VARIATIONS IN MONOTERPENES IN SCOTCH PINE (PINUS SYLVESTRIS L.)

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This is to certify that the

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(*PINUS SYLVESTRIS* L.)

presented by

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Major professor

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ABSTRACT

VARIATIONS IN MONOTERPENES IN SCOTCH PINE
(PINUS SYLVESTRIS L.)

by James J. Tobolski

The objectives of this study were: (1) to determine the qualitative and quantitative variations in monoterpenes of Scotch pine, (2) to determine the following physiological and environmental sources of variation in monoterpenes: (a) the variation in monoterpene composition among needle, xylem and cortex tissue; (b) the effects of cortex age; (c) effects due to site; (d) the changes in monoterpene composition due to defoliation by the European pine sawfly, and (e) the effects of season on monoterpene composition, (3) to determine the variation between and within half-sib families and seed lots, and (4) to determine the degree of correlation between monoterpenes, growth rate and existent varietal classes.

Variation in Scotch pine monoterpenes was investigated in 7 to 9 year-old trees growing in replicated provenance tests in southern Michigan. Quantitative and qualitative analyses were performed using gas-liquid chromotography. Scotch pine normally contained the

following 11 monoterpenes: α-pinene, camphene, β-pinene, myrcene, 3-carene, α-terpinene, limonene, β-phellandrene, γ-terpinene, cymene and terpinolene.

Cortical oleoresin was found to contain larger concentrations of limonene, β-phellandrene, β-pinene, 3-carene, and terpinolene than xylem or needle oleoresin. Needle tissue was high in α-pinene (averaging 61 percent) and was characterized by having the highest concentrations of cymene and camphene. Xylem oleoresin contained high concentrations of α-pinene with some trees having a concentration of 94 percent. Differences between tissues were statistically significant (at the 1 percent level) for all monoterpenes except γ-terpinene.

Cortical monoterpenes were found to vary with age of the cortex tissue. Proceeding from current-year tissues formed in 1967 to tissue formed in 1965 the concentration of α-pinene and β-pinene increased while myrcene, 3-carene and limonene decreased.

The effects of site and sawfly defoliation on cortical terpenes were small. Only for β-phellandrene was there a significant interaction between seed source and site. Defoliation by the European pine sawfly significantly increased the α-pinene concentration and the total terpene concentration in defoliated branches as compared to foliated branches within a tree. The effect was most pronounced on moderately defoliated (35-65 percent) trees.

Seven terpenes were found to vary significantly from season to season as determined from eight trees sampled at nine intervals during a thirteen-month period. This variation, however, was small and never exceeded 5 percent for any terpene. The between-tree variation was considerably larger than the between-season variation for the principal monoterpenes.

From studies of individual trees and half-sib-families the monoterpenes 3-carene, myrcene, limonene, β-phellandrene and terpinolene appeared to be under simple genetic control. Multiple inheritance patterns were indicated for the remaining terpenes. The variation among half-sib families was significant for the principal terpenes.

Tree-to-tree variability within seedlots was large for simply inherited monoterpenes having low gene frequencies. Thus, large sample sizes (100-200 trees) may be necessary to detect small differences between populations.

Simple correlations between monoterpenes support the hypothesis that all terpenes are derived from the stable precursor geranylpyrophosphate. A consistent, positive correlation was found only between 3-carene and terpinolene. The cause of this association is unknown.

Geographical variation of cortex monoterpenes was determined from 108 Scotch pine provenances from Europe and Asia. Monoterpene composition was found to parallel

geographic variation. Thus, terpenes are a valuable chemotaxonomic aid in Scotch pine. Of the 11 terpenes the most variable were α-pinene and 3-carene which were inversely correlated in a general north-south direction. For example, 3-carene varied from 0-60 percent south to north, respectively. The absence of 3-carene in most isolated southern populations indicates that they are probably Tertiary relics. Apparently little gene exchange has taken place between them and the more continuous northern populations. Similarity in terpene composition between Middle Europe, southern Scandinavia and Scotland, lends credence to the hypothesis that Scotch pine migrated from middle Europe across land bridges which had once connected these land masses.

VARIATIONS IN MONOTERPENES IN SCOTCH PINE

(PINUS SYLVESTRIS L.)

By

James J. Joseph Tobolski

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CHAPTER I

INTRODUCTION

Scotch pine (Pinus sylvestris L.) is one of the most variable tree species in the world, and during the past 154 years numerous varieties have been described. Ruby (1964) recognized 21 geographic variables as valid. The native range of Scotch pine includes most of Europe and northern and west-central Asia (Figures 1 and 2). In the north, it is a valuable timber and pulp species where its range is continuous over large areas of low and medium elevation. It is less important in southern Europe where it is confined to scattered mountainous areas.

Scotch pine has been widely planted outside its natural range both as an ornamental and forest tree. It is an important exotic in the United States, especially in the northeastern and northcentral states, where millions of seedlings have been planted. Recently, it has become one of America's most important Christmas trees.

Provenance Testing of Scotch Pine

A provenance in forestry, as I use the term, refers to a population of trees growing at a specific place of origin. Provenance research provides information about the

Figure 1.--Natural distribution of Scotch pine in Europe (shaded) and provenances included in this study (numbered dots).


15° 10° 5° 0° 5° 10° 15° 20° 25° 30° 35° 40° 45° 50° 65°
70° 65° 60° 55° 50° 45° 40°
60° 55° 50° 45° 40° 35°
5° 0° 5° 10° 15° 20°
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204 528
311 308 307
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525-6
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318 208 209
306 305
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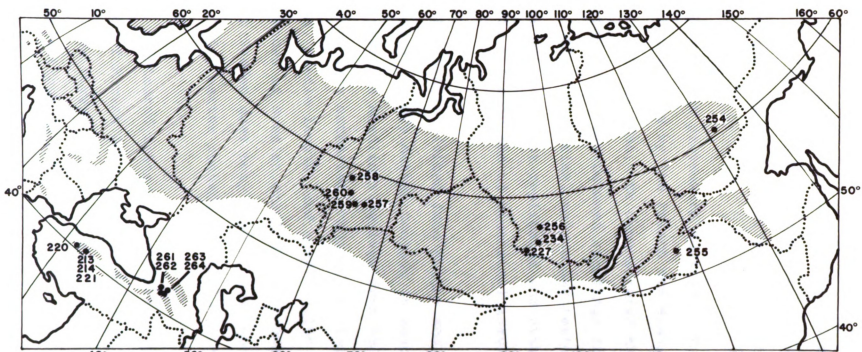
Figure 2.--Natural distribution of Scotch pine in Asia (shaded) and provenances included in this study (numbered dots).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environmental and genetic components of variation associated with geographic source and thus can be useful in directing breeding programs. Furthermore, these tests are an adjunct in defining the evolutionary patterns of species or higher taxon.

Some of the earliest provenance testing of forest trees was done on Scotch pine by the French seedsman, DeVilmorin between 1820 and 1850. He demonstrated that large growth differences existed between seedlings from different regions. Since that time, many other tests have been conducted, but most were not replicated and either have limited genetic value or are of historical interest only.

In the 1930's Langlet (cited from Wright and Bull, 1963) conducted a study of dry matter content in Scotch pine needles of 2-year old seedlings derived from 582 stands in Sweden. In less extensive studies, he also measured height growth, needle length, and needle color of Scotch pine provenances of Swedish origins. He showed that trees from northern Sweden grew very slowly, had short needles with a high dry matter content and yellow winter coloration.

Widespread replicated tests were initiated by the International Union of Forest Research Organizations (IUFRO) in 1907 and 1938. The first of these tests included 13 origins and 16 outplantings in Sweden, Germany, Belgium,

Hungary, and the Netherlands. Wiedemann in 1930 (cited from Wright and Bull, 1963) summarized the separate published reports for the entire experiment. The 1938 IUFRO test included 55 provenances from Scotland to Latvia and from Germany to northern Scandinavia. Each cooperator established one or more plots of as many origins as he chose to include.

All 55 origins were planted in a replicated test at Hillsboro, New Hampshire and some origins were also planted in New York and Michigan. Results of various aspects of these test plantations are summarized in a series of reports by Baldwin (1956), Wright and Baldwin (1957), Echols (1958), Gerhold (1959).

The IUFRO investigations showed that the Belgian origins consistently grew faster but were sometimes inferior in stem form. Latvian origins had good stem form but grew more slowly. Differences were also observed in carotenoid and mineral content of foliage. Slow growing Scandinavian trees produced wood of high density, but cellulose production was much greater for faster growing origins from Belgium and Germany.

The potential of Scotch pine on many infertile sites of the north-central region of the United States as well as inquiries by Christmas tree growers prompted the NC-51 Regional Tree Improvement Committee to initiate extensive provenance tests of the species. Three of these

test plantations were used in this study. They were established from seed collected from 108 native Scotch pine stands throughout Europe and Asia.

Monoterpenes in Pines

The monoterpenes and their oxygenated derivatives have been found in over 350 plant species. Over 150 monoterpenes are known to exist. They are among the oldest studied natural products because of their fragrance and use in medicinal preparations.

In Pinus, Picea, Larix and Pseudotsuga the monoterpenes comprise a fraction of the oleoresin which is synthesized in the thin-walled epithelial cells surrounding the resin canals. These ducts are found in the needles, cortex of the bark, and in the heartwood and sapwood. The oleoresin within the canals is normally under pressure and when they are severed droplets of oleoresin are exuded.

Oleoresin can be divided into two components: turpentine and rosin. Turpentine is a mixture of monoterpenes ($C_{10}H_{16}$); rosin is a mixture of resin acids which are diterpene derivatives ($C_{20}H_{30}O_2$), and are classified into two types, abietic and pimaric.

The role of monoterpenes in survival and growth of pines has been a topic of lively conjecture for many years. Some workers feel that the monoterpenes are merely metabolic wastes while others believe they may be important in disease resistance, insect resistance or as useful metabolic

constitutents in the growth processes. Since it is postulated that the pines originated in the Mesozoic era some 150,000,000 years ago, the resin duct system may be nothing more than a "human appendix," once important, but now simply a relic of the past.

Objectives of Study

This study is part of a long range research program directed towards defining the patterns of genetic variation and inheritance of physiological traits of forest trees. It focuses on the monoterpene compounds in Scotch pine and seeks to provide genetic and physiological information about these compounds in the species. Hopefully, this information will contribute to our general knowledge about genetic differentiation in trees and eventually to the improvement of Scotch pine planted in the United States.

The specific objectives of this study were:

1. To determine the qualitative and quantitative variations in monoterpenes of Scotch pine.
2. To determine the following physiological and environmental sources of variation in monoterpenes:
   a) the effects of season on monoterpene composition;
   b) the changes in monoterpene composition due to defoliation by the European pine sawfly;
   c) the variation in monoterpene composition among needle, xylem and cortex tissue;

d) the effects of tissue age on cortical monoterpenes, and

e) the effects of site on cortical monoterpenes.

3. To determine the variation between and within half-sib families and seedlots.

4. To determine the degree of correlation between monoterpenes, growth rate and existent varietal classes.

CHAPTER II

NON-GENETIC VARIATION

Investigations in pine monoterpenes have been diverse and unrelated. Some studies have implicated the monoterpenes as having a role in disease and insect resistance. Others were directed at terpene physiology, inheritance mechanisms or chemosystematics.

It is essential therefore, that factors affecting monoeterpene levels be clarified in order to plan and interpret experiments meaningfully. The environmental sources of variation which I studied included tissue differences (needles, cortex and xylem), effects associated with the age of cortex tissue, time of sampling, and effects due to site and defoliation. These factors are considered in more detail under the respective investigations.

Materials and Methods

Oleoresin samples were obtained from a provenance-test plantation established at the Rose Lake Wildlife Experiment Station, located 10 miles northeast of East Lansing, Michigan. This plantation was established in 1961 with 2-0 stock and was 7-9 years old at the time of sampling. The planatation contains 75 origins of trees planted

in an 8-by-8 foot spacing in four-tree plots and eight replications (Wright and Bull, 1963). The 75 origins represent 75 stand collections from throughout the natural range of the species. A single row of trees composed of Austrian and Swedish sources borders the planting. A similar plantation at the Fred Russ Memorial Forest was also sampled. The samples were placed in small vials or centrifuge tubes stored at 35°C and analyzed by gas-liquid chromatography within 10 days.

Details of oleoresin collection varied and are described separately under each study.

At the time of analysis each sample was diluted with acetone or pentane and a three microliter aliquot was immediately injected into an F and M model 700 gas chromatograph. It was equipped with a thermal conductivity detector, a Hewlett Packard automatic attenuator model 50B, and a Honeywell disc-chart integrator Model 227. The chromatograph column was stainless steel, 1/4-inch in diameter and 8 feet long, and packed with 10% polypropylene glycol on 60/80 mesh chromasorb G-AW. Column temperatures were 95°C-105°C, injection port and detector temperatures were 190°C-200°C, and the helium flow rate was 100-110 ml/min.

The monoterpenes were tentatively identified by comparing relative retention times of the unknowns with those of known compounds. To check identification, several

samples were rerun at 60°C on a column containing the polar substrate β, β'-oxydipropionitrile.

When the data is expressed as a percent of the total monoterpenes, concentration was determined by integration and summation of areas under the peaks. In one study (Effect of Defoliation) monoterpene concentrations are expressed as a percentage of the oleoresin. Here, concentrations were derived from area integrator values on a column in which standard curves were prepared from a series of known monoterpene concentrations. The same conditions were used when analyzing the unknown oleoresin samples.

VARIATION IN NEEDLE, CORTEX AND XYLEM TISSUES

Several investigations have shown that monoterpene composition varies between tissues of the same tree (Squillace and Fisher, 1966; Juvonen, 1966). To date, however, differences among all three major tissues (needles, cortex and xylem) of individual trees in unknown. To obtain such information the following investigation was undertaken.

Ten trees, representing nine diverse seed sources were sampled at the Rose Lake plantation in June and August 1967. From each tree, 20 µl. of cortex oleoresin was obtained from incisions on year-old branches of the 1965 or 1966 whorl. The same branches were cut into 6 or 8 cm. sections and from 3 to 12 µl. of xylem oleoresin was obtained from the cut surfaces. Finally, the foliage was removed from

these sections, placed in polyethylene bags and extracted the same day in the laboratory.

The monoterpenes were extracted from 10 grams of needles by homogenizing them in a Waring blendor for two minutes in a sufficient volume of pentane to cover the foliage. The extract was filtered into a beaker and the remaining homogenate was washed three times with 15 ml. of pentane, filtered and added to the initial extract. To remove water, 4 to 5 grams of anhydrous sodium sulfate were stirred into the extract which was then evaporated with an air stream down to 15 or 20 ml. This remaining solution was filtered into a test tube and further evaporated to a final volume of .5 ml.

Results and Discussion

Differences between the June and August collections were less than 2 percent for all monoterpenes with the exception of α-pinene and 3-carene in the xylem. In this tissue α-pinene was 8.4 percent lower and 3-carene was 6.6 percent higher in the June collection. Since differences in sampling time were generally small, the data was combined and the mean variation among tissues is presented in Table 1. The differences between tissues were significant for all monoterpenes except γ-terpinene.

Needle tissues was consistently higher in camphene and cymene than xylem or cortex. The mean concentrations

Table 1.--Monoterpene composition in different tissues in 10 trees from 9 seed sources.

Monoterpenes	Tissue		
	Needle	Cortex	Xylem
	Mean Percent of Total Monoterpenes		
α-Pinene**	61.0 ± 5 %[1]	14.2 ± 29%	59.5 ± 12%
Camphene**	11.4 ± 11	.5 ± 40	.7 ± 23
β-Pinene**	8.5 ± 21	12.2 ± 25	6.8 ± 29
Myrcene**	4.8 ± 10	15.0 ± 35	2.4 ± 29
3-Carene**	8.6 ± 22	32.6 ± 24	23.7 ± 24
α-Terpinene**	.4 ± 25	1.0 ± 20	.9 ± 33
Limonene**	1.2 ± 8	10.8 ± 36	1.5 ± 20
β-Phellandrene**	.9 ± 11	8.8 ± 43	1.2 ± 8
Cymene**	1.8 ± 17	.8 ± 13	.3 ± 33
γ-Terpinene	.4 ± 25	.6 ± 33	.4 ± 25
Terpinolene**	1.3 ± 23	3.8 ± 24	3.1 ± 26

**Between-tissue differences significant at the 1 percent level.

[1]Standard error of the mean expressed as a percent.

of α-pinene were equally high in xylem and cortex tissue (60 percent); however, the variation between trees for each tissue was considerably different. In the xylem α-pinene ranged from 28 to 94 percent with a standard error of 12 percent. The α-pinene concentration in the foliage was more consistent. It varied from 46-66 percent with a standard error of only 5 percent. The concentration of α-pinene was consistently lower in the cortex ranging from 6 to 46 percent but the tree-to-tree variability was highest with a standard error of 29 percent. The high α-pinene concentration in xylem oleoresin was also found in Pinus elliottii Englem. (Squillace and Fisher, 1966). Juvonen (1966) also found that α-pinene was high in needle tissue from several sources of Scotch pine.

In the cortex limonene ranged from 0-40 percent and β-phellandrene varied from 1-31 percent. Apparently, the large tree-to-tree variability for these terpenes is characteristic of this tissue. Limonene and β-phellandrene in the other tissues varied from only 0-3 percent.

At this time, I can only speculate on the physiological basis accounting for these differences. Sucrose, the most abundant and highly transported product of photosynthesis, is thought to be a precursor for monoterpene synthesis. Thus, the monoterpene concentration in a particular tissue may reflect the utilization of sucrose which could be influenced by such factors as enzyme levels, enzyeme

activities and conditions causing spontaneous conversions. For example, cymene and camphene are spontaneously formed from α-pinene under acid conditions (Mutton, 1962). The higher cymene and camphene concentrations found in the foliage is associated with higher pH levels which may subsequently influence enzyme activities or terpene conversion involving these terpenes.

In chemosystematic studies, the choice of tissue to be sampled is an important consideration. To distinguish trees or populations from one another, variation in monoterpene composition must be present. Thus, the monoterpenes from needle tissue would be of little value since there was only slight variation among these 10 trees. The variation between trees in the xylem and cortex monoterpenes was much larger. In these tissues, α-pinene, β-pinene, myrcene, and 3-carene would be equally effective in the separation of these trees. However, the cortical monoterpenes were the most suitable because of their additional variation in the concentration of limonene and β-phellandrene. Cortical oleoresin is also more abundant and easier to collect than xylem or needle oleoresin in young branches of Scotch pine.

VARIATION ASSOCIATED WITH TISSUES OF DIFFERENT AGE

Cortical monoterpene concentration has been shown to vary among different age tissues. Hanover (1966a) reported that in three trees of western white pine (Pinus

monticola Dougl.), current year cortex tissue had less α-pinene, β-pinene and limonene and more myrcene and 3-carene than that of older tissue. In contrast, R. M. Hilton (personal communication) found that 1966 cortex tissue of 23 Pinus strobus L. provenances had significantly higher concentrations of β-pinene and γ-terpinene and lower amounts of camphene, β-phellandrene and terpinolene than 1965 tissue.

To determine the effects of tissue age in Scotch pine, four trees from different seed sources were sampled. Approximately 20 microliters of oleoresin were collected from cortical incisions made on a lateral branch of the 1964 whorl. Collections were made only from the 1965, 1966 and 1967 internodes.

The concentration of the major monoterpenes was as follows:

Year Tissue Formed	Monoterpenes				
	α-Pinene	β-Pinene	Myrcene	3-Carene	Limonene
	Percent of Monoterpenes				
1965	23.8	30.1	15.1	23.4	2.0
1966	18.5	29.9	18.7	24.8	2.5
1967	15.9	21.2	21.0	29.7	4.2

Proceeding from current-year tissue to older tissue, the concentrations of α-pinene and β-pinene increased while those of myrcene, 3-carene and limonene decreased.

For most monoterpenes, the largest change occurred between the current-year tissue formed in 1967 and year-old tissue formed in 1966. These results are in general agreement with Hanover's (1966a) data on western white pine.

EFFECTS OF DEFOLIATION ON CORTICAL MONOTERPENES

The use of monoterpenes as a taxonomic tool is based in part on the evidence that terpenes are only slightly influenced by the environment. Thus, factors affecting cortical monoterpene composition, which have not been previously studied, such as defoliation, are important if valid interpretations are to be made.

As will be shown from the study on site effects, the average level of α-pinene concentration at the Rose Lake plantation was 4.9 percent higher than at the Russ Forest plantation. It was suspected that this difference as well as other changes may have been due to defoliation at Rose Lake by the European pine sawfly (Neodiprion sertifer (Geoff.)). In addition, two of the three replicates sampled at Rose Lake, which were heavily defoliated, were also higher in α-pinene concentration.

To determine the effects of defoliation, samples were obtained from defoliated and non-defoliated branches of each of 31 trees. Of the trees sampled, 9 were classified as lightly defoliated (5 to 25 percent of the branches defoliated) while 12 and 10 trees were classified in the

medium to heavy defoliation classes, 35-65 and 75-95 percent of branches defoliated, respectively. Normally only year-old old needles are eaten by the sawfly and current-year needles are not damaged. Because the plantation has been infested by sawflies for the past four years, repeated defoliation had removed all but the current year needles on some trees. The samples were collected in mid-July 1967 and from 1966 cortex tissue in the upper two-thirds of the crown. Twenty microliters of oleoresin were obtained from cortical incisions on a defoliated and non-defoliated branch of each tree.

Results and Discussion

Differences in monoterpene concentrations were small and not significant between defoliated and normal (non-defoliated) branches of lightly defoliated trees. However, differences did occur within the medium and heavy defoliated trees. Since the effects were similar in both classes of defoliation, their data was combined and analyzed together (Table 2).

There was a significant increase in the concentration of α-pinene (1.26 percent) and in the total monoterpene concentration (2.17 percent). To explain these changes, it is helpful to compare differences between defoliated and normal branches in each of the three defoliation classes.

The monoterpene concentration in defoliated branches increased (+) or decreased (-) as indicated in Table 3.

Table 2.--The effect of individual trees and defoliation by the European pine sawfly on the monoterpene composition of Scotch pine.[1]

Monoterpenes	Monoterpene Concentration: Range of Tree Means	Monoterpene Concentration: Mean Increase (+) or Decrease (-) Due to Defoliation	Portion of Total Variance Due to: Tree	Defoliation	Error
	Percent of Oleoresin			Percent	
α-Pinene	2.1 - 24.6	+1.26	93**	3**	4
β-Pinene	1.0 - 20.6	+ .23	96**	0	4
Myrcene	1.2 - 13.9	+ .06	98**	0	2
3-Carene	.0 - 21.3	+ .43	96**	0	4
Limonene	.3 - 11.1	+ .19	98**	0	2
β-Phellandrene[2]	.4 - 4.4	- .06	--	--	--
γ-Terpinene	.0 - .4	.00	--	--	--
Cymene	.0 - .5	+ .01	--	--	--
Terpinolene	.0 - 2.2	+ .04	--	--	--
Camphene	.3 - 1.1	+ .03	--	--	--
α-Terpinene	.0 - .7	- .02	--	--	--
Total Monoterpenes	25.6 - 40.0	+2.17	60**	8**	32

**Significant at the 1 percent level.

[1]Only the medium to heavy defoliation classes (35-95 percent of year-old needles) are included in the analysis.

[2]Concentration determined from the calibration curve for limonene.

Table 3.--Changes in monoterpene concentration associated with different degrees of defoliation.

Degree of Defoliation	Monoterpene				
	α-Pinene	β-Pinene	3-Carene	α-Terpinene	Total
	Percent of Oleoresin				
Light	+ .18	+ .12	+ .51	+.02	+ .49
Medium	+1.36***	+1.06*	+1.23*	-.06	+3.86*
Heavy	+1.16**	- .59	- .40	+ .02	+ .45

*, **, ***Significant at the 10, 5, and 1 percent levels, respectively.

Note that trees which were moderately defoliated exhibited the largest changes in monoterpene composition. In lightly defoliated trees no significant change occurred, and the small differences shown are primarily due to experimental error. With heavy defoliation, differences between defoliated and non-defoliated branches decreased and only the concentration of α-pinene was significantly different. Apparently the almost total lack of foliage also influenced the monoterpenes in the few remaining foliated branches decreasing the difference between the normal and defoliated branches. This effect seems to be reversed in lightly defoliated trees where the presence of foliage overrides the effect of defoliation.

Thus, changes in monoterpene composition reflect the degree of defoliation. As defoliation increases the mononterpene composition is subsequently altered, but the exact degree of this change in unknown in heavy defoliated trees since the

monoterpene composition in the remaining foliated branched is also affected. Thielges (1968) reported that in the same provenances of Scotch pine defoliation caused a similar general response in phenol metabolism. An unknown compound almost doubled in the foliage of partially defoliated trees.

The mechanisms involved in these monoterpene changes are unknown. Foliage or its absence may be altering substrates, enzyme activities and/or enzyme levels involved in monoterpene metabolism.

EFFECTS OF SITE ON CORTICAL MONOTERPENES

A number of studies have indicated that oleoresin derived from wood has a stable monoterpene composition whether the tree is growing in its native habitat or planted in a foreign environment (Mirov, 1961; Williams and Bannister, 1962). Recent studies of the monoterpenes derived from cortex oleoresin also indicate that site has little influence (Squillace and Fisher, 1956; Hanover, 1966a). However, site affects were apparent in provenances of Pinus strobus (R. M. Hilton, personal communication) which were growing in several Michigan planatations.

The influence of site on monoterpene composition is an important consideration for their use in systematic studies. This study was undertaken to determine if different sites affect the monoterpene composition in provenances of Scotch pine.

Ten selected seed sources encompassing the entire range of Scotch pine were sampled in early July, 1967 at both the Fred Russ Forest and at Rose Lake. The Fred Russ plantation is near Dowagiac, Michigan, about 120 miles southwest of the Rose Lake plantation. The Russ plantation is level and the soil is a fertile sandy loam. Chemical weed control had been used to eliminate competing vegetation since plantation establishment. The Rose Lake plantation had rolling hills with slopes up to 10 percent. The soil is an infertile loamy sand. No weed control was used. The growth rate in both plantings was similar.

Twenty microliters of oleoresin were collected from cortical incisions made on year-old branches of the 1964 whorl. Three 8-tree bulked samples (totaling 24 trees) were collected from each seed source in each plantation.

Results and Discussion

The mean difference between plantations ranged from zero (camphene and cymene) to 4.9 percent (α-pinene). The variation between sources is highly significant and it accounts for the major portion of the total variance (Table 4). There were significant differences between locations in the concentration of α-pinene, myrcene and β-phellandrene. The changes in α-pinene and myrcene concentrations were consistent between plantations for most sources and thus no interaction occurred. For β-phellandrene, however, irregular source differences between plantations resulted in a small

Table 4.--Monoterpene composition of 10 seed sources growing at two locations.

Monoterpenes	Location		Percent of Variance Due to			
	Russ	Rose Lake	Source	Location	Source x Location	Error
	Percent of Monoterpenes					
α-Pinene	14.9[1]	19.8	73.7**	10.8**	0	15.5
Camphene	.7	.7	52.4**	0	0	47.6
β-Pinene	28.0	26.4	79.4**	0	0	20.6
Myrcene	17.7	14.6	57.8**	5.0**	3.8	33.4
3-Carene	18.6	20.7	87.2**	0	0	12.8
α-Terpinene	.9	.8	83.2**	0	0	16.8
Limonene	9.3	8.5	58.4**	.4	1.2	40.0
β-Phellandrene	6.3	5.1	77.5**	1.0**	9.4**	12.1
Cymene	.9	.9	21.5**	0	37.8	40.7
γ-Terpinene	.5	.4	81.0**	.7	.9	17.4
Terpinolene	2.1	2.0	90.3**	0	.6	9.1

[1]A mean value of 24 trees; 8 in each of 3 replicates.

**Significant at the 1 percent level.

but significant source X location interaction. Because of the small sample size, 24 trees, this apparent interaction may have been due to chance. β-phellandrene is a simply inherited monoterpene (Chapter III) whose genes were in low frequency in 9 of the 10 sources sampled. In such a case, a much larger sample is necessary to obtain a precise estimate of its true mean concentration.

A portion of the location differences was thought to be due to the heavy defoliation of the Rose Lake plantation by the European pine sawfly. The Russ Forest plantation was lightly attacked in 1963 and 1964. The attack at Rose Lake began in 1963 and was heavy in 1965, 1966, and 1967 (Wright et al., 1967). A portion of the data from a study on defoliation affects (the preceding investigation in this chapter) indicated that differences between locations were due partly to defoliation. The mean increase (+) or decrease (-) in monoterpene concentration at Rose Lake was comparable to changes due to defoliation. These differences are illustrated in the following array of data:

Average Difference in	Monoterpenes		
	α-Pinene	Myrcene	β-Phellandrene
	Percent of Total Monoterpenes		
Sources at Rose Lake	+4.9	-3.1	-1.2
Defoliated Branches	+3.1	-2.0	- .6

This study indicates that the monoterpenes in Scotch pine are under strong genetic control. Site had little influence on monoterpene composition and defoliation may have been responsible for the significant location differences in the concentrations of α-pinene, myrcene and β-phellandrene. The small size of the sample may explain the source X site interaction in β-phellandrene.

SEASONAL VARIATION OF CORTICAL MONOTERPENES

A knowledge of seasonal variation in monoterpenes is a fundamental prerequisite to planning and interpreting other investigations on these compounds. This is especially true for studies related to insect and disease resistance, chemosystematics, inheritance mechanisms and physiology.

Two previous studies (Bannister et al., 1962, Blight and McDonald, 1964) on wood oleoresin of Pinus radiata D. Don have indicated that monoterpene composition is highly stable, varying only 1-3 percent between any sampling date. Monthly samples obtained over a one-year period from a Pinus ponderosa Dougl. var. ponderosa tree also showed little variation in wood monoterpenes (Smith, 1964).

In contrast to this evidence for seasonal stability, a study (Hanover and Furniss, 1966) of monoterpenes obtained from wood oleoresin of 15 Douglas-fir (Psueudotsuga menziesii (Mirb.) Franco var. menziesii) showed that α-pinene and β-pinene increased significantly between June and October.

Some seasonal variation of cortical monoterpenes was also detected by R. M. Hilton (personal communication) in a study involving 23 seed sources of eastern white pine. Camphene, γ-terpinene, and terpinolene varied significantly between the March and October collections.

To determine the degree and pattern, if any, of seasonal variation in Scotch pine, eight border row trees, four from each of two seed sources, were selected for sampling because of their wide variation in monoterpene composition.

Oleoresin samples were collected at nine intervals from December 1966 through December 1967. Five to twenty microliters of oleoresin were obtained from cortex tissue of lateral branches by either scraping off a droplet of oleoresin from a severed branch or by drawing up a droplet in a capillary tube from a small cortical incision made with a razor blade. The means of 14 paired collections are included in this study. These samples were obtained from seven of the trees on three of the sampling dates to determine the repeatability of multiple samples taken within a tree.

Results and Discussion

Seven of the eleven monoterpenes varied significantly between sampling times (Table 5). For the major monoterpenes, the amount of seasonal variation was slight compared to the between-tree variation. Camphene, cymene and γ-terpinene

Table 5.--Analysis of seasonal variation of monoterpenes from eight Scotch pine trees sampled on nine dates.

Monoterpenes	Range of Tree Means	Error Mean Square	F Value Due to		Percent of Variance Due to	
			Tree	Time of Sampling[1]	Tree	Time of Sampling
	Percent Monoterpene					
α-Pinene	6.5-19.0	3.697	60.29**	2.86**	81.4	3.5
Camphene	.2- .6	0.032	5.34**	4.23**	21.8	22.5
β-Pinene	6.1-71.3	8.751	552.36**	2.43*	97.7	0.3
Myrcene	2.6-21.3	3.523	197.89**	2.32*	93.8	0.8
3-Carene	.2-68.4	3.456	2242.42**	1.05	99.5	0.0
α-Terpinene	.0- 1.3	0.122	20.03**	1.63	61.5	2.8
Limonene	1.1-17.8	6.734	188.05**	2.32*	93.5	0.9
β-Phellandrene	.0-27.1	1.165	808.71**	1.51	98.5	0.0
Cymene	.2- 1.5	0.115	21.76**	4.80**	56.1	14.1
γ-Terpinene	.0- 1.1	0.028	64.97**	2.39*	83.1	2.5
Terpinolene	.1- 8.2	0.157	661.23**	1.32	98.2	0.0

[1]F-value for time of sampling also includes some effects due to tissue age and position and defoliation by the sawfly.

*,**Significant at the 5 and 1 percent level, respectively.

varied significantly although they were present in very small quantities which made their precise measurement difficult.

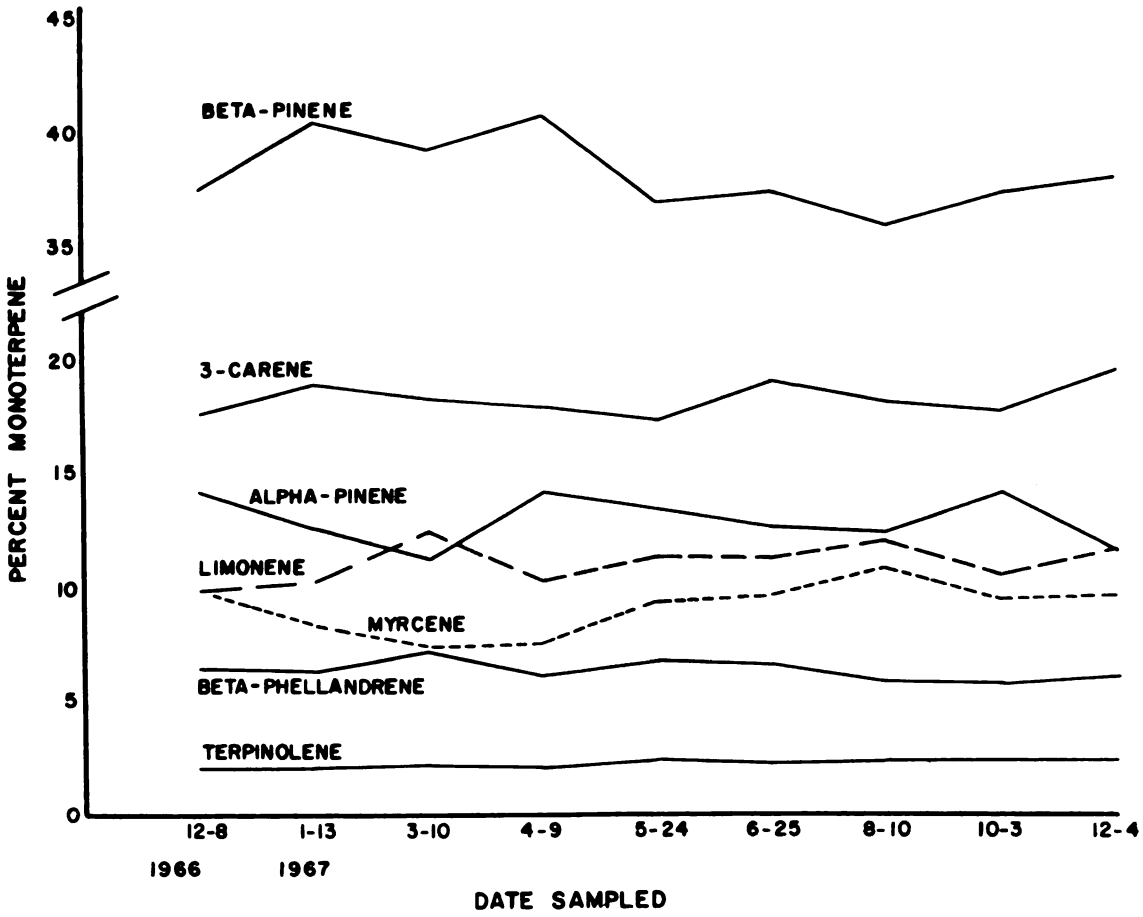
The pattern of seasonal variation for the major monoterpenes is shown in Figure 3. Alpha-pinene and myrcene decreased from December to March, increased from April to August and then decreased again. However, the maximum variation throughout the year was only 2.9 and 3.4 percent for α-pinene and myrcene, respectively. From December, 1966 to March, 1967 α-pinene averaged 2.3 percent higher than during the May to December, 1967 period. Variation in the other monoterpenes appears to be random with respect to season.

In addition to sampling time other factors may have influenced the results. These are: sampling errors, the methods of expressing monoterpene concentration, defoliation of a sampled branch and tissue age.

Sampling Errors

During the course of the seasonal variation study, four to six branches were sampled on each tree. For the majority of these collections, only one sample was obtained for each tree on a specific date. However analyses of 14 paired samples obtained to estimate branch-to-branch differences indicated that some within-tree variation was present. The detailed results are given below.

Figure 3.--The mean seasonal variation in the principal monoterpenes in eight Scotch pines. The maximum standard error of the means is 1.8 percent.


45
40
35
20
15
10
5
0
PERCENT MONOTERPENE
BETA-PINENE
3-CARENE
ALPHA-PINENE
LIMONENE
MYRCENE
BETA-PHELLANDRENE
TERPINOLENE
12-8
1-13
3-10
4-9
5-24
6-25
8-10
10-3
12-4
1966
1967
DATE SAMPLED

	Monoterpenes					
	α-Pinene	β-Pinene	Myrcene	3-Carene	Limonene	β-Phellandrene
	Percent of Monoterpenes					
Mean	12.9	36.3	10.5	13.6	13.6	9.1
Standard Error	1.9	5.3	2.9	4.0	4.8	2.6

Camphene, α-terpinene, cymene, γ-terpinene and terpinolene occurred in very low concentrations and had standard errors of less than 0.5 percent. In addition to the variation between branches, a portion of these standard errors is due to errors in the chromatographic analysis.

Methods of Expressing Data

Expressing oleoresin monoterpene composition either as a percent of the total monoterpene fraction or as a percent of the total oleoresin can affect the results. Table 6 illustrates how this may occur using data from western white pine.

Expressed as a percent of oleoresin, all monoterpenes decreased from February to May, while little change is evident from the data when expressed as a percentage of the monoterpene fraction. The latter conclusion could only result if all monoterpenes decreased, in a like manner, either from evaporation, translocation or metabolism, or if the resin acid fraction increased while the monoterpene

Table 6.--Concentration of five cortical monoterpenes of western white pine sampled at different seasons (Hanover, personal communication).

Month Sampled	Monoterpenes					
	α-Pinene	β-Pinene	Myrcene	3-Carene	Limonene	Total
	Percent of Oleoresin					
February	7.6	21.3	2.5	13.3	3.9	48.6
May	5.7	17.0	1.4	11.2	3.4	38.7
August	4.3	12.2	0.8	11.6	3.0	31.9
	Percent of Monoterpenes					
February	15.6	43.9	5.1	27.4	8.0	100.0
May	14.6	44.0	3.7	29.0	8.7	100.0
August	13.5	38.3	2.6	36.3	9.3	100.0

fraction remained unchanged. All monoterpenes except 3-carene and limonene decreased from May to August regardless of the method of expression. Based on percent of oleoresin, 3-carene increased slightly, while limonene decreased. However, both 3-carene and limonene increased considerably when the results are expressed as a percentage of the monoterpene fraction.

The seasonal variation data of Scotch pine is expressed as a percentage of the total monoterpenes. Thus changes in the absolute amount of the monoterpenes or resin acids could have occurred but would not be detected. However, as indicated from the western white pine data, any dissimilar change in one or more monoterpenes would be evident although the results are considerably different depending on the manner of expressing the monoterpene concentrations.

Defoliation

All sample trees were heavily defoliated by the European pine sawfly in June and July, 1967, and thus the August and October samples were collected from defoliated branches. Defoliation, as indicated by the previous study, significantly increases the α-pinene concentration and also affects other terpenes in an unpredictable manner.

Effects of Tissue Age

Small changes in monoterpene composition are known to occur between cortex tissue of different ages as indicated by the previous study. Changes associated with tissue

age may have influenced the seasonal variation data for Scotch pine in two ways. First, the sampling began on the current, 1966 tissue and as the sampling progressed the tissue aged one year. Second, in order to terminate the sampling cycle with the current year's growth, the December, 1967 samples were collected from 1967 cortex tissue. Thus, part of the variation observed between the October and December 1967 samples could have been due to a change in tissue age.

Thus, this study indicates that although 7 of the 11 monoterpenes varied significantly between sampling times, changes in their concentrations were small and may in part be due to tissue aging, sampling errors and defoliation. With a well designed, replicated experiment, these sources of variation can be eliminated in a seasonal variation study. Further, additional information may be obtained by collecting known volumes of oleoresin and expressing the monoterpene concentration as a percent of the oleoresin.

CHAPTER III

MONOTERPENE VARIATION WITHIN SEEDLOTS

The variability of the monoterpenes between and within populations may provide useful information for such studies as the modes of monoterpene inheritance, the biosynthesis of monoterpenes and the taxonomy and evolution of natural populations.

My reasons for sampling individual trees within seedlots were twofold. First, information on the magnitude of monoterpene variation is indispensable in predicting the sample size necessary to achieve given levels of significance. Second, for traits under gene control, individual tree data can be used to obtain information on inheritance patterns. For a monoterpene that is simply inherited, concentration may indicate directly the genotype of an individual. Thus, by sampling a number of trees in a population it may be possible to determine gene frequency.

Materials and Methods

Oleoresin samples for this study were obtained from trees growing in the Rose Lake provenance plantation. Details of the planting site are discussed in Chapter II.

In early December, 1967, samples were collected from the following seedlots: Southern Sweden, No. 541 (14 trees); western Germany, No. 252 (19 trees) and Yugoslavia, No. 242 (21 trees).

Several small incisions were made on a tree in the cortical tissue of the current years growth of the 1966 (next-to-top) whorl. A 20-microliter sample of oleoresin was collected from these incisions on each tree. The collection and analytical procedures were the same as those described previously (Chapter II under the section on defoliation).

Results and Discussion

Inheritance of Monoterpenes

The concentrations of monoterpenes in all 54 trees are shown in Table 7. Camphene, α-terpinene, cymene and γ-terpinene occurred in relatively small concentrations and varied little. Alpha-pinene is more variable than the above terpenes and its normal pattern of distribution is suggestive of multiple gene inheritance. Similar patterns in concentrations of α-pinene have been shown for individual trees of Pinus elliottii (Squillace and Fisher, 1966) and for individuals of half-sib families of Pinus strobus (Hilton, personal communication). However, the normal pattern of distribution in the concentration of α-pinene could be due to environmental modifications such as defoliation. Another possibility is that α-pinene may be simply inherited, but it

Table 7.--Variation in cortex monoterpenes of individual trees from three seedlots grown at the Rose Lake Wildlife Experiment Station, Shiawassee County, Michigan.

Monoterpenes											
α-Pinene	Camphene	β-Pinene	Myrcene	3-Carene	α-Terpinene	Limonene	β-Phellandrene	Cymene	γ-Terpinene	Terpinolene	Total
percent of oleoresin											
Seedlot 541 Southern Sweden											
.76	.21	.89	.98	19.86	.33	.34	.51	.18	.10	1.76	25.93
1.39	.44	1.28	1.46	20.61	.26	.34	3.42	.18	.37	2.30	32.05
1.57	.33	2.55	1.27	19.01	.41	.34	2.31	.11	.19	1.94	30.01
3.27	.33	9.65	6.11	10.36	.26	.51	.77	.11	.01	.77	32.13
1.84	.33	2.94	1.46	19.97	.41	.51	2.74	.18	.28	1.76	32.40
2.28	.33	3.91	6.59	8.65	.41	1.88	4.02	.26	.46	1.13	29.91
1.03	.21	1.48	1.36	24.46	.41	.34	.60	.03	.19	2.75	32.84
1.93	.21	1.67	1.46	27.13	.41	.34	.60	.03	.37	2.93	37.06
2.28	.33	7.12	1.27	11.43	.33	.34	2.56	.03	.01	.95	26.65
1.75	.21	.99	13.90	.21	.03	.85	6.50	.11	.00	.23	24.78
1.30	.33	3.42	.89	14.74	.33	.34	.51	.18	.10	1.40	23.53
1.57	.44	1.97	1.46	14.10	.41	.51	3.42	.49	.28	2.12	26.75
1.21	.33	.99	.98	18.90	.41	.42	.51	.11	.19	1.94	25.99
1.84	.33	4.88	1.27	11.32	.26	.42	5.05	.26	.10	1.04	26.76
$\bar{X}$ 1.71	.29	3.13	2.91	15.76	.33	.51	2.39	.16	.20	1.64	29.06
Seedlot 252 Western Germany											
2.01	.33	4.01	1.27	.00	.03	14.29	.51	.41	.01	.05	22.92
1.84	.33	5.18	1.27	11.96	.26	4.88	.85	.26	.19	1.31	28.31
1.48	.33	7.02	1.17	17.09	.41	.51	.60	.11	.10	1.67	30.47
1.39	.33	5.18	.89	14.42	.26	.42	.51	.18	.10	1.40	25.06
1.75	.21	1.67	1.74	22.75	.56	.60	3.85	.41	.37	2.57	36.47
2.19	.33	2.55	4.59	13.24	.41	.51	.60	.26	.10	1.40	26.17
2.91	.33	10.04	6.30	8.44	.26	.34	.77	.26	.10	1.22	30.95
1.93	.33	.89	1.17	17.73	.56	4.11	.77	.71	.19	1.85	30.23
1.39	.33	2.74	1.27	26.49	.64	.51	.60	.18	.19	2.39	36.71
2.28	.33	1.38	8.49	10.57	.49	.51	1.02	.18	.10	1.22	26.57
3.45	.33	11.60	10.77	.32	.18	3.68	.60	.11	.00	.14	31.16
3.45	.33	12.38	7.25	.32	.18	2.82	.77	.33	.00	.14	27.97
3.00	.44	8.48	1.08	8.33	.18	5.05	.68	.41	.10	.86	28.61
.85	.33	1.19	1.46	25.31	.56	.42	.51	.18	.37	2.57	33.75
3.54	.33	5.76	9.63	.32	.18	5.65	.51	.41	.01	.14	26.46
2.37	.33	7.32	1.74	9.18	.18	3.51	3.76	.18	.19	1.22	29.98
1.48	.33	3.13	3.64	6.83	.18	.34	1.97	.64	.01	.59	19.13
2.37	.33	4.88	1.08	11.96	.26	2.39	.51	.11	.01	1.13	25.02
1.03	.33	2.35	1.17	19.12	.56	.42	.68	.26	.28	2.30	28.50
$\bar{X}$ 2.14	.30	5.15	3.48	11.80	.35	2.67	1.06	.30	.13	1.27	28.65
Seedlot 242 Central Yugoslavia											
2.91	.33	3.81	9.06	.53	.26	6.07	3.85	.41	.10	.14	27.47
1.93	.21	.80	10.96	.32	.26	1.37	3.76	.18	.10	.14	20.02
3.54	.33	12.38	1.65	.11	.03	15.06	.85	.41	.01	.05	34.40
1.84	.21	2.35	6.78	.32	.11	4.88	4.45	.11	.01	.14	21.18
2.37	.33	4.59	8.77	.21	.11	11.30	.68	.33	.01	.14	28.84
1.57	.33	.70	6.30	.32	.18	10.44	4.62	.33	.10	.14	25.03
2.46	.33	1.58	9.15	.43	.18	9.16	6.59	.49	.19	.23	30.77
1.66	.33	.12	1.36	.11	.03	17.72	1.71	.41	.28	.14	23.85
3.18	.33	8.29	1.65	.21	.11	9.41	3.59	.41	.01	.14	27.32
3.89	.33	13.15	6.68	.64	.18	5.47	2.22	.26	.10	.14	33.07
3.80	.44	.99	8.68	.53	.18	3.68	4.19	.33	.10	.32	23.25
3.63	.33	1.67	14.38	.32	.26	.25	4.88	.33	.00	.14	26.18
3.89	.33	1.09	6.21	.21	.03	5.56	4.02	.11	.00	.14	21.59
2.64	.33	1.19	6.78	.21	.11	2.14	6.76	.18	.00	.14	20.47
1.57	.21	.51	1.36	.11	.11	15.75	2.14	.18	.01	.14	22.07
3.72	.44	11.70	8.30	1.07	.41	2.91	1.19	.33	.19	.23	30.48
5.68	.33	6.64	14.76	.00	.18	2.82	.94	.18	.01	.05	31.58
4.88	.44	3.81	14.38	1.07	.41	.85	5.30	.26	.01	.14	31.55
2.73	.21	5.86	6.59	.43	.18	5.39	4.45	.26	.01	.14	26.23
1.84	.21	1.67	1.93	.21	.11	13.44	6.33	.26	.01	.14	26.14
3.63	.33	13.06	1.55	.43	.18	11.04	.42	.33	.01	.05	31.02
$\bar{X}$ 3.01	.29	4.58	7.03	.36	.18	7.37	3.47	.29	.06	.12	26.79

is metabolized at different rates in individual trees; consequently, a normal distribution is manifested. Obviously, to confirm the exact nature of inheritance for any of the terpenes, parent-progeny relationships obtained from selected crosses are necessary.

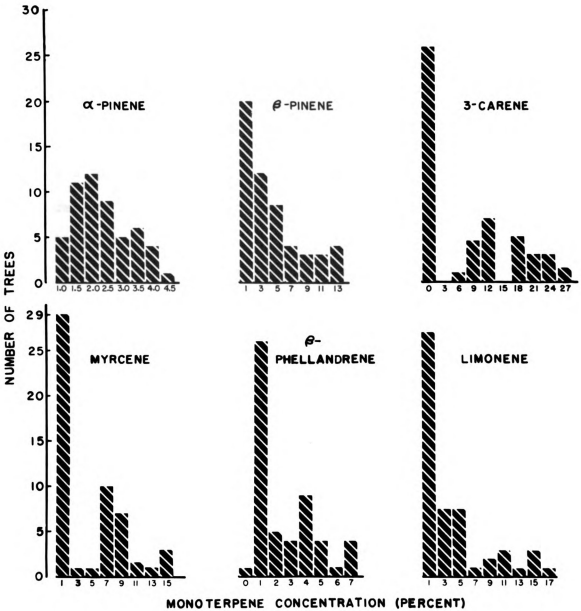
Indications of the inheritance patterns were more easily discerned by plotting histograms of the data (Figure 4). Such frequency distributions were particularly interesting for β-pinene, 3-carene, myrcene, limonene, β-phellandrene and terpinolene. The concentrations of these monoterpenes formed bimodal or trimodal patterns suggestive of control by one or two pairs of genes. However, distinct classes were not always evident because of the small size of the sample. Simple inheritance has also been suggested for 3-carene in Pinus monticola (Hanover, 1966b); for β-pinene and β-phellandrene in Pinus elliottii (Squillace and Fisher, 1966) and for myrcene and limonene in Pinus strobus (Hilton, personal communication).

When the exact modes of simply inherited monoterpenes become known, it may then be possible to measure gene frequencies for these terpenes in a population. The frequencies of such genes could be a valuable aid in determining the genetic structure and evolution of natural populations.

Minimum sample size

A knowledge of individual tree variation within a population is fundamental to studies of geographic variation.

Figure 4.--Frequency distributions of the major cortical monoterpenes. Basis, 54 trees.


NUMBER OF TREES
α-PINENE
β-PINENE
3-CARENE
MYRCENE
β-
PHELLANDRENE
LIMONENE
MONOTERPENE CONCENTRATION (PERCENT)

Obviously, differences in terpene composition between populations can be discerned only if an adequate number of samples is analyzed. Therefore, the number of trees needed to show significance for a certain difference between seedlot means was calculated using the following formula:

$$R = \frac{2V\ t^2}{(\bar{X}_1 - \bar{X}_2)^2}$$

where R = number of trees, t = Students' t, V = within-seedlot variance and $(\bar{X}_1 - \bar{X}_2)$ = minimum detectable difference between seedlot means.

It is evident from Table 7 that simply inherited monoterpenes are highly variable within a seedlot and to obtain a precise estimate of their mean concentrations a large sample size is necessary (Table 8). To detect a difference of 1/10 of the range of concentration between seedlots from 8 to 238 individuals would have to be sampled. The 8-tree sample for camphene is a reflection of its low variability within a seedlot while a highly variable terpene like myrcene requires a sample size of 238 trees. The sample sizes indicated are probably underestimated because the variances of simply inherited terpenes are unequal. The sample sizes presented in Table 8 illustrate one of the considerations involved in monoterpene studies and the detectable population differences (1/10 of the total range in concentration) were arbitrarily chosen. Smaller or larger sample

Table 8.--Size of sample needed to detect significance (5 percent level) of a given difference in monoterpene concentration between seedlots.

Monoterpenes	Error Mean Square	Range in Concentration[1]	Trees Needed to Detect a Difference of 1/10 of Range
		Percent of Oleoresin	Number[2]
α-Pinene	.82	17.86	10
Camphene	.003	.59	8
β-Pinene	14.16	12.79	68
Myrcene	14.77	6.92	238
3-Carene	36.97	17.39	94
α-Terpinene	.02	.64	40
Limonene	14.82	9.44	132
β-Phellandrene	2.89	6.22	60
Cymene	.018	.53	52
γ-Terpinene	.015	.34	103
Terpinolene	.39	1.60	14

[1]Determined from the 108 seedlots of the geographic variation study.

[2]These data and the formula on which they are based probably underestimates the number of samples needed. For a more conservative estimate, the following formula would be more appropriate:

$$r = \frac{2v(t_0 + t_1)^2}{(\bar{x}_1 - \bar{x}_2)^2}$$

sizes may be necessary depending upon the objectives of a particular study.

In conclusion, this investigation indicates that several monoterpenes appear to be under simple genetic control, and therefore, are highly variable within a population. Thus, to detect small differences between populations for these monoterpenes, large sample sizes are necessary.

Monoterpene analyses may be conducted on samples obtained from individual trees or replicated bulked samples. The choice will depend upon such factors as the specific objectives of the study, the number of trees available, and the costs involved.

CHAPTER IV

MONOTERPENE VARIATION IN HALF-SIB FAMILIES

In the past few years several studies have been conducted on the inheritance of monoterpenes in pines. Such data have been obtained from parent-progeny and other relationships studied in full-sib families (Squillace and Fisher, 1966; Hanover, 1966c) or from the progeny of half-sib families (Hilton, personal communication). In addition, analyses of half-sib families derived from natural stands may provide information about the genetic structure and evolution of a species.

The purpose of this study was to examine the variation in monoterpene composition among 30 half-sib families derived from three European stands.

Materials and Methods

The trees sampled are a portion of a larger study involving 140 open-pollinated families derived from nine European stands (Wright, 1963). The seed was collected in 1958 by European cooperators and was kept separate by parent tree and by stand. The identity of the seedling progeny derived from these parent trees was maintained in the nursery and in the plantation.

The trees used in this study are growing at the Fred Russ Memorial Forest. The plantation was established in 1961 with 2-0 stock, and the 10 families derived from each stand were planted in a replicated design.

The families sampled came from a native stand in southern Norway (Nos. 275 to 284); and from two native stands in East Germany (Nos. 341 to 350 and Nos. 501 to 510).

Cortical oleoresin was collected in late July, 1966 from one-year-old lateral branches of the 1964 whorl. Droplets of oleoresin were collected from the cut surfaces of severed branches and bulked for each four-tree replicate. Four replicates were obtained for 10 families and five replicates were obtained for the remaining 20 families to give a total of 140 samples. The samples were placed in 2 ml. stoppered vials and stored at 2°C until analysis. Details of the analytical procedures are described in Chapter II.

Results and Discussion

The mean monoterpene concentrations for each family are shown in Table 9. Two of the most variable monoterpenes were limonene (1.2 to 25.8 percent) and β-phellandrene (1.6 to 17.9 percent). Considering all of the monoterpenes, the 10 families in the Norwegian stand are less variable than the 20 families of the combined East German stands; however, the variability of the Norwegian families is similar to that in families of either East German stand.

Table 9.--Concentrations of the principal monoterpenes[1] in half-sib families growing at the Fred Russ Forest.

Family (MSFG Number)	α-Pinene	β-Pinene	Myrcene	3-Carene	Limonene	β-Phellandrene	Terpinolene
	Mean Percent of Total Monoterpenes						
			Norwegian Stand				
275	9.5	26.6	4.4	39.9	11.9	3.2	1.4
276	7.4	14.1	6.6	56.2	4.6	6.4	2.5
277	11.5	12.2	11.6	44.6	5.6	10.6	1.8
278	10.3	17.7	7.0	48.8	4.8	7.2	1.5
279	12.9	26.1	5.8	33.9	15.3	3.2	1.1
280	9.3	24.9	4.9	35.2	17.9	3.3	2.5
281	15.6	34.7	6.2	21.8	17.5	1.6	.9
282	8.3	16.1	8.8	42.6	10.3	8.5	2.5
283	6.2	12.0	3.2	66.1	1.9	5.2	2.8
284	12.8	13.8	5.1	51.7	5.6	4.4	2.6
			East German Stand				
341	6.9	16.0	5.1	61.0	1.2	3.5	3.9
342	7.7	11.1	3.4	45.7	9.8	15.5	4.4
343	10.6	11.5	3.4	40.5	12.8	16.2	2.9
344	6.1	13.4	3.6	66.1	3.2	2.9	2.8
345	5.0	14.3	2.7	65.0	3.6	2.3	5.0
346	10.2	18.6	4.0	37.8	14.4	9.5	2.5
347	8.7	27.5	7.9	41.7	3.5	4.3	4.0
348	8.5	21.4	2.7	40.7	16.9	4.4	2.7
349	7.2	19.0	3.3	50.8	4.1	9.5	3.9
350	8.3	8.6	3.6	61.4	1.7	8.3	5.3
			East German Stand				
501	13.7	28.1	6.7	38.2	2.7	6.7	1.7
502	4.9	11.5	3.7	70.7	1.3	2.5	3.1
503	8.6	14.9	3.1	56.4	6.4	5.8	2.4
504	9.1	20.6	4.0	57.5	2.1	1.8	2.7
505	7.1	8.0	3.5	64.2	5.2	6.2	3.7
506	12.1	17.8	3.3	56.0	3.6	2.4	3.0
507	8.2	15.2	5.1	50.9	13.3	3.3	2.1
508	6.1	16.0	2.9	67.0	1.8	1.6	3.4
509	9.3	16.3	4.5	54.6	6.4	3.5	2.5
510	11.0	19.5	6.7	27.4	25.8	6.3	1.7

[1]Does not include camphene, cymene and γ-terpinene which were present in small concentrations (0.2-2.4 percent).

In order to determine the significance of the variation between families, the data were subjected to an analysis of variance. The percentage of the total variation within and between families was calculated for each monoterpene. The results show a consistent significant difference between families of each stand in the concentrations of α-pinene, β-pinene, 3-carene, limonene, and β-phellandrene. The remaining terpenes were significantly different between families in only one or two stands (Table 10).

Some indication of the modes of inheritance of the monoterpenes is given by the amount of within-family variation. Large differences within families were observed for myrcene, 3-carene, limonene, β-phellandrene, and terpinolene. These differences may be due to the segregation of a few genes. Consistently large differences were not observed within families for α-pinene, camphene, cymene and γ-terpinene which suggests a more complex type of gene control. The mode of inheritance of β-pinene is not clarified by this data. The within-family differences were not as large as they would have been if one rather than four-tree bulked samples had been used.

The gene frequency of simply inherited monoterpenes like myrcene and 3-carene have a major influence on the within and between variance components. For example, in the German progenies only one sample each in family 501, 507, and 510 had high concentrations of myrcene (averaging

Table 10.--Analysis of monoterpene variation in half-sib families growing at the Fred Russ Forest.

Monoterpenes	MSFG 501-510[1]			MSFG 341-350			MSFG 275-284		
		Percent of Variance			Percent of Variance			Percent of Variance	
	Mean	Between Families	Within Families	Mean	Between Families	Within Families	Mean	Between Families	Within Families
α-Pinene	9.2	26**	71	7.9	46**	54	10.4	36**	64
Camphene	.4	60**	40	.3	17	83	.4	9	84
β-Pinene	16.8	23*	77	16.1	63**	37	19.8	70**	30
Myrcene	4.3	0	100	4.0	16	82	6.4	27**	65
3-Carene	54.3	42**	58	51.0	59**	41	44.1	60**	39
Limonene	6.9	59**	39	7.1	67**	33	9.6	37**	62
β-Phellandrene	4.0	21*	79	7.6	65**	30	5.4	55**	41
Cymene	1.1	8	11	1.4	16	69	1.5	35**	57
γ-Terpinene	.6	0	85	.8	41**	48	.6	8	84
Terpinolene	2.6	0	89	3.7	24*	75	2.0	26**	74

[1]501-510, Germany; 341-350, Germany; 275-284, Norway.

*, **,Significant at the 5 and 1 percent level, respectively.

15.9 percent). Thus, the gene frequency for myrcene is very low in this stand and 100 percent of the total variance is within families. If myrcene is simply inherited, the high concentration in a sample is probably a result of pollination by a heterozygous male. A decrease in within-family variance and significant between-family differences would result if by chance progency from this heterozygote parent were included in the sample. The gene frequency for myrcene is higher in the families of the Norwegian stand. Possibly the parent trees of families 277 and 282 were heterozygous because 3 of the 5 samples in each of these families had high myrcene concentrations. In this stand 65 percent of the variance was within families. The remaining between-family differences (35 percent) were significant. The gene(s) for 3-carene are intermediate in these three stands resulting in significant between-family differences. In addition, the proportion of the total variance is more equally divided between the two variance components.

For a terpene like α-pinene which appears to be under multiple gene control, the between-family differences were significant in all stands. The within-family variances are intermediate to high.

Thus, this study indicates that the three stands sampled are highly heterozygous for genes controlling the synthesis of myrcene, 3-carene, limonene, β-phellandrene and terpinolene. This is evident from the large within-family variances for these simply inherited monoterpenes.

CHAPTER V

INTERRELATIONSHIPS AMONG MONOTERPENES

The occurence and quantity of cortical monoterpenes are known to be under strong genetic control in Scotch pine as well as several other pine species (Squillace and Fisher, 1966; Hanover, 1966c). The enzymes, which are the functional products of these genes, apparently regulate the synthesis and ultimate concentration of the various terpenes. These facts suggest that the biosynthetic pathways leading to the formation of the monoterpenes may be indirectly determined by examining their relationship to one another.

The work of several investigators has provided some information on monoterpene biosynthesis. Stanley (1958) showed that labeled mevalonic acid gave rise to radioactive α-pinene in shoots of Pinus attenuata Lemm.. Other investigations indicated that the active isoprene molecule (derived from mevalonic acid) was isopentenylpyrophosphate and that it condensed with dimethylallylpyrophosphate to form the C_{10} compound geranylpyrophosphate (Lynen et al., 1959; Chaykin et al., 1958). This compound can be converted to myrcene by the loss of the pyrophosphate unit or through intramolecular electrophilic rearrangements give rise to monocyclic (limonene)

and bicyclic (α-pinene) terpenes (Sanderman and Schweers, 1962).

Juvonen (1966) hypothesized a very complete and detailed scheme of monoterpene biosynthesis. The pathways were based in part on the above work and the observations by many investigators of terpene fluctuations. The latter correlations suggested the idea that several common precursors were involved in the synthesis of the monoterpenes. The precursors, believed to be carbonium ions, gave rise to two or more structurally similar terpenes. The involvement of enzymes in this scheme was completely ignored.

To determine interrelationships between the monoterpenes, simple correlation analyses were performed on the cortical terpene composition of 54 trees. The origins and methods of oleoresin collection and analysis of these trees were described in Chapter III. Three simple correlation analyses were performed. One on all 54 trees, one on 28 of these trees with high concentrations of 3-carene and terpinolene and the third on the 26 remaining trees with only trace amounts of 3-carene and terpinolene. All correlations were performed on transformed data (arc sine) which had been expressed as a percent of the total monoterpenes.

Results and Discussion

The correlation coefficients (Table 11) based on all trees or only on those containing large concentrations of

Table 11.--Correlations between monoterpenes for 54 trees from southern Sweden, western Germany and Yugoslavia.

	Monoterpenes							
	α-Pinene	β-Pinene	Myrcene	3-Carene	α-Terpinene	Limonene	β-Phellandrene	γ-Terpinene
	r[1]							
β-Pinene	.44[2]	--						
	NS	--						
	.69	--						
Myrcene	.64	NS	--					
	NS	NS	--					
	.53	NS	--					
3-Carene	-.71	NS	-.63	--				
	NS	NS	*	--				
	-.87	-.74	-.59	--				
α-Terpinene	-.39	NS	NS	.73	--			
	NS	NS	*	.67	--			
	-.54	-.69	NS	.61	--			
Limonene	NS	NS	NS	-.71	-.73	--		
	-.59	NS	-.87	-.51	-.54	--		
	*	NS	NS	*	*	--		
β-Phellandrene	NS	-.34	.45	-.42	*	NS	--	
	NS	-.66	NS	NS	NS	NS	--	
	NS	NS	NS	*	NS	NS	--	
γ-Terpinene	-.61	*	.50	.60	.55	NS	NS	--
	NS	NS	NS	NS	NS	*	NS	--
	-.56	-.65	NS	*	*	NS	NS	--
Terpinolene	-.71	*	-.58	.98	.72	-.71	-.33	.62
	NS	*	*	.61	NS	NS	.61	NS
	-.84	-.79	-.50	.89	.63	*	NS	.63

[1]Values listed are significant at the 1 percent level. NS and * indicate non-significance and significance at the 5° level, respectively.

[2]Upper value based on 54 trees.
Middle value based on 26 of the above trees which have only a trace amount of 3-carene and terpinolene.
Lower value based on the 28 remaining trees which contain large amount of 3-carene and terpinolene.

3-carene and terpinolene were similar except in the case of β-pinene. Correlation of that chemical with 3-carene was r = -.74, with α-terpinene r = -.69, with γ-terpinene r = -.65 and with terpinolene r = -.79 when based only on trees with high 3-carene and terpinolene concentrations. But β-pinene was not correlated with those same terpenes if all trees were considered.

On the other hand, monoterpene correlations with α-pinene varied drastically among the three sets of analyses. When all trees were included or those containing 3-carene, most correlations were significant. However, these correlations were not significant when based on trees lacking 3-carene. The two notable exceptions to this trend are evident in the correlations between limonene and α-pinene (r = -.57) and limonene and myrcene (r = -.87). These correlations were either not significant or significant at the 5 percent level when performed on trees containing 3-carene.

A negative correlation between any two terpenes supports the hypothesis that both are derived from a common precursor. Thus, as one or two terpenes greatly increases others are driven down since the total monoterpenes synthesized is fairly constant. Negative correlations by themselves do not indicate whether the precursors are separate and distinct carbonium ions or if all terpenes are derived from a single substrate such as a pool of geranylpyrophosphate.

Positive correlations may be due to one of several factors. For example the presence of 3-carene is apparently

responsible for the positive correlation of α-pinene with β-pinene and with myrcene. Both of these correlations are not significant when 3-carene is absent. Only the positive correlation between 3-carene and terpinolene was consistent regardless of the variation in all other terpenes. This association may be due to a specific common precursor (other than geranylpyrophosphate) or one of these terpenes may serve as a precursor in the synthesis of the other. Finally, this and other positive correlations could be a result of genetic linkage.

Correlations were performed on trees with or without 3-carene and terpinolene as a technique to clarify relationships which may have been obscured when all trees were analyzed together. However, these groupings unexpectedly showed that many correlations could be completely altered by including or excluding one of the terpenes. Thus, many correlations given here and published elsewhere have no real significance in relation to biosynthetic pathways.

I feel that the data of this study is consistent with the hypothesis that all monoterpenes are derived from one precursor, geranylpyrophosphate. Hypothesizing that several other intermediates are involved, based on terpene correlations, is not supported by the fact that these correlations can be easily altered. The only consistent association observed was between 3-carene and terpinolene.

CHAPTER VI

GEOGRAPHIC VARIATION IN SCOTCH PINE MONOTERPENES

Introduction

Since the advent of gas chromatography, the monoterpene composition of very small samples can be measured precisely and rapidly. This fact along with the evidence that monoterpenes are under strong genetic control makes it possible to undertake intensive studies of variation within species or local populations.

Historically, taxonomy and classification have been based on morphological characteristics. The more characteristics used in a system the more probable it is that the system will express the natural relations among populations. In the last decade plant chemicals have been used increasingly as another dimension in systematic classification. This has come to be known as chemotaxonomy or chemical systematics. Chemical studies in several genera and species have been helpful in elucidating their classification and evolution. In fact, chemicals may be particularly useful in delineating subtle differences between races, varieties and hybrid populations where morphological features, influenced by the environment, may be of little value.

Monoterpene Variation Within Species

Geographic variation in monoterpenes has been reported in several species of Pinus. Mirov (1961) reported considerable variation in monoterpenes of Pinus ponderosa oleoresin samples collected from 12 localities. Peloquin (1964) conducted a more intensive study in Pinus ponderosa and showed that there was a general correspondence between morphological and monoterpene variation patterns. Squillace and Fisher (1966) determined that the cortical oleoresin in Pinus elliottii var. elliottii in northern Florida was low in β-phellandrene and high in β-pinene. These trends were reversed in Pinus elliottii var. densa in southern Florida. Varieties of Pinus muricata exhibit especially interesting monoterpene patterns (Forde and Blight, 1964; Mirov et al., 1965). Within this California species, the northern variety consists largely of α-pinene, the central variety is composed of 3-carene and terpinolene, and the southern varieties are composed largely of sabinene and terpinolene. The insular populations are high in α-pinene, sabinene and terpinolene. Geographic variation has also been shown in three populations of Pseudotsuga menziesii in Montana and Idaho (Hanover and Furniss, 1966); and in five populations of Pinus radiata in California (Bannister et al., 1962). R. M. Hilton found differences between Pinus strobus from Michigan's Upper and Lower Peninsulas.

Variation in Scotch pine monoterpene composition throughout Europe and Asia was summarized by Mirov (1961) and more recently by Juvonen (1966). These reviews indicate that Scotch pine monoterpenes vary extensively from region to region. However, these investigations usually consisted of analyzing the oleoresin in only a few native trees. In addition, some of the analyses were conducted on oleoresin obtained from xylem tissue, other investigators analyzed the oleoresin from needle or cortex tissue, and still others determined the monoterpene composition from two or more tissues combined. There have been no extensive systematic studies of the monoterpenes in Scotch pine.

Taxonomy of Scotch Pine

Numerous varieties of Scotch pine have been designated by different taxonomists and many variants have been named. The NC-51 Scotch pine provenance test is the most extensive one to date. As such, it has been a valuable aid in clarifying the taxonomy of the species. Recently, the assigning of valid varietal names was based on multivariate analysis of several traits measured in two-year old seedlings and from cone and needle characteristics of wild tress (Ruby, 1964). Ruby recognized 21 geographic varieties of Scotch pine as valid. However, the type variety, *Pinus sylvestris* var. *sylvestris* is still in doubt because it is unknown

whether Linneaus' type specimen was collected in Germany or southern Sweden.

Sampling Considerations

Before embarking upon a study of geographic variation, several sampling procedures should be considered. Some of the more important of these are choice of tissue to be sampled, size of sample needed to characterize a population and whether analyses should be based on bulked or individual tree samples. On the basis of preliminary investigations, oleoresin from cortex tissue was selected for sampling. Cortical oleoresin was more abundant than xylem oleoresin, and also cortex monoterpenes were more variable--between trees--an important chemotaxonomic consideration. Needle tissue requires a time consuming extraction procedure, and further, the monoterpenes appear to be less variable than those in cortex tissue.

This portion of the study was primarily concerned with characterizing the monoterpene composition of a population or seedlot. Ideally, sampling every tree of a seedlot would provide the maximum information. Since a sample size of this magnitude was impossible, bulking the oleoresin for a number of trees of each seedlot appeared to be a logical compromise. In a preliminary study the variation between replicates of five-tree bulked samples indicated that a 20-tree bulked sample would provide a good estimate of the monoterpene composition of a seedlot.

In the near future, individual tree analyses may provide information that is lost when samples are bulked (Chapter III). This is especially true for monoterpenes, such as 3-carene, which are simply inherited (Hanover, 1966b). The concentration of 3-carene could indicate whether an individual is homozygous or heterozygous for the genes controlling 3-carene synthesis. Thus, the gene frequency for 3-carene could easily be determined in a population. This knowledge would furnish the means for more directly measuring the degree of relatedness between populations.

Materials and Methods

Samples were collected from 108 seedlots of an NC-51 plantation growing at the W. K. Kellogg Forest, located in Kalamazoo county, two miles west of Augusta, Michigan. The plantation was established in 1961 with 2-0 stock and each seedlot is represented in 10-replicated, four-tree plots. Details of the nursery procedures and other establishment information are given by Wright and Bull (1963).

A 20-tree bulked sample was obtained by collecting oleoresin from two trees in each of the 10 replicates. Samples were obtained by scraping off a droplet of oleoresin from the cortex tissue of a one-year old lateral branch severed at the 1964 whorl. The oleoresin was placed in one-half dram vials, tightly sealed and stored at 35°C. Samples were collected during a four-day period in June, 1966, and

analyzed in December, 1966, and January, 1967. In order to determine the amount of variation within a source, two replicated, bulked samples were collected from 21 seedlots. Each replicate consisted of oleoresin bulked from 10 trees collected from plantation replicates 1-5 and 6-10.

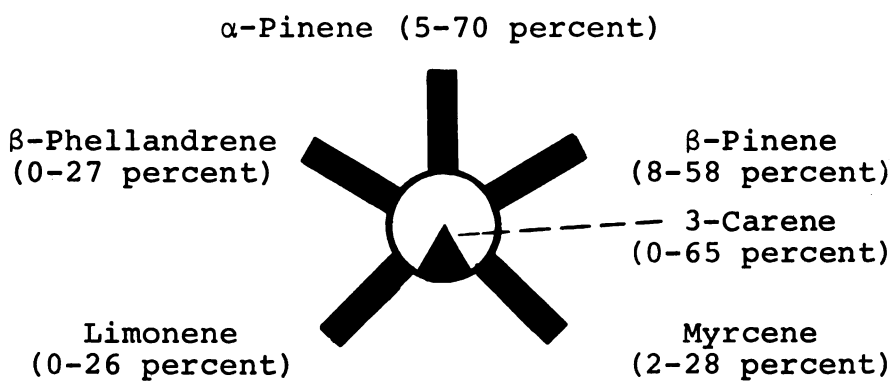
Samples were analyzed by gas-liquid chromatography as described in Chapter II under the section on seasonal variation. The column used was 6' x 1/4" stainless steel, packed with 10 percent polyproplyene glycol on 60/80 mesh chromasorb G-AW. Column temperatures were 95°C to 97°C, injection port and detector temperatures were 200°C and the helium flow rate was 110 ml/min. Twenty-four samples were rerun on a 6' x 1/4" column containing β, β'-oxydipropionitrile at 60°C. The re-chromatographed samples further substantiated identification of the monoterpenes and also aided in the quantitative determination of limonene and β-phellandrene. These monoterpenes are not completely separated by polypropylene glycol.

Results and Discussion

Geographic Variation

The variation in monoterpenes among the 108 seed sources sampled was amazingly large. One of the most variable monoterpenes was 3-carene as indicated from Figures 5 and 6. Most of the isolated southern populations either lacked 3-carene or possessed it in small amounts, while

Figure 5.--Geographic variation in the principal monoterpenes in Scotch pine from Europe. The key to the symbol is shown below. Each monoterpene is divided into nine equal classes and the amount of each is represented by the length of bar or degree of shading of the circle.



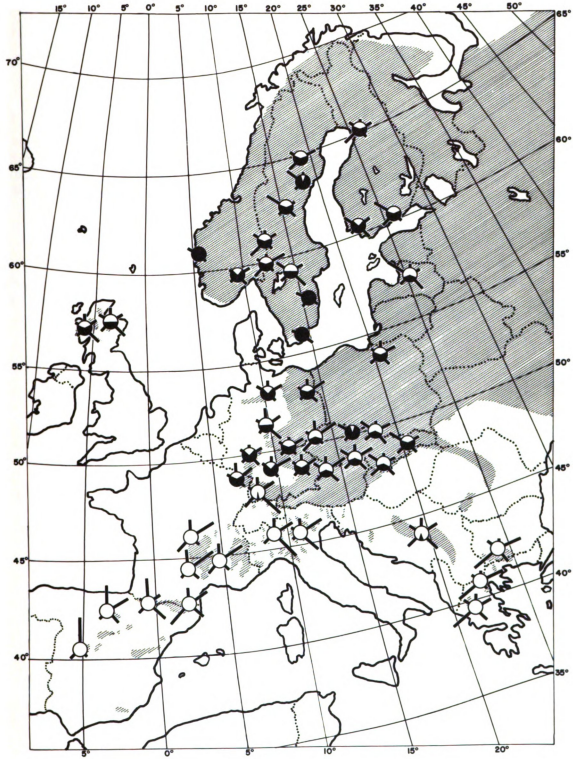
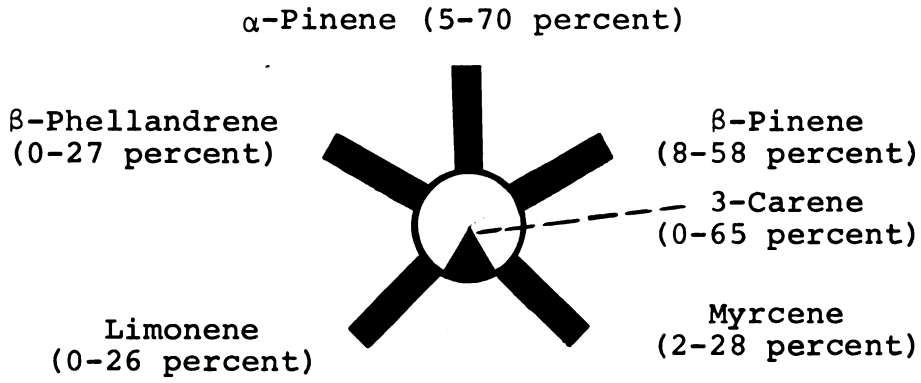
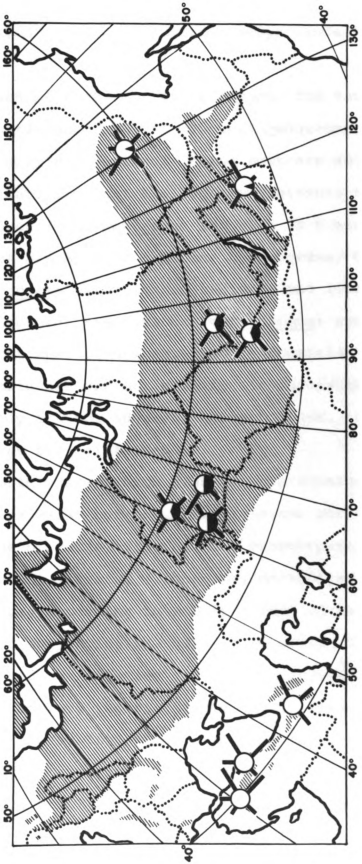

15° 10° 5° 0° 5° 10° 15° 20° 25° 30° 35° 40° 45° 50° 65°
70°
65°
60°
55°
50°
45°
40°
60°
55°
50°
45°
40°
35°
5° 0° 5° 10° 15° 20°

Figure 6.--Geographic variation in the principal monoterpenes in Scotch pine from Asia. The key to the symbol is shown below. Each monoterpene is divided into nine equal classes and the amount of each is represented by the length of bar or degree of shading of the circle.





northern populations generally contained large concentrations of 3-carene.

Within each of these two major groups, the variation in other monoterpenes exhibit distinct geographic patterns. This is especially evident in the southern sources. Spanish sources (var. iberica) are high in α-pinene; sources from southern France (var. aquitana) are high in β-pinene; 'N. Italy' sources are high in β-pinene and myrcene; Greek sources (var. rhodopaea) are high in β-pinene and limonene and Turkish and Georgian SSR sources (var. armena) are high in β-pinene and myrcene. The monoterpene composition of the latter two varieties are not clearly distinguishable; however, since they are not adjacent to each other, their separate identities are maintained.

In the north where Scotch pine is more continuous, geographic patterns exist but no sharp divisions are evident.

The degree of correlation between monoterpene composition and existent varietal classes was determined by grouping the sources according to Ruby's (1964) varietal classification and subjecting the data to an analysis of variance. Three sources adjacent to varietal boundaries were regrouped to improve the fit of the data. Seedlots 254 and 255 were removed from their respective varieties, combined and analyzed as a separate group. Seedlot 542 was regrouped from variety rigensis into variety septentrionalis and variety rigensis was divided into Latvian and

Swedish sources--a division that had been made in the 1938 IUFRO tests. These minor changes did not conflict with Ruby's data and the naturalness of the geographic varieties was maintained. Planted stands and varieties represented by a single seedlot were omitted from the analysis. Seedlots comprising each variety are given in Table 12 and the varietal means are given in Table 13.

An analysis of variance of the replicated 10-tree bulked samples of 21 seedlots showed that the within-seedlot variance was small. The variation between varieties (Table 14) was significant at the 1 percent level for all monoterpenes except cymene. The most suitable monoterpenes for distinguishing varieties was 3-carene and α-pinene. The between-variety variances for these compounds were 87 and 86 percent of the total variances, respectively.

The middle European variety hercynica contributed substantially to the within variety variation; 3-carene varied between 13 and 54 percent and α-pinene between 6 and 15 percent. Also, the central Scandinavian variety septentrionalis varied from 32 to 63 percent in 3-carene. Both of these varieties encompass regions of considerable geographic diversity and complex patterns of plant distribution. Ruby separated the East German and Czechoslovakian sources of hercynica. However, a simple natural division was not obvious on the basis of monoterpene variation. Within Czechoslovakia, 3-carene varied between 16 and 54 percent. On the

Table 12.--Classification of Scotch pine into varieties according to Wright et al. (1966).

Variety	Countries	Seedlot MSFG Nos.
lapponica	Northern Finland	229
	Northern Sweden	546,547,548,549
mongolica	Eastern Siberia	254
altaica	Southern Siberia	227, 234, 255, 256
septentrionalis	Central Sweden	222, 521, 522, 523, 524, 543, 544, 545
	Central Norway	201, 273, 274
	Southern Finland	228, 230, 232, 233
rigensis	Latvian SSR	223, 224
	Southern Sweden	541, 542, 543
uralensis	Ural Mtns., Russia	257, 258, 259, 260
polonica	Poland	211, 317
borussica	Northeastern Germany	202, 210
hercynica	Germany	203, 204, 207, 208, 209, 525, 526, 527, 528, 529
	Czechoslovakia	305, 306, 307, 308, 309, 310, 311, 312, 313, 314, 315
haguenensis	Western Germany	206, 250, 251, 252, 253
	Vosges Mtns., France	236, 237, 241
	Belgium	318, 530
'East Anglia'	England	269, 270
pannonica	Hungary	552, 553
'North Italy'	Italy	554, 555, 556, 557
illyrica	Yugoslavia	242
scotica	Scotland	265, 266, 267, 268
iberica	Spain	218, 219, 246, 247
aquitana	Central Massif, France	212, 238, 239, 240, 316, 320
rhodopaea	Greece	243, 244, 271, 272, 551
armena	Caucasus Mtns., Turkey	213, 214, 220, 221
	Georgian SSR	261, 262, 263, 264

Table 13.--Variation in monoterpene concentrations in Scotch pine varieties grown at the W. K. Kellogg Forest.[1]

Variety	Concentration of α-Pinene	β-Pinene	Myrcene	3-Carene	Limonene	β-Phellandrene	Terpinolene
	Percent of Total Monoterpenes						
	Scandinavian and Siberian Varieties						
lapponica	9.1	17.0	5.5	41.1	9.3	10.9	3.2
mongolica	15.4	28.7	11.5	8.7	16.2	16.4	1.3
altaica	10.6	17.3	7.4	26.3	14.1	17.4	3.7
septentrionalis	7.6	17.3	8.2	44.1	6.4	9.5	4.0
rigensis							
Sweden	5.6	13.6	4.3	58.8	4.4	5.5	4.6
Latvia	8.2	14.4	15.3	29.7	6.9	19.6	2.7
uralensis	9.1	19.9	11.3	25.0	11.3	17.2	3.1
	Central European Varieties						
polonica	9.5	22.1	8.9	38.5	8.1	6.4	3.0
borussica	10.1	22.8	8.7	41.0	3.7	6.1	4.8
hercynica	10.4	22.9	11.9	30.7	8.6	8.9	2.9
haguenensis	9.5	19.5	9.7	41.6	4.6	4.9	3.2
'East Anglia'	17.2	31.6	11.4	26.4	4.4	3.3	2.4
pannonica	8.3	12.9	5.5	49.9	6.0	8.9	4.7
'N. Italy'	17.1	41.6	23.7	4.4	6.4	3.7	.7
illyrica	11.8	24.3	17.9	20.2	12.9	7.9	1.8
	West and South European Varieties						
scotica	10.6	21.9	11.8	39.7	5.0	4.5	3.1
iberica	46.1	15.3	12.7	.8	7.1	14.7	.3
aquitana	18.5	47.1	10.4	4.9	11.7	3.4	.3
rhodopaea	12.4	34.9	11.5	5.8	23.1	7.9	.9
armena	19.1	42.7	17.7	4.4	9.8	3.4	.5

[1]Camphene, cymene, α-terpinene, and γ-terpinene are omitted because they were present in very small amounts (0-2 percent).

Table 14.--Percentage of variation in monoterpene concentration accounted for by differences between and within varieties.

Monoterpenes	Percent of Variance Due to Differences	
	Between Varieties	Within Varieties
α-Pinene	86**	14
Camphene	61**	39
β-Pinene	73**	27
Myrcene	41**	59
3-Carene	87**	13
α-Terpinene	50**	50
Limonene	53**	47
β-Phellandrene	72**	28
Cymene	22	78
γ-Terpinene	50**	50
Terpinolene	73**	27

**Significant at the 1 percent level.

basis of terpenes alone, hercynica could be divided into 3 or 4 subunits, but this additional splitting would not be supported by morphological differences.

The high correspondence between existent varietal classes and monoterpene composition indicates that the monoterpenes are indeed a useful taxonomic tool in Scotch pine.

Evolution of Scotch Pine

The evolution of monoterpenes and the resin duct system is strictly a matter of conjecture. However, the patterns of geographic variability in monoterpenes do reflect the evolution and migration of Scotch pine. In the south, tree growth is confined to isolated stands located at high elevations. These forests were south of the maximum extent of glaciation during the Pleistocene. Evolution has probably proceeded uninterrupted for a much longer time than in northern Europe where the species was obliterated during glaciation.

Two opposing theories of plant distribution in response to glaciation are evident from the literature. Bertsch (1953) in his description of the German forests contends that middle Europe, directly south of the glacier of the last ice age, was covered with tundra and below this there was a scrub zone. The forest survived only in the

lower elevations of the Mediterranean region. All of middle Europe was devoid of forest.

A more recent hypothesis contends that the glaciers had little influence on plant distribution in unglaciated areas. The zone of tundra and scrub was very narrow and the retreating Scotch pine never came in contact with the isolated southern populations. The distribution of 3-carene appears to support the later theory, assuming that 3-carene was present in the pre-Pleistocene populations in northern Europe. The genes for 3-carene synthesis are entirely absent in most southern populations. This would not be the case if the northern populations had come into contact with the southern stands or if the northern forest was derived from the southern stands. The exchange of genetic material has also been limited between Spain, the Central Massif of France, Italy, Yugoslavia, Greece, Turkey and Georgian SSR. Apparently these populations are Tertiary relics and their extended isolation is reflected in their distinct morphological and chemical differentiation.

During the Pleistocene glaciation, probably a number of refugia existed just south of the ice and perhaps some within the glaciated area (Wulff, 1943). Some of the present patterns of variation in northern Europe and Asia reflect the migration of several well-differentiated populations. Paleobotanical evidence indicates that refugia probably existed in the Carpathean and Ural mountains, in the south

of western Siberia and even possibly in the Scandinavian highlands and the Gulf of Finland. Reinvasion eventually formed a more or less continuous forest in a complex arrangement. The free exchange of genetic material created additional diversity. Selection pressures acting upon this complex gene pool have allowed more recent morphological and chemical differentiation. The heterogeneous monoterpene patterns found especially in Middle Europe manifest these recent geological events.

The retreat of the ice coincided with a rise of the land, connecting the Scandinavian peninsula with western Europe via Denmark. Also, the shallow southern part of the North Sea formed a land bridge between England and the continent. The high concentrations of 3-carene in southern Scandinavia and in some populations in Germany, lend further support to the concept of the formation of a land bridge. The similarity of Scottish populations and those of middle Europe also indicate recent gene exchange between these populations.

The present distribution of Scotch pine and perhaps some of its complexity may be accounted for by early man. The complete extermination of Scotch pine in England and Denmark happened recently after man arrived there (Godwin, 1956). A change from a continental to an oceanic climate contributed to this obliteration. Further, man has artificially established populations of trees by either a directed program of reforestation or as a matter of chance, and it is often difficult to distinguish them from natural populations.

CHAPTER VII

CONCLUSIONS AND RECOMMENDATIONS

The environmental effects on monoterpene composition in Scotch pine were small but usually predictable. Although 7 of the 11 monoterpenes varied significantly between sampling times, these changes were confounded by the effects of defoliation, errors in sampling and tissue age effects. The effects of sawfly defoliation and errors in sampling can be easily eliminated from seasonal variation studies by obtaining replicated samples on protected trees. Tissue age effects are difficult to separate from seasonal effects on plantation grown trees. However, the major environmental influences (soil moisture, temperature and photoperiod) could be eliminated from the effects of tissue age by using clonal material in growth chamber investigations. In such studies, material of the same age could be tested simultaneously under various conditions.

Cortical monoterpene changes associated with different aged tissue and defoliation were small. Oleoresin from older tissue formed in 1965 was higher in α-pinene and β-pinene and lower in myrcene, 3-carene and limonene than younger tissue formed in 1967. Defoliation significantly increased (at the 5

or 10 percent level) the concentration of α-pinene, β-pinene, 3-carene and the total monoterpenes. This effect was most pronounced on moderately defoliated trees. In heavy defoliated trees, branches with and without foliage differed only in α-pinene concentration. I believe the almost total lack of foliage altered the monoterpene concentrations throughout the tree, including the few remaining foliated branches. Such changes would not be detected by the within-tree sampling scheme that was utilized. Therefore, to investigate this hypothesis and to determine the effects of defoliation more precisely, clonal material should be used. In such a study, monoterpene concentrations would be determined before and after artificial defoliation. The mechanism(s) of these changes would be difficult to determine since they probably involve enzyme activities, enzyme concentrations or changes in substrates.

In order to plan and interpret other related investigations on terpenes, a knowledge of changes associated with tissue age and defoliation may be important. For example, to obtain valid comparisons in chemosystematic studies, I would recommend that all oleoresin samples be collected from the same aged tissue of uninjured trees.

Site effects, another source of environmental influence, were minor. Although a significant seed source X site interaction was determined for β-phellandrene, the small size for this simply inherited terpene may have been responsible

for this interaction. It is apparent that in future investigations site effects can be determined more precisely and with fewer samples from clones established in diverse location.

Different tissues (cortex, xylem and needle) had distinct monoterpene compositions. Each tissue appears to act as a separate compartment having a distinct terpene metabolism. Probably little or no monoterpene transport occurs between tissues. Tree-to-tree variability of terpene composition was smallest in needle tissue and largest in cortex tissue. Thus, in chemosystematic studies the analysis of cortical monoterpenes is recommended since the presence of variability is essential in distinguishing trees or populations from one another.

From studies on individual trees and half-sib families, the monoterpenes 3-carene, myrcene, limonene, β-phellandrene and terpinolene appeared to be under simple genetic control. More complex gene action was indicated for α-pinene and β-pinene, camphene, α-terpinene, cymene and γ-terpinene. To clarify the nature of these inheritance patterns, parent-progeny relationships obtained from selected crosses are needed.

Large tree-to-tree variation occurred in the simply inherited terpenes, especially when their gene frequency in a population was low. In such cases large sample sizes are necessary to detect small difrerences between populations. This is most easily accomplished by replicated bulked samples.

However, in the near future additional knowledge of terpene inheritance may make it possible to determine the genotype of an individual directly from terpene concentration. Thus, gene frequencies of populations could be determined which would aid in chemosystematic studies and especially in investigations related to the evolution of natural populations.

Simple monoterpene correlations support the hypothesis that all the terpenes are enzymatically derived from the stable precursor geranlypyrophosphate. The enzyme and subsequent terpene concentrations are under strong genetic control, and the presence or absence of a terpene reflects the gene status. The only positive correlation that persisted, despite changes in any other terpene, was between 3-carene and terpinolene. At present the cause of this common association is entirely speculative. From time course studies using $14CO_2$, it may be possible to directly determine terpene biosynthetic pathways and turnover. Selected genotypes which are lacking in one or more terpenes could aid such studies.

The monoterpenes in Scotch pine exhibited wide geographical variation. They proved to be an excellent chemotaxonomic tool based on the fact that there was a high correspondence between terpenes and existent varietal classes. The highly variable middle European area, in morphology and in terpene composition, indicates that additional sampling is necessary to further delineate natural groupings.

In addition, geographic variability of the monoterpenes is useful in explaining evolution and migration patterns in Scotch pine. For example, the absence of 3-carene in most isolated southern populations indicates that little gene exchange has taken place and that these populations are probably Tertiary relics. The similarity in terpene composition between Germany and lower Scandinavia lend further support to the hypothesis that Scotch pine migrated across a land bridge which had once connected these land masses. Also there probably has been recent gene exchange between the Scottish populations and those of Middle Europe since they have similar terpene compositions.

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APPENDICES

TABLE 1. MONOTERPENE VARIATION IN CORTEX, XYLEM, AND NEEDLE TISSUES IN 10 SCOTCH PINES

COLLECTED 6/22/1967
SINGLE TREE SAMPLES
YEAR OLD TISSUE(1966)

COLLECTED FROM 1965-66 WHORLS
ROSE LAKE
GLC ANALYSIS 6/23/67

PERCENT MONOTERPENE

TISSUE	MSFG	REP	TR. NO.	ALPHA-PINENE	CAMPHENE	BETA-PINENE	MYRCENE	3-CARENE	ALPHA-TERPINENE	LIMONENE	BETA-PHELL.	CYMENE	GAMMA-TERPINENE	TERPINOLENE
NEEDLE	218	5	4	59.1	19.2	7.4	7.4	0.5	0.5	1.0	1.0	2.5	1.0	0.5
CORTEX	218	5	4	49.7	0.6	6.8	40.8	0.2	0.2	0.6	1.0	0.2	0.0	0.0
XYLEM	218	5	4	91.4	0.9	2.1	3.7	0.2	0.0	0.7	0.2	0.2	0.2	0.2
NEEDLE	219	1	1	64.6	16.3	8.2	4.8	0.0	0.7	1.4	1.4	2.7	0.0	0.0
CORTEX	219	1	1	33.6	0.8	2.6	19.0	0.8	0.3	40.5	1.9	0.3	0.0	0.3
XYLEM	219	1	1	92.5	0.9	1.9	1.4	0.5	0.5	0.9	0.5	0.0	0.5	0.5
NEEDLE	239	3	1	55.4	10.2	14.7	3.9	10.9	0.4	0.7	0.4	1.1	0.4	2.1
CORTEX	239	3	1	8.0	0.6	31.5	4.3	29.8	1.1	17.9	2.8	0.3	0.6	3.1
XYLEM	239	3	1	36.2	0.5	10.6	1.9	41.7	0.7	1.9	0.7	0.5	0.2	5.0
NEEDLE	250	3	2	48.0	8.9	19.6	4.5	10.1	0.0	1.1	1.7	3.9	0.0	2.2
CORTEX	250	3	2	4.5	0.3	13.9	23.1	43.4	1.5	3.0	1.8	2.1	0.9	5.3
XYLEM	250	3	2	33.4	0.5	30.8	3.1	26.2	0.3	0.8	1.5	0.0	0.3	3.1
NEEDLE	250	5	4	66.4	10.2	5.3	4.5	8.7	0.4	1.1	0.4	1.5	0.8	0.8
CORTEX	250	5	4	9.0	0.3	3.9	3.9	58.1	0.9	15.1	2.1	0.3	0.6	5.7
XYLEM	250	5	4	66.9	0.9	2.6	1.3	23.5	0.4	0.9	0.4	0.2	0.2	2.6

TABLE 1. (CONTINUED)

NEEDLE	252	3	2	78.8	8.4	5.1	3.3	0.4	0.0	1.1	0.7	1.5	0.4	0.4
CORTEX	252	3	2	9.6	0.5	29.0	32.2	0.9	0.2	13.1	14.0	0.2	0.0	0.2
XYLEM	252	3	2	87.3	0.8	4.2	3.9	0.3	0.0	1.9	1.4	0.0	0.0	0.3
NEEDLE	257	2	2	62.9	11.0	5.3	4.1	11.8	0.4	0.8	0.8	0.8	0.4	1.6
CORTEX	257	2	2	9.7	0.4	8.4	5.0	33.2	1.3	6.3	32.4	0.4	0.0	2.9
XYLEM	257	2	2	44.7	0.8	2.7	1.9	40.1	1.2	1.2	3.1	0.8	0.4	3.1
NEEDLE	308	3	4	66.9	9.0	4.5	3.8	11.7	0.3	1.4	0.7	0.3	0.3	1.0
CORTEX	308	3	4	6.2	0.3	6.2	5.3	36.0	1.5	8.6	30.7	0.6	0.6	4.1
XYLEM	308	3	4	52.9	0.7	3.0	1.5	30.3	0.7	3.6	2.8	0.2	0.6	3.7
NEEDLE	317	3	4	56.9	6.8	7.7	4.0	15.4	1.5	2.2	0.6	3.1	0.6	1.2
CORTEX	317	3	4	7.7	0.5	13.6	3.6	59.6	1.5	1.3	2.1	2.1	1.3	6.7
XYLEM	317	3	4	28.1	0.5	14.3	2.3	45.7	1.3	1.0	1.3	0.3	0.8	4.4
NEEDLE	530	6	4	54.5	11.3	4.8	5.6	18.6	0.4	0.9	0.4	1.3	0.4	1.7
CORTEX	530	6	4	6.8	0.3	12.4	4.0	65.7	1.5	0.8	1.8	0.0	0.5	6.3
XYLEM	530	6	4	19.1	0.2	3.3	2.9	61.3	1.8	1.3	1.6	0.2	0.7	7.6

TABLE 2. MONOTERPENE VARIATION IN CORTEX, XYLEM, AND NEEDLE TISSUES IN 10 SCOTCH PINES

COLLECTED 8/13/1967 — COLLECTED FROM 1965-66 WHORLS
SINGLE TREE SAMPLES — ROSE LAKE
YEAR OLD TISSUE(1966) — GLC ANALYSIS 8/15/67

PERCENT MONOTERPENE

TISSUE	MSFG	REP	TR. NO.	ALPHA-PINENE	CAMPHENE	BETA-PINENE	MYRCENE	3-CARENE	ALPHA-TERPINENE	LIMONENE	BETA-PHELL.	CYMENE	GAMMA-TERPINENE	TERPINOLENE
NEEDLE	218	6	4	57.7	19.8	8.6	8.9	0.2	0.2	1.1	1.1	1.8	0.2	0.2
CORTEX	218	6	4	45.1	0.8	3.4	48.5	0.4	0.0	0.4	1.1	0.4	0.0	0.0
XYLEM	218	6	4	91.3	0.5	3.1	2.0	0.5	0.0	1.0	0.5	0.5	0.0	0.5
NEEDLE	219	1	1	65.5	16.8	7.2	5.6	0.3	0.0	1.0	1.0	2.0	0.3	0.3
CORTEX	219	1	1	30.3	0.6	4.8	19.7	0.6	0.3	40.4	2.5	0.3	0.0	0.3
XYLEM	219	1	1	94.1	1.0	2.0	1.0	0.0	0.0	1.0	0.5	0.0	0.0	0.5
NEEDLE	239	3	1	54.6	11.1	14.1	4.6	9.0	0.5	1.4	0.9	1.4	0.5	2.1
CORTEX	239	3	1	10.3	0.3	32.6	4.0	29.2	1.0	15.9	2.7	0.3	0.3	3.3
XYLEM	239	3	1	50.3	0.6	3.6	3.0	32.7	1.8	2.4	0.6	0.0	0.6	4.2
NEEDLE	250	3	2	45.8	9.2	22.9	4.6	10.6	0.3	0.9	0.9	2.6	0.3	2.0
CORTEX	250	3	2	6.2	0.4	14.5	25.7	40.6	1.4	2.2	1.4	2.5	0.7	4.3
XYLEM	250	3	2	46.3	1.1	22.9	3.2	17.6	2.1	1.6	1.6	0.5	0.5	2.7
NEEDLE	250	6	4	64.3	11.2	5.0	4.6	9.5	0.4	1.2	0.4	1.7	0.4	1.2
CORTEX	250	6	4	7.4	0.3	3.7	4.4	56.7	1.0	15.4	1.7	1.0	1.0	7.4
XYLEM	250	6	4	72.2	0.5	2.8	2.3	15.7	0.9	1.4	0.9	0.5	0.5	2.3

TABLE 2. (CONTINUED)

CORTEX	252	3	2	9.4	0.3	22.1	37.5	0.5	0.0	16.7	12.9	0.3	0.0	0.3
XYLEM	252	3	2	89.4	1.4	3.9	1.4	0.5	0.5	1.4	1.0	0.0	0.0	0.5
NEEDLE	257	2	2	62.9	10.3	5.2	4.4	10.7	0.6	1.6	1.0	0.8	0.2	2.4
CORTEX	257	2	2	9.3	0.4	7.1	5.2	32.3	1.1	7.4	31.2	0.7	1.1	4.1
XYLEM	257	2	2	60.4	0.7	2.9	2.2	27.3	1.1	1.1	0.7	0.0	0.0	3.6
NEEDLE	308	3	4	65.8	10.6	4.7	3.7	10.8	0.4	1.4	0.8	0.8	0.2	1.0
CORTEX	308	3	4	6.4	0.4	5.1	5.1	38.1	1.3	8.1	28.8	0.8	0.8	5.1
XYLEM	308	3	4	68.3	0.4	3.1	2.7	16.2	1.9	3.1	1.9	0.4	0.4	1.5
NEEDLE	317	3	4	54.9	7.8	9.2	4.2	15.6	0.6	1.1	1.1	2.8	1.1	1.7
CORTEX	317	3	4	5.9	0.3	10.5	3.6	63.4	1.6	1.3	1.6	2.3	1.3	8.2
XYLEM	317	3	4	36.3	0.4	8.4	2.7	40.7	1.3	1.3	1.3	0.4	0.9	6.2
NEEDLE	530	6	4	56.3	12.0	5.0	5.5	16.0	0.3	1.2	0.9	0.9	0.3	1.7
CORTEX	530	6	4	8.9	0.4	12.8	4.3	62.4	1.6	0.8	1.2	0.0	0.8	7.0
XYLEM	530	6	4	28.4	0.5	3.8	2.8	53.1	1.4	0.9	0.9	0.0	0.5	7.6

TABLE 3. VARIATION IN SCOTCH PINE CORTEX MONOTERPENES BETWEEN DEFOLIATED AND NON-DEFOLIATED BRANCHES OF THE SAME TREE

COLLECTED 7/19-20/1967 — COLLECTED FROM UPPER 2/3 OF CROWN
1 TREE, 20 UL, SAMPLE — ROSE LAKE
1966 CORTEX OLEORESIN — GLC ANALYSIS 7/20/67

5-25 PERCENT OFTHE 1966 NEEDLES REMOVED BY THE EUROPEAN PINE SAWFLY

PERCENT MONOTERPENE

DEFOLIATION	MSFG	REP	TR. NO.	ALPHA-PINENE	CAMPHENE	BETA-PINENE	MYRCENE	3-CARENE	ALPHA-TERPINENE	LIMONENE	BETA-PHELL.	CYMENE	GAMMA-TERPINENE	TERPINOLENE
NONDEF	220	3	2	25,4	0,7	48,6	11,4	0,4	0,0	11,4	1,4	0,4	0,0	0,4
DEF	220	3	2	31,5	0,7	42,8	10,6	0,3	0,0	12,0	1,4	0,3	0,0	0,3
NONDEF	220	5	1	33,3	1,1	38,9	18,1	0,8	0,5	5,3	1,3	0,3	0,0	0,3
DEF	220	5	1	30,7	1,0	39,9	19,2	0,8	0,5	5,4	2,0	0,3	0,0	0,3
NONDEF	239	2	3	14,2	0,7	44,8	34,5	0,7	0,4	0,7	1,8	0,7	0,4	1,1
DEF	239	2	3	20,2	0,8	41,4	30,9	0,8	0,3	0,6	2,5	1,1	0,6	0,8
NONDEF	239	8	1	35,6	1,3	48,0	4,0	1,0	0,3	5,7	2,7	1,0	0,0	0,3
DEF	239	8	1	35,4	1,4	49,5	3,8	1,0	0,3	5,2	2,4	0,7	0,0	0,3
NONDEF	250	3	1	18,5	0,7	41,5	20,7	1,1	0,7	13,0	2,2	0,7	0,4	0,4
DEF	250	3	1	20,3	0,6	34,0	23,8	1,3	0,6	16,2	1,6	1,0	0,3	0,3
NONDEF	250	7	2	9,2	0,9	24,4	4,1	42,1	0,9	1,3	11,7	0,3	0,6	4,4
DEF	250	7	2	8,1	0,7	22,1	4,4	43,0	1,7	1,3	11,1	1,0	1,0	5,7
NONDEF	251	8	1	23,0	0,3	40,9	2,8	26,4	0,6	1,6	1,6	0,3	0,3	2,2
DEF	251	8	1	14,1	0,3	53,7	2,7	22,1	1,0	2,0	1,7	0,3	0,3	1,7
NONDEF	317	3	4	14,0	0,3	18,4	3,7	42,5	1,0	13,0	1,0	0,3	0,7	5,0
DEF	317	3	4	14,6	0,3	14,2	4,1	42,0	1,0	16,3	1,4	0,3	0,7	5,1
NONDEF	317	8	3	14,6	0,3	34,2	3,7	25,6	0,7	9,6	7,6	0,3	0,3	3,0
DEF	317	8	3	15,2	0,4	36,5	3,3	24,2	0,4	8,6	8,2	0,4	0,4	2,5

TABLE 4. VARIATION IN SCOTCH PINE CORTEX MONOTERPENES BETWEEN DEFOLIATED AND NON-DEFOLIATED BRANCHES OF THE SAME TREE

COLLECTED 7/19-20/1967
1 TREE, 20 UL. SAMPLE
1966 CORTEX OLEORESIN

COLLECTED FROM UPPER 2/3 OF CROWN
ROSE LAKE
GLC ANALYSIS 7/20/67

5-25 PERCENT OFTHE 1966 NEEDLES REMOVED BY THE EUROPEAN PINE SAWFLY

PERCENT OF OLEORESIN

DEFOLIATION	MSFG	REP	TR. NO.	ALPHA-PINENE	CAMPHENE	BETA-PINENE	MYRCENE	3-CARENE	ALPHA-TERPINENE	LIMONENE	BETA-PHELL.	GAMMA-TERPINENE	CYMENE	TERPINOLENE	TOTAL
NONDEF	220	3	2	6,67	0,44	13,25	3,26	0,11	0,03	2,91	0,51	0,11	0,00	0,14	27,43
DEF	220	3	2	8,55	0,44	12,18	3,17	0,11	0,03	3,16	0,51	0,11	0,00	0,14	28,40
NONDEF	220	5	1	11,50	0,68	14,22	6,68	0,32	0,18	1,88	0,60	0,11	0,00	0,14	36,31
DEF	220	5	1	11,05	0,68	15,20	7,35	0,32	0,18	1,97	0,85	0,11	0,00	0,14	37,84
NONDEF	239	2	3	3,89	0,44	12,28	9,44	0,21	0,11	0,34	0,60	0,18	0,01	0,32	27,82
DEF	239	2	3	6,85	0,56	14,61	10,86	0,32	0,11	0,34	0,94	0,33	0,10	0,32	35,34
NONDEF	239	8	1	9,80	0,68	13,93	1,36	0,32	0,11	1,62	0,85	0,26	0,00	0,14	29,08
DEF	239	8	1	9,53	0,68	14,03	1,27	0,32	0,11	1,45	0,77	0,18	0,00	0,14	28,48
NONDEF	250	3	1	4,79	0,44	10,92	5,54	0,32	0,18	3,16	0,68	0,18	0,01	0,14	26,37
DEF	250	3	1	6,04	0,44	10,43	7,35	0,43	0,18	4,53	0,60	0,26	0,01	0,14	30,41
NONDEF	250	7	2	2,91	0,56	7,51	1,46	14,20	0,26	0,51	3,33	0,11	0,10	1,31	32,26
DEF	250	7	2	2,46	0,44	6,44	1,46	13,67	0,41	0,51	2,99	0,26	0,19	1,58	30,41
NONDEF	251	8	1	6,85	0,33	12,67	1,08	8,97	0,18	0,60	0,60	0,11	0,01	0,68	32,06
DEF	251	8	1	4,07	0,33	15,59	0,98	7,05	0,26	0,68	0,60	0,11	0,01	0,50	30,16
NONDEF	317	3	4	4,07	0,33	5,37	1,27	13,56	0,26	3,51	0,42	0,11	0,10	1,40	30,39
DEF	317	3	4	4,16	0,33	4,11	1,36	13,24	0,26	4,28	0,51	0,11	0,10	1,40	29,85
NONDEF	317	8	3	4,25	0,33	10,04	1,27	8,22	0,18	2,65	2,14	0,11	0,01	0,86	30,05
DEF	317	8	3	3,63	0,33	8,68	0,98	6,30	0,11	1,97	1,88	0,11	0,01	0,59	24,57

TABLE 5. VARIATION IN SCOTCH PINE CORTEX MONOTERPENES BETWEEN DEFOLIATED AND NON-DEFOLIATED BRANCHES OF THE SAME TREE

COLLECTED 7/19-20/1967
1 TREE, 20 UL, SAMPLE
1964 CORTEX OLEORESIN

COLLECTED FROM UPPER 2/3 OF CROWN
ROSE LAKE
GLC ANALYSIS 7/20/67

35-65 PERCENT OF THE 1966 NEEDLES REMOVED BY THE EUROPEAN PINE SAWFLY

PERCENT MONOTERPENE

DEFOLIATION	MSFG	REP	TR. NO.	ALPHA-PINENE	CAMPHENE	BETA-PINENE	MYRCENE	3-CARENE	ALPHA-TERPINENE	LIMONENE	BETA-PHELL.	CYMENE	GAMMA-TERPINENE	TERPINOLENE
NONDEF	220	3	4	39,0	1,2	27,3	15,7	0,4	0,0	13,7	2,0	0,4	0,0	0,4
DEF	220	3	4	42,3	1,8	30,8	12,2	0,4	0,0	10,4	1,4	0,4	0,0	0,4
NONDEF	220	8	1	20,1	0,5	47,8	25,8	0,9	0,7	0,9	2,1	0,7	0,2	0,2
DEF	220	8	1	29,5	0,5	46,6	20,9	0,3	0,0	0,5	1,0	0,5	0,0	0,3
NONDEF	239	4	2	20,6	0,7	49,8	11,4	1,1	0,7	10,7	3,2	1,1	0,4	0,4
DEF	239	4	2	18,4	0,7	54,6	9,6	1,0	0,3	10,9	2,7	1,0	0,3	0,3
NONDEF	250	8	1	12,7	0,3	24,1	29,4	25,9	1,6	0,6	1,6	0,6	0,3	2,8
DEF	250	8	1	18,0	0,3	19,1	27,8	28,7	1,1	0,6	1,7	0,3	0,3	2,2
NONDEF	250	3	2	5,6	0,4	14,9	20,4	45,0	1,1	1,5	1,1	2,6	1,1	6,3
DEF	250	3	2	10,5	0,3	14,1	20,4	41,9	0,9	2,7	1,2	2,1	0,6	5,4
NONDEF	250	6	4	10,4	0,3	2,7	3,6	56,3	1,4	16,5	0,8	0,5	0,8	6,6
DEF	250	6	4	9,0	0,3	2,9	3,5	56,1	1,2	17,4	0,9	0,9	0,9	7,0
NONDEF	250	2	3	12,7	0,7	33,3	48,1	0,7	0,3	0,7	1,7	1,0	0,3	0,3
DEF	250	2	3	13,6	0,9	36,5	43,5	0,9	0,3	0,6	2,3	0,9	0,3	0,3
NONDEF	251	7	2	17,3	0,3	44,6	3,5	21,5	0,6	7,4	2,2	0,3	0,3	1,9
DEF	251	7	2	12,7	0,5	44,5	3,2	22,4	0,7	10,4	1,8	0,5	0,5	3,0
NONDEF	251	5	3	6,5	0,3	3,3	21,2	40,7	2,3	2,3	15,6	1,3	1,3	5,2
DEF	251	5	3	10,9	0,3	4,0	20,3	40,6	1,4	1,4	15,1	0,6	0,6	4,9

TABLE 5. (CONTINUED)

NONDEF	251	1	1	9.3	0.3	33.3	20.0	29.6	0.8	0.8	1.9	0.3	0.3	3.5
DEF	251	1	1	14.4	0.3	31.6	16.9	29.0	0.5	1.0	2.0	0.3	0.3	3.8
NONDEF	317	3	1	7.0	0.4	5.5	4.3	53.1	1.2	1.6	17.6	0.0	0.8	8.6
DEF	317	3	1	17.3	0.3	3.9	3.3	58.6	1.2	0.9	6.8	0.0	0.6	7.1
NONDEF	317	8	4	11.4	1.7	10.8	4.0	39.7	1.7	22.2	3.0	1.0	0.7	3.7
DEF	317	8	4	12.5	1.5	18.6	4.0	36.3	0.9	19.8	2.1	0.6	0.6	3.0

TABLE 6. VARIATION IN SCOTCH PINE CORTEX MONOTERPENES BETWEEN DEFOLIATED AND NON-DEFOLIATED BRANCHES OF THE SAME TREE

COLLECTED 7/19-20/1967
1 TREE, 20 UL. SAMPLE
1966 CORTEX OLEORESIN

COLLECTED FROM UPPER 2/3 OF CROWN
ROSE LAKE
GLC ANALYSIS 7/20/67

35-65 PERCENT OF THE 1966 NEEDLES REMOVED BY THE EUROPEAN PINE SAWFLY

PERCENT OF OLEORESIN

DEFOLIATION	MSFG	REP	TR. NO.	ALPHA-PINENE	CAMPHENE	BETA-PINENE	MYRCENE	3-CARENE	ALPHA-TERPINENE	LIMONENE	BETA-PHELL.	CYMENE	GAMMA-TERPINENE	TERPINOLENE	TOTAL
NONDEF	220	3	4	9.00	0.56	6.64	3.93	0.11	0.03	3.08	0.60	0.11	0.00	0.14	24.18
DEF	220	3	4	10.88	0.80	8.39	3.45	0.11	0.03	2.65	0.51	0.11	0.00	0.14	27.05
NONDEF	220	8	1	8.01	0.44	19.87	10.67	0.43	0.26	0.51	0.94	0.26	0.01	0.14	41.53
DEF	220	8	1	10.70	0.44	17.83	8.01	0.11	0.03	0.34	0.51	0.18	0.00	0.14	38.28
NONDEF	239	4	2	5.51	0.44	13.64	3.26	0.32	0.18	2.74	0.94	0.26	0.01	0.14	27.43
DEF	239	4	2	5.15	0.44	15.59	2.88	0.32	0.11	2.91	0.85	0.26	0.01	0.14	28.65
NONDEF	250	8	1	3.89	0.33	7.41	6.21	8.76	0.41	0.34	0.60	0.18	0.01	0.86	28.99
DEF	250	8	1	4.04	0.33	6.64	9.63	10.89	0.33	0.34	0.68	0.11	0.01	0.77	35.76
NONDEF	250	3	2	1.66	0.33	3.91	5.45	12.92	0.26	0.51	0.42	0.56	0.19	1.58	27.78
DEF	250	3	2	3.45	0.33	4.59	6.68	14.95	0.26	0.94	0.51	0.56	0.10	1.67	34.03
NONDEF	250	6	4	3.72	0.33	0.99	1.46	21.89	0.41	5.30	0.42	0.18	0.19	2.21	37.10
DEF	250	6	4	3.09	0.33	0.99	1.36	20.61	0.33	5.30	0.42	0.26	0.19	2.21	35.10
NONDEF	250	2	3	3.63	0.44	9.46	13.52	0.21	0.11	0.34	0.60	0.26	0.01	0.14	28.71
DEF	250	2	3	4.52	0.56	12.28	14.47	0.32	0.11	0.34	0.85	0.26	0.01	0.14	33.86
NONDEF	251	7	2	5.15	0.33	13.54	1.27	7.15	0.18	2.14	0.77	0.11	0.01	0.59	31.23
DEF	251	7	2	5.24	0.44	18.80	1.55	10.36	0.26	4.02	0.85	0.18	0.10	1.22	43.02
NONDEF	251	5	3	2.10	0.33	0.99	6.40	13.35	0.56	0.77	4.28	0.33	0.28	1.49	30.88
DEF	251	5	3	3.72	0.33	1.38	6.97	15.16	0.41	0.60	4.70	0.18	0.10	1.58	35.12

TABLE 6. (CONTINUED)

NONDEF	251	1	1	1.45	0.33	12.18	7.35	11.85	0.26	0.42	0.77	0.11	0.01	1.22	37.94
DEF	251	1	1	5.42	0.33	12.18	6.59	12.28	0.18	0.51	0.85	0.11	0.01	1.40	39.85
NONDEF	317	3	1	4.93	0.33	1.38	1.27	14.52	0.26	0.51	4.02	0.03	0.10	2.03	26.37
DEF	317	3	1	5.51	0.33	1.28	1.27	21.04	0.33	0.42	2.14	0.03	0.10	2.21	34.65
NONDEF	317	8	4	1.36	0.80	3.13	1.36	12.60	0.41	5.82	0.94	0.26	0.10	1.04	29.81
DEF	317	8	4	1.98	0.80	5.95	1.46	12.71	0.26	5.73	0.77	0.18	0.10	0.95	32.89

TABLE 7. VARIATION IN SCOTCH PINE CORTEX MONOTERPENES BETWEEN DEFOLIATED AND NON-DEFOLIATED BRANCHES OF THE SAME TREE

COLLECTED 7/19-20/1967 — COLLECTED FROM UPPER 2/3 OF CROWN
1 TREE, 20 UL. SAMPLE — ROSE LAKE
1966 CORTEX OLEORESIN — GLC ANALYSIS 7/20/67

75-95 PERCENT OF THE 1966 NEEDLES REMOVED BY THE EUROPEAN PINE SAWFLY

PERCENT MONOTERPENE

DEFOLIATION	MSFG	REP	TR. NO.	ALPHA-PINENE	CAMPHENE	BETA-PINENE	MYRCENE	3-CARENE	ALPHA-TERPINENE	LIMONENE	BETA-PHELL.	CYMENE	GAMMA-TERPINENE	TERPINOLENE
NONDEF	220	3	1	30.7	1.3	38.2	5.6	0.0	0.0	21.9	1.0	1.0	0.0	0.3
DEF	220	3	1	37.9	1.3	31.8	6.1	0.0	0.0	20.6	0.6	1.3	0.0	0.3
NONDEF	220	4	2	32.2	1.7	33.3	18.1	0.3	0.0	1.7	11.9	0.6	0.0	0.3
DEF	220	4	2	30.8	1.7	34.5	18.5	0.3	0.0	1.7	11.7	0.6	0.0	0.3
NONDEF	220	7	4	57.1	1.9	36.4	2.3	0.5	0.0	0.5	1.2	0.0	0.0	0.2
DEF	220	7	4	61.9	1.9	31.7	2.1	0.2	0.0	0.6	1.4	0.0	0.0	0.2
NONDEF	239	5	2	16.5	0.6	65.1	10.5	0.3	0.3	3.2	2.5	0.3	0.3	0.3
DEF	239	5	2	17.6	0.6	56.9	12.8	1.6	1.3	5.1	2.9	0.6	0.3	0.3
NONDEF	250	4	3	14.6	0.5	26.9	14.9	26.1	1.6	1.6	9.8	0.3	0.8	2.9
DEF	250	4	3	18.9	0.5	23.9	13.3	25.5	2.7	2.1	8.5	1.1	0.8	2.7
NONDEF	250	1	4	12.6	0.2	51.4	4.0	0.2	0.0	29.6	1.5	0.2	0.0	0.2
DEF	250	1	4	13.1	0.2	49.8	3.7	0.2	0.0	31.3	1.2	0.2	0.0	0.2
NONDEF	251	4	2	11.0	0.3	22.9	5.0	51.8	1.1	0.6	1.1	0.8	0.6	5.0
DEF	251	4	2	19.7	0.3	19.7	3.8	47.1	0.6	0.3	1.3	1.0	0.6	5.4
NONDEF	251	8	4	13.2	0.6	21.0	4.3	49.7	1.4	0.6	1.4	1.1	0.9	5.7
DEF	251	8	4	17.0	0.7	23.2	3.3	44.4	1.0	0.7	2.0	1.6	0.7	5.6
NONDEF	317	5	4	5.8	0.4	5.0	3.6	53.6	3.6	2.5	13.3	2.5	2.2	7.6
DEF	317	5	4	7.7	0.3	4.6	3.1	56.0	2.8	1.9	12.4	2.2	1.9	7.1
NONDEF	317	8	1	9.7	0.4	15.4	4.2	38.6	0.8	15.4	9.3	0.8	0.4	5.0
DEF	317	8	1	7.2	0.3	17.2	3.8	36.9	1.0	16.9	9.7	0.7	0.7	5.5

TABLE 8. VARIATION IN SCOTCH PINE CORTEX MONOTERPENES BETWEEN DEFOLIATED AND NON-DEFOLIATED BRANCHES OF THE SAME TREE

COLLECTED 7/19-20/1967
1 TREE, 20 UL. SAMPLE
1966 CORTEX OLEORESIN

COLLECTED FROM UPPER 2/3 OF CROWN
ROSE LAKE
GLC ANALYSIS 7/20/67

75-95 PERCENT OF THE 1966 NEEDLES REMOVED BY THE EUROPEAN PINE SAWFLY

PERCENT OF OLEORESIN

DEFOLIATION	MSFG	REP	TR. NO.	ALPHA-PINENE	CAMPHENE	BETA-PINENE	MYRCENE	3-CARENE	ALPHA-TERPINENE	LIMONENE	BETA-PHELL.	CYMENE	GAMMA-TERPINENE	TERPINOLENE	TOTAL
NONDEF	220	3	1	8,73	0,68	11.40	1,84	0,00	0,03	5,90	0,42	0,26	0,00	0,14	29,40
DEF	220	3	1	10,88	0,68	9.65	2,03	0,00	0,03	5,65	0,34	0,33	0,00	0,14	29,72
NONDEF	220	4	2	10,52	0,91	11.50	6,30	0,11	0,03	0,68	3,76	0,18	0,00	0,14	34,14
DEF	220	4	2	9,98	0,91	11.79	6,40	0,11	0,03	0,68	3,68	0,18	0,00	0,14	33,90
NONDEF	220	7	4	22,33	1,15	15.30	1,17	0,21	0,03	0,34	0,60	0,03	0,00	0,14	41,30
DEF	220	7	4	27,07	1,27	14.91	1,17	0,11	0,03	0,42	0,77	0,03	0,00	0,14	45,92
NONDEF	239	5	2	4,97	0,44	19.97	3,36	0,11	0,11	1,02	0,85	0,11	0,01	0,14	31,08
DEF	239	5	2	5,24	0,44	17.34	4,02	0,53	0,33	1,54	0,94	0,18	0,01	0,14	30,71
NONDEF	250	4	3	5,24	0,44	9.85	5,54	10,47	0,49	0,68	3,33	0,11	0,19	1,04	37,37
DEF	250	4	3	6,67	0,44	8.78	4,97	10,25	0,79	0,85	2,91	0,33	0,19	0,95	37,13
NONDEF	250	1	4	4,88	0,33	20.26	1,74	0,11	0,03	10,44	0,68	0,11	0,00	0,14	38,71
DEF	250	1	4	5,42	0,33	21.04	1,74	0,11	0,03	11,81	0,60	0,11	0,00	0,14	41,31
NONDEF	251	4	2	3,89	0,33	8.10	1,93	20,08	0,33	0,34	0,51	0,26	0,10	1,67	37,53
DEF	251	4	2	5,86	0,33	6.05	1,36	15,81	0,18	0,25	0,51	0,26	0,10	1,58	32,29
NONDEF	251	8	4	4,43	0,44	7.12	1,65	18,48	0,41	0,34	0,60	0,33	0,19	1,85	35,83
DEF	251	8	4	4,97	0,44	6.93	1,17	14,52	0,26	0,34	0,68	0,41	0,10	1,58	31,40
NONDEF	317	5	4	1,75	0,33	1.38	1,17	15,91	0,79	0,77	3,33	0,56	0,46	1,94	28,39
DEF	317	5	4	2,55	0,33	1.48	1,17	19,33	0,71	0,68	3,59	0,56	0,46	2,12	32,98
NONDEF	317	8	1	2,55	0,33	3.91	1,27	10,68	0,18	3,99	2,22	0,18	0,01	1,22	26,14
DEF	317	8	1	2,19	0,33	4.88	1,27	11,43	0,26	4,36	2,56	0,18	0,10	1,49	29,05

TABLE 9. VARIATION IN SCOTCH PINE CORTEX MONOTERPENES AMONG SELECTED SEED SOURCES

COLLECTED 7/3-6/1967
6-TREE PULKED SAMPLES
1964 CORTEX OLEORESIN

COLLECTED FROM 1964 WHORL
ROSE LAKE (L)
GLC ANALYSIS 7/7-9/1967

PERCENT MONOTERPENE

MSFG	REP	ALPHA-PINENE	CAMPHENE	BETA-PINENE	MYRCENE	3-CARENE	ALPHA-TERPINENE	LIMONENE	BETA-PHELL.	CYMENE	GAMMA-TERPINENE	TERPINOLENE
220	1	34,5	1,5	31,6	17,0	1,0	0,0	11,7	1,9	0,5	0,0	0,5
239	1	19,9	0,6	46,3	16,1	5,5	0,0	7,7	1,9	1,0	0,0	1,0
245	1	41,3	1,7	12,3	18,4	0,6	0,0	23,5	0,6	1,1	0,0	0,6
250	1	18,9	0,3	16,2	11,5	35,5	0,3	9,5	3,0	0,7	0,7	3,4
251	1	21,6	1,0	18,0	18,0	31,7	1,0	1,3	3,6	0,7	0,3	2,9
256	1	11,2	0,3	22,4	19,3	25,9	0,9	4,3	12,6	0,6	0,3	2,3
317	1	9,2	0,3	8,9	4,1	53,6	1,2	6,2	9,2	1,2	0,6	5,6
320	1	25,0	1,1	37,9	7,6	9,8	0,8	10,6	4,5	1,1	0,4	1,1
521	1	6,1	0,3	9,4	3,7	56,3	2,0	1,6	13,5	1,2	0,8	4,9
556	1	17,8	1,1	48,7	28,0	2,0	1,4	2,5	5,9	1,1	0,8	0,6
220	2	39,1	0,7	32,6	13,0	0,7	0,0	9,4	2,9	0,7	0,0	0,7
239	2	25,2	0,8	54,5	10,2	0,8	0,0	4,9	2,8	0,4	0,0	0,4
245	2	41,0	1,0	6,3	29,3	0,0	0,0	21,0	0,5	0,5	0,0	0,5
250	2	13,2	0,2	28,7	15,0	27,9	0,5	0,0	3,5	0,2	0,2	2,5
251	2	20,7	0,3	24,0	9,8	34,1	0,8	3,9	2,0	0,6	0,6	3,4
256	2	5,4	0,1	8,1	7,0	68,1	0,5	7,1	2,1	0,4	0,2	1,1
317	2	15,4	0,7	14,2	10,8	34,9	1,4	5,0	10,8	1,0	1,0	4,8
320	2	22,9	1,0	43,6	8,3	1,2	1,0	18,3	1,2	1,7	0,7	0,2
521	2	9,7	0,6	14,2	9,1	57,9	1,5	7,9	11,8	1,2	1,5	4,5
556	2	18,0	1,0	27,3	35,6	2,1	1,0	8,2	4,6	1,0	0,5	0,5

TABLE 9. (CONTINUED)

220	3	24.6	0.5	34.7	26.6	0.5	0.0	10.6	1.5	0.5	0.0	0.5
239	3	28.9	1.7	47.7	8.1	0.4	0.0	8.1	3.0	1.7	0.0	0.4
246	3	30.3	0.9	26.0	22.6	0.9	0.6	10.8	0.6	0.9	0.0	0.3
250	3	8.7	0.3	17.2	12.1	50.4	1.1	1.3	2.6	0.5	0.8	5.0
251	3	13.1	0.5	34.0	15.7	26.1	0.7	2.1	4.5	0.5	0.2	2.6
256	3	15.0	0.5	29.8	11.5	11.2	0.8	14.5	14.2	0.5	0.3	1.8
317	3	8.6	1.0	12.7	4.6	39.0	1.6	12.1	12.7	1.6	1.3	4.8
320	3	23.8	1.1	47.5	10.2	5.2	0.6	8.3	1.9	0.8	0.3	0.3
521	3	7.2	0.3	10.1	10.1	46.9	1.6	3.5	11.9	1.6	1.3	5.7
556	3	17.1	0.9	36.6	24.8	10.0	1.7	4.6	2.6	0.6	0.3	1.1

TABLE 10. VARIATION IN SCOTCH PINE CORTEX MONOTERPENES AMONG SELECTED SEED SOURCES

COLLECTED 7/6-7/1967
8-TREE BULKED SAMPLES
1964 CORTEX OLEORESIN

COLLECTED FROM 1964 WHORL
RUSS FOREST (R)
GLC ANALYSIS 7/7-9/1967

		PERCENT MONOTERPENE										
MSFG	REP	ALPHA-PINENE	CAMPHENE	BETA-PINENE	MYRCENE	3-CARENE	ALPHA-TERPINENE	LIMONENE	BETA-PHELL.	CYMENE	GAMMA-TERPINENE	TERPINOLENE
220	1	23.9	0.9	36.5	23.9	0.4	0.0	11.7	1.3	0.9	0.0	0.4
239	1	21.2	0.8	50.6	18.4	0.8	0.0	5.5	1.6	0.8	0.0	0.4
246	1	38.1	1.8	9.4	29.6	0.4	0.0	17.5	1.3	0.9	0.4	0.4
250	1	8.1	0.4	19.3	28.3	30.9	1.3	3.1	4.9	0.4	0.4	2.7
251	1	9.1	0.4	16.5	5.6	48.1	1.4	6.3	4.2	1.4	1.1	6.0
256	1	9.0	0.3	15.9	14.2	18.9	0.8	14.5	22.5	0.8	0.5	2.5
317	1	6.4	0.3	14.7	8.8	45.7	1.3	6.1	10.2	0.8	0.8	4.8
320	1	19.9	1.3	43.3	13.1	9.2	1.0	6.8	2.9	1.0	0.5	0.8
521	1	7.1	0.3	13.8	5.7	42.8	2.0	6.1	15.2	1.0	1.0	5.1
556	1	17.4	0.7	46.1	15.2	7.6	1.0	7.6	2.2	0.7	0.7	0.7
220	2	17.8	0.8	29.1	23.9	0.4	0.0	25.9	0.8	0.8	0.0	0.4
239	2	17.3	0.4	54.8	14.3	0.4	0.0	10.7	1.5	0.4	0.0	0.4
246	2	24.7	0.6	29.0	32.1	0.0	0.0	11.1	1.2	0.6	0.0	0.6
250	2	11.0	0.3	29.0	13.8	29.7	1.0	6.6	4.5	0.7	0.3	3.1
251	2	11.7	0.3	23.4	16.7	30.6	1.1	7.2	4.2	0.8	0.8	3.1
256	2	9.3	0.3	19.0	12.3	26.3	1.0	12.0	15.8	0.8	0.5	2.8
317	2	6.7	0.7	9.2	4.6	45.2	1.8	10.6	12.4	1.4	1.8	5.7
320	2	21.2	2.0	35.3	21.6	1.0	0.7	14.4	2.0	1.3	0.3	0.3
521	2	7.1	0.3	14.0	11.0	44.2	2.3	2.6	11.0	1.3	1.3	4.9
556	2	16.0	1.3	34.2	25.9	5.8	1.3	11.2	2.2	1.3	0.6	0.3

TABLE 10. (CONTINUED)

220	3	24.3	1.0	39.8	20.4	0.5	0.0	11.7	1.5	0.5	0.0	0.5
239	3	18.5	0.7	52.6	14.2	0.3	0.0	8.6	4.0	0.7	0.0	0.3
246	3	20.4	0.7	22.1	33.3	0.7	0.4	19.3	1.4	0.7	0.0	1.1
250	3	10.8	0.6	20.5	32.4	22.2	0.6	2.3	6.8	1.1	0.6	2.3
251	3	12.5	0.6	32.3	18.7	22.8	1.1	4.2	5.0	0.6	0.3	1.9
256	3	10.6	0.5	14.4	22.9	17.3	1.3	8.8	20.2	0.8	0.8	2.4
317	3	5.9	0.4	9.2	4.8	52.2	1.5	4.8	13.2	1.1	1.5	5.5
320	3	20.7	0.7	49.3	10.7	0.4	0.0	14.4	2.2	1.1	0.0	0.4
521	3	7.4	0.3	19.1	10.2	44.0	1.2	2.2	9.2	0.9	0.6	4.9
556	3	14.0	1.2	37.0	25.7	8.1	2.1	6.3	2.7	1.5	0.6	0.9

TABLE 11. SEASONAL VARIATION OF SCOTCH PINE MONOTERPENES

1965-67 CORTEX OLEORESIN COLLECTED FROM 1964-66 WHORLS
1 TREE SAMPLES ROSE LAKE (BORDER ROW TREES)

PERCENT MONOTERPENE

TREE MSFG	O R W	COL- UM	DATE SAMPLED	TIS- SUE AGE	ALPHA-PI-NENE	CAM-PHENE	BETA-PI-NENE	MYR-CENE	3-CAR-ENE	ALPHA-TERP-INENE	LIMO-NENE	BETA-PHELL.	CYM-ENE	GAMMA-TERP-INENE	TERP-INO-LENE
249	1	K	12-08-66	65	19.5	0.6	71.0	3.0	0.0	0.0	2.4	2.4	0.6	0.0	0.6
249	1	K	12-08-66	66	21.5	0.6	69.9	3.7	0.0	0.0	1.8	1.8	0.6	0.0	0.0
249	1	K	01-13-67	66	18.6	0.6	74.1	1.4	0.2	0.0	2.0	2.2	0.8	0.0	0.0
249	1	K	03-10-67	66	18.6	0.3	74.6	1.9	0.3	0.0	2.2	1.6	0.3	0.0	0.3
249	1	K	04-09-67	66	19.5	0.8	72.9	1.5	0.0	0.0	2.3	2.3	0.8	0.0	0.0
249	1	K	05-24-67	66	18.1	0.7	67.6	3.4	0.7	0.0	5.5	2.7	1.4	0.0	0.0
249	1	K	06-25-67	66	18.0	0.9	70.7	3.6	0.5	0.0	2.7	2.3	0.9	0.0	0.5
249	1	K	08-10-67	66	19.3	0.5	69.0	2.0	0.2	0.0	5.5	2.3	1.0	0.0	0.2
249	1	K	10-03-67	66	20.7	0.8	65.3	3.3	0.8	0.0	4.1	2.5	1.7	0.0	0.8
249	1	K	10-03-67	67	17.3	0.7	71.8	2.7	0.3	0.0	3.0	2.3	1.7	0.0	0.3
249	1	K	12-04-67	67	16.8	0.7	75.2	2.0	0.0	0.0	2.0	2.0	1.3	0.0	0.0
249	1	M	12-08-66	65	17.5	0.8	52.4	3.2	0.4	0.0	25.8	0.0	0.0	0.0	0.0
249	1	M	12-08-66	66	13.1	0.6	47.9	4.5	0.3	0.0	33.3	0.0	0.3	0.0	0.0
249	1	M	01-13-67	66	13.7	0.4	51.8	3.1	0.2	0.0	30.7	0.0	0.0	0.0	0.0
249	1	M	03-10-67	66	11.5	0.4	46.2	4.2	0.4	0.0	36.9	0.0	0.4	0.0	0.0
249	1	M	04-09-67	66	13.8	0.2	48.9	2.8	0.2	0.0	34.0	0.0	0.0	0.0	0.0
249	1	M	05-24-67	66	15.1	0.7	46.1	4.0	0.2	0.0	33.7	0.0	0.2	0.0	0.0
249	1	M	06-25-67	66	13.1	0.5	47.5	3.8	0.5	0.0	34.3	0.0	0.3	0.0	0.0
249	1	M	08-10-67	66	15.0	0.4	48.6	3.5	0.1	0.0	32.1	0.0	0.3	0.0	0.1
249	1	M	10-03-67	66	16.8	0.7	49.7	3.0	0.3	0.0	29.2	0.0	0.3	0.0	0.0
249	1	M	10-03-67	67	11.7	0.4	43.6	4.2	0.2	0.0	39.2	0.0	0.6	0.0	0.2
249	1	M	12-04-67	67	13.8	0.6	47.5	3.0	0.2	0.0	34.7	0.0	0.0	0.0	0.2

TABLE 11. (CONTINUED)

249	1	N	12-08-66	65	14.4	0.5	50.9	21.4	0.5	0.0	6.8	3.2	0.5	0.0	0.0
249	1	N	12-08-66	66	13.6	0.5	51.2	24.9	0.5	0.0	6.1	2.8	0.5	0.0	0.0
249	1	N	01-13-67	66	13.3	0.4	57.3	19.4	0.4	0.0	6.5	2.4	0.4	0.0	0.0
249	1	N	03-10-67	66	13.9	0.3	57.0	19.9	0.6	0.0	5.4	2.5	0.3	0.0	0.0
249	1	N	04-09-67	66	13.9	0.4	57.8	18.7	0.4	0.0	6.1	2.4	0.2	0.0	0.2
249	1	N	05-24-67	66	14.7	0.5	49.2	22.3	0.8	0.0	7.9	2.7	1.9	0.0	0.0
249	1	N	06-25-67	66	13.3	0.7	54.8	20.7	1.5	0.0	5.9	2.2	0.7	0.0	0.0
249	1	N	08-10-67	66	13.4	0.3	46.4	26.3	0.3	0.0	10.8	1.5	1.0	0.0	0.0
249	1	N	10-03-67	66	14.7	0.5	50.7	22.1	0.2	0.0	7.6	2.8	1.2	0.0	0.2
249	1	N	10-03-67	67	14.1	0.5	56.6	18.5	0.5	0.0	6.8	2.4	0.5	0.0	0.0
249	1	N	12-04-67	67	13.3	0.4	54.9	20.8	0.4	0.0	8.2	1.6	0.4	0.0	0.0
249	1	N	08-10-67	64	22.3	0.7	56.8	14.2	0.7	0.0	3.4	2.0	0.0	0.0	0.0
249	1	N	08-10-67	65	17.5	0.7	58.0	16.1	0.7	0.0	4.9	2.1	0.0	0.0	0.0
249	1	N	08-10-67	67	11.5	1.0	44.2	25.0	1.0	0.0	13.5	2.9	1.0	0.0	0.0
249	1	Q	12-08-66	65	19.8	0.9	59.5	12.1	0.9	0.0	4.3	1.7	0.9	0.0	0.0
249	1	Q	12-08-66	66	16.0	0.7	49.3	19.4	0.7	0.0	9.0	4.2	0.7	0.0	0.0
249	1	Q	01-13-67	66	16.4	0.5	53.0	16.4	0.5	0.0	9.8	2.7	0.5	0.0	0.0
249	1	Q	03-10-67	66	12.9	0.4	50.6	7.1	0.4	0.0	24.9	3.3	0.4	0.0	0.0
249	1	Q	04-09-67	66	17.3	0.4	55.3	14.9	0.4	0.0	9.0	2.0	0.4	0.0	0.4
249	1	Q	05-24-67	66	23.6	0.5	46.0	16.2	0.5	0.0	9.3	2.7	0.8	0.0	0.3
249	1	Q	06-25-67	66	18.5	0.4	45.3	19.8	0.9	0.0	11.2	2.2	1.3	0.0	0.4
249	1	Q	08-10-67	66	15.6	0.4	45.4	23.4	0.6	0.0	10.8	2.2	1.5	0.0	0.2
249	1	Q	10-03-67	66	19.1	0.9	50.0	15.7	0.4	0.0	10.0	2.6	1.3	0.0	0.0
249	1	Q	10-03-67	67	20.0	0.5	45.4	19.5	0.5	0.0	10.7	2.9	0.5	0.0	0.0
249	1	Q	12-04-67	67	17.6	0.5	42.3	21.4	0.5	0.0	14.3	2.2	1.1	0.0	0.0

TABLE 12. SEASONAL VARIATION OF SCOTCH PINE MONOTERPENES

1965-67 CORTEX OLEORESIN — COLLECTED FROM 1964-66 WHORLS
1 TREE SAMPLES — ROSE LAKE (BORDER ROW TREES)

PERCENT MONOTERPENE

TREE MSFG	R O W	COLUM	DATE SAMPLED	TIS-SUE AGE	ALPHA-PINENE	CAMPHENE	BETA-PINENE	MYRCENE	3-CARENE	ALPHA-TERPINENE	LIMONENE	BETA-PHELLANDRENE	CYMENE	GAMMA-TERPINENE	TERPINOLENE
222	2	DB	12-08-66	65	8.4	0.7	5.4	3.7	63.5	2.3	2.3	2.3	2.0	1.3	8.0
222	2	DB	12-08-66	66	7.5	0.6	8.6	3.3	66.0	1.7	1.1	1.4	1.4	1.1	7.5
222	2	DB	01-13-67	66	5.6	0.3	6.5	2.9	72.0	0.8	0.9	1.1	1.1	0.8	8.2
222	2	DB	03-10-67	66	5.2	0.5	6.1	3.3	69.3	2.4	0.9	1.9	1.4	0.9	8.0
222	2	DB	04-09-67	66	7.3	0.9	8.5	3.3	66.7	0.9	0.7	1.2	1.2	0.9	8.3
222	2	DB	05-24-67	66	7.3	1.0	8.6	4.2	64.0	1.3	1.6	2.1	1.6	1.0	7.3
222	2	DB	06-25-67	66	8.4	0.5	5.9	4.0	68.7	1.3	1.1	1.6	1.3	1.1	8.9
222	2	DB	08-10-67	66	6.7	0.5	4.0	3.6	69.9	1.4	0.8	1.4	1.6	1.4	8.8
222	2	DB	10-03-67	66	7.8	0.9	4.6	4.1	66.2	0.9	1.4	3.2	1.8	1.4	7.8
222	2	DB	10-03-67	67	5.3	0.8	5.1	4.1	69.4	1.0	0.8	1.8	2.3	1.3	8.4
222	2	DB	12-04-67	67	4.7	0.0	3.9	3.1	76.0	0.8	0.8	0.8	0.8	0.8	8.5
222	2	EB	12-08-66	65	9.5	0.4	32.2	3.5	36.0	0.4	11.7	2.5	0.0	0.4	3.5
222	2	EB	12-08-66	66	8.2	0.3	28.7	4.9	33.3	0.8	18.6	1.6	0.3	0.3	3.0
222	2	EB	01-13-67	66	13.7	0.3	31.3	1.8	32.6	0.0	15.8	1.8	0.0	0.0	2.6
222	2	EB	03-10-67	66	7.7	0.3	29.5	3.3	32.7	0.6	19.3	2.1	0.3	0.6	3.6
222	2	EB	04-09-67	66	10.2	0.4	32.4	2.9	30.5	0.4	18.5	1.5	0.4	0.0	2.9
222	2	EB	05-24-67	66	9.0	0.3	26.8	3.0	33.1	0.6	19.0	2.4	0.6	0.6	4.5
222	2	EB	06-25-67	66	7.9	0.2	26.6	3.4	33.1	0.5	22.2	2.2	0.2	0.3	3.3
222	2	EB	08-10-67	66	8.0	0.0	29.5	3.5	33.7	1.0	17.4	2.1	0.7	0.7	3.5
222	2	EB	10-03-67	66	7.9	0.4	28.0	3.5	35.0	0.8	17.7	1.2	0.4	0.4	4.7
222	2	EB	10-03-67	67	8.9	0.4	31.4	3.7	31.0	0.7	18.1	1.1	0.4	0.7	3.7
222	2	EB	12-04-67	67	8.1	0.7	29.1	3.4	33.1	0.7	17.6	2.0	0.0	0.7	4.7

TABLE 12. (CONTINUED)

222	2	GB	12-08-66	65	9,7	0,6	21,6	4,8	40,8	0,6	0,8	14,1	1,6	0,8	4,8
222	2	GB	12-08-66	66	9,8	0,3	22,8	4,6	40,4	1,0	1,3	12,1	2,0	1,0	4,9
222	2	GB	01-13-67	66	8,6	0,3	23,1	3,0	47,1	0,3	1,2	12,0	0,6	0,3	5,4
222	2	GB	03-10-67	66	8,5	0,4	22,1	3,7	43,8	0,9	1,5	14,1	1,3	0,7	5,0
222	2	GB	04-09-67	66	14,9	0,5	17,9	3,0	46,3	0,5	1,0	10,4	0,5	0,5	4,5
222	2	GB	05-24-67	66	7,1	0,6	23,9	4,6	39,9	0,6	1,4	13,4	1,4	0,9	6,3
222	2	GB	06-25-67	66	8,1	0,4	18,5	3,6	47,6	0,4	0,8	14,1	0,8	0,4	5,2
222	2	GB	08-10-67	66	9,2	1,0	23,3	4,5	40,1	1,0	1,4	12,0	1,7	1,0	4,8
222	2	GB	10-03-67	66	9,3	1,3	25,3	5,3	38,7	1,3	1,3	9,3	1,3	1,3	5,3
222	2	GB	10-03-67	67	7,3	0,9	20,5	4,1	40,0	1,4	1,8	14,1	2,3	1,4	6,4
222	2	GB	12-04-67	67	7,1	0,5	20,9	4,0	44,4	0,7	1,4	13,3	1,9	0,7	5,0
222	2	LB	12-08-66	65	15,9	0,8	26,3	17,1	1,0	0,3	7,4	29,2	0,8	0,3	1,0
222	2	LB	12-08-66	66	23,5	0,5	24,2	13,8	0,9	0,2	7,3	27,7	0,7	0,2	0,9
222	2	LB	01-13-67	66	12,6	0,2	24,6	19,6	0,3	0,2	13,8	27,5	0,5	0,2	0,5
222	2	LB	03-10-67	66	13,5	0,3	26,7	15,5	0,5	0,0	10,4	31,9	0,5	0,3	0,5
222	2	LB	04-09-67	66	15,7	0,4	30,5	13,6	0,4	0,4	10,2	28,0	0,4	0,0	0,4
222	2	LB	05-24-67	66	12,7	0,7	25,0	17,8	0,7	0,4	12,7	27,5	1,1	0,4	1,1
222	2	LB	06-25-67	66	15,5	0,6	25,0	17,9	0,6	0,6	11,9	26,8	0,6	0,0	0,6
222	2	LB	08-10-67	66	13,6	0,5	21,5	20,8	0,7	0,2	17,7	22,9	1,0	0,2	1,0
222	2	LB	10-03-67	66	15,8	0,6	23,7	19,5	0,9	0,3	13,1	23,7	0,9	0,0	1,5
222	2	LB	10-03-67	67	12,4	0,4	28,5	18,5	0,8	0,0	11,8	26,3	0,6	0,0	0,8
222	2	LB	12-04-67	67	10,8	0,4	26,3	19,3	0,9	0,2	14,4	26,1	0,8	0,0	0,8

TABLE 13. VARIATION IN SCOTCH PINE CORTEX MONOTERPENES IN INDIVIDUAL TREES FROM SOUTHERN SWEDEN (SEED LOT MSEG 541)

COLLECTED 12/5-6/1967
1 TREE, 20 UL, SAMPLE
1967 CORTEX OLEORESIN

COLLECTED FROM 1965-66 WHORLS
ROSE LAKE
GLC ANALYSIS 12/11-14/1967

PERCENT MONOTERPENE

REP	TREE NO.	ALPHA-PINENE	CAMPHENE	BETA-PINENE	MYRCENE	3-CARENE	ALPHA-TERPINENE	LIMONENE	BETA-PHELL.	CYMENE	GAMMA-TERPINENE	TERPINOLENE
1	3	2.1	0.0	3.7	3.3	77.2	1.7	0.8	1.7	0.8	0.8	7.9
1	4	3.9	0.6	4.2	4.2	62.7	1.0	0.6	12.3	0.6	1.6	8.1
2	1	4.1	0.4	4.1	3.3	72.8	2.1	1.2	1.6	0.4	1.2	8.6
2	2	6.4	0.4	18.9	4.2	40.2	1.1	1.1	21.6	1.1	0.8	4.2
3	1	4.9	0.3	9.1	3.8	62.0	1.7	0.7	8.7	0.3	1.0	7.3
3	2	10.4	0.3	31.3	19.6	30.7	0.9	1.3	2.2	0.3	0.3	2.5
3	3	5.4	0.3	9.6	4.2	59.9	1.6	1.3	9.6	0.6	1.3	6.1
4	1	7.3	0.3	13.2	22.2	26.8	1.7	6.6	14.9	1.0	2.0	4.0
4	2	2.6	0.0	4.9	3.9	74.1	1.6	0.6	1.6	0.0	1.0	9.7
4	3	5.1	0.0	4.8	3.7	72.4	1.4	0.6	1.4	0.0	1.4	9.1
6	1	8.5	0.4	28.2	4.2	41.3	1.5	0.8	10.8	0.0	0.4	3.9
6	2	6.2	0.0	3.9	56.0	0.8	0.0	3.1	28.8	0.4	0.0	0.8
6	3	5.0	0.5	15.8	3.2	62.4	1.8	0.9	1.8	0.9	0.9	6.8
6	4	5.4	0.8	7.7	5.0	50.6	1.9	1.5	14.6	2.3	1.5	8.8

TABLE 14. VARIATION IN SCOTCH PINE CORTEX MONOTERPENES IN INDIVIDUAL TREES FROM SOUTHERN SWEDEN (SEED LOT MSFG 541)

COLLECTED 12/5-6/1967 — COLLECTED FROM1965-66 WHORLS
1 TREE, 20 UL, SAMPLE — ROSE LAKE
1967 CORTEX OLEORESIN — GLC ANALYSIS 12/11-14/1967

PERCENT OF OLEORESIN

REP	TREE NO.	ALPHA-PINENE	CAMPHENE	BETA-PINENE	MYRCENE	3-CARENE	ALPHA-TERPINENE	LIMONENE	BETA-PHELL.	CYMENE	GAMMA-TERPINENE	TERPINOLENE	TOTAL
1	3	0,76	0,21	0,89	0,98	19,86	0,33	0,34	0,51	0,18	0,10	1.76	25.93
1	4	1,39	0,44	1,28	1,46	20,61	0,26	0,34	3,42	0,18	0,37	2,30	32.05
3	1	1,57	0,33	2,55	1,27	19,01	0,41	0,34	2,31	0,11	0,19	1.94	30.01
3	2	3,27	0,33	9,65	6,11	10,36	0,26	0,51	0,77	0,11	0,01	0,77	32.13
3	3	1,84	0,33	2,94	1,46	19,97	0,41	0,51	2,74	0,18	0,28	1,76	32.40
4	1	2,28	0,33	3,91	6,59	8,65	0,41	1,88	4,02	0,26	0,46	1,13	29.91
4	2	1,03	0,21	1,48	1,36	24,46	0,41	0,34	0,60	0,03	0,19	2,75	32.84
4	3	1,93	0,21	1,67	1,46	27,13	0,41	0,34	0,60	0,03	0,37	2,93	37.06
6	1	2,28	0,33	7,12	1,27	11,43	0,33	0,34	2,56	0,03	0,01	0,95	26.65
6	2	1,75	0,21	0,99	13,90	0,21	0,03	0,85	6,50	0,11	0,00	0,23	24.78
6	3	1,30	0,33	3,42	0,89	14,74	0,33	0,34	0,51	0,18	0,10	1,40	23.53
6	4	1,57	0,44	1,97	1,46	14,10	0,41	0,51	3,42	0,49	0,28	2,12	26.75
2	1	1,21	0,33	0,99	0,98	18,90	0,41	0,42	0,51	0,11	0,19	1,94	25.99
2	2	1,84	0,33	4,88	1,27	11,32	0,26	0,42	5,05	0,26	0,10	1.04	26.76

TABLE 15. VARIATION IN SCOTCH PINE CORTEX MONOTERPENES IN INDIVIDUAL TREES FROM WESTERN GERMANY (SEED LOT MSFG 252)

COLLECTED 12/5-6/1967
1 TREE, 20 UL. SAMPLE
1967 CORTEX OLEORESIN

COLLECTED FROM 1965-66 WHORLS
ROSE LAKE
GLC ANALYSIS 12/11-14/1967

PERCENT MONOTERPENE

REP	TREE NO.	ALPHA-PINENE	CAMPHENE	BETA-PINENE	MYRCENE	3-CARENE	ALPHA-TERPINENE	LIMONENE	BETA-PHELL.	CYMENE	GAMMA-TERPINENE	TERPINOLENE
1	3	7,7	0,4	16,6	4,5	0,0	0,0	66,8	1,6	2,0	0,4	0,0
2	2	6,1	0,4	18,9	3,9	40,0	1,1	19,6	2,9	1,1	1,1	5,0
2	3	4,5	0,3	24,7	3,4	55,0	1,7	1,4	1,7	0,3	0,7	6,2
2	4	5,1	0,4	22,4	3,0	57,0	1,3	1,3	1,7	0,8	0,8	6,3
3	1	4,5	0,0	4,8	4,5	60,0	2,0	1,4	12,1	1,4	1,4	7,9
3	3	8,3	0,4	10,3	18,3	49,2	2,0	1,6	2,0	1,2	0,8	6,0
4	1	9,5	0,3	33,7	20,9	25,8	1,0	0,7	2,3	1,0	0,7	4,2
4	2	6,1	0,3	3,0	3,4	56,1	2,4	15,5	2,4	3,0	1,0	6,8
4	4	3,4	0,3	8,0	3,2	71,3	2,3	1,1	1,4	0,6	0,9	7,5
6	2	8,5	0,4	5,4	33,5	38,1	2,3	1,5	3,8	0,8	0,8	5,0
6	3	11,0	0,3	37,3	34,8	0,9	0,6	12,9	1,6	0,3	0,0	0,3
6	7	12,3	0,4	44,6	26,0	1,1	0,7	10,9	2,2	1,4	0,0	0,4
7	2	10,5	0,7	30,3	3,1	27,2	0,7	19,9	2,1	1,7	0,7	3,1
7	3	1,9	0,3	3,8	4,1	74,5	2,2	0,9	1,3	0,6	1,6	8,8
7	4	13,1	0,4	21,5	36,0	1,1	0,7	23,3	1,2	1,8	0,4	0,4
8	1	7,6	0,3	24,8	5,3	28,5	0,7	12,9	13,9	0,7	1,0	4,3
8	2	7,0	0,5	17,2	19,4	34,4	1,1	1,1	11,3	4,3	0,2	3,2
8	3	9,5	0,4	20,7	3,7	46,3	1,2	10,7	1,7	0,4	0,4	5,0
8	4	3,0	0,4	8,9	3,7	66,3	2,6	1,1	2,2	1,1	1,3	9,3

TABLE 16. VARIATION IN SCOTCH PINE CORTEX MONOTERPENES IN INDIVIDUAL TREES FROM WESTERN GERMANY (SEED LOT MSEG 252)

COLLECTED 12/5-6/1967
1 TREE, 20 UL. SAMPLE
1967 CORTEX OLEORESIN

COLLECTED FROM 1965-66 WHORLS
ROSE LAKE
GLC ANALYSIS 12/11-14/1967

PERCENT OF OLEORESIN

REP	TREE NO.	ALPHA-PINENE	CAMPHENE	BETA-PINENE	MYRCENE	3-CARENE	ALPHA-TERPINENE	LIMONENE	BETA-PHELL.	CYMENE	GAMMA-TERPINENE	TERPINOLENE	TOTAL
1	3	2.01	0.33	4.01	1.27	0.00	0.03	14.29	0.51	0.41	0.01	0.05	22.92
2	2	1.84	0.33	5.18	1.27	11.96	0.26	4.88	0.85	0.26	0.19	1.31	28.31
2	3	1.48	0.33	7.02	1.17	17.09	0.41	0.51	0.60	0.11	0.10	1.67	30.47
2	4	1.39	0.33	5.18	0.89	14.42	0.26	0.42	0.51	0.18	0.10	1.40	25.06
3	1	1.75	0.21	1.67	1.74	22.75	0.56	0.60	3.85	0.41	0.37	2.57	36.47
3	3	2.19	0.33	2.55	4.59	13.24	0.41	0.51	0.60	0.26	0.10	1.40	26.17
4	1	2.91	0.33	10.04	6.30	8.44	0.26	0.34	0.77	0.26	0.10	1.22	30.95
4	2	1.93	0.33	0.89	1.17	17.73	0.56	4.11	0.77	0.71	0.19	1.85	30.23
4	4	1.39	0.33	2.74	1.27	26.49	0.64	0.51	0.60	0.18	0.19	2.39	36.71
6	2	2.28	0.33	1.38	8.49	10.57	0.49	0.51	1.02	0.18	0.10	1.22	26.57
6	3	3.45	0.33	11.60	10.77	0.32	0.18	3.68	0.60	0.11	0.00	0.14	31.16
6	7	3.45	0.33	12.38	7.25	0.32	0.18	2.82	0.77	0.33	0.00	0.14	27.97
7	2	3.00	0.44	8.48	1.08	8.33	0.18	5.05	0.68	0.41	0.10	0.86	28.61
7	3	0.85	0.33	1.19	1.46	25.31	0.56	0.42	0.51	0.18	0.37	2.57	33.75
7	4	3.54	0.33	5.76	9.63	0.32	0.18	5.65	0.51	0.41	0.01	0.14	26.46
8	1	2.37	0.33	7.32	1.74	9.18	0.18	3.51	3.76	0.18	0.19	1.22	29.98
8	2	1.48	0.33	3.13	3.64	6.83	0.18	0.34	1.97	0.64	0.01	0.59	19.13
8	3	2.37	0.33	4.88	1.08	11.96	0.26	2.39	0.51	0.11	0.01	1.13	25.02
8	4	1.03	0.33	2.35	1.17	19.12	0.56	0.42	0.68	0.26	0.28	2.30	28.50

TABLE 17. VARIATION IN SCOTCH PINE CORTEX MONOTERPENES IN INDIVIDUAL TREES FROM YUGOSLAVIA (SEED LOT MSFG 242)

COLLECTED 12/5-6/1967
1 TREE, 20 UL, SAMPLE
1967 CORTEX OLEORESIN

COLLECTED FROM 1965-66 WHORLS
ROSE LAKE
GLC ANALYSIS 12/11-14/1967

PERCENT MONOTERPENE

REP	TREE NO.	ALPHA-PINENE	CAMPHENE	BETA-PINENE	MYRCENE	3-CARENE	ALPHA-TERPINENE	LIMONENE	BETA-PHELL.	CYMENE	GAMMA-TERPINENE	TERPINOLENE
1	1	10,0	0,3	13,4	32,1	1,7	1,0	23,8	14,8	1,7	0,7	0,3
1	2	8,7	0,0	3,9	54,9	1,5	1,5	6,8	20,4	1,0	1,0	0,5
1	3	9,8	0,3	34,5	4,1	0,3	0,0	47,3	2,2	1,4	0,3	0,0
1	4	7,7	0,0	11,8	31,1	1,4	0,5	24,8	22,5	0,5	0,5	0,5
2	1	7,5	0,3	15,4	29,4	0,7	0,3	42,5	2,0	1,3	0,3	0,3
2	2	5,2	0,4	9,6	23,7	1,1	0,7	44,4	19,3	1,5	0,7	0,4
2	3	7,2	0,3	4,8	28,3	1,2	0,6	31,6	22,6	1,8	0,9	0,6
2	4	5,7	0,4	0,4	4,6	0,4	0,0	77,9	6,8	1,9	1,5	0,4
3	3	11,0	0,3	29,2	5,2	0,7	0,3	37,1	13,7	1,7	0,3	0,3
5	1	11,6	0,3	39,2	19,8	1,7	0,6	18,0	7,0	0,9	0,6	0,3
5	3	16,0	0,8	4,1	36,5	2,0	0,8	16,8	19,3	1,6	0,8	1,2
6	1	13,7	0,4	6,3	55,0	1,1	1,1	0,4	20,3	1,5	0,0	0,4
6	2	17,6	0,4	4,8	27,8	0,9	0,0	27,8	19,8	0,4	0,0	0,4
6	3	12,1	0,5	5,6	32,2	0,9	0,5	10,7	36,0	0,9	0,0	0,5
7	2	5,8	0,0	2,1	5,0	0,4	0,4	75,2	9,5	0,8	0,4	0,4
7	3	12,1	0,6	38,3	27,2	3,2	1,6	10,2	3,8	1,3	1,0	0,6
7	4	18,3	0,3	21,8	46,8	0,0	0,6	9,5	2,8	0,6	0,3	0,0
8	1	15,5	0,6	11,9	45,3	3,0	1,5	2,4	18,2	0,9	0,3	0,3
8	2	9,8	0,0	21,7	24,3	1,4	0,7	22,1	18,1	1,1	0,4	0,4
8	3	5,9	0,0	5,9	6,3	0,7	0,3	54,0	25,1	1,0	0,3	0,3
8	4	11,3	0,3	41,0	4,3	1,2	0,6	38,8	0,9	1,2	0,3	0,0

TABLE 18. VARIATION IN SCOTCH PINE CORTEX MONOTERPENES IN INDIVIDUAL TREES FROM YUGOSLAVIA (SEED LOT MSFG 242)

COLLECTED 12/5-6/1967
1 TREE, 20 UL. SAMPLE
1967 CORTEX OLEORESIN

COLLECTED FROM 1965-66 WHORLS
ROSE LAKE
GLC ANALYSIS 12/11-14/1967

PERCENT OF OLEORESIN

REP	TREE NO.	ALPHA-PINENE	CAMPHENE	BETA-PINENE	MYRCENE	3-CARENE	ALPHA-TERPINENE	LIMONENE	BETA-PHELL.	CYMENE	GAMMA-TERPINENE	TERPINOLENE	TOTAL
1	1	2,91	0,33	3,81	9,06	0,53	0,26	6,07	3,85	0,41	0,10	0,14	27.47
1	2	1,93	0,21	0,80	10,96	0,32	0,26	1,37	3,76	0,18	0,10	0,14	20.02
1	3	3,54	0,33	12,38	1,65	0,11	0,03	15,06	0,85	0,41	0,01	0,05	34.40
1	4	1,84	0,21	2,35	6,78	0,32	0,11	4,88	4,45	0,11	0,01	0,14	21.18
2	1	2,37	0,33	4,59	8,77	0,21	0,11	11,30	0,68	0,33	0,01	0,14	28.84
2	2	1,57	0,33	0,70	6,30	0,32	0,18	10,44	4,62	0,33	0,10	0,14	25.03
2	3	2,46	0,33	1,58	9,15	0,43	0,18	9,15	6,59	0,49	0,19	0,23	30.77
2	4	1,66	0,33	0,12	1,36	0,11	0,03	17,72	1,71	0,41	0,28	0,14	23.85
3	3	3,18	0,33	8,29	1,65	0,21	0,11	9,41	3,59	0,41	0,01	0,14	27.32
5	1	3,89	0,33	13,15	6,68	0,64	0,18	5,47	2,22	0,26	0,10	0,14	33.07
5	3	3,80	0,44	0,99	8,68	0,53	0,18	3,68	4,19	0,33	0,10	0,32	23.25
6	1	3,63	0,33	1,67	14,38	0,32	0,26	0,25	4,88	0,33	0,00	0,14	26.18
6	2	3,89	0,33	1,09	6,21	0,21	0,03	5,56	4,02	0,11	0,00	0,14	21.59
6	3	2,64	0,33	1,19	6,78	0,21	0,11	2,14	6,76	0,18	0,00	0,14	20.47
7	2	1,57	0,21	0,51	1,36	0,11	0,11	15,75	2,14	0,18	0,01	0,14	22.07
7	3	3,72	0,44	11,70	8,30	1,07	0,41	2,91	1,19	0,33	0,19	0,23	30.48
7	4	5,68	0,33	6,64	14,76	0,00	0,18	2,82	0,94	0,18	0,01	0,05	31.58
8	1	4,88	0,44	3,81	14,38	1,07	0,41	0,85	5,30	0,26	0,01	0,14	31.55
8	2	2,73	0,21	5,86	6,59	0,43	0,18	5,39	4,45	0,26	0,01	0,14	26.23
8	3	1,84	0,21	1,67	1,93	0,21	0,11	13,44	6,33	0,26	0,01	0,14	26.14
8	4	3,63	0,33	13,06	1,55	0,43	0,18	11,04	0,42	0,33	0,01	0,05	31.02

TABLE 19. VARIATION IN SCOTCH PINE CORTEX MONOTERPENES AMONG 10 HALF SIB-FAMILIES DERIVED FROM NORWAY

COLLECTED 7/26/1966 — COLLECTED FROM 1964 WHORL
4-TREE BULKED SAMPLE — RUSS FOREST
1965 CORTEX OLEORESIN — ANALYZED FEB., MAR., 1967

MSFG	REP	ALPHA-PINENE	CAMPHENE	BETA-PINENE	MYRCENE	3-CARENE	LIMONENE	BETA-PHELL.	CYMENE	GAMMA-TERPINENE	TERPINOLENE
		PERCENT MONOTERPENE									
275	1	8.6	0.3	27.0	2.8	33.8	19.6	4.0	2.0	0.8	1.3
275	2	12.1	1.0	20.2	7.1	31.3	18.2	5.1	3.0	1.0	1.0
275	3	7.6	0.4	20.3	4.2	56.4	4.2	2.5	3.4	0.0	0.8
275	4	10.4	0.8	29.6	5.6	40.0	8.0	2.4	1.6	0.0	1.6
275	5	8.7	0.1	35.9	2.4	37.8	9.6	2.1	0.8	0.3	2.4
276	1	5.9	0.3	9.4	7.2	59.9	2.2	9.2	1.2	0.8	3.9
276	2	6.4	0.2	12.1	3.7	63.3	1.7	6.9	1.5	0.7	3.4
276	3	9.8	0.4	23.6	13.1	38.8	2.5	7.4	1.2	0.5	2.7
276	4	7.9	0.3	15.4	3.3	64.9	3.8	2.1	0.8	0.3	1.3
276	5	7.0	0.7	9.9	5.6	54.2	12.7	6.3	1.4	0.7	1.4
277	1	9.0	0.2	11.8	9.6	49.4	2.0	13.1	0.8	0.6	3.4
277	2	9.9	0.4	11.3	5.1	62.3	2.2	4.6	2.4	0.7	1.1
277	3	9.1	0.2	16.5	14.0	41.9	3.9	9.9	1.2	0.7	2.5
277	4	11.9	0.3	7.5	7.5	49.7	9.6	11.4	0.8	0.3	1.0
277	5	17.8	0.4	13.7	21.8	19.8	10.4	14.1	0.7	0.2	1.1
278	1	7.3	0.2	13.0	6.3	51.3	5.6	11.1	1.5	1.0	2.7
278	2	14.7	0.6	24.6	9.0	30.6	9.0	8.4	1.5	0.9	0.6
278	3	9.5	0.3	17.3	7.0	50.0	4.8	7.5	1.8	0.3	1.5
278	4	12.9	0.6	17.9	5.6	49.7	3.5	5.6	2.1	0.3	1.8
278	5	7.2	0.2	15.9	7.2	62.5	1.2	3.4	1.4	0.2	0.7

TABLE 19. (CONTINUED)

279	5	12.2	0.4	27.0	5.1	28.7	20.7	3.8	0.8	0.4	0.8
279	1	12.9	0.3	25.8	5.2	37.2	13.2	2.8	0.9	0.3	1.2
279	2	19.2	0.6	28.2	3.7	34.2	8.2	3.7	1.7	0.3	0.3
279	3	10.4	0.5	25.8	11.0	19.8	25.8	4.9	0.5	0.0	1.1
279	4	9.9	0.2	23.8	4.0	49.4	8.7	1.0	0.8	0.2	2.1
280	1	10.3	0.5	19.2	3.7	29.3	24.8	6.8	1.0	0.7	3.7
280	2	8.9	0.2	22.6	5.1	50.1	6.1	3.0	1.2	0.7	2.1
280	3	10.0	0.4	31.3	2.9	26.6	22.5	2.0	1.3	0.7	2.2
280	4	8.8	0.2	27.3	5.7	33.3	18.4	3.1	0.8	0.4	2.0
280	5	8.5	0.3	24.0	7.0	36.8	17.9	1.5	0.9	0.6	2.7
281	1	11.5	0.3	34.6	2.7	17.3	31.0	0.9	0.5	0.4	0.8
281	2	22.4	0.5	41.5	7.7	20.8	4.4	1.1	0.5	0.5	0.5
281	3	19.0	0.7	42.3	7.0	19.7	8.5	1.4	1.4	0.0	0.0
281	4	11.2	0.2	24.1	4.3	32.6	22.6	2.6	0.8	0.2	1.4
281	5	13.9	0.3	31.2	9.2	18.5	21.0	1.9	1.6	0.8	1.6
282	1	9.9	0.4	18.4	9.9	35.0	12.6	9.4	1.8	0.9	1.8
282	2	7.9	0.2	19.1	8.1	44.5	3.8	10.5	1.5	1.1	3.4
282	3	9.3	0.9	13.0	9.3	50.0	3.7	8.3	2.8	0.9	1.9
282	4	7.4	0.2	15.4	2.9	40.8	26.2	3.2	1.0	0.5	2.6
282	5	7.2	0.2	14.8	13.9	42.5	5.1	11.1	1.6	0.9	2.8
283	1	6.7	0.4	5.2	3.0	70.5	2.2	8.4	1.7	0.2	1.7
283	2	4.8	0.3	9.6	3.0	75.0	1.3	2.8	2.0	0.5	0.8
283	3	7.4	0.7	12.3	3.5	58.8	2.8	7.7	1.8	1.1	3.9
283	4	5.5	0.3	16.7	3.1	63.4	1.5	3.5	0.7	0.6	4.7
283	5	6.7	0.5	16.3	3.5	63.0	1.9	3.5	1.4	0.5	2.8
284	1	22.1	0.8	14.6	8.8	43.8	2.9	2.9	1.7	0.4	2.1
284	2	10.0	0.8	7.3	3.0	63.7	1.9	6.2	2.4	0.8	3.8
284	3	9.8	1.1	14.1	4.3	46.7	16.3	3.3	2.2	0.0	2.2
284	4	13.0	0.4	13.0	4.9	54.3	4.0	4.5	2.2	0.9	2.7
284	5	9.5	0.5	20.0	4.5	50.0	3.0	5.0	3.5	2.0	2.0

TABLE 20. VARIATION IN SCOTCH PINE CORTEX MONOTERPENES AMONG 10 HALF SIB-FAMILIES DERIVED FROM EAST GERMANY

COLLECTED 7/26/1966
4-TREE BULKED SAMPLE
1965 CORTEX OLEORESIN

COLLECTED FROM 1964 WHORL
RUSS FOREST
ANALYZED FEB., MAR., 1967

MSFG	REP	ALPHA-PINENE	CAMPHENE	BETA-PINENE	MYRCENE	3-CARENE	LIMONENE	BETA-PHELL.	CYMENE	GAMMA-TERPINENE	TERPINOLENE
		PERCENT MONOTERPENE									
341	1	6,9	0,6	14,9	4,0	65,9	1,1	2,6	2,0	0,3	1,7
341	2	6,1	0,3	16,5	3,1	59,3	1,2	4,4	1,2	1,3	6,6
341	3	6,5	0,3	13,0	11,1	56,6	1,0	5,0	1,0	1,0	4,3
341	4	8,2	0,2	19,7	2,2	62,2	1,3	1,8	1,1	0,4	2,9
342	1	6,8	0,2	9,1	2,3	54,7	7,3	13,2	1,1	1,1	4,1
342	2	9,7	0,1	13,6	3,8	33,2	12,0	20,9	1,4	1,3	4,0
342	3	7,7	0,3	13,9	2,7	47,8	8,4	12,7	0,8	1,2	4,5
342	4	6,6	0,3	7,6	4,7	47,1	11,4	15,0	1,0	1,3	5,0
343	1	13,4	0,5	15,8	3,1	37,7	13,6	12,9	0,7	0,2	2,1
343	2	8,4	0,3	11,3	3,3	49,2	12,1	10,2	1,5	0,8	3,0
343	3	9,7	0,3	8,3	3,1	52,1	6,9	12,5	1,7	1,0	4,2
343	4	11,0	0,3	10,6	4,2	22,9	18,6	29,0	0,6	0,6	2,3
344	1	7,2	0,6	20,1	2,0	63,6	0,8	1,6	1,2	0,2	2,8
344	2	5,6	0,2	12,7	4,9	68,1	1,7	2,4	1,7	0,2	2,4
344	3	7,3	0,3	16,7	4,6	53,4	8,9	4,9	0,8	0,3	3,0
344	4	4,4	0,3	4,1	2,7	79,2	1,4	2,5	1,9	0,5	3,0
345	1	5,1	0,3	12,5	2,8	63,7	4,5	4,2	1,1	0,8	4,8
345	2	3,8	0,5	11,5	2,9	71,8	1,4	1,4	1,4	0,5	4,8
345	3	5,7	0,1	17,9	2,5	60,9	4,6	1,4	0,7	0,7	5,3
345	4	5,2	0,2	15,3	2,6	63,4	4,0	2,1	1,4	0,7	5,2

TABLE 20. (CONTINUED)

346	1	8.4	0.3	19.6	4.2	48.5	11.4	3.6	2.4	0.3	1.2
346	2	10.3	0.2	16.0	3.4	38.9	16.7	9.4	2.2	1.0	1.7
346	3	9.4	0.5	17.8	3.6	38.6	13.5	10.4	1.8	0.6	3.9
346	4	12.7	0.8	20.8	4.9	25.2	15.8	14.7	1.7	0.5	3.0
347	1	8.4	0.2	29.4	10.0	35.9	8.0	2.0	0.9	0.7	4.4
347	2	9.6	0.6	29.5	4.5	41.0	2.6	4.5	1.9	1.3	4.5
347	3	8.8	0.3	27.8	14.6	41.2	1.2	1.5	0.6	0.6	3.4
347	4	8.0	0.2	23.4	2.5	48.6	2.3	9.1	1.5	0.8	3.6
348	1	8.5	0.3	20.9	2.7	35.0	24.8	3.2	1.4	1.0	2.0
348	2	7.8	0.5	20.6	2.3	36.0	27.7	1.9	1.9	1.0	0.4
348	3	8.5	0.9	27.5	2.6	40.9	8.3	5.6	1.0	0.9	3.9
348	4	9.0	0.6	16.7	3.1	50.8	6.6	6.7	0.9	0.9	4.6
349	1	7.7	0.2	21.4	3.3	51.9	1.9	8.5	1.4	0.8	3.0
349	2	6.8	0.2	19.3	3.2	49.6	5.9	8.9	1.4	1.1	3.6
349	3	6.0	0.2	16.0	3.6	59.6	2.2	5.6	1.4	0.8	4.6
349	4	8.2	0.3	19.2	3.2	42.0	6.3	14.8	1.0	0.8	4.2
350	1	4.2	0.1	4.5	3.0	68.4	1.5	8.4	1.5	1.0	7.3
350	2	8.3	0.2	11.1	3.2	60.3	2.0	6.3	1.7	1.1	5.8
350	3	7.7	0.2	10.5	3.8	58.3	2.0	10.5	1.4	0.8	4.9
350	4	13.0	0.4	8.1	4.6	58.6	1.4	8.1	2.1	0.7	3.2

TABLE 21. VARIATION IN SCOTCH PINE CORTEX MONOTERPENES AMONG 10 HALF SIB-FAMILIES DERIVED FROM EAST GERMANY

COLLECTED 7/25/1966
4-TREE BULKED SAMPLE
1965 CORTEX OLEORESIN

COLLECTED FROM 1964 WHORL
RUSS FOREST
ANALYZED FEB., MAR., 1967

PERCENT MONOTERPENE

MSFG	REP	ALPHA-PINENE	CAMPHENE	BETA-PINENE	MYRCENE	3-CARENE	LIMONENE	BETA-PHELL.	CYMENE	GAMMA-TERPINENE	TERPINOLENE
501	1	21,4	0,4	45,6	2,8	22,2	0,8	4,4	0,8	0,4	1,2
501	2	16,5	0,7	20,3	2,9	40,2	1,4	13,8	0,9	0,7	2,7
501	3	17,1	0,9	41,4	3,6	18,9	6,8	9,0	0,9	0,5	0,9
501	4	7,2	0,3	21,7	19,4	40,0	3,6	3,3	0,6	0,8	3,1
501	5	6,3	0,5	11,6	4,8	69,8	1,1	3,2	1,6	0,5	0,5
502	1	5,6	0,6	13,9	6,7	67,2	1,7	1,1	2,2	0,6	0,6
502	2	4,6	0,2	11,1	2,7	70,0	1,0	3,4	1,7	1,2	4,1
502	3	4,7	0,2	9,2	4,1	74,7	0,6	4,1	0,6	0,2	1,6
502	4	3,2	0,2	7,1	2,4	74,5	2,1	2,6	1,3	0,9	5,8
502	5	6,5	0,2	16,4	2,6	67,1	1,0	1,4	1,0	0,4	3,4
503	1	8,0	0,2	19,6	3,0	56,5	1,2	5,2	1,4	0,7	4,1
503	2	7,6	0,2	13,7	3,1	59,9	3,1	7,4	1,3	0,7	3,1
503	3	12,9	1,0	14,9	5,0	39,6	17,8	5,0	2,0	1,0	1,0
503	4	6,8	0,2	14,1	2,6	55,9	7,0	9,4	1,4	0,9	1,6
503	5	7,9	0,3	12,3	1,9	70,0	2,8	1,8	0,5	0,1	2,3
504	1	11,8	0,5	26,1	3,8	51,2	1,9	1,9	1,9	0,5	0,5
504	2	6,6	0,3	17,4	6,9	55,4	3,1	2,3	1,1	1,7	5,1
504	3	14,1	0,3	28,1	4,8	46,7	2,4	1,6	1,3	0,3	0,5
504	4	6,4	0,2	14,6	2,5	67,6	1,0	2,3	0,8	0,4	4,1
504	5	6,8	0,2	16,8	1,9	66,7	2,3	0,8	1,0	0,4	3,1

TABLE 21. (CONTINUED)

505	1	5,8	0,3	11,3	2,3	71,9	1,0	1,9	1,3	0,6	3,5
505	2	9,4	0,4	7,5	2,9	63,4	1,2	6,5	1,4	1,0	6,3
505	3	3,3	0,1	7,5	1,5	81,2	1,2	0,9	1,2	0,4	2,7
505	4	8,9	0,2	5,3	3,8	50,8	5,9	18,4	1,1	0,8	4,8
505	5	7,9	0,2	8,4	7,0	53,7	16,8	3,3	1,1	0,2	1,5
506	1	10,5	0,3	16,0	2,8	54,5	3,7	6,0	1,5	0,9	3,7
506	2	11,6	0,2	14,5	5,1	60,2	1,8	3,6	1,3	0,4	1,4
506	3	23,4	0,4	34,5	3,6	29,0	7,1	0,4	0,8	0,4	0,4
506	4	9,6	0,2	16,3	2,5	59,9	4,4	1,3	0,2	0,4	5,3
506	5	5,5	0,2	7,7	2,7	76,5	0,9	0,6	0,9	0,5	4,4
507	1	11,0	0,4	13,2	3,6	50,8	13,2	2,4	1,0	0,8	3,6
507	2	7,4	0,2	23,1	2,5	56,4	5,3	1,4	0,5	0,2	3,0
507	3	4,7	0,5	3,6	3,1	54,2	24,5	5,2	1,6	0,5	2,1
507	4	8,9	0,6	12,2	12,8	52,8	7,8	2,2	0,0	2,2	0,6
507	5	9,1	0,2	23,9	3,3	40,1	15,5	5,3	0,7	0,5	1,4
508	1	6,3	0,2	17,4	2,9	65,0	2,0	1,7	0,8	0,5	3,5
508	2	4,0	0,2	10,5	2,8	74,4	1,1	0,8	0,3	0,6	5,2
508	3	7,5	0,1	20,7	3,1	58,5	1,8	3,0	0,6	0,4	4,5
508	4	7,1	0,1	23,8	2,8	58,8	3,2	1,2	1,1	0,4	1,6
508	5	5,4	0,3	7,6	2,7	78,4	1,1	1,1	1,1	0,3	2,2
509	1	9,4	1,7	12,7	5,5	66,9	0,8	0,6	1,9	0,3	0,3
509	2	10,6	1,6	14,0	3,0	43,7	20,9	2,3	1,8	0,5	1,6
509	3	7,5	0,6	10,3	2,9	63,6	1,6	6,9	0,9	0,6	5,1
509	4	9,0	1,0	27,3	2,9	46,9	6,3	1,8	1,0	0,4	3,3
509	5	10,1	1,3	17,0	8,0	52,1	2,2	6,0	0,9	0,4	2,1
510	1	11,3	0,3	24,2	2,7	42,7	11,3	4,4	1,0	0,0	2,0
510	2	7,8	0,3	12,3	3,9	35,7	25,6	10,4	1,6	0,3	1,9
510	3	14,0	0,3	26,0	8,0	12,3	34,3	4,0	0,6	0,3	0,3
510	4	5,3	0,2	10,6	3,1	45,6	24,3	5,3	0,9	0,9	3,8
510	5	16,7	0,5	24,6	15,7	0,8	33,4	7,3	0,5	0,3	0,3

TABLE 22. VARIATION IN SCOTCH PINE CORTEX MONOTERPENES AMONG 21 SEED SOURCES FROM EUROPE AND ASIA

COLLECTED 6/27-30/1966
10-TREE BULKED SAMPLE
1966 CORTEX OLEORESIN

COLLECTED FROM 1964 WHORL
KELLOGG FOREST
ANALYZED DEC., JAN., 1966-67

PERCENT MONOTERPENE

VARIETY	ORIGIN	SEED LOT MSFG	REP	ALPHA-PINENE	CAMPHENE	BETA-PINENE	MYRCENE	3-CARENE	ALPHA-TERPINENE	LIMONENE	BETA-PHELL.	CYMENE	GAMMA-TERPINENE	TERPINOLENE
9	GER	202	1	9.0	0.6	19.9	5.7	47.2	1.6	3.9	7.0	1.0	0.8	4.5
9	GER	202	2	10.7	0.5	21.7	7.7	44.3	1.9	1.6	6.4	0.7	0.5	3.0
19	TUR	213	1	18.6	1.2	12.6	53.9	1.2	0.6	7.2	3.0	1.2	0.0	0.6
19	TUR	213	2	19.2	0.5	44.7	21.9	0.9	0.5	9.1	2.7	0.5	0.0	0.0
19	TUR	214	1	27.0	0.9	47.2	16.0	3.0	0.9	2.7	1.5	0.6	0.3	0.0
19	TUR	214	2	17.6	1.3	37.7	25.2	0.6	0.6	6.9	9.4	0.6	0.0	0.0
16	FRA	238	1	20.1	0.8	52.3	8.8	2.2	1.1	10.5	2.5	0.8	0.3	0.6
16	FRA	238	2	14.9	1.4	57.4	6.8	0.7	0.0	16.2	2.0	0.7	0.0	0.0
10	YUG	242	1	11.4	0.9	27.0	18.0	6.2	1.4	20.9	11.4	1.9	0.5	0.5
10	YUG	242	2	14.6	0.7	24.3	23.3	3.7	1.5	21.2	12.5	0.9	0.5	0.7
18	GRE	243	1	17.6	1.4	48.2	5.4	4.1	1.4	21.6	4.1	0.0	0.0	1.4
18	GRE	243	2	11.9	0.6	42.9	4.8	0.6	0.6	35.9	4.2	0.6	0.0	0.6
11	GER	251	1	9.6	0.5	27.3	3.9	44.2	1.0	7.1	2.5	1.2	0.5	2.2
11	GER	251	2	9.7	0.5	29.7	5.4	43.8	1.1	1.6	2.7	1.4	0.5	3.5
11	GER	252	1	11.9	0.5	39.2	5.7	28.4	0.5	8.8	2.1	0.5	0.5	2.1
11	GER	252	2	12.2	0.7	21.6	13.7	41.7	0.7	2.2	2.9	2.2	0.7	1.4
11	GER	253	1	6.3	0.4	27.5	5.3	49.4	1.1	1.1	2.6	0.6	0.4	3.0
11	GER	253	2	13.6	0.4	35.8	11.3	32.3	0.8	2.7	1.6	1.2	0.0	0.4
6	JPL	259	1	11.7	0.4	18.7	22.3	15.0	0.7	14.7	14.3	0.7	0.4	1.1
6	JPL	259	2	11.4	0.5	28.4	11.4	11.4	0.6	11.7	21.2	0.6	0.5	1.9
6	JPL	260	1	9.5	0.3	20.4	11.9	22.4	0.7	17.0	13.9	0.7	0.3	2.7
6	JPL	260	2	7.0	0.7	20.5	9.4	36.9	1.7	7.7	11.7	1.0	0.3	3.0

TABLE 22. (CONTINUED)

19	GFO	261	1	21.1	1.3	54.6	6.6	5.3	0.0	7.9	2.6	0.7	0.0	0.7
19	GFO	261	2	18.4	0.4	48.6	20.7	0.6	0.2	8.5	1.7	0.4	0.2	0.2
8	C7E	305	1	16.1	0.6	33.3	17.3	8.8	0.3	16.4	4.2	0.9	0.6	1.5
8	C7E	305	2	10.6	0.5	18.3	25.6	23.3	0.9	5.4	12.4	0.6	0.5	1.8
8	C7E	306	1	13.0	0.9	30.9	5.6	27.8	0.0	10.2	1.9	1.9	0.0	0.0
8	C7E	306	2	10.6	0.4	28.7	8.0	24.4	1.1	18.1	6.7	0.4	0.2	1.5
8	C7E	310	1	8.3	0.6	25.0	15.0	32.8	1.9	4.2	8.9	0.8	0.6	1.9
8	C7E	310	2	10.3	0.3	25.1	12.6	20.6	1.1	12.9	14.6	1.1	0.3	1.1
8	C7E	314	1	6.1	0.4	12.5	5.4	51.8	2.1	5.4	12.1	0.7	0.4	3.2
8	C7E	314	2	7.5	0.6	19.8	9.4	32.4	2.5	6.0	14.2	1.6	1.3	4.7
7	POL	317	1	9.2	0.7	19.5	7.9	41.8	1.7	6.8	8.2	0.7	0.3	3.1
7	POL	317	2	11.5	0.7	26.0	5.4	42.9	1.4	6.1	2.4	0.7	0.3	2.7
5	SWE	541	1	4.3	0.4	6.4	2.5	67.9	2.5	2.9	6.4	1.1	0.7	5.0
5	SWE	541	2	6.3	0.5	11.3	6.2	52.8	1.6	5.6	8.7	0.5	0.3	4.0
4	SWE	543	1	9.1	0.6	32.9	4.9	37.2	1.2	7.3	3.0	1.2	0.6	1.8
4	SWE	543	2	9.1	1.2	18.1	7.8	39.1	1.2	11.5	4.9	2.9	1.2	2.9
13	ITA	555	1	20.7	0.9	37.3	29.3	0.6	0.3	6.5	2.4	0.9	0.3	0.9
13	ITA	555	2	14.2	0.4	40.8	26.6	5.2	0.4	7.7	3.4	0.4	0.4	0.4
13	ITA	556	1	16.9	0.6	30.5	25.8	9.3	0.8	5.9	6.6	0.8	0.4	1.7
13	ITA	556	2	19.2	1.0	42.4	29.1	0.5	0.0	2.5	3.4	1.0	0.5	0.5

TABLE 23. VARIATION IN SCOTCH PINE CORTEX MONOTERPENES AMONG 108 SEED SOURCES FROM EUROPE AND ASIA

COLLECTED 6/27-30/1966
20-TREE BULKED SAMPLE
1966 CORTEX OLEORESIN

COLLECTED FROM 1964 WHORL
KELLOGG FOREST
ANALYZED DEC., JAN., 1966-67

VARIETY	ORIGIN	SEED LOT MSFG	ALPHA-PINENE	CAMPHENE	BETA-PINENE	MYRCENE	3-CARENE	ALPHA-TERPINENE	LIMONENE	BETA-PHELL.	CYMENE	GAMMA-TERPINENE	TERPINOLENE
			PERCENT MONOTERPENE										
1	FIN	229	11.4	0.7	18.9	6.2	36.2	0.7	13.7	9.4	1.0	0.3	1.6
1	SWE	546	10.4	0.5	19.0	5.0	38.9	1.4	13.6	6.8	1.4	0.5	2.7
1	SWE	547	6.4	0.6	13.6	8.4	42.2	0.9	5.4	16.3	1.2	0.9	3.9
1	SWE	548	9.3	0.5	10.3	3.7	51.6	1.1	4.2	13.0	1.1	0.8	4.5
1	SWE	549	7.8	0.7	23.2	4.1	36.5	2.7	9.6	8.9	2.4	1.0	3.1
2	SIB	234	10.3	0.8	19.1	6.7	27.4	1.0	14.2	14.2	1.0	0.8	4.4
2	SIB	254	16.4	0.5	23.0	13.0	9.5	0.5	15.2	19.2	0.9	0.5	1.4
3	SIB	227	9.9	0.7	18.1	7.4	28.7	1.1	14.9	16.0	0.7	0.4	2.8
3	SIB	255	14.1	0.6	34.4	10.0	7.8	0.0	17.2	13.9	0.6	0.0	1.1
3	SIB	256	11.4	0.4	14.7	8.2	22.9	1.6	13.1	22.0	1.1	0.7	3.8
4	NOR	201	5.1	0.8	9.9	4.6	62.9	1.1	1.6	7.3	0.8	0.8	5.1
4	SWE	222	8.8	0.4	24.0	9.4	34.8	0.6	4.2	12.5	0.6	0.6	4.0
4	FIN	228	6.2	0.6	10.0	5.3	40.6	1.5	12.0	17.1	1.1	1.1	4.5
4	FIN	230	6.5	0.3	15.7	10.7	48.8	0.6	3.8	9.8	0.9	0.3	2.7
4	FIN	232	9.4	0.6	18.0	13.4	32.3	0.4	12.1	10.0	0.6	0.4	2.5
4	FIN	233	8.1	0.4	13.9	17.4	36.5	1.1	6.1	11.3	0.6	0.7	3.9
4	NOR	273	7.1	0.3	17.1	9.2	45.3	1.3	6.4	6.4	1.0	0.8	4.9

TABLE 23. (CONTINUED)

4	NOR	274	5,7	0,7	9,8	7,0	56,9	1.6	5,0	6.3	0,9	0.7	5.4
4	SWE	521	5,6	0,6	10,1	3,0	53,4	1.3	7,3	11.2	1.5	0.9	5,2
4	SWE	522	9,5	0,5	16,8	2,5	54,3	1.5	3,0	6.5	0.7	0.7	4,0
4	SWE	523	7,3	0,2	19,1	6,7	40,0	1.0	9.2	11.2	0.6	0.6	4.0
4	SWE	524	8,5	0,8	19,6	6,5	47,0	2.3	4,0	6.0	0.5	0.5	4,3
4	SWE	543	9,1	1,0	24,1	6,6	38,3	1.2	9,8	4.2	2.2	1.0	2,5
4	SWE	544	7,8	0,5	18,9	7,1	45,3	1.3	5,0	9.3	0.8	0.5	3,5
4	SWE	545	8,7	0,8	14,9	9,0	38,7	1.8	6,2	14.1	1.3	0.8	3,8
5	LAT	223	6,7	0,4	14,0	14,7	34,5	0.9	7,1	16,5	0.9	0.7	3,6
5	LAT	224	9,4	0,7	15,2	15,8	24,9	2.0	6.7	22.6	0.7	0.3	1.7
5	SWE	541	5,5	0,3	9,4	5,8	59,3	1.8	4,6	7.9	0.6	0.3	4.6
5	SWE	542	8,0	0,6	17,2	13,6	33,1	1.2	8,6	11.8	1.5	0.9	3.6
5	SWE	550	5,8	0,7	17,8	2,7	58,3	1.4	4,1	3.1	0.7	0.7	4,6
6	URL	257	6,1	0,4	11,3	7,8	31,3	1.7	12,6	23,9	0.9	0.4	3,5
6	URL	258	10,4	0,8	23,6	10,9	25,9	1.6	7,5	13,7	0,8	0.5	4,4
6	URL	259	11,7	0,3	24,3	16,0	12,9	0.6	12,9	18,2	0.9	0.6	1,5
6	URL	260	8,3	0,5	20,4	10,6	29,7	1.2	12,3	12.8	0.8	0.3	2,9
7	POL	211	8,5	0,5	21,4	11,2	34,7	1.7	9,7	7,5	1,0	0.7	3,0
7	POL	317	10,4	0,7	22,8	6,6	42,3	1.5	6,5	5.3	0.7	0.3	2,9
8	GER	203	13,0	0,8	26,6	26,3	13,0	0.6	13,3	5,1	0,6	0.3	0,6
8	GER	204	12,6	0,7	21,7	15,9	29,7	0.7	6,3	7.7	0.7	0.7	3,1
8	GER	207	8,7	0,8	20,8	6,4	41,5	2.3	6.4	6.4	1.1	0.8	4,9
8	GER	208	9,0	0,5	25,8	8,8	37,7	1.5	4,9	5.8	1.5	1.0	3,6
8	GER	209	13,0	1,3	25,4	9,4	34,2	2.0	6,2	4.2	1.6	0.7	2,0
8	CZE	305	13,1	0,6	25,3	21,7	16,4	0.6	10,6	8,6	0,8	0.6	1,7
8	CZE	306	11,1	0,3	30,2	7,7	25,0	0.9	16,7	5.9	0.6	0.3	1.2

(CONTINUED)

TABLE 23. VARIATION IN SCOTCH PINE CORTEX MONOTERPENES AMONG 108 SEED SOURCES FROM EUROPE AND ASIA

COLLECTED 6/27-30/1966
20-TREE BULKED SAMPLE
1966 CORTEX OLEORESIN

COLLECTED FROM 1964 WHORL
KELLOGG FOREST
ANALYZED DEC., JAN., 1966-67

PERCENT MONOTERPENE

VARIETY	ORIGIN	SEED LOT MSEG	ALPHA-PINENE	CAMPHENE	BETA-PINENE	MYRCENE	3-CARENE	ALPHA-TERPINENE	LIMONENE	BETAPHELL.	CYMENE	GAMMA-TERPINENE	TERPINOLENE
8	CZE	307	10.7	0.7	23.3	13.3	26.7	2.3	8.0	10.0	1.3	1.0	2.7
8	CZE	308	14.0	0.7	21.8	13.4	22.3	0.7	10.4	12.6	0.7	0.5	2.0
8	CZE	309	10.0	0.9	32.3	12.5	25.0	1.3	7.3	6.3	0.9	0.6	2.2
8	CZE	310	9.3	0.4	25.1	13.8	24.8	1.3	8.5	11.7	1.0	0.4	1.6
8	CZE	311	8.7	0.4	21.4	8.9	35.5	1.1	10.8	8.9	0.4	0.6	3.4
8	CZE	312	7.3	0.3	8.2	4.1	53.9	1.7	5.2	12.5	1.2	0.9	4.7
8	CZE	313	6.3	0.6	11.0	5.0	53.0	1.9	4.1	10.1	1.3	0.9	5.7
8	CZE	314	7.3	0.3	16.3	7.7	41.3	2.3	5.7	13.3	1.0	0.7	4.0
8	CZE	315	8.0	0.4	18.8	13.3	27.1	1.5	12.5	12.1	1.1	0.8	3.4
8	GER	525	14.0	1.0	34.3	5.5	21.9	0.7	11.5	6.2	0.8	0.7	2.5
8	GER	526	11.0	0.5	25.9	15.9	24.0	1.2	6.5	9.0	1.3	1.2	3.5
8	GER	527	9.5	0.7	22.7	21.6	19.4	1.3	9.5	11.5	0.9	0.7	2.2
8	GER	528	9.0	0.6	19.7	9.3	32.5	1.2	10.4	12.8	0.9	0.6	3.2
8	GER	529	9.5	0.4	26.2	9.5	37.1	1.1	5.1	5.9	0.7	0.7	4.0
9	GER	202	9.7	0.5	20.5	6.5	45.4	0.7	2.8	7.6	0.8	0.6	4.8
9	GER	210	10.4	0.4	25.0	10.9	36.6	1.4	4.6	4.6	0.7	0.7	4.8
10	YUG	242	11.9	0.9	24.3	17.9	20.2	0.9	12.9	7.9	0.9	0.5	1.8

TABLE 23. (CONTINUED)

11	GER	206	7.8	0.8	21.1	12.2	36.7	1.7	5.8	8.1	1.4	1.1	3.3
11	FRA	236	14.4	1.2	34.6	10.6	25.9	0.7	6.1	4.2	0.7	0.2	1.4
11	FRA	237	15.9	0.4	25.2	6.6	42.0	1.3	1.8	3.5	0.4	0.4	2.2
11	FRA	241	9.0	1.1	24.1	12.9	38.2	1.5	5.3	3.7	0.9	0.4	2.9
11	GER	250	7.6	0.9	17.0	9.1	47.5	2.1	3.8	4.4	1.5	1.2	5.0
11	GER	251	9.7	0.5	28.5	4.6	44.1	1.0	4.5	2.6	1.2	0.5	2.8
11	GER	252	12.4	0.6	32.8	9.3	31.9	0.6	6.2	2.5	1.2	0.6	1.9
11	GER	253	10.9	0.4	31.6	8.2	41.0	1.0	1.9	2.1	1.0	0.2	1.7
11	BEL	318	10.2	0.6	24.3	19.2	28.8	1.8	3.1	7.3	0.8	0.6	3.3
11	BEL	530	8.0	0.6	19.4	10.8	42.3	1.1	3.2	9.1	0.9	0.6	3.9
12	HUN	552	8.3	1.3	12.9	5.5	49.9	0.8	6.0	8.9	0.9	0.8	4.7
12	HUN	553	14.4	1.5	25.7	11.1	13.5	0.9	17.5	11.5	1.1	0.7	2.2
13	ITA	554	16.4	0.8	48.3	19.5	3.2	0.4	5.9	4.4	0.6	0.2	0.2
13	ITA	555	18.2	0.4	38.6	28.4	2.5	0.4	7.0	2.8	0.7	0.4	0.7
13	ITA	556	18.0	0.9	35.6	27.0	5.4	0.5	4.5	5.4	0.9	0.5	1.4
13	ITA	557	15.9	0.5	44.0	19.9	6.6	0.8	8.2	2.1	0.8	0.5	0.5
14	SCO	265	11.7	1.5	16.5	14.0	43.4	0.8	3.3	2.8	1.0	0.5	4.6
14	SCO	266	10.0	0.7	18.9	16.6	35.2	1.0	7.3	7.3	0.7	0.3	2.0
14	SCO	267	10.1	1.1	21.6	10.1	41.0	2.2	5.6	2.6	1.9	0.7	3.0
14	SCO	268	9.3	0.7	30.6	6.5	39.0	1.2	3.6	5.3	0.7	0.5	2.6
15	ENG	269	13.9	0.9	26.6	15.0	29.2	1.6	4.4	3.8	0.9	0.6	3.8
15	ENG	270	21.1	0.6	36.6	7.8	23.6	0.9	4.3	2.8	0.9	0.3	0.9

(CONTINUED)

TABLE 23. VARIATION IN SCOTCH PINE CORTEX MONOTERPENES AMONG 108 SEED SOURCES FROM EUROPE AND ASIA

COLLECTED 6/27-30/1966 — COLLECTED FROM 1964 WHORL
20-TREE BULKED SAMPLE — KELLOGG FOREST
1965 CORTEX OLEORESIN — ANALYZED DEC., JAN., 1966-67

PERCENT MONOTERPENE

VARIETY	ORIGIN	SEED LOT MSFG	ALPHA-PINENE	CAMPHENE	BETA-PINENE	MYRCENE	3-CARENE	ALPHA-TERPINENE	LIMONENE	BETA-PHELL.	CYMENE	GAMMA-TERPINENE	TERPINOLENE
16	FRA	212	15,8	0,9	44,7	15,9	7,5	1.3	7,8	5,0	0,9	0,6	0,3
16	FRA	235	13,4	1,1	24,6	38,0	5,9	0.5	9,1	4,3	2,1	0,5	0,5
16	FRA	238	18,6	1,0	53,9	8,2	1,8	0.8	12,2	2,4	0,8	0,0	0,4
16	FRA	239	18,9	1,3	52,9	6,6	1,6	0.5	12,1	3,7	1,6	0,5	0,3
16	FRA	240	20,6	1,7	32,0	15,1	2,1	0.7	24,1	1,7	0,7	0,3	1,0
16	FRA	316	21,9	2,1	57,3	10,4	1,0	0.0	5,2	1,0	1,0	0,0	0,0
16	FRA	320	16,1	0,8	41,8	6,5	15,4	1.5	8,8	6,3	0,8	0,5	1,5
17	SPA	218	68,9	2,3	11,4	6,8	0,8	0.0	6,8	1.5	0,8	0,0	0,8
17	SPA	219	29,4	0,9	1,8	9,2	0,0	0.0	8,3	49.5	0,9	0,0	0,0
17	SPA	246	43,8	2,5	15,0	22,5	1,3	0.0	8,8	5.0	1,3	0,0	0,0
17	SPA	247	42,2	2,2	32,9	12,4	0,9	0.4	4,4	3.1	0,9	0,0	0,4
18	GRE	243	11,7	0,8	34,2	12,2	3,7	0.8	26,3	8,2	1,3	0,3	0,5
18	GRE	244	12,6	0,6	39,7	5,8	7,4	0.6	25,2	6,2	0,9	0,3	0,6
18	GRE	271	12,1	0,8	38,9	21,6	3,8	0.5	11,1	9.0	1,0	0,8	0,5
18	GRE	272	14,3	0,9	24,8	11,5	0,9	0.5	35,3	7,8	2,3	1,4	0,5
18	GRE	551	11,5	0,7	36,9	6,3	13,1	1.3	17,4	8,5	1,3	0,5	2,5
19	TUR	213	18,8	0,5	30,7	35,9	1,0	0.5	8,3	3,1	0,5	0,0	0,5

TABLE 23. (CONTINUED)

19	TUR	214	23.8	0.8	44.0	19.0	2.4	0.6	4.0	4.0	0.8	0.4	0.0
19	TUR	220	20.7	0.6	37.7	21.4	1.3	0.2	11.0	5.8	0.9	0.4	0.2
19	TUR	221	26.7	1.0	59.0	4.8	1.9	0.0	1.0	4.8	1.0	0.0	0.0
19	GEO	261	19.0	0.6	49.7	17.1	1.9	0.3	8.2	1.9	0.6	0.3	0.3
19	GEO	262	15.4	0.9	46.1	15.4	4.9	0.9	13.3	2.0	0.6	0.3	0.3
19	GEO	263	15.2	1.0	39.4	16.3	12.1	1.3	10.2	2.7	0.6	0.2	1.0
19	GEO	264	13.9	0.7	34.6	11.8	18.0	0.7	22.5	2.5	1.1	0.7	1.4
20	AUS	205	13.2	0.5	39.2	12.0	17.9	1.7	6.1	7.1	0.7	0.5	1.0
20	NY	225	13.9	1.4	46.6	10.2	9.2	0.9	7.6	7.8	0.7	0.5	1.2