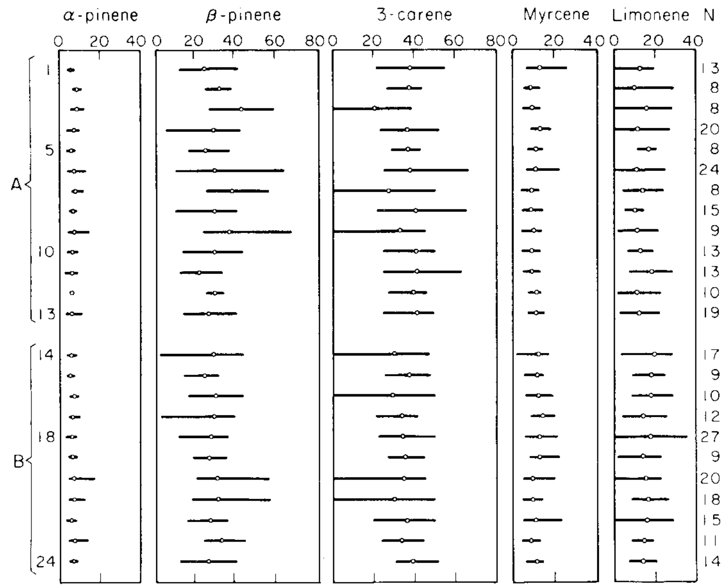

Figure 3.—*Mean (o) and range (—) in percent of the five major monoterpene components in plots 1 to 24 of ponderosa pine in El Dorado County, Calif:* A, *at different elevations decreasing from 6,700 feet at No. 1 to 1,800 ft. at No. 13, with Nos. 8, 9, and 10 all at 2,700 ft.;* B, *at 3,500 ft. ± 300 ft. elevation. N is number of trees per plot.*

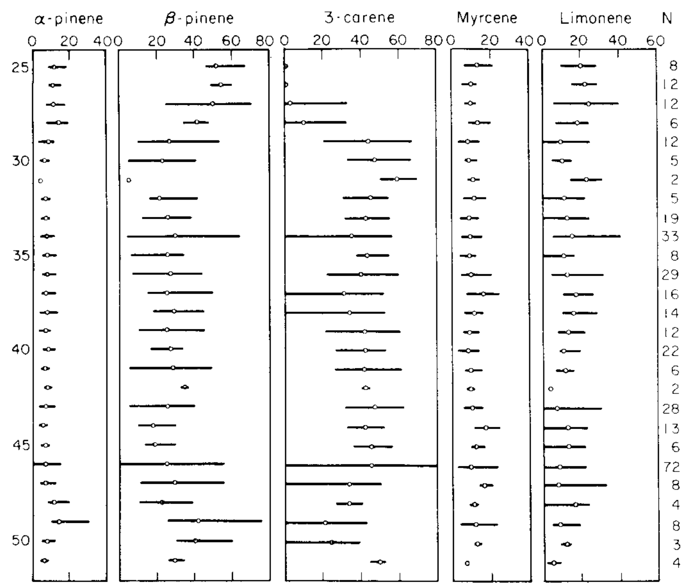

Figure *4.—Mean (o) and range (—) in percent of the five major monoterpene components in plots Nos. 25 to 51 of ponderosa pine in counties of California. Plots Nos. 37, 44, and 46 are natural plots; the remainder are plantation plots. Plot numbers refer to figure 2. N is number of trees per plot.*

unusual to find trees with near-equal amounts of β-pinene, 3-carene, and a somewhat less amount of limonene.

Trees in the northern and central Coast Ranges appear to be somewhat intermediate between the southern California type and the Sierra Nevada-Cascades type in the percentages of 3-carene and β-pinene. The average α-pinene is above 10 percent in both the southern California mountains and northern Coast Ranges.

The Cascades and the Sierra Nevada differ in at least one component if a large sample of trees is used for an analysis. Limonene was found to be significantly greater in 78 trees from the three central Sierra Nevada plots than in 49 trees in three Cascade plots ($\bar{X}_1 - \bar{X}_2 = 7.9$ percent, $t = 1.93$, $t_{.05} = 1.67$).

The highest average for 3-carene, about 60 percent, was found in Fresno County (plot 31), but the plot consisted of only two trees and therefore may not be too representative. The average for 3-carene levels off to about 40 percent to the north. It again rises in the Cascades, going above an average of 45 percent. Individual trees with the highest 3-carene, nearly 80 percent, are found in the Warner Mountains in the extreme northeast corner of the State; 3-carene may be absent from any of the three regions of the State.

The average for limonene is highest in the southern California mountains, but its range is not appreciably greater than in other regions of the State. Trees without limonene occur most often in the Cascades.

Two trees which might be classed as hybrids between ponderosa pine and Jeffrey pine *(P. jeffreyi* Grey. & Balf.*)* were found during this study in the plantations at IFG; none was found in natural plots. One of the hybrids was from Kern County, the other from El Dorado County. In both instances, the composition of these two trees was similar to the artificially produced F_1 (Smith 1967). Probably not more than 100 to 200 of the trees sampled came from the zone common to the range of the two species. Artificial hybrids between ponderosa and Jeffrey pine have been developed (Liddicoet and Righter 1960), and natural hybrids have been found (Haller 1962).

Western North America

Figure 5, arranged in the numerical order given in figure 1, is the average and range for each plot outside California.

At least two types of ponderosa pine, in addition to those in California, may be distinguished in western North America; and several intermediate ones may exist. A large amount of α-pinene generally characterizes trees from Arizona, particularly southern Arizona; the average for the other four major terpenes is quite low. However, some individual trees are not too different from those in other regions.

Northward from Arizona, trees tend to have a larger amount of 3-carene. Though the data show a clear break in the high α-pinene and high 3-carene between Arizona and the Wyoming and Nebraska plots, the sampling was insufficient to establish a cline or a clear break. There are irregular shifts from northern Wyoming through British Columbia to western Oregon, particularly in the mean and range of β-pinene and 3-carene. The amounts of myrcene and limonene may increase as the circuit is traversed. The Carter County, Mont., plot No. 62 is difficult to explain, since it resembles the southern Rocky Mountain plots as much as nearby plots.

There is a shift toward less 3-carene southward from Washington to southern Oregon. There is a divergence in southern Oregon, with the samples from the more easterly counties resembling those of the Sierra Nevada-Cascades of California and the more westerly ones resembling the samples from northern California Coast Ranges.

The mean composition was calculated for plots which could be closely grouped geographically. Plots were grouped as follows, using the plot numbers of figures 1 and 2 and designating these groups by Roman numerals: I = plots 25, 26, 27, 28; II = plots 35, 36, 37, 38; IIa = plots 48, 49. 50, 51; IIb = plots 70, 72; III = plots 57, 58, 59, 60, 61; IIIa = plots 64, 65, 66, 67; IIIb = plot 56; IV = plots 52, 53. This grouping used 290 of the trees; the remaining trees were, very largely, from the Sierra Nevada and were considered superfluous in this regional picture. A few other trees outside California were not used, such as plots 54 and 55, which consisted of so few trees and which would not be geographically grouped with other plots.

From these data eight regional types of ponderosa pine, based on xylem monoterpenes, can be envi-

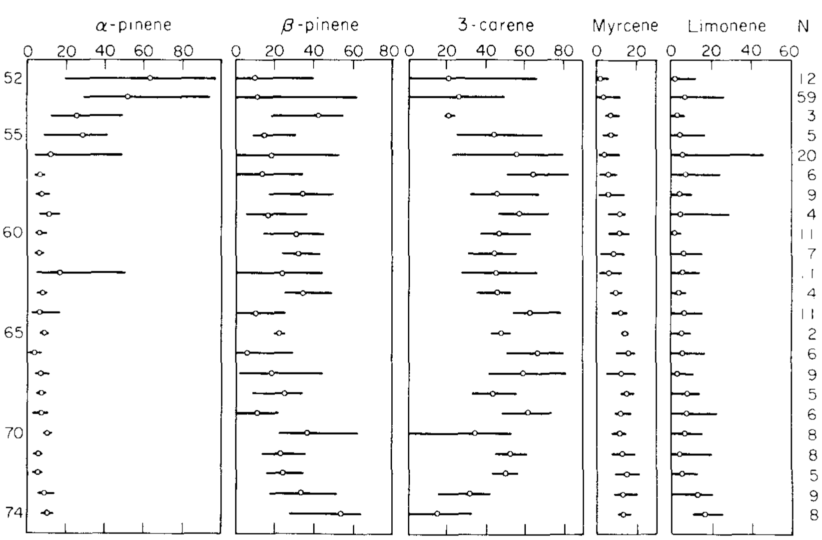

Figure 5.—*Mean (o) and range (—) in percent of the five major monoterpenes in plots Nos. 52 to 74 of ponderosa pine in western Canada and United States. All plots are plantations. N is number of trees per plot. See figure] for location of plot numbers.*

sioned *(fig. 6)*. A further breakdown of these was made into four major types–I, Southern California; II, Sierra-Cascade; III, northern-central Rocky Mountains; IV, Arizona—and four minor types—IIa, northern coast; IIb, central Cascade; IIIa, northern plateau; IIIb, central Rocky Mountains. Characteristics of the four major types are: I, high β-pinene; II, no component markedly higher than others; III, high 3-carene; IV, high α-pinene. Each of the four minor types is somewhat similar to a major type, yet has some distinctiveness. More thorough study now being made in the Arizona region may call for some changes in this classification.

A t-test was made between each of these eight regions for 3-carene by using arc-sin transformation of percents. The results (*table 1)* show a significant difference at the 99 percent level of confidence or greater in 23 of the 28 comparisons. Analyses of the other components are not presented because the statistical validity of comparing more than one element of a normalized system has been questioned.

These eight types do not fit the most recent subdivisions of ponderosa pine proposed by Wells (1964), who used seed and seedling characteristics to subdivide var. *ponderosa* into California and north plateau ecotypes, and var. *scopulorum* into southern, central, and northern ecotypes. For example, he establishes one type for California; we suggest three types.

General

The composition of individual trees varies widely throughout the range, and individual variants may be more meaningful than regional types. Twenty-five trees were selected to illustrate some of the individual variants of trees found in this study *(table 2)*. Bias was used in the selection to see how many types could be found in California. Most of the types listed

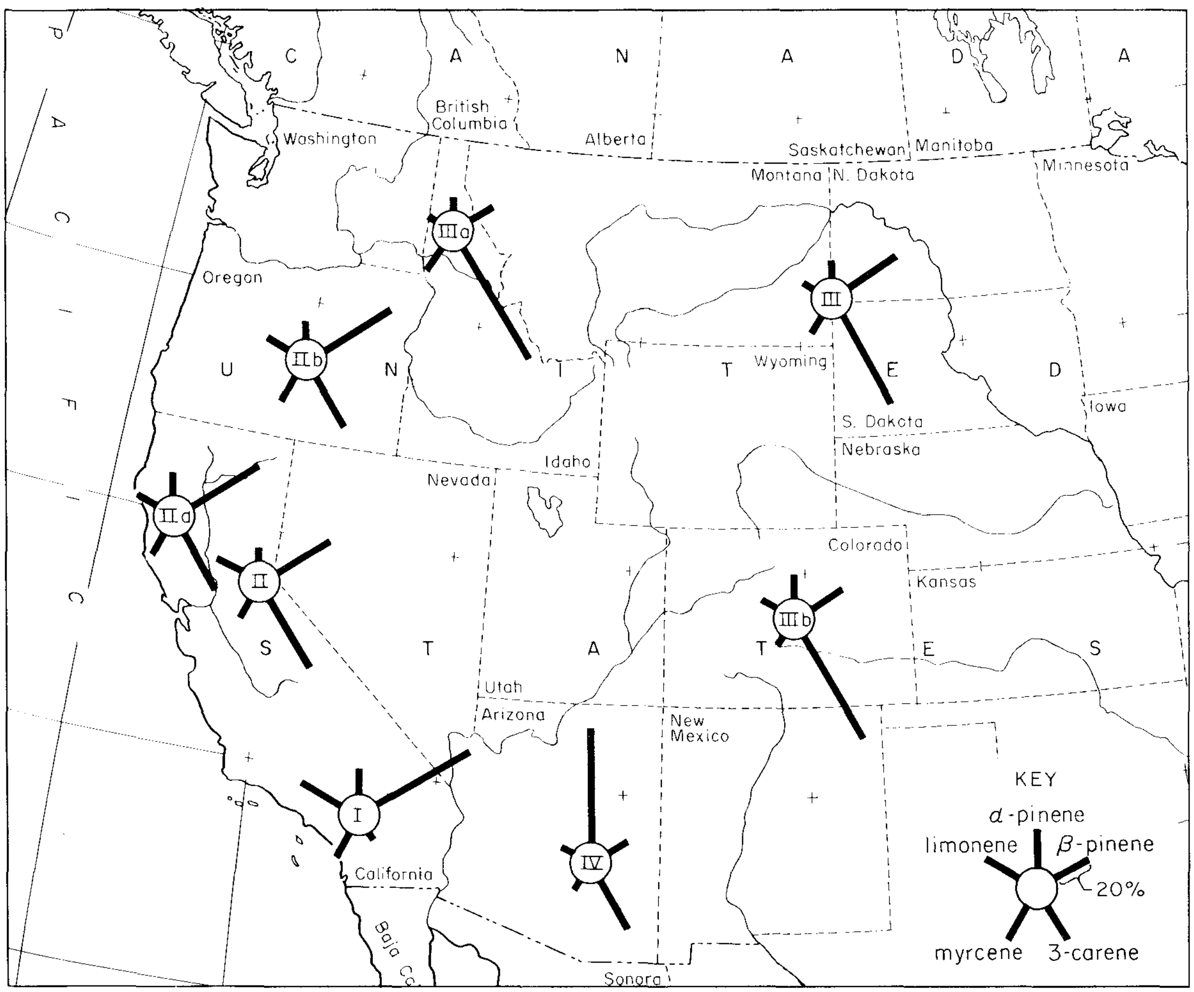

Figure 6.—*Mean monoterpene composition from plots of ponderosa pine in western North America.*

Table 1.– *Difference ($\overline{X}_1$ percent - $\overline{X}_z$ percent) in 3-carene for the eight regions shown in figure 6 and the 99 percent (**) confidence level of significance of this difference.*

Region	No. of trees	II	IIa	IIb	III	IIa	IIIb	IV
I	37	36.5**	27.4**	23.0**	47.9**	58.2**	53.5**	23.3**
II	55		9.1**	13.5**	11.4**	21.7**	17.0**	13.2**
IIa	18			4.4	20.5**	30.8**	26.1**	4.1
IIb	23				24.9**	35.2**	30.5**	.3
III	37					10.3**	5.6	24.6**
Ma	28						4.7	34.9**
Mb	20							30.2**
IV	72							

for California can be found outside the State. However, there was insufficient sampling to determine the diversity of types in each of the other regions. From this list it is evident that a large or small amount of one component may be associated with varying quantities of all the other four. The range of each major component was as follows: (a) α-pinene, 1 to 98 percent; (b) β-pinene, trace to 76 percent; (c) 3-carene, trace to 81 percent; (d) myrcene, trace to 25 percent; and (e) limonene, trace to 46 percent.

On the other hand it was possible to find a "typical" tree in every region except Arizona. Twenty-six trees were selected from all regions except southern Arizona to show this narrow range. Tree No. 21 in table 2 approximates this average tree. The

Table 2. – Monoterpene composition of individual ponderosa pines selected to show the wide range of types and association

Tree no.	Plot no.	α-pinene	α-thujene	Camphene	β-pinene	3-carene	Sabinene	Myrcene	Limonene	β-phellan-drene	γ-terpinene	Terpinolene
		Percent										
1	52	84.6	–	0.5	1.0	–	0.5	0.5	11.8	([1])	([1])	1.2
2	52	98.2	–	.7	.7	–	([1])	.4	([1])	([1])	–	–
3	52	28.6	–	.2	26.0	40.1	–	1.8	([1])	.4	([1])	2.9
4	52	70.7	([1])	.2	.6	([1])	11.2	5.4	.8	.4	([1])	10.7
5	56	47.1	–	.7	2.6	([1])	–	1.3	46.3	2.0	–	–
6	53	35.1	–	([1])	.3	31.8	–	3.4	26.4	([1])	([1])	3.0
7	69	9.0	([1])	([1])	.6	53.9	–	11.5	23.1	([1])	([1])	1.9
8	35	7.8	([1])	([1])	31.7	43.7	–	13.2	.4	.8	([1])	2.4
9	41	4.8	([1])	([1])	50.8	26.0	–	8.6	8.9	.3	([1])	.6
10	48	19.9	–	([1])	39.1	26.5	–	13.2	([1])	([1])	([1])	1.2
11	28	16.9	–	.3	48.0	([1])	–	8.8	24.6	1.4	–	–
12	31	3.2	([1])	([1])	5.6	48.3	–	8.7	31.5	([1])	([1])	2.5
13	49	30.5	–	.4	41.1	([1])	–	24.1	.7	3.2	–	–
14	38	5.9	–	([1])	29.4	26.8	–	10.5	24.8	1.3	([1])	1.3
15	26	8.5	–	([1])	52.4	([1])	–	10.0	28.6	.5	–	
16	36	7.7	([1])	([1])	8.9	65.9	–	8.5	5.0	.9	([1])	3.1
17	34	10.2	–	([1])	36.4	([1])	–	11.4	42.0	([1])	–	–
18	34	3.3	([1])	([1])	3.3	57.4	–	16.4	16.9	([1])	([1])	2.7
19	46	7.9	([1])	([1])	22.1	59.3	–	6.4	.3	.8	.1	3.0
20	46	1.0	([1])	.3	.3	80.6	–	12.3	([1])	1.0	.6	3.9
21	46	5.5	([1])	([1])	27.6	38.1	–	13.5	13.5	([1])	([1])	1.8
22	49	19.5	–	([1])	75.8	([1])	–	2.9	.6	1.2	–	–
23	44	4.9	([1])	([1])	25.8	40.8	–	23.6	.8	1.2	.3	2.4
24	44	4.3	([1])	([1])	9.2	39.7	–	24.8	19.1	1.7	([1])	1.2
25	36	4.0	([1])	([1])	14.4	27.3	–	24.9	26.5	1.8	([1])	1.1

[1] Trace amount.

range of the five major components in these selected trees was as follows: (a) α-pinene, 5 to 11 percent; (b) β-pinene, 20 to 55 percent; (c) 3-carene, 19 to 55 percent; (d) myrcene, 3 to 15 percent; and (e) limonene, trace to 17 percent. Thus, though there are numerous types of individual composition extremes which might lead one to fragment the pine into a number of variants, there is also a thread of "standard" trees which binds the species together.

The coefficient of variation, calculated from arcsin values, of each component in each plot *(fig. 7)* shows limonene to be by far the most variable component, having the highest coefficient of variation in 48 out of 74 plots. Increasing the sample size did not, in general, decrease this coefficient. This relationship was particularly evident in the two Modoc plots, Nos. 45 and 46.

Several ponderosa pines also were found to have a monoterpene composition like Washoe pine *(P. washoensis* Mason & Stockwell*)*. In this study, trees Nos. 16 and 20 in table 2 approximate the monoterpene composition of this pine. This composition is somewhat characteristic of trees from the north-central Rockies. Haller (1962) suggests that Washoe is related to ponderosa. Mirov (1961) suggested that it is a chemical mutant of ponderosa or a hybrid between two varieties of ponderosa, one of which may now be extinct. On the basis of monoterpene studies, this relationship would appear to be closest to trees in the north central Rockies.

Three-carene may provide a clue to the type of inheritance in a tree. This component is found either in trace amounts or in an amount in excess of about 20 percent; there is no percentage between. The maximum amount found was nearly 80 percent. But between 20 and 80 percent there is no distinct 20 percent grouping.

Variations in Minor Components

The analysis of minor components provided little help in understanding the species. It was difficult to work with the minor components because they often eluted during chromatographing near a major com-

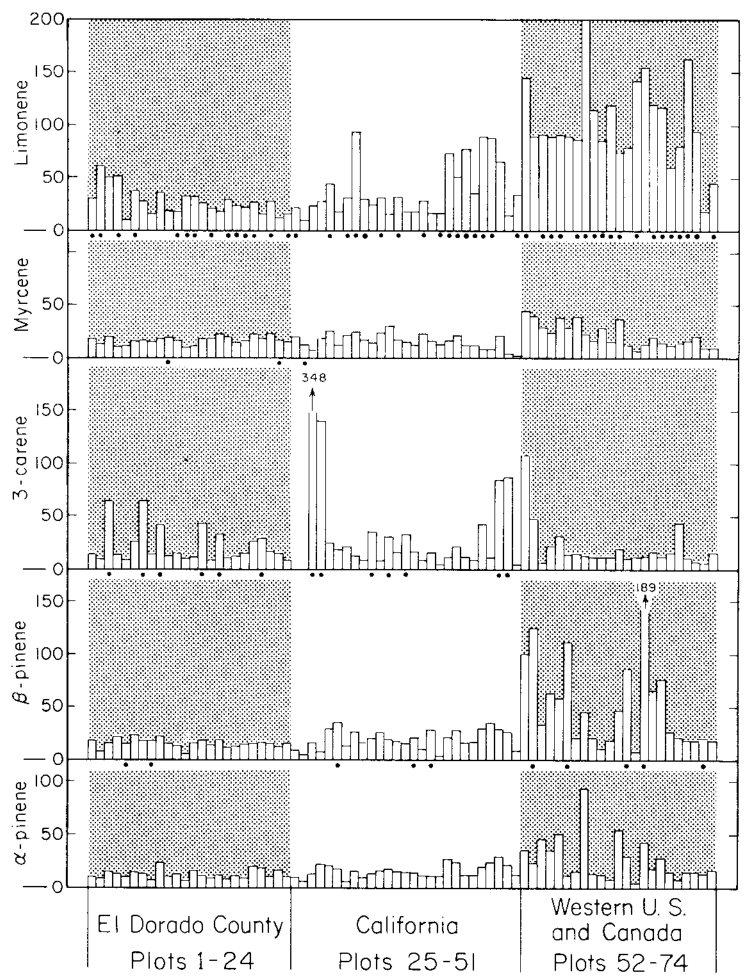

Figure 7.—*Coefficient of variation for the five major monoterpene components of ponderosa pine xylem resin from 74 sources. Plot numbers run consecutively from left and refer to figures 3, 4, and 5; • denotes component from each source with the largest coefficient.*

ponent. And a large amount of the major component may mask the presence of the trace amount of the minor component. This difficulty was most apparent in working with sabinene and 3-carene.

One or more of seven minor components-heptane, α-thujene, camphene, γ-terpinene, sabinene, β-phellandrene, and terpinolene—were found in trees in all regions. Traces of heptane were found in trees from Utah, Colorado, and California. One tree from Utah may have a trace of nonane. Traces of α-thujene, camphene, and γ-terpinene were found in some trees in all regions. Camphene tended to be in measurable amounts, between 0.1 and 0.5 percent, in trees from the southern Rockies. Sabinene was found in small amounts in trees from Cochise County, Ariz., plot 52; one particular tree had 11 percent. Sabinene was not found in all trees from Arizona. It may occur in trees in other regions, but the chromatographic procedures will have to be improved to detect it with more assurance. Undecane was found in trees in four counties in California—Santa Cruz, Kern, El Dorado, and Lassen—and in Utah. Mirov (1961) found undecane in trees from Santa Cruz County, Calif., and considered this a link between ponderosa and Coulter, *Pinus coulteri* D. Don. This might now be questioned, since no undecane was found in the southern California mountains where ponderosa and Coulter often grow together.

Two minor components, β-phellandrene and terpinolene, occur in measurable amounts in all regions; β-phellandrene averages about 1 percent, with a high near 3 percent; terpinolene averages about 2 percent, with a high near 10 percent. This 10 percent was uniquely associated with the 11 percent sabinene; without this particular tree the high would be about 6 percent. Outside southern Arizona the presence of γ-terpinene and terpinolene is associated with 3-carene; trees without 3-carene have neither of these two; when 3-carene is high these two are comparatively high.

DISCUSSION

Any explanation of the lack of coincidence of the range of ponderosa pine and the western pine beetle is still quite speculative. The distribution of the beetle (Miller and Keen 1960) generally follows the distribution usually assigned to var. *ponderosa.* The average monoterpene composition of trees in this distribution tends to have a more even concentration of the five major monoterpenes than that of trees in other regions, though individual trees exhibit a wide variation. The beetle is not found in the region assigned to var. *scopulorum,* where trees tend to have a high concentration of 3-carene. Likewise, the beetle is not found in regions assigned to var. *arizonica,* where trees tend to have a high concentration of a-pinene. The southwestern pine beetle, which has habits quite similar to those of the western pine beetle, however, is found in this region. Therefore, the western pine beetle tends to be associated with ponderosa pine where no monoterpene occurs as a large percentage of the composition in the average tree, with one exception; in southern California, the beetle occurs where the average pine has a large percentage of β-pinene.

The study did little to clarify the taxonomy within ponderosa pine; in fact, it may have added to the uncertainty which now exists. Trees in southern California have always been grouped with var. *ponderosa,* yet the trees in that region are as chemically distinct as trees assigned to regions of var. *scopulorum* and var. *arizonica.* Likewise, trees in Arizona are often split between var. *scopulorum* in the north and var. *arizonica* in the south; yet, chemically, they may be quite similar. Appreciable differences in average values can be found from region to region. However, the range of values for the various monoterpene components often overlaps. In most cases the sampling in this study probably was too restricted to demonstrate the existing variation. Larger and more extensive samples would be needed before real differences can be confidently ascertained.

Our data, covering the Western United States, and Mirov's (1961) show similarities as well as differences. Mirov did not report large local variation, particularly of trees either nearly lacking or having large amounts of 3-carene, β-pinene, α-pinene, and limonene. He also reported generally smaller amounts of myrcene, limonene, β-phellandrene, and terpinolene. And he did not report small amounts of heptane, α-thujene, sabinene, and γ-terpinene.

Several studies, in addition to the more extensive and intensive sampling, are suggested by these results. The use of more sensitive chromatographic detectors would enable more work to be done on the minor constituents. Possibly these minor constituents may help clarify taxonomical relationships as well as or better than the five major constituents. The chemical relationship between ponderosa and Washoe pine needs additional work. An investigation of the sesqui- and diterpenes could reveal valuable data about resin properties.

SUMMARY

A gas chromatographic analysis of the monoterpenes of 927 ponderosa pines, representing to some degree a major portion of the species' range, showed considerable local and regional diversity in composition. Five major monoterpenes— α-pinene, β-pinene, 3-carene, myrcene, and limonene—were analyzed. There is some evidence to support the establishment of at least eight regional types of ponderosa pine, and a further breakdown of these into four major and four minor ones on the basis of greater differences. More meaningful than regional types may be individual tree variants; at least 25 of these have been identified. However, despite regional types and the large number of individual variants, trees with similar composition were found in all regions except southern Arizona. Limonene had the largest coefficient of variation in 48 of 74 plots. Neither elevation nor age of the tree had an apparent effect on composition. Minor components found were heptane, α-thujene, camphene, sabinene, undecane, β-phellandrene, -γ-terpinene, and terpinolene; however, only the last three were commonly found.

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