Classification of *Pinus patula, P. tecunumanii, P. oocarpa, P. caribaea* var. *hondurensis*, and Related Taxonomic Entities

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Abstract

Stem xylem terpenes of 75 pine populations were studied to determine relationships among taxonomic entities. Typical *Pinus patula* populations occurring in areas north and west of Oaxaca, Mexico, had very high proportions of β-phellandrene and low proportions of other constituents. Terpene compositions of populations of variety *longipedunculata* in northern Oaxaca were similar to that of the typical variety, while those of populations in southern Oaxaca resembled that of *P. tecunumanii*. Typical *P. tecunumanii* from populations in Chiapas (Mexico), Guatemala, and southwestern Honduras contained high proportions of α-pinene, carene, limonene, and β-phellandrene. Populations in southern Mexico, Guatemala, Honduras, Nicaragua, and Belize that contained very high proportions of α-pinene and low proportions of other constituents were judged to be typical *P. oocarpa*. Other populations in Guatemala, Honduras, and Nicaragua tended to resemble both P. *oocarpa* and *P. tecunumanii* and were judged to be atypical *P. oocarpa*. Our results suggest that the two species hybridize at middle elevations, where they occur together. Other researchers regard the atypical *P. oocarpa* populations as *P. oocarpa*, *P. patula* ssp. *tecunumanii*, or *P. oocarpa* var. *ochoterenae*. Most atypical *P. oocarpa* were more similar to *P. oocarpa* than to *P. tecunumanii*. They were definitely more similar to *P. oocarpa* than to *P. patula* and hence should not be referred to the latter taxonomically. *P. caribaea* var. *hondurensis* trees differed from others mainly in that they contained high proportions of α-pinene and β-phellandrene and low proportions of other constituents. Hybridization with *P. oocarpa* occurs where the two species occur together at low elevations.

Keywords: Monoterpenes, taxonomy.

Introduction

Although differences between *Pinus patula* Schiede and Deppe and *P. oocarpa* Schiede are usually clear, there is considerable controversy about the taxonomy and identities of the related entities *P. patula* var. *longipedunculata* Loock., *P. tecunumanii* (Schwd.) Eguiluz-Piedra and Perry (1983) [syn. *P. patula* ssp. *tecunumanii* (Eguiluz and Perry) Styles], and *P. oocarpa* var. *ochoterenae* Martínez. The history of the problems involved has been discussed well by others including Styles (1976 and 1985), Styles and Hughes (1983), Lockhart (1985, 1990b), Dvorak and Raymond (1991), and Perry (1991). In particular, there is disagreement about (1) the taxonomic status of *P. oocarpa* var. *ochoterenae* and *P. patula* var. *longipedunculata*, (2) the extent of the range of *P. tecunumanii* (Styles and McCarter 1988), and (3) the extent of variation within entities.

Here we analyze data on terpenes obtained from populations of the species in an attempt to shed light on various problems of identification and taxonomy. Data previously reported by others and our own previously unreported data are utilized. We also report results of a study of natural hybridization between *P. oocarpa* and *P. caribaea* var. *hondurensis* (hereafter the varietal epithet will be omitted for the sake of brevity). These results explain some of the variation among *P. oocarpa* populations. We also briefly summarize morphological data reported by others for the taxa discussed here.

Materials and Methods

Terpene compositions of 2,196 trees in 75 populations (apps. 1 and 2) were studied. Thirty of the populations were sampled by the authors. The remainder, and some of those we sampled, were sampled by others. Data from populations sampled by more than one author were combined when the results were similar. When results were not similar, names were changed slightly and data kept separately. In all cases, oleoresin was obtained from stem xylem tissue about 1.5 m above ground level. Most of our samples were collected over several years prior to 1988 and were analyzed by techniques described by Perry (1987). In these analyses, the sesquiterpene longifolene was not identified. In 1988, six additional populations (Nos. 17, 18, 19, 27, 39, and 42) were sampled as part of a study of hybridization between *P. oocarpa* and *P. caribaea*. Proportions of longifolene were determined for these populations.

In the 1988 sampling, composition of the turpentine was obtained by gas chromatography of a sample of the whole oleoresin dissolved in methyl *tert*-butyl ether (20 mg in 1 mL) using a 15-m (0.25-mm od) DX-1 fused silica column (J&W Scientific,[1] Folsom, CA), with a temperature program of 50 °C (15 min) followed by 2 °C/min at 110 °C to remove free resin acids from the column.

In statistical analyses, we considered only the monoterpenes that frequently occurred in large proportions (α-pinene, β-pinene, carene, limonene, and β-phellandrene) and the sesquiterpene longifolene. Some authors reported large proportions of terpenes other than those listed above. Inclusion or exclusion of particular terpenes can change the relative proportion of each terpene appreciably. In order to minimize such effects, we renormalized data for all reports in which longifolene was assessed so that the sum of all constituents (the five monoterpenes plus longifolene) added to 100 percent. For those samples in which longifolene was not assessed, we renormalized the proportions to sum to 90 percent to provide an approximate allowance for the omission of longifolene (the proportion of this constituent averaged roughly 10 percent).

A preliminary examination of individual tree data for some populations showed that some individuals had relatively high proportions of both limonene and β-phellandrene, while others did not. We determined the percentage of trees having at least 10 percent limonene and at least 6 percent β-phellandrene in each population for which individual tree data were available. Such trees were characterized as "high-LP trees."

Relationships among populations were determined mainly by means of principal component analyses (Isebrands and Crow 1975) of population mean proportions of terpenes. The first of the 3 analyses involved only the 5 monoterpenes and all 75 populations (P.C. Analysis 1). The second involved populations 1–48, in which both longifolene and the five monoterpenes were assessed (P.C. Analysis 2). The third analysis involved the five monoterpenes of populations 49–75 (P.C. Analysis 3).

We tentatively classified all populations into five major groups, mainly on the basis of major differences in terpene composition, but also partly on geographic location:

Groups A-1 and A-2. Populations having very high β-phellandrene, in areas north of Oaxaca and northern Oaxaca, Mexico, respectively.

Groups B-1, B-2, B-3, and B-4. Populations having high α-pinene, high carene or high limonene or both, and high β-phellandrene, in southern Oaxaca (Mexico), Chiapas (Mexico), Guatemala, and Honduras, respectively.

Group C. Populations having both high α-pinene and high β-phellandrene.

Group D. Populations having very high α-pinene with low proportions of other terpenes.

Groups E-1 and E-2. Populations having very high α-pinene and moderate proportions of carene or limonene or both, and populations having lower proportions of α-pinene and higher proportions of carene or limonene or both, respectively.

Analyses of variance were conducted on the population means of terpenes. These compared all possible pairs of groups, mainly to determine the extent of interaction between groups and terpenes. As an example, the analysis comparing groups A-1 and A-2 (containing 4 and 3 populations, respectively) was as follows:

Source of variation	**Degrees of freedom**
Groups	1
Populations in groups	5
Terpenes	4
Groups x terpenes	4
Total	14

We also summarized data on morphological traits of needles and cones reported by others. These were used mainly to aid in judging results of terpene analyses.

[1] The use of trade or firm names in this publication is for reader information and does not imply endorsement by the U.S. Department of Agriculture of any product or service.

Results

Principal Component Analyses

In PC Analysis 1, the first three principal components accounted for about 91 percent of the variation in mean relative contents of terpenes in the 75 populations. The first component was heavily weighted for α-pinene, β-pinene, β-phellandrene, and limonene in that order. The second and third components were most heavily weighted for carene and for limonene, respectively. In PC Analyses 2 and 3, the first three components accounted for similarly large proportions of variation.

Ordination of the populations along pairs of principal components (eigenvectors) is shown in figures 1–4. Figures 1 and 2 strongly suggest that two major clusters are present. Group A and B populations are on the left side of both figures, while populations of other groups tend to be on the right. Group A and B populations usually had relatively lower proportions of α-pinene and higher proportions of β-phellandrene than had those on the right.

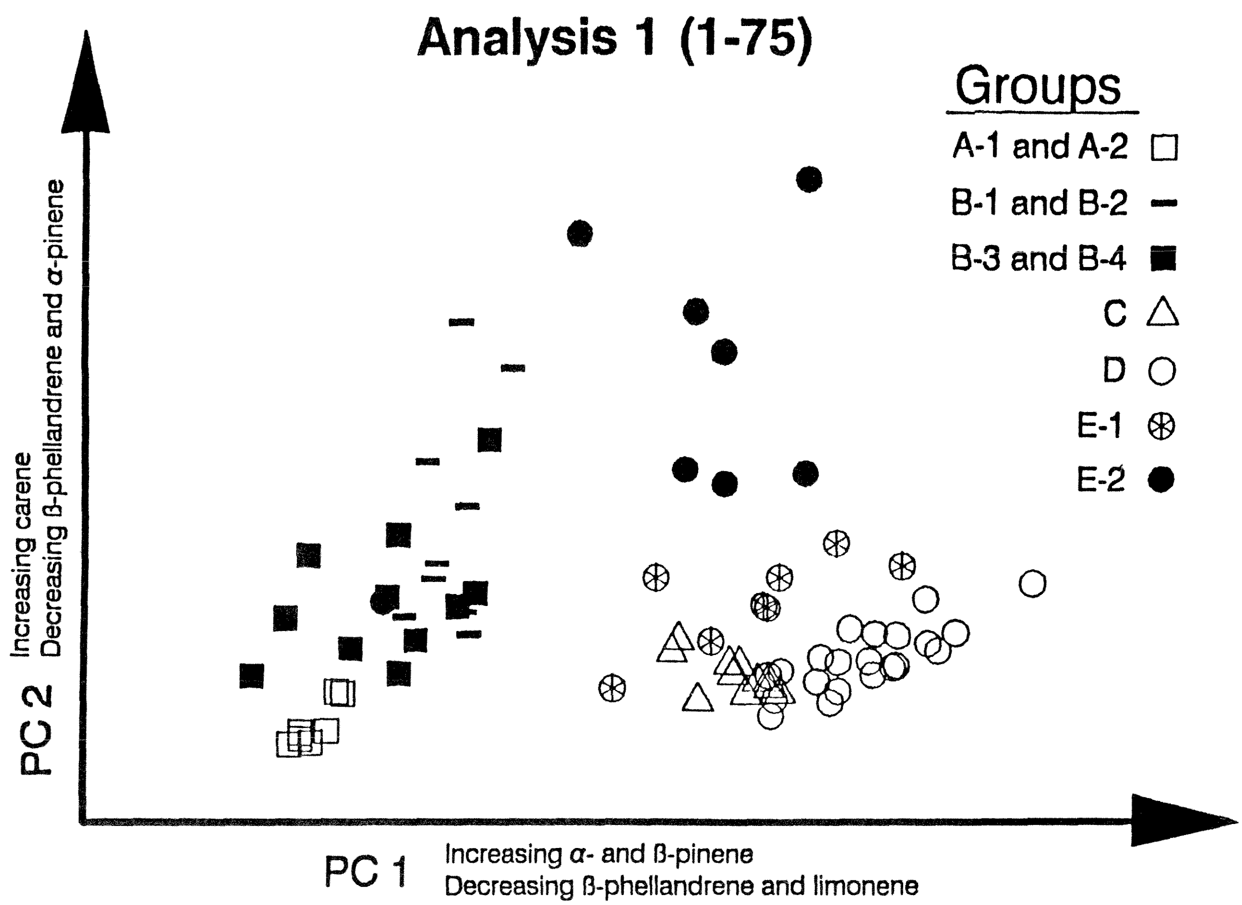

Figure 1—Ordination of all 75 populations by principal components 1 and 2 of P.C. Analysis 1.

Groups A-1 and A-2

Terpene compositions of the seven populations in these groups were very similar. Each population had an average of at least 75 percent β-phellandrene and only small amounts of other constituents (table 1). Very few individuals had both high limonene and high β-phellandrene (were LP trees). The four populations located northwest of Oaxaca, Mexico (group A-1), were considered *P. patula* by authors reporting terpene composition, and the three in northern Oaxaca (group A-2) were considered *P. patula* var. *longipedunculata* (see app. 1).

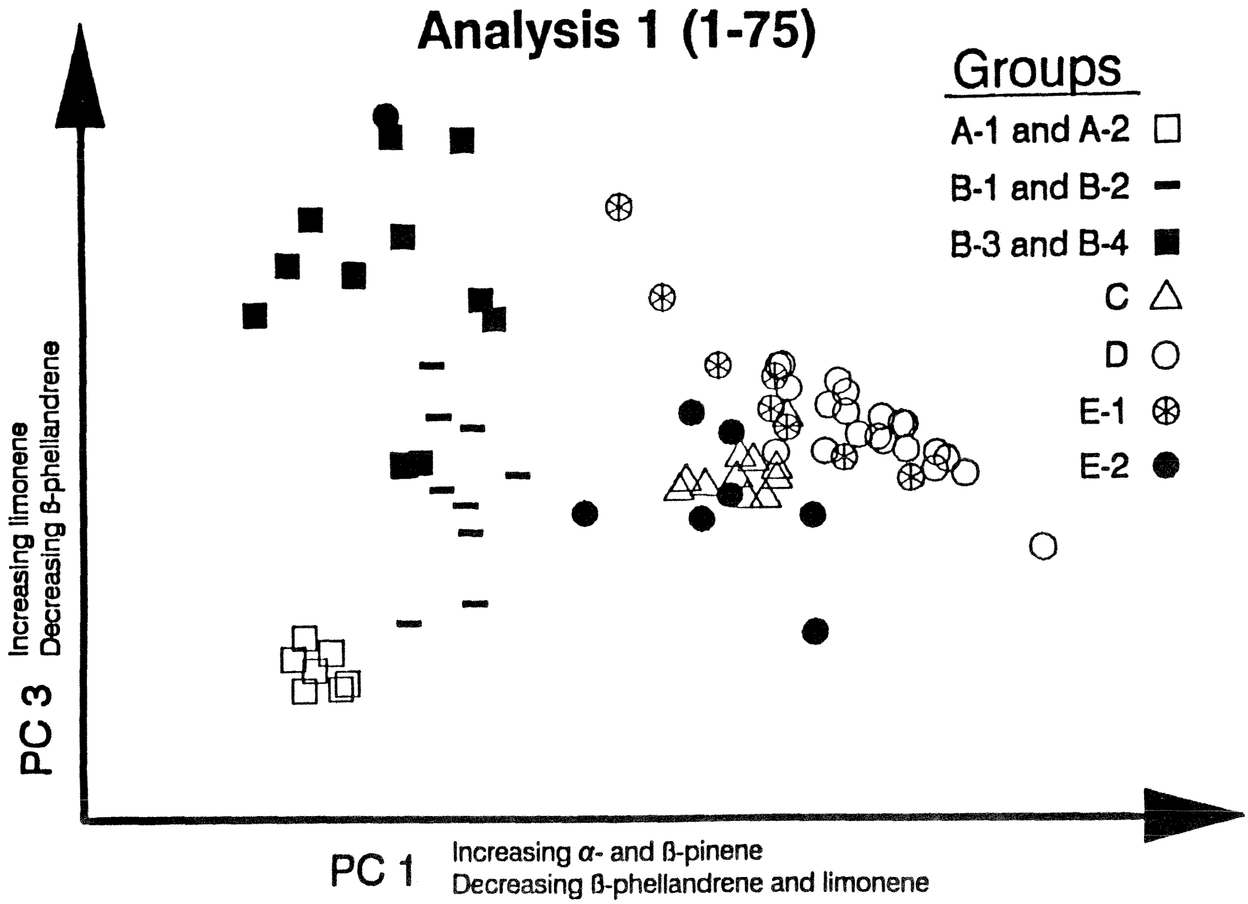

Figure 2—Ordination of all 75 populations by principal components 1 and 3 of P.C. Analysis 1.

P.C. analyses (figs. 1, 2, and 4) showed that groups A-1 and A-2 are closely clustered and indistinguishable on the basis of terpenes alone. Morphological data were available for only a few of the seven populations (table 2). Group A-1 trees had shorter peduncles and smaller ratios of cone length to width than had group A-2 trees. The Santa Maria Papalo population, which was considered *P. patula* by Dvorak and Raymond (1991), differed from *P. patula* populations only in having greater ratios of cone length to width. Cone shape in the Ixtlan population was similar to cone shape for *P. patula*, but trees of the Ixtlan population had longer peduncles than had *P. patula* trees and were more typical of the *longipedunculata* variety.

Groups B-1, B-2, B-3, and B-4

Trees in these groups had less β-phellandrene, more α-pinene, and more carene or limonene or both, than had trees in the A groups, and there were more LP trees in groups B-1, B-2, B-3, and B-4 than in the A groups (table 1). Trees in groups B-1, B-2, B-3, and B-4 also tended to have shorter needles, more needles per fascicle, and longer peduncles than had A-group trees (table 2).

Terpenes and morphological traits of two of the B-1 populations (64 and 67) tended to resemble those of populations in group A-2. Terpenes of populations 58 and 70 tended to be more like those in other B groups (table 1 and fig. 4), but populations 58 and 70 had many more internal resin ducts than had populations in other B groups.

Most of the remaining group B populations had high limonene and β-phellandrene and rather similar morphological traits. Most were considered by the authors to be *P. tecunumanii*, especially those in Guatemala and Honduras. There were several appreciable differences within and between these groups:

(1) The Chiapas populations (B-2) tended to have higher carene than others, and one of them (population 61) had no LP trees even though proportions of limonene and β-phellandrene were substantial.

(2) Like the B-2 populations, the Guatemala populations (B-3) had relatively high limonene and β-phellandrene, but their carene content was variable.

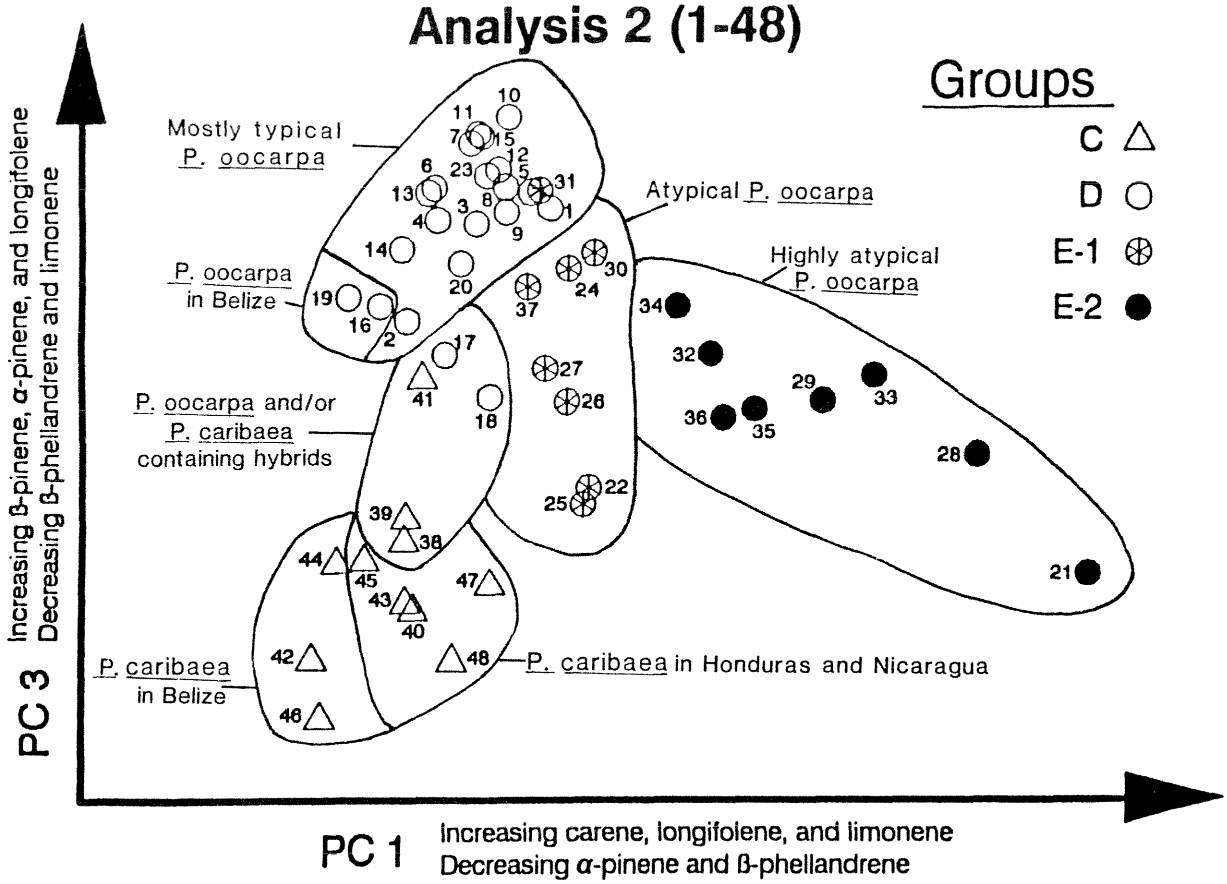

Figure 3—Ordination of populations 1 through 48 by principal components 1 and 3 of P.C. Analysis 2.

(3) Most of the Honduras populations (B-4) had less β-phellandrene, but they had appreciable percentages of LP trees. Content of carene was variable, and peduncles were longer than in other groups.

(4) P.C. analyses (fig. 4) showed fairly distinct clustering of the B-2, B-3, and B-4 populations. Populations 62, 63, 68, and 75 tended to be outliers, but their morphological traits do not seem to be out of line with those of typical *P. tecunumanii*.

(5) Cone length/width ratios decreased and peduncle lengths increased, going from B-1 to B-4 populations (table 2).

Group C

The authors judged that all of these populations (table 1) were *P. caribaea* (app. 1). The group as a whole differed from others in having high α-pinene, high β-phellandrene, and small amounts of other constituents. Mean proportion of longifolene was generally lower for group C populations than for others. Terpene composition varied little among locations, although the three Belize populations had lower than average longifolene.

β-phellandrene content of populations 38, 39, and 41 was somewhat lower than average, possibly because some *P. oocarpa* x *P. caribaea* hybrids were present. On average, trees in populations 38 and 39 had fewer internal ducts than others, and this suggests hybridization (such data were not available for population 41). Note that populations 38, 39, and 41 occur at relatively high elevations (app. 1) and are in a somewhat intermediate position between *P. oocarpa* and *P. caribaea* in figure 3. Presence of hybrids in population 38 (Santa Clara) was also suggested by Salazar (1983).

Group D

Most of these populations were considered *P. oocarpa* (app. 1) and had similar terpene compositions. The group D populations had much higher proportions of α-pinene and lower proportions of β-phellandrene than had the A and B populations. Proportions of β-pinene averaged 0.9, 1.5, 4.4, 6.2, and 5.9 percent in the A, B, C, D, and E populations.

Morphological data were scanty, but trees in most group D populations had more needles per fascicle, more resin canals (more of which were in the septal position), and much lower cone length/width ratios than had trees in the group A and B populations (table 2).

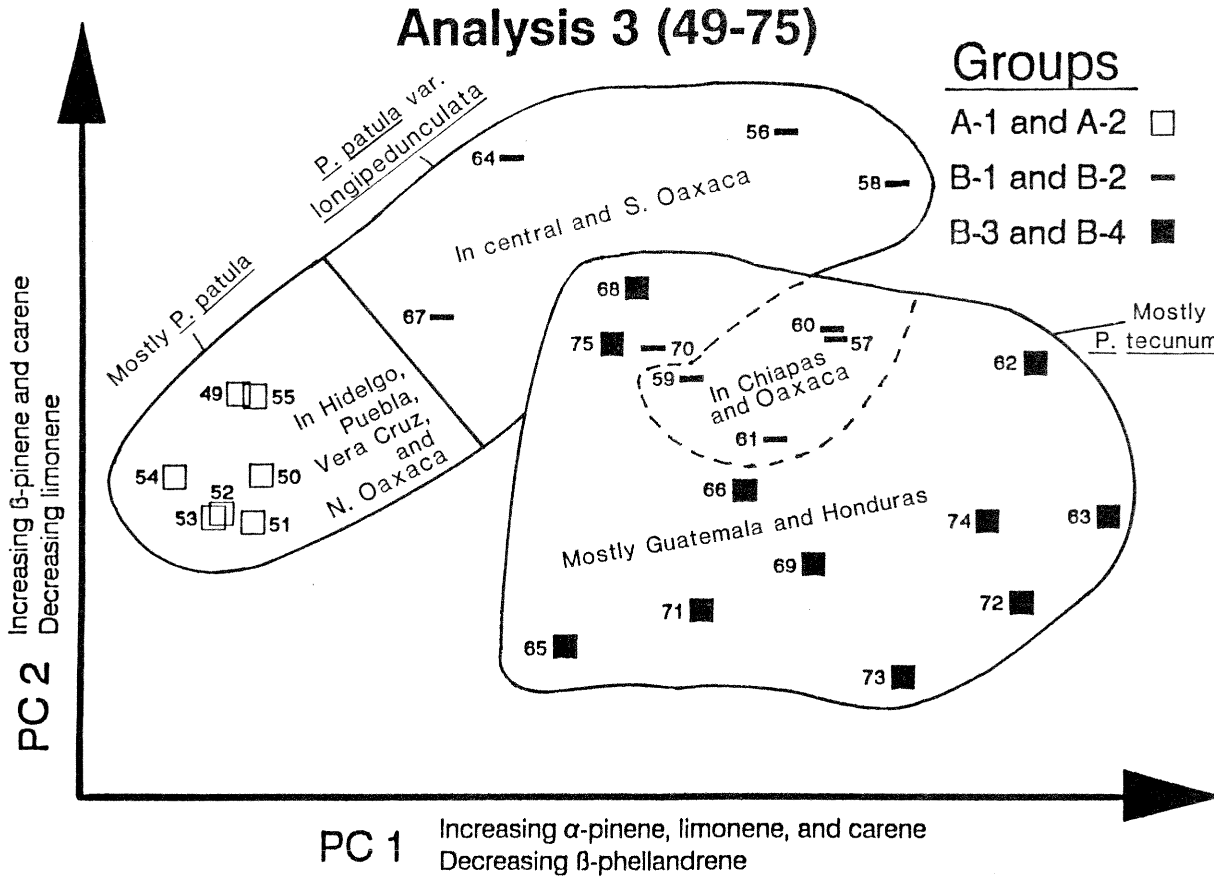

Figure 4—Ordination of populations 49 through 75 by principal components 1 and 2 of P.C. Analysis 3.

The two Belize populations differed from others in having lower than average proportions of longifolene, which is curious because Belize populations in group C also had lower proportions of longifolene than had others in group C. Morphological data were available only for population 19, and trees in that population, unlike most *P. oocarpa*, had no septal resin canals.

Populations 17 and 18 had higher than average proportions of β-phellandrene. They were sampled because appearance suggested that *P. oocarpa* x *P. caribaea* hybrids were present. Roughly equal numbers of suspected hybrids and typical *P. oocarpa* trees were selected for sampling. High content of β-phellandrene is believed to be indicative of natural hybridization, which will be discussed later.

Group E

These populations (table 1), like populations of *P. oocarpa*, are characterized by high proportions of α-pinene and low β-phellandrene, but they differ from populations of *P. oocarpa* in having appreciable proportions of carene or limonene or both. Many of these populations were considered to be *P. oocarpa* or its variety *ochoterenae*, but several were considered *P. tecunumanii* or *P. patula* spp. *tecunumanii* (app. 1). We separated group E populations having moderate proportions of carene or limonene or both (group E-1) from those having relatively high proportions of those terpenes (group E-2). The former also had higher proportions of α-pinene than had the latter, as would be expected because of constraint.

Principal component analyses showed that group E-1 populations were relatively similar to each other and were close to the typical *P. oocarpa* populations, and that the group E-2 populations were more variable and more distinct from typical *P. oocarpa* (figs. 1, 2, and 4). Also, both of the E groups were closer to *P. oocarpa* than to *P. patula* populations (figs. 1 and 2). Population 31 (group E-1) is an outlier and is within the cluster of *P. oocarpa* populations (fig. 3). Population 21 (group E-2) is within the cluster of *P. tecunumanii* populations (figs. 1 and 2).

Morphological differences between group E-1 and group E-2 populations were not appreciable. But these populations had fewer resin canals and fewer canals in the internal and septal positions than had group D populations. Population 28 (La Lagunilla) has very high carene but resembles typical *P. oocarpa* in most of its morphological traits. McCarter and Birks (1985) considered it typical *P. oocarpa*.

Analyses of Variance

Analyses of variance often showed highly significant differences among relative terpene contents of the various groups, but groups had been formed partly on the basis of terpene composition. However, interactions between terpenes and groups also often differed appreciably and were indicative of the degree of similarity among groups (table 3).

The data suggest relative similarity among groups as follows, the distance between points representing approximate averages of pertinent interactions:

	200		90		185		190		30		60	
A-1 A-2		B-1		B-2 B-3 B-4		E-2		E-1		D		C

Thus, groups A-1 and A-2 are very similar and are more similar to B-1 than to other groups. Groups B-2, B-3, and B-4 are also similar and are closer to B-1 than to others, and so on. We think it significant that questionable group E-2 falls between group D (mostly *P. oocarpa*) and the B-2, B-3, B-4 cluster (mostly *P. tecunumanii*). Also, groups E-1 and E-2 are closer to D than to the A-1, A-2 cluster (mostly *P. patula*). These results agree well with the P.C. analyses.

Evidence of Clinal Trends

Correlations between elevation and terpene contents in putative *P. tecunumanii*, atypical *P. oocarpa*, and typical *P. oocarpa* populations are given in table 4. The following points are of interest.

1. The strong negative correlation (-0.67) between elevation and α-pinene content in *P. tecunumanii* populations may indicate that there is appreciable introgression of *P. oocarpa* (which has very high α-pinene) at low elevations and little or no introgression at high elevations. The same situation may be true for the strong positive correlation (0.55) between elevation and percent LP trees. The increasing trend in LP trees may be due to introgression of *P. oocarpa* (which has very few LP trees) into *P. tecunumanii* stands at the lower elevations.

2. Although carene content was very low in typical *P. oocarpa*, level of this terpene was strongly correlated (0.56) with elevation. This correlation probably results from introgression of *P. tecunumanii* (which has appreciable carene content) into high-elevation *P. oocarpa* stands.

3. The strong negative correlation (-0.66) between elevation and β-pinene content in atypical *P. oocarpa* populations suggests that at least some trees in these populations are *P. tecunumanii* x *P. oocarpa* hybrids. Atypical populations at relatively high elevations probably receive genes from *P. tecunumanii* (which has low β-pinene), while those at low elevations receive genes from *P. oocarpa* (which has relatively high β-pinene). William S. Dvorak[2] contends—based on numerous field observations—that the two species hybridize frequently where they occur together at middle elevations.

Among the 23 A and B populations for which data on peduncle length were available, values of this trait increased, going from northwest to southeast. Barrett (1972) showed a similar trend for *P. patula* and its variety *longipedunculata*. When latitude and longitude were independent variables and peduncle length the dependent variable, the multiple correlation coefficient was 0.90 and was highly significant. The trend, however, appeared to be "stepped"—that is, peduncle lengths were relatively consistent within locations other than northern Oaxaca (table 5). Data for the E and D populations were scarce and did not show a trend. The results suggest that the B populations are related to (and may have originated from) *P. patula* and that the E and D populations are not related to *P. patula*.

Evidence of Hybridization between *P. oocarpa and P. caribaea*

As we have mentioned, the presence of high β-phellandrene trees in low-elevation *P. oocarpa* populations was thought to indicate that some populations contained hybrids. Table 1 and data from Nikles (1966) and Burley and Green (1977), indicate that *P. caribaea* trees generally contain appreciable proportions of β-phellandrene, while most *P. oocarpa* trees have low β-phellandrene. High β-phellandrene in cortical oleoresin is dominant over low in some pine species (Squillace 1982). This may also be true in xylem oleoresin. But even if it is not, the progeny of crosses between the two species are likely to have higher average content of β-phellandrene. Since *P. caribaea* occurs at low elevations (10 to 700 m in this study), hybridization is most likely to occur in *P. oocarpa* stands at relatively low elevations and within the range of *P. caribaea*.

To estimate the extent of hybridization, we compared proportions of high β-phellandrene trees in populations at

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[2] Dvorak, William S. 1992. Letter dated March 4 to Anthony E. Squillace. On file with: A.E. Squillace, School of Forest Resources and Conservation, University of Florida, Gainesville, FL 32611.

875 to 1550 m with proportions of high β-phellandrene trees in populations at 550 to 700 m (table 6). Only populations for which individual-tree data were available and that were within the range of *P. caribaea* were considered. Only 3.8 percent of the trees in the eight high-elevation populations contained high proportions of β-phellandrene, whereas 16.3 percent of trees in the five low-elevation populations had high proportions of β-phellandrene. All of the 15 individual *P. caribaea* trees had high β-phellandrene. Thus, appreciable hybridization seems to be occurring in the low-elevation *P. oocarpa* populations. Evidence of hybridization between *P. oocarpa* and *P. caribaea* also has been reported by Burley and Green (1979), Styles and others (1982), and Fernandez de la Reguera and others (1988a, 1988b).

The apparent presence of hybrids in the five low-elevation populations (Nos. 16, 17, 18, 19, and 20) is also reflected in the principal component analyses in figure 3. The low-elevation populations tend to occur between other *P. oocarpa* and *P. caribaea* populations. Note also that three *P. caribaea* populations (Nos. 38, 39, and 41) tend to be in somewhat intermediate positions between *P. caribaea* and *P. oocarpa* in figure 3. As might be expected, these three *P. caribaea* populations were at relatively high elevations for the species (700, 675, and 500 m, respectively). Salazar (1983) found evidence of hybridization in the Santa Clara population.

Discussion and Conclusions

Styles (1985) reported that populations usually considered to be *P. patula* var. *longipedunculata* and *P. tecunumanii* are extensions of *P. patula*. Partly because of this apparent clinal trend, he declared the former two entities to be *P. patula* ssp. *tecunumanii*. However, he and other authors (Birks and Barnes 1985; McCarter and Birks 1985; Styles and McCarter 1988) also designated a number of populations—previously considered *P. oocarpa* or its variety *ochoterenae*—as belonging to the new subspecies (see app. 1). Most often mentioned are the populations showing rapid growth in provenance tests, such as Yucul, San Rafael, and Las Camelias in Nicaragua and Mt. Pine Ridge in Belize. Our results strongly suggest that these four populations (plus other atypical *P. oocarpa* populations) are more related to *P. oocarpa* than to *P. patula*.

Rapid growth may not be a reliable criterion for judging taxonomic status. The volume growth at ages 6 to 9 years of 24 populations designated as either *P. oocarpa* or subspecies *tecunumanii* in international provenance trials (Birks and Barnes 1990) was found to be significantly correlated with mean annual rainfall of the provenance origin. The four populations mentioned above were located in areas of high rainfall. The trend was apparent also for *P. oocarpa* populations in Guatemala, where populations in the northeast received high rainfall and exhibited rapid growth. The relationship agrees with Squillace's (1966) report suggesting that natural selection favors trees with inherent rapid growth more in areas of favorable climate than in areas of unfavorable climate. It may be that the populations designated as members of the new subspecies are the more rapid growers among *P. oocarpa* or var. *ochoterenae* populations as a result of natural selection and are not genetically related to *P. tecunumanii*.

Our results agree with Lockhart's reports (1990a, 1990b) indicating that populations considered to be members of the subspecies are highly variable and not similar to *P. patula*. Our results also agree fairly well with Dvorak and Raymond's report (1991) on morphological traits. That report suggested (1) that many of the high-elevation populations (greater than 1800 m) in Chiapas, Guatemala, and Honduras are *P. tecunumanii* rather than *P. oocarpa* var. *ochoterenae*; (2) the probable absence of *P. tecunumanii* from Oaxaca; and (3) the tendency for similarity among populations within species that are closely associated geographically.

In spite of the clinal trend in peduncle lengths noted earlier, there is some evidence of discontinuity between the Oaxaca populations and those to the south and east. That is, most of the group B populations in Chiapas, Guatemala, and Honduras are sufficiently alike and clustered to be considered a separate species (*P. tecunumanii*) from variety *longipedunculata* in Oaxaca and Chiapas. Outliers occur, as mentioned earlier, but these may be the result of hybridization or other factors (Perry 1991).

The relationships and taxonomy of the populations we considered typical and atypical *P. oocarpa* are also controversial. Our results suggest that the highly atypical populations are more related to *P. oocarpa* than to *P. patula*. They may contain *P. oocarpa* x *P. tecunumanii* hybrids and possibly also some *P. oocarpa* var. *ochoterenae*. The Belize populations differ somewhat from typical *P. oocarpa* both in terpene composition and in some morphological traits. But they lack high carene and limonene, unlike the populations we termed highly atypical *P. oocarpa* or the *ochoterenae* variety, and this is at variance with Hunt's (1962) designation of the Belize populations as *ochoterenae*. More study on this is needed.

A summary of prominent differences between species and our opinions as to the taxonomic status of each population are given in table 7. Although the Belize populations of *P. oocarpa* are shown separately from those in other areas, we do not consider them separate taxonomic entities. The same is true for the Belize populations of *P. caribaea*. The populations we considered atypical *P. oocarpa* certainly need further study. A comprehensive study of morphological traits, especially location of resin canals, would be helpful in judging the taxonomic status of each population.

Although this study was fairly successful in determining degrees of relationship among populations, we should keep in mind that a number of investigators who employed somewhat different techniques collected and analyzed the terpene samples. Further sampling of both cortical and stem xylem oleoresin by a single team would be desirable.

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Table 1— Mean relative content (percent) of terpenes, and percent high-LP trees

Population	Mean percent content α-pinene	β-pinene	Carene	Limonene	β-phellandrene	Longifolene[a]	Percent high-LP trees[a]
	High β-phellandrene						
	Group A-1[b] (Vera Cruz, Puebla, and Hidalgo, Mexico)						
49 Zacultipán[c]	6	2	6	0	76	--	0
50 El Chico[d]	9	1	1	3	76	--	0
51 Xoxocatla	8	1	1	5	77	8	0
52 Huauchinango[e]	8	1	1	1	80	10	0
Mean	8	1	2	2	77	9	0
	Group A-2 (northern Oaxaca, Mexico)						
55 Santa M. Papalo	7	2	6	0	75	--	0
53 Llano d. Flores	7	1	0	4	82	6	7
54 Ixtlan	4	1	1	1	83	10	0
Mean	6	1	2	2	80	8	2
	High α-pinene, high carene or limonene or both, and high β-phellandrene						
	Group B-1 (southern Oaxaca, Mexico)						
58 Tlacuache	23	2	43	8	14	--	16
64 Las Trancas	17	4	9	5	54	--	0
67 El Manzanal	13	2	14	2	58	--	0
70 Juquila	25	2	13	6	43	11	21
Mean	20	2	20	5	42	11	9
	Group B-2 (Chiapas, Mexico)						
56 San Jose	12	2	49	8	19	--	--
57 Las Piedrecitas	17	2	28	22	16	15	24
59 Rancho Nuevo	22	1	19	11	37	--	17
60 Napite & Teopisca	25	2	24	15	24	--	12
61 Camino-Chanal[f]	26	1	15	17	31	--	0
Mean	20	2	26	15	24	15	13
	High α-pinene, high carene or limonene or both, and high β-phellandrene						
	Group B-3 (Guatemala)						
65 Pachoc	8	0	0	36	45	11	92
66 La Soledad	17	2	1	37	32	10	68
68 San Vicente	12	3	20	18	38	--	23
71 San Jose Pinula	12	1	6	38	33	--	52
73 San Lorenzo	33	0	0	33	21	13	--
74 San Jeronimo	38	1	12	24	16	10	36
Mean	20	1	6	31	31	11	54
	Group B-4 (Honduras)						
62 Montana Sumpul	30	1	30	21	5	13	21
63 La Paz	37	2	4	42	5	10	20
69 Las Trancas	13	1	13	41	22	--	33
72 Guajiquiro	29	1	6	44	9	10	30
75 Celaque	17	3	6	18	43	13	11
Mean	25	2	12	33	17	12	23

See footnotes at end of table.

Table 1— Mean relative content (percent) of terpenes, and percent high-LP trees—Continued

Population	Mean percent content						Percent high-LP trees[a]
	α-pinene	β-pinene	Carene	Limonene	β-phellandrene	Longifolene[a]	
High α-pinene and β-phellandrene							
Group C (Honduras)							
39 Los Limones	67	6	1	1	18	7	0
40 Miravelles	62	5	3	3	21	5	--
41 Culmi	78	3	1	1	8	8	--
43 Guanaja Island	62	6	4	1	22	6	--
Mean	67	5	2	2	17	6	0
Group C (Nicaragua)							
38 Santa Clara	69	4	4	1	16	6	--
45 Alamicamba	71	4	1	1	18	5	--
47 Karawala	59	3	9	0	20	9	--
48 Laguna d. Pinar	57	3	7	1	24	7	--
Mean	64	4	5	1	20	7	--
High α-pinene and β-phellandrene							
Group C (Belize)							
42 Mt. Pine Ridge	66	6	2	1	24	1	0
44 Los Lomitas	72	5	2	1	18	3	--
46 Melinda	66	4	2	1	26	2	--
Mean	68	5	2	1	23	2	0
High α-pinene							
Group D (Mexico)							
2 Dos Aguas	87	1	2	1	2	7	0
3 Abosola	80	5	3	1	1	10	0
Mean	84	3	2	1	2	8	0
Group D (Guatemala)							
23 Unknown	74	10	7	1	1	8	--
1 Pueblo Viejo	78	2	4	1	0	14	--
4 La Cumbre	86	4	1	0	0	9	--
14 Unknown	88	3	0	1	0	8	--
20 Conacaste	86	1	0	1	2	11	0
Mean	82	4	2	1	1	10	0
Group D (Honduras)							
5 San Juan	75	6	6	0	1	12	--
7 Siguatepeque	78	10	0	1	2	10	0
8 Zamorano	76	7	5	1	1	11	--
10 El Corozo	76	9	1	1	0	12	0
11 Guaimaca	76	11	1	1	2	10	0
12 Villa Santa	76	8	4	1	1	11	--
15 Pimientilla	66	16	3	1	5	9	--
17 Ocotillo	73	6	0	1	10[g]	10	0
18 V.d. Lepaguare	68	5	2	1	12[g]	12	0
Mean	74	9	2	1	4	12	0
High α-pinene							
Group D (Nicaragua)							
6 Cusmapa	83	7	1	0	0	9	--
9 Dipilto	79	4	4	1	0	12	--
13 Las Camelias	83	7	1	1	0	8	--
Mean	82	6	2	1	0	10	--

See footnotes at end of table.

Table 1— Mean relative content (percent) of terpenes, and percent high-LP trees—Continued

Population	Mean percent content						Percent high-LP trees[a]
	α-pinene	β-pinene	Carene	Limonene	β-phellandrene	Longifolene[a]	
			Group D (Belize)				
16 S.P. Pine Ridge	81	6	3	1	4	5	0
19 Mt. Pine Ridge	86	6	2	1	2	3	0
Mean	84	6	2	1	3	4	0
			Moderately high carene or limonene or both				
			Group E-1 (Mexico)				
22 Rancho Nuevo	70	0	0	23	0	7	--
			Group E-1 (Guatemala)				
24 Huehuetenango	72	3	12	1	0	12	0
30 Bucaral	69	4	15	1	0	12	--
			Group E-1 (Honduras)				
31 Jocón	68	10	11	1	1	10	0
25 Zambrano	64	2	14	17	0	4	0
26 Siguatepeque	67	3	6	9	5	10	4
27 Cusuco	67	5	8	10	2	7	4
37 Culmi	68	7	17	1	1	7	0
Mean	69	4	10	8	1	9	1
			High carene or limonene or both				
			Group E-2 (Mexico)				
21 San Cristobal	26	0	5	43	3	23	--
			Group E-2 (Guatemala)				
28 La Lagunilla	23	2	60	0	0	14	--
			High carene or limonene or both				
			Group E-2 (Honduras)				
32 San Francisco	51	5	24	6	1	11	0
35 Villa Santa	40	7	41	3	1	8	0
36 San Esteban	48	4	27	9	2	10	2
			Group E-2 (Nicaragua)				
29 San Rafael	35	6	48	1	1	10	0
33 Yucul	18	14	57	0	3	8	0
34 Las Mangas	50	8	24	1	5	12	--
Mean	36	6	36	8	2	12	0

[a] Indicates contents were not assessed or that individual tree data necessary for determining percent high-LP trees were not available.

[b] See text for more detailed definitions of groups.

[c] Includes Pinal de Amoles, Queretaro.

[d] Includes District 0 Federal.

[e] Includes Zacapoaxtla, Puebla.

[f] Includes Chempil.

[g] The relatively high means here are likely due to hybridization with P. caribaea (see text).

Table 2—Morphological traits of needles and cones[a]

Group	Needles/ fasicle	Needle length	Resin canals	Location of resin canals: Internal	Medial	External	Septal	Cone length	Cone length ÷ width	Peduncle length
	Number	MM	Number	Percent				MM		MM
A-1	3.2	218	2.2	8	91	0	1	72	1.47	2.1
A-2	3.4	216	2.2	14	86	0	0	78	1.86	5.0
B-1	4.3	189	2.0	45	54	1	0	61	1.56	9.6
B-2	4.1	181	2.7	4	96	0	0	62	1.38	11.8
B-3	4.4	184	3.5	9	87	2	2	57	1.31	12.5
B-4	4.5	168	2.8	8	91	0	1	63	1.23	17.7
C	3.2	219	3.1	88	12	0	0	85	--	--
D	4.5	197	3.2	22	40	9	30	59	1.00	21.4
E-1	3.8	184	2.4	6	94	0	0	65	1.04	21.0
E-2	4.4	192	2.8	5	95	0	0	58	.99	18.8

[a] Based on data from Dvorak and Raymond (1991), McCarter and Birks (1985), Eguiluz-Piedra (1984), CAMCORE Cooperative (unpubl.), Eguiluz-Piedra and Perry (1983), Salazar (1983), Hunt (1962), and Perry (1991).

Table 3--Estimates of components of variance for groups x terpene interaction (s_{GT}), obtained from analyses of variance of population means of terpene concentrations, in all possible pairs of groups[a]

Group[b]	Population	Groups[b] A-2	A-1	B-1	B-3	B-2	B-4	E-2	C	E-1	D
	Number						S_{GT}				
A-2	3		0	210**	417**	482**	663**	992**	903**	1265**	1418**
A-1	4			188**	383**	443**	608**	936**	840**	1188**	1337**
B-1	4				93**	26	151**	238**	360**	505**	674**
B-3	6					74**	10	294**	392**	465**	655**
B-2	5						59*	94**	354**	392**	594**
B-4	5							166**	339**	329**	526**
E-2	8								277**	192**	365**
C	11									52**	57**
E-1	8										27**
D	21										

** = significant at the 0.01 level.

* = significant at the 0.05 level.

[a] $S_{GT} = \frac{\text{interaction mean square - error mean square}}{n_0}$, where n_0 is a type of average between the numbers of populations in the two groups involved (Snedecor 1956).

[b] See text for definitions.

Table 4—Terpene composition and correlation with elevation (R) in *Pinus tecunumanii* and atypical and typical *P. oocarpa* populations

Elevation class	Mean elevation	Population	Terpene composition (percent)						High-LP trees
			α-pinene	β-pinene	Carene	Limonene	β-phellandrene	Longifolene	
	Meters	Number							Percent
			Groups B-2, B-3, and B-4 (mostly *P. tecunumanii*)						
High	2425	5	15	2	19	23	30	12	50
Medium	2142	6	20	1	14	29	26	10	25
Low	1875	5	31	1	10	28	18	12	22
R w/elev.[a]			(-0.67**)	(-0.05)	(0.34)	(-0.17)	(0.31)	(0.06)	(0.55**)
			Groups E-1 and E-2 (atypical *P. oocarpa*)						
High	1809	4	57	2	9	17	2	12	1
Medium	1175	5	52	5	28	2	1	11	1
Low	868	6	46	8	32	3	2	9	0
R w/elev.[a]			(-0.11)	(-0.66**)	(-0.39)	(0.77**[b])	(0.08)	(0.63**[b])	(0.27)
			Group D (typical *P. oocarpa*)						
High	1521	7	80	5	3	1	1	10	0
Medium	1028	7	78	8	2	1	1	11	0
Low	654	7	78	6	1	1	5	8	0
R w/elev.[a]			(0.07)	(-0.14)	(0.56**)	(-1.0)	(-0.50*)	(0.20)	(0.00)

** = significant at the 0.01 level.

* = significant at the 0.05 level.

[a] Indicates correlations with elevations.

[b] These high correlations were mainly due to one very erratic value.

Table 5—Average lengths of peduncles (mm) for 33 populations, arrayed by groups and locations

Location	Population groups					
	A-1	A-2	B-1	B-2, B-3, B-4	E-1, E-2	D[a]
Mexico:						
Areas NW of Oaxaca	2, 2, 2					
Northern Oaxaca		2, 8				
Southern Oaxaca			8, 9, 10, 10			
Chiapas				11, 12, 12, 12, 13	16	18
Guatemala				10, 12, 12, 12, 14, 15	21	
Honduras				16, 16, 21	21, 21	23, 24, 25
Nicaragua					17	24

A-1 = *Pinus patula*
A-2 and B-1 = mostly *P. patula* var. *longipedunculata*
B-2, B-3, B-4 = mostly *P. tecunumanii*
E-1, E-2 = atypical *P. oocarpa*
D = typical *P. oocarpa*

[a] A single population in Belize, for which peduncle length averaged 16 mm, is not shown.

Table 6—Frequency distributions of percent β-phellandrene in relatively high vs. low elevation *Pinus oocarpa* populations within the range of *P. caribaea* and in *P. caribaea* populations

Class	*P. oocarpa* populations[a] 875 to 1550 m elevation[b]	*P. oocarpa* populations[a] 550 to 700 m elevation[c]	*P. caribaea*[d]	
	Number of trees			
0-0.9	219	50		Relatively low β-phellandrene
1.0-1.9	34	33		
2.0-2.9	11	22		
3.0-3.9	10	3		
4.0-4.9	2			
5.0-5.9	3			
6.0-6.9				
7.0-7.9				
8.0-8.9		1	2	Relatively high β-phellandrene
9.0-9.9	1			
10.0-10.9		2	1	
11.0-11.9	1	3		
12.0-12.9				
13.0-13.9			1	
14.0-14.9			1	
15.0-15.9		1		
16.0-16.9	1	2	1	
17.0-17.9		1		
18.0-18.9	1			
19.0-19.9				
20.0 +	6	11	9	
Total	289	129	15	

Chi-square test of independence:

	High elev.	Low elev.	Total	
High β-phellandrene	10	21	31	$\chi^2 = 21.34^{**}$
Low β-phellandrene	279	108	387	
Total	289	129	418	

** Significant at the 0.01 level.

[a] Including atypical populations.

[b] Population numbers 10, 11, 25, 27, 31, 32, 35, and 36.

[c] Population numbers 16, 17, 18, 19, and 20.

[d] Population numbers 39 and 42.

Table 7—Summary of major differences noted between taxonomic entities

Taxonomic entity	Average terpene content						Avg. needles \fasicle	Avg. needle length	Resin canals	Location of resin canals[a]	Avg. cone length/width	Avg. peduncle length	Identity of—	
	α-pin.	β-pin.	Car.	Lim.	β-phell.	Longi.							Typical population	Questionable population
	Percent						Number	MM	Number	Percent	Ratio	MM	Population number	
Pinus patula	8	1	2	2	77	9	3.2	215	2.2	8-90-0-2	1.47	2	49, 50, 51, 52	55[b]
P. patula var. longipedunculata	10	2	6	3	69	8	3.6	200	2.1	18-82-0-0	1.71	7	53, 54, 64, 67	58, 70[c]
P. tecunumanii	22	1	11	29	26	11	4.3	179	3.1	7-91-1-1	1.31	14	57, 59, 60, 61, 62, 63 66, 69, 71, 72, 73, 74	56, 68, 75
P. oocarpa, highly atypical[d]	38	6	40	3	2	10	4.4	192	2.8	6-94-0-0	1.01	20	28, 29, 32, 33, 34 35, 36	21
P. oocarpa, moderately atypical[d]	68	3	10	9	1	8	3.8	184	24	6-94-0-0	1.04	21	22, 24, 25, 26, 27 30, 37	—
P. oocarpa[e]	78	7	3	1	2	10	4.6	198	3.4	24-34-10-33	.96	23	1 through 15, 17, 18 20, 23, 31	—
P. oocarpa - Belize	84	6	2	1	3	4	4.2	185	2.6	1-98-1-0	1.47	16	16, 19	—
P. caribaea - Honduras and Nicaragua	64	4	4	1	20	6	3.4	226	2.7	83-17-0-0	1.42	15	38, 39, 40, 43, 45, 47, 48	41
P. caribaea - Belize	68	5	2	1	23	2	3.0	209	3.6	94-6-0-0	([f])	16	42, 44, 46	—

[a] Internal, medial, external, and septal, respectively.

[b] Population 55 differs from typical P. patula only in having longer cone length/width ratios.

[c] Populations 58 and 70 tend to resemble P. tecunumanii.

[d] These populations may contain P. oocarpa var. ochoternae trees, hybrids between P. tecunumanii and P. oocarpa, or both. Such hybrids are probably more common in E-2 than in E-1. Populations in E-2 tend to resemble P. tecunumanii, while those in E-1 tend to resemble P. oocarpa.

[e] Mexico, Guatemala, Honduras, and Nicaragua.

[f] No specific data available, but Barrett and Golfari (1962) indicate that the ratios were greater than in other areas.

Appendix 1

Descriptive data for the 75 populations analyzed for terpene composition

Population		Country[a]	Latitude	Longitude	Elevation	Trees sampled	Authors[b] and species given[c]
					Meters	Number	
1	Pueblo Viejo	G	15°22′	91°36′	1800	94	6 (OOC)
2	Dos Aguas	M	18 55	103 07	1700	30	1, 3, 6 (OOC)
3	Abosola	M	17 20	92 07	1300	24	2 (OOC)
4	La Cumbre	G	15 02	90 13	1300	21	6 (OOC)
5	San Juan	H	18 24	88 23	1300	27	6 (OOC)
6	Cusmapa	N	13 17	86 39	1250	14	6 (OOC)
7	Siguatepeque	H	14 37	87 54	1200	34	2, 6 (OOC)
8	Zamorano	H	14 02	87 03	1200	66	6 (OOC)
9	Dipilto	N	13 43	86 32	1150	30	6 (OOC)
10	El Corozo	H	15 13	87 02	950	11	1 (OOC)
11	Guaimaca	H	14 33	86 46	900	27	2 (OOC)
12	Villa Santa-1	H	14 12	86 25	900	19	6 (OOC)
13	Las Camelias	N	13 46	86 18	900	6	6 (OOC)
14	Location unknown	G	--	--	800	20	7 (OOC)
15	Pimientilla	H	14 54	87 30	700	21	6 (OOC)
16	San Pastor Pine Ridge	B	16 41	88 58	700	30	2 (PAT-t)
17	Ocotillo	H	15 18	87 09	650	10	1 (OOC)
18	Valle de Lepaguare	H	14 33	86 23	600	9	1, 6 (OOC)
19	Mt. Pine Ridge	B	17 00	88 55	575	102	1, 6 (OOC); 2 (PAT-t)
20	Conacaste	G	15 10	89 21	550	29	2 (OOC)
21	San Cristobal[d]	M	16 45	92 39	2450	12	5 (OOC-o)
22	Rancho Nuevo	M	16 20	93 00	(*)	10	8 (OOC)
23	Location unknown	G	--	--	2000	18	7 (OOC)
24	Huehuetenango	G	15 13	91 32	1760	19	2, 6 (OOC)
25	Zambrano	H	14 16	87 25	1550	6	2 (PAT-t)
26	Siguatepeque	H	14 32	87 50	1475	23	2 (PAT-t)
27	Cusuco	H	15 30	88 11	1325	46	1 (OOC-o); 2 (PAT-t)
28	La Lagunilla	G	14 42	89 57	1300	79	6 (OOC)
29	San Rafael	N	13 14	86 08	1150	26	2 (PAT-t); 6 (OOC)
30	Bucaral	G	15 01	90 09	1100	6	6 (OOC)
31	Jocón	H	15 16	86 55	1000	37	2 (PAT-t)
32	San Francisco	H	14 57	86 07	960	42	1 (TEC); 2 (PAT-t)
33	Yucul	N	12 55	85 47	950	55	2 (PAT-t); 6 (OOC)
34	Las Mangas	N	12 50	86 18	950	35	6 (OOC)
35	Villa Santa-2	H	14 11	86 19	875	69	1 (OOC,TEC); 2 (PAT-t)
36	San Esteban	H	15 15	85 38	875	55	1 (TEC); 2 (PAT-t)
37	Culmi	H	15 06	85 21	600	51	2 (PAT-t)
38	Santa Clara	N	13 48	86 12	700	15	6 (CAR)
39	Los Limones	H	14 03	86 42	675	30	1, 6 (CAR)
40	Miravelles	H	14 35	86 50	650	13	6, 11 (CAR)
41	Culmi	H	15 05	85 37	500	5	6 (CAR)
42	Mt. Pine Ridge	B	17 00	88 55	400	53	1, 6, 10, 12 (CAR)
43	Guanaja Island	H	16 27	85 54	75	15	6, 10 (CAR)
44	Las Lomitas	B	16 28	88 33	30	28	6 (CAR)

See footnotes at end of table.

Descriptive data for the 75 populations analyzed for terpene composition—Continued

Population		Country[a]	Latitude	Longitude	Elevation	Trees sampled	Authors[b] and species given[c]
					Meters	Number	
45	Alamicamba	N	13°34′	84°17′	25	30	6 (CAR)
46	Melinda	B	17 01	88 20	20	30	6 (CAR)
47	Karawala	N	13 00	83 42	10	42	9, 12 (CAR)
48	Laguna del Pinar	N	12 13	83 42	10	8	6 (CAR)
49	Zacualtipán	M	20 33	98 37	3000	11	1 (PAT)
50	El Chico	M	20 12	98 48	2850	10	1 (PAT)
51	Xoxocatla	M	18 40	97 06	2550	40	2 (PAT)
52	Huauchinango	M	20 11	98 02	2050	30	1, 3 (PAT)
53	Llano de Flores	M	17 27	96 29	2800	27	2 (PAT-l)
54	Ixtlan	M	17 24	96 27	2500	22	1, 4 (PAT-l)
55	Santa Maria Papalo	M	17 49	96 48	2200	13	1 (PAT-l)
56	San Jose[d]	M	16 42	92 41	2500	22	1 (OOC-o, PAT-l)
57	Las Piedrecitas	M	16 44	92 33	2425	43	1 (OOC-o, PAT-l); 2 (PAT-t)
58	Tlacuache	M	16 44	97 09	2350	27	1 (PAT-l)
59	Rancho Nuevo	M	16 41	92 35	2300	12	1 (OOC-o, PAT-l)
60	Napite & Teopisca	M	16 34	92 19	2200	24	1 (OOC-o, PAT-l)
61	Camino-Chanal	M	16 45	92 23	2150	20	1 (OOC-o, PAT-l)
62	Montana Sumpul	H	14 24	89 08	2000	24	2 (PAT-t)
63	La Paz	H	14 19	87 45	1875	40	2 (PAT-t)
64	Las Trancas	M	17 10	96 45	2750	19	1 (PAT-l)
65	Pachoc	G	14 56	91 16	2600	25	2 (PAT-t)
66	La Soledad	G	14 31	90 18	2400	51	2 (PAT-t); 4, 5 (OOC-o)
67	El Manzanal	M	16 06	96 33	2400	12	1 (PAT-l)
68	San Vicente	G	15 05	90 07	2200	13	1 (TEC)
69	Las Trancas	H	14 07	87 49	2150	18	1 (TEC)
70	Juquila	M	16 15	97 17	2125	33	1 (TEC, OOC-o, PAT-l); 2 (PAT-t)
71	San Jose Pinula	G	14 35	90 25	2100	21	1 (TEC, OOC-o)
72	Guajiquiro	H	14 11	87 50	2050	46	2 (PAT-t)
73	San Lorenzo	G	15 05	89 40	1900	26	4 (TEC)
74	San Jeronimo	G	15 03	90 18	1850	57	1, 4 (TEC); 2 (PAT-t)
75	Celaque	H	14 34	88 39	1750	28	1 (TEC); 2 (PAT-t)

[a] M = Mexico, G = Guatemala, H = Honduras, N = Nicaragua, B = Belize.

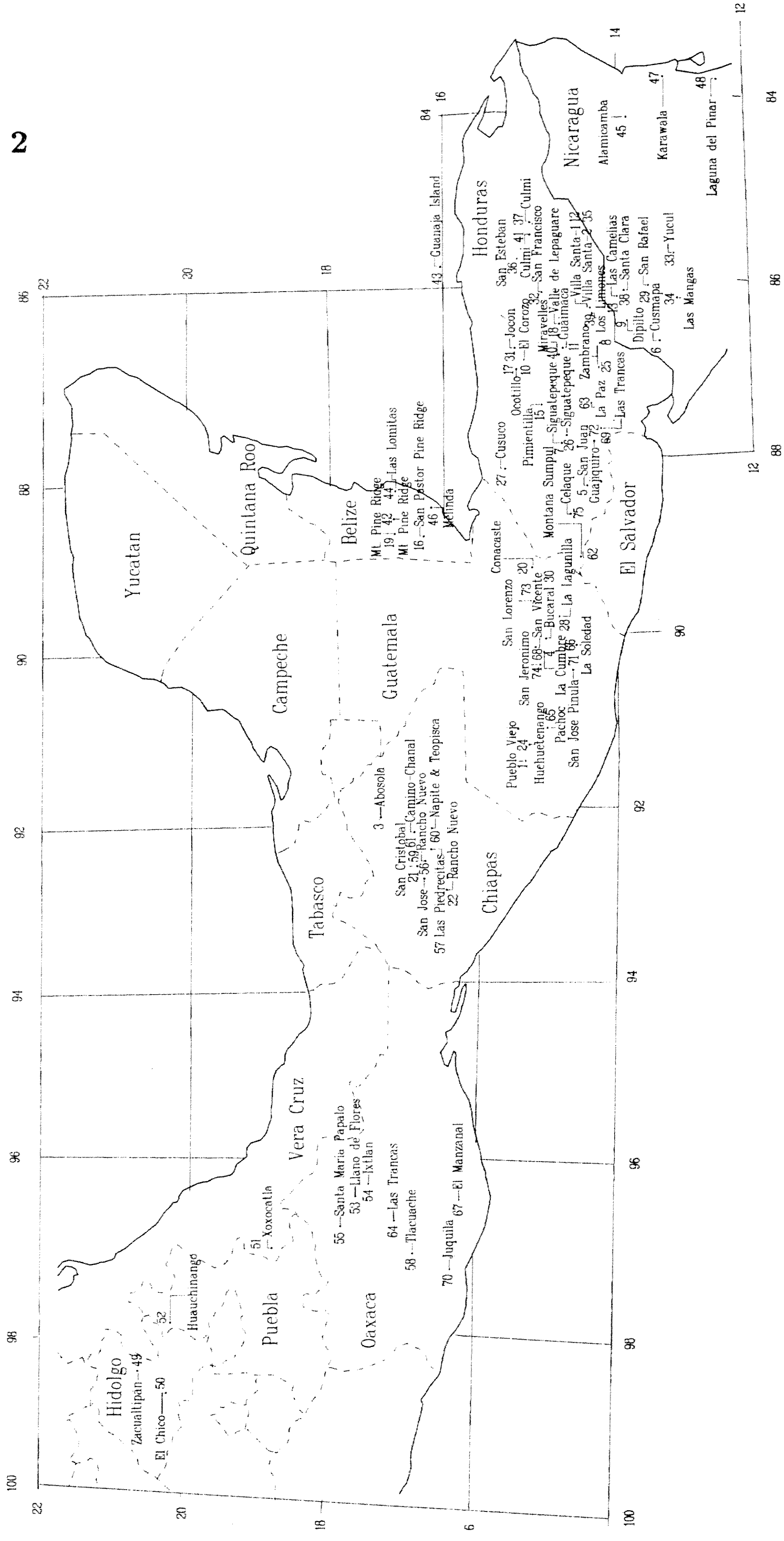
[b] 1 = present authors, 2 = Lockhart (1985), 3 = Mirov (1961), 4 = Eguiluz-Piedra (1986), 5 = Eguiluz-Piedra and Perry (1983), 6 = Burley and Green (1977), 7 = Coppen and others (1988), 8 = Iloff and Mirov (1953), 9 = Iloff and Mirov (1954), 10 = Nikles (1966), 11 = Coyne and Critchfield (1974), 12 = Burley and Green (1979).

[c] OOC = *P. oocarpa*, OOC-o = *P. oocarpa* var. *ochoterenae*, PAT = *P. patula*, PAT-t = *P. patula* ssp. *tecunumanii*, PAT-l = *P. patula* var. *longipedunculata*, TEC = *P. tecunumanii*, CAR = *P. caribaea* var. *hondurensis*.

[d] Numbers 21 and 56 may be in the same area, but are kept separate because of major differences in terpene composition.

[e] Elevation not given.

Appendix 2



Location and identity of populations sampled for terpene composition.

Dos Aguas, No. 2, located in Michoacan, Mexico, and "Unknown" populations, Nos. 14 and 23, in Guatemala are not shown.

Squillace, A.E.; Perry, Jesse P., Jr. 1992. Classification of *Pinus patula, P. tecunumanii, P. oocarpa, P. caribaea* var. *hondurensis*, and related taxonomic entities. Res. Pap. SE-285. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southeastern Forest Experiment Station. 23 pp.

Relationships among trees in 75 populations variously considered as *Pinus patula, P. patula* var. *longipedunculata, P. tecunumanii* (syn. *P. patula* ssp. *tecunumanii*), *P. oocarpa, P. oocarpa* var. *ochoterenae*, and *P. caribaea* var. *hondurensis* were studied using terpene composition and some morphological traits in an attempt to reconcile taxonomic disagreements.

Keywords: Monoterpenes, taxonomy.

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