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The taxonomic status of closely related closed cone pines in Mexico and Central America

W. S. DVORAK[1] and R. H. RAYMOND[2]

[1] *CAMCORE Cooperative, Box 7626, College of Forest Resources, North Carolina State University, Raleigh, NC 27695, U.S.A.;* [2] *Wallace Laboratories, 301 B College Road East, Princeton, NJ 08540, U.S.A.*

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Abstract. A taxonomic study on 14 cone and needle traits of 281 trees from 33 provenances of *Pinus oocarpa, P. oocarpa* var. *ochoterenae, P. patula* var. *longipedunculata, P. patula* var. *patula* and *P. tecunumanii* in Central America and Mexico was conducted to quantify the affinity between closely related species. A second objective was to determine the geographic range of *P. tecunumanii* in Mexico. Cluster analysis placed 52% of all provenances in taxa different from those assigned by field foresters. Trees from 15 provenances of what was locally known as *Pinus oocarpa* var. *ochoterenae* from Chiapas were statistically indistinguishable from high elevation Central American sources of *P. tecuncumanii* when assessed for cone and needle characteristics. However, trees from two provenances known locally as *P. oocarpa* var. *ochoterenae* from southwestern Oaxaca, Juquila and Tlacuache, were found to be distinct from *P. tecunumanii* and may be a variant of *P. patula.* Canonical discriminant analysis was used to determine the taxonomic affinity among newly formed clusters. The spatial (Mahalanobis) distance between *P. tecunumanii* and *P. patula* var. *patula, P. patula* var. *longipedunculata*, and *P. oocarpa* was 42.0, 44.4, and 109.4 respectively, and highly significant. The geographic range of *Pinus tecunumanii* in Mexico appears to be confined to the state of Chiapas.

Application. The northern and western limit of the geographic range of *Pinus tecunumanii* is Chiapas, Mexico. Within the taxon were groups of several populations that were more morphologically related to each other than to neighboring populations in other subgroups. Morphological studies in combination with monoterpene analysis and genetic (DNA) research are needed to better understand the evolutionary history of the subgroups.

Introduction

Pinus tecunumanii (Schwd.) Eguiluz and Perry was originally described as occurring in Guatemala, Honduras and "possibly Chiapas, Mexico" (Eguiluz and Perry 1983). Reclassification of trees from several *P. oocarpa* Schiede provenances as *P. tecunumanii* (syn. *P. patula* ssp.

tecunumanii [Eguiluz & Perry] Styles) by McCarter and Birks (1985) extended the known southern and eastern range of the species to Belize and Nicaragua. Botanical specimens collected at Juquila, Oaxaca, Mexico by McCarter and Birks (1985) were also classified as *P. tecunumanii* and indicated that the western range extended further than Chiapas as suggested by Eguiluz and Perry (1983). When reporting about seed collections at Juquila, Oaxaca, Dvorak (1986) also referred to trees in the provenance as *P. tecunumanii* but suggested that it represented an outlier population that required more taxonomic investigation. Recently, Styles and McCarter (1988) hypothesized that the western limit of the geographic range of *P. tecunumanii* may reach the state of Guerrero, Mexico (Fig. 1).

Forest taxonomists disagree about whether the *P. tecunumanii* trees recently sighted in southern Mexico are not actually closely related *P. oocarpa* var. *ochoterenae* Martinez or *P. patula* var. *longipedunculata* Loock. The debate centers around the legitimacy of *P. oocarpa* var. *ochoterenae* and *P. patula* var. *longipedunculata* as distinct taxa (Styles 1976; Eguiluz 1986). Until questions about the taxonomic legitimacy of

Fig. 1. Suggested geographic range of *Pinus tecunumanii* in Mexico and Central America. Hatched areas in Chiapas and Oaxaca indicate regions of taxonomic dispute.

P. oocarpa var. *ochoterenae* and *P. patula* var. *longipedunculata* are resolved, the western and northern boundaries of *P. tecunumanii* in Mexico will vary by taxonomic authority and will be subject to change.

The objective of this study was to determine the taxonomic relationships among *P. tecunumanii, P. oocarpa* var. *ochoterenae*, and *P. patula* var. *longipedunculata* in order to define the geographic range of *P. tecunumanii* in Mexico. This taxonomic study differs from past attempts to distinguish among closely related taxa in the region in two respects. First, the botanical samples examined come from a much broader geographic range in Mexico and Central America than most past studies which allowed us to better quantify true morphological differences. Second, our statistical analysis approach was first to cluster provenances by taxonomic similarities without regards to names given them by collectors and subsequently assess the spatial distance between newly formed groups (taxa) to determine if they were significantly differrent. Such an approach does not restrict the number of distinct groups (taxa) that could form.

All references to *P. tecunumanii* in this study pertain to high elevation sources found at altitudes above 1500 m. For a more detailed description of high and low elevation sources see Dvorak (1985 and 1986). Species names are sometimes abbreviated in the tables and figures of this paper as follows: *P. patula* var. *longipedunculata* (LPA), *P. patula* Schiede & Deppe var. *patula* (PAT), *P. tecunumanii*, (TEC), *P. oocarpa* var. *ochoterebae* (OCH), and *P. oocarpa* (OOC). A variant of *P. patula* is also mentioned in the text and has been abbreviated (VPA).

Materials and methods

Botanical samples (needles and cones) were collected from 256 dominant and co-dominant trees of what was locally known as *Pinus tecunumanii, P. oocarpa* var. *ochoterenae*, and *P. patula* var. *longipedunculata* in 29 provenances in El Salvador, Guatemala, Honduras, and Mexico by staff of the Central America and Mexico Coniferous Resources Cooperative (CAMCORE), North Carolina State University and forest taxonomist J. P. Perry, Jr.[1] (Fig. 2). Voucher specimens from the collection are kept in Mr. Perry's herbarium in Hertford, North Carolina. The 29 provenances sampled included some from the same locations that Martinez (1940), Loock (in Martinez 1948) and Schwerdtfeger (1953) used originally as specimen types to classify *P. oocarpa* var. *ochoterenae, P. patula* var. *longipedunculata* and *P. tecunumanii*, respectively.[2]

Botanical samples were sent to North Carolina State University for

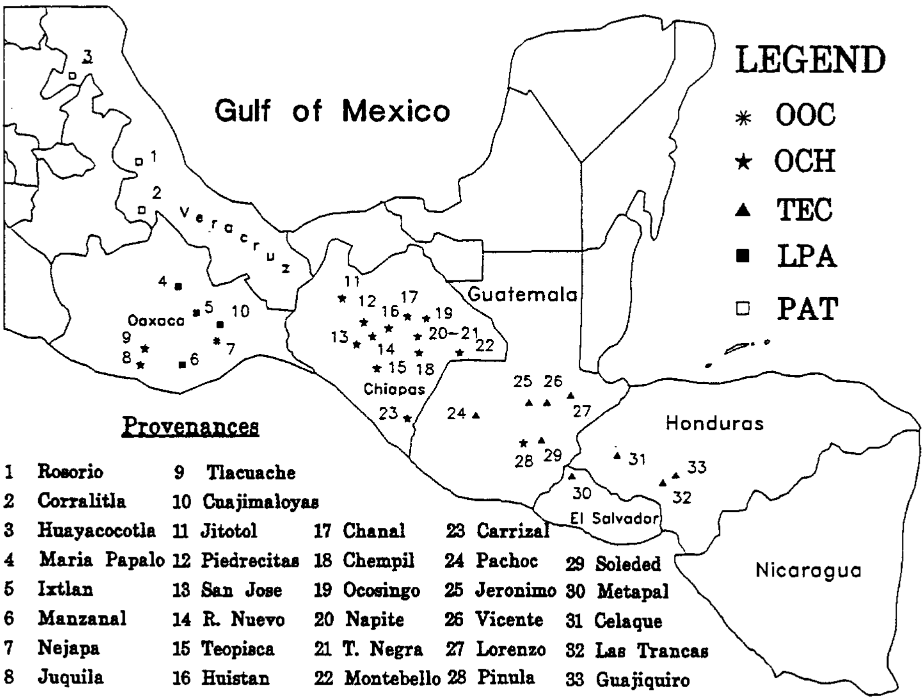

Fig. 2. Map showing the locations in Mexico and Central America where botanical samples were collected. Names given taxa were those provided by field foresters.

assessment. The species or varietal name given to each provenance were those assigned to it by well-trained local foresters; no taxonomic reclassification was attempted prior to data analysis (Table 1). Botanical sample of *Pinus patula* var. *patula* and *P. oocarpa* from four locations in Mexico were also collected as controls to represent the extremes in morphological variation between which *P. tecunumanii, P. oocarpa* var. *ochoterenae*, and *P. patula* var. *longipedunculata* were believed to exist (Fig. 2). The authenticity of both controls, *P. patula* var. *patula* and *P. oocarpa*, were verified by the use of taxonomic keys, needle and cone measurements and needle dissections at North Carolina State University.

Five needle fascicles were randomly chosen from botanical samples of each tree. From these, one needle was selected per fascicle and assessed. Two mature cones per tree were also measured. Individual tree means were computed for each of the fourteen needle and cone characteristics that were studied (Table 2). Provenance means and standard errors were also calculated for each trait (Appendix 1).

Cluster analysis was conducted on provenance means using the method of average linkage to determine affinity between groups of provenances.

Table 1. Summary of species, provenances, and number of trees sampled in the collection of botanical samples. Taxon names were assigned to provenances by local collectors.

Provenance	species	Number of trees
Nejapa, Mexico	OOC*	7
Santa Maria Papalo, Mexico	LPA	8
Ixtlan, Mexico	LPA	8
Cuajimaloyas, Mexico	LPA[a]	8
Manzanal, Mexico	LPA	8
Huayacocotla, Mexico	PAT*	8
Ingenio del Rosario, Mexico	PAT*	8
Corralitla, Mexico	PAT*	8
Chempil, Mexico	OCH	10
Ocosingo, Mexico	OCH	8
San Jose, Mexico	OCH[a]	10
Las Piedrecitas, Mexico	OCH	10
El Carrizal, Mexico	OCH	8
Chanal, Mexico	OCH	9
Teopisca, Mexico	OCH	10
Rancho Nuevo, Mexico	OCH	10
Tierra Negra, Mexico	OCH	7
Juquila, Mexico	OCH	10
Tlacuache, Mexico	OCH	8
Montebello, Mexico	OCH	8
Jitotol, Mexico	OCH	10
Napite, Mexico	OCH	10
Huixtan, Mexico	OCH	10
San Jose Pinula, Guatemala	OCH	8
La Soledad, Guatemala	TEC	8
Pachoc, Guatemala	TEC[a]	6
San Jeronimo, Guatemala	TEC[a]	10
San Lorenzo, Guatemala	TEC	8
San Vicente, Guatemala	TEC	8
Celaque, Honduras	TEC	8
Guajiquiro, Honduras	TEC	6
Las Trancas, Honduras	TEC	11
Metapal, El Salvador	TEC	5
	33 provenances and 281 trees	

Asterisks (*) denote checklots. Celaque was deleted from the analysis because of no cone data. Provenances followed by (a) denote locations where Martinez (1940), Loock (in Martinez, 1948) and Schwerdtfeger (1953) collected specimen types to describe OCH, LPA and TEC, respectively.

Table 2. Summary of morphological traits assessed and their trait codes.

Trait	Trait code
Percent Open Scales	POPEN
Cone Length (mm)	CLENG
Cone Width (mm)	CWIDT
Cone Length/Width Ratio	LWRAT
Peduncle Length (mm)	PLENG
Peduncle Width (mm)	PWIDT
Number of Needles per Fascicle	NUMFAS
Needle Length (mm)	NLENG
Fascicle Sheath Length (mm)	FSLENG
Number of Resin Canals	NUMCAN
Resin Canal Location:	
Percent Medial	PMED
Percent Internal	PINT
Percent External	PEXT
Percent Septal	PSEP

Each provenance mean began in a cluster by itself and through an iterative process, the two clusters separated by the smallest average distance were grouped together regardless of the taxonomic name given it by field collectors. Divisions were easily identified by observing the normalized root mean square distance between clusters. Because cluster analysis does not require "a prior" knowledge about the identity of a species or variety it is extremely useful whenever the identity of closely related taxa is in question.

Canonical discriminant analysis was conducted on the 14 needle and cone traits, subsequent to the clustering procedure, to compute and test the statistical significance of spatial distances between pairs of the newly formed clusters. Canonical discriminant analysis derives linear combinations of the quantitative variables that summarizes between class (taxa) variation in much the same way that principal components summarizes total variation (Statistical Analysis System 1985).

Univariate analysis of variance was conducted on the regrouped data to identify the most important morphologic traits across all clusters. The Waller-Duncan multiple comparison procedure was used to determine which traits differed significantly between any two pairs of clusters.

Results and discussion

The normalized root mean square distance among the 33 provenances generated by the cluster analysis suggested that five subdivisions of the data were appropriate. Clusters 3 and 5 were the controls, *P. patula* var. *patula* and *P. oocarpa*, respectively (Fig. 3). Cluster 1 contained all the Chiapas sources of what was locally known as *P. oocarpa* var. *ochoterenae* and the Central American populations of *P. tecunumanii*. Cluster 1 was called *P. tecunumanii* (Fig. 3). Cluster 2 contained three provenances of *P. patula* var. *longipedunculata* (Cuajimaloyas, Ixtlan, and Manazal). Because it contained one of the locations (Cuajimaloyas) that Loock used trees from to originally described the variety, cluster 2 was labelled *P. patula* var. *longipedunculata*. Eguiluz (1986) also classified Ixtlan as *P. patula* var. *longipedunculata*. Cluster 4 contained two provenances from southwestern Oaxaca, Juquila and Tlacuache, that were originally labelled *P. oocarpa* var. *ochoterenae* by local foresters. However, because it was morphologically most similar to *P. patula* var. *longipedunculata*, but still taxonomically separable from it, (discussed later) it was called "variant *patula*" (VPA). The geographical arrangement of these five clusters in Mexico and Central America is shown in Fig. 3.

Fifty-two percent of all provenances were placed in a taxon different from those assigned by field foresters (Fig. 3). The greatest confusion

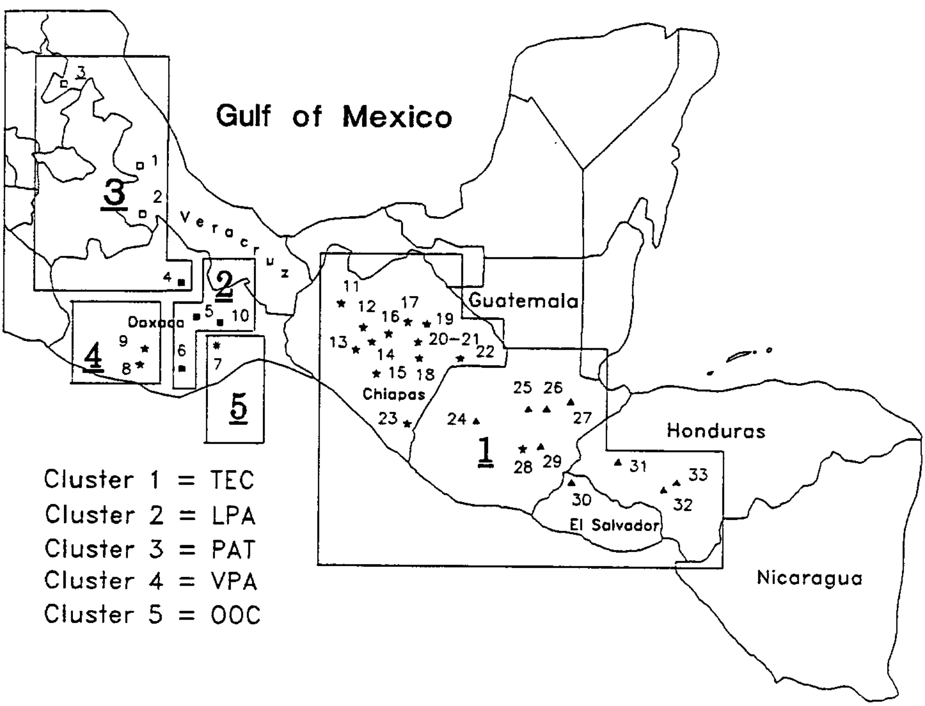

Fig. 3. Map showing the location of newly formed clusters.

occurred with the Chiapas provenances of *P. oocarpa* var. *ochoterenae.* All sources were found to be statistically indistinguishable from high elevation provenances in Guatemala, Honduras, and El Salvador. None of the Chiapas sources clustered with *P. patula* var. *longipedunculata* or *P. patula* var. *patula* as Styles (1976) hypothesized they might, nor did they remain distinct from Central American *P. tecunumanii* as Eguiluz (1986) reported.

The controls, *P. patula* var. *patula* and *P. oocarpa*, were not grouped with other taxa by the cluster analysis thus substantiating their taxonomic distinctness. However, one provenance, Santa Maria Papalo, originally labelled *P. patula* var. *longipedunculata* was reclassified as *P. patula* var. *patula.* Geographically, it was located nearest to the other *P. patula* var. *patula* provenances examined in this study (Fig. 3).

Morphological trait means, by cluster, are shown in Table 3. Small standard errors for cluster means suggest relatively little variation in important cone and needle traits within a taxon (Fig. 4). This may be the result of taking measurement on a relatively few cones per tree, and a small number (11 or less) of trees per provenance.

Canonical discriminant analysis conducted on the reclustered data indicate that the newly defined taxa were all statistically different from each other at the 0.0001 probability level, except for *Pinus patula* var. *patula* and var. *longipedunculata* (Table 4). The *P. patula* and *P. patula* var. *longipedunculata* clusters were statistically different at the 0.07 probability level and were the most closely related of the 5 groups. This was also verified by forcing the data to only four clusters: the vars. *patula* and *longipedunculata* were the first to merge.

The map in Fig. 3 gives the impression of an allopatric distribution of the five clusters. For the most part, this is an artifact of incomplete sampling. *Pinus oocarpa* (cluster 5) occurs throughout the region, sympatric with the other species. The geographic range of *P. patula* vars. *longipedunculata* and *patula* (clusters 2 and 3) is sympatric in northern Oaxaca. However, we did not find any *P. tecunumanii* in Oaxaca despite the fact that most of the known sites of related species that it could be confused with were sampled in this analysis.

Within the newly defined *P. tecunumanii* cluster, six subgroups of several provenances each were identified that were more taxonomically related to each other than to neighboring populations in other subgroups (Fig. 5). Close geographical proximity appears to be a major factor in the provenance composition of subgroups. For example, in subgroup (a), the provenances of Las Trancas and Guajiquiro are located 10 km from each other in Honduras. In subgroup (b), San Vicente, La Soledad, San Lorenzo, and (San Jose) Pinula are all eastern Guatemalan provenances.

Table 3. Means and Waller-Duncan K-ratio T-tests for morphological traits. Clusters marked with the same letter have trait means which are *not* significantly different*.

Cluster	Morphological characteristic												
	POPEN	CLENG	CWIDT	LWRAT	PLENG	PWIDT	NUMFAS	NLENG	FSLENG	NUMCAN	PMED	PINT	PSEP
		(mm)	(mm)		(mm)	(mm)		(mm)	(mm)		(%)	(%)	(%)
TEC													
Cluster 1	8.0 ab	59.9 b	45.6 bc	1.3 b	12.5 b	5.6 a	4.1 b	182 cd	14.1 d	3.0 a	92.4 a	6.3 c	0.4 b
LPA													
Cluster 2	8.1 ab	68.2 a	42.4 c	1.6 a	8.5 c	5.1 ab	3.9 c	203 b	18.2 b	1.5 b	76.0 b	23.1 b	0.0 b
PAT													
Cluster 3	6.2 c	74.2 a	47.2 b	1.6 a	2.2 d	4.9 b	3.2 d	218 a	20.6 a	1.8 b	90.5 a	8.6 c	0.9 b
VPA													
Cluster 4	8.2 a	56.7 bc	35.1 d	1.6 a	9.8 c	4.8 bc	4.5 a	180 d	15.0 d	1.9 b	34.7 c	65.3 a	0.0 b
OOC													
Cluster 5	7.5 b	50.8 c	57.8 c	0.9 c	17.4 a	4.3 c	4.4a	191 c	16.4 c	3.3 a	19.3 d	20.1 b	60.6 a

* $p < 0.05$. PEXT showed no statistical difference across taxa and was not included in the table.

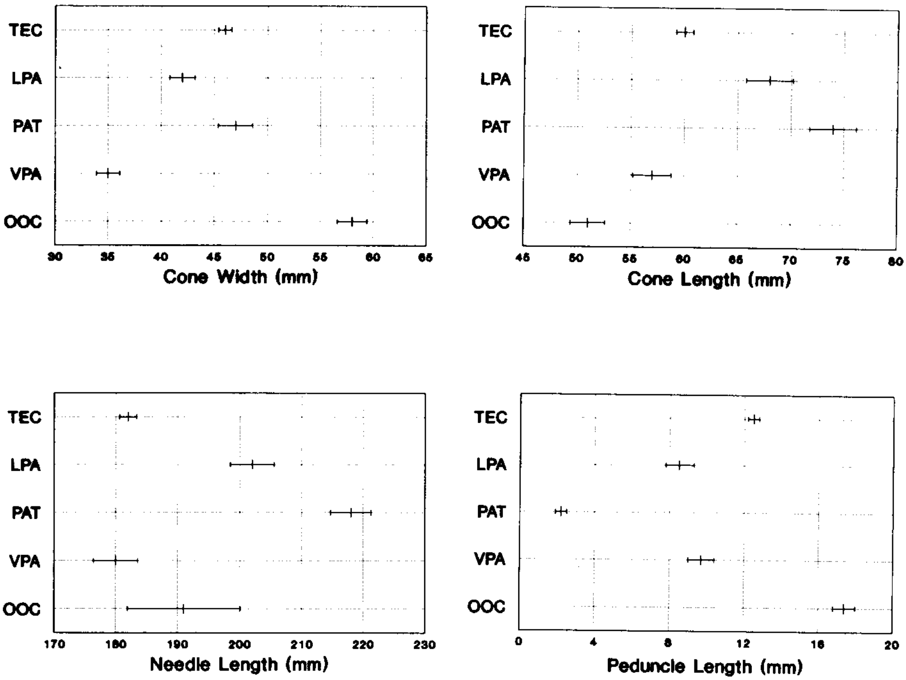

Fig. 4. Cluster means and standard errors for cone width, cone length, needle length and peduncle length.

Table 4. Canonical discriminant analysis-spatial (Mahalanobis) distances between groups formed by the cluster analysis.*

	TEC	LPA	PAT	VPA	OOC
TEC	—	44.4	42.0	81.0	109.4
LPA	—	—	10.6	37.9	79.2
PAT	—	—	—	43.9	79.9
VPA	—	—	—	—	67.7

* The probability of spatial distances greater than the ones given above is 0.0001 for all pair-wise comparisons except LPA vs. PAT which is 0.0656.

In subgroup (d), Tierra Negra, Chanal, and Napite are located within 50 km of each other. The composition of the subgroups were not always geographically perfect (e.g. subgroup (e) with provenances Chempil, Mexico and Metapal, El Salvador) nor did they always agree with our own field observations (for example, San Jeronimo, Guatemala, appeared to us to be morphologically much more similar to provenances in subgroup (b)

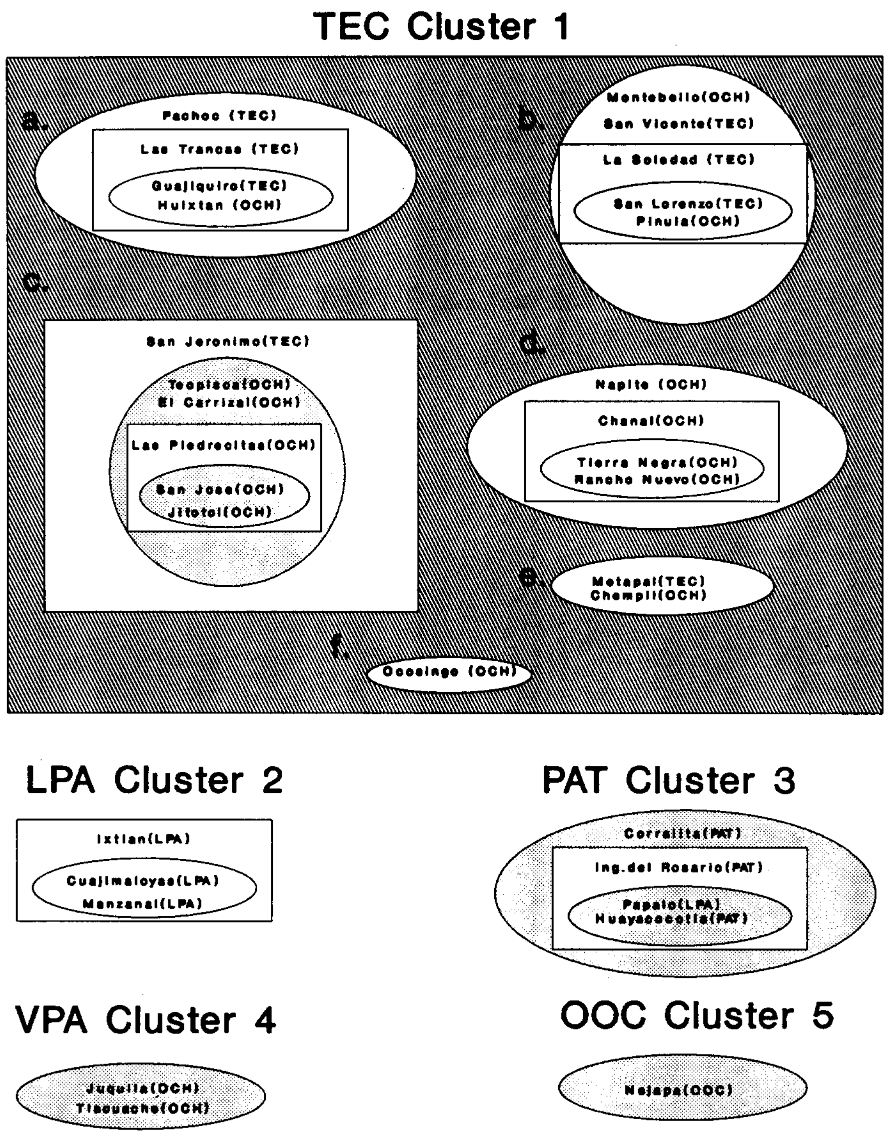

Fig. 5. Diagram showing the taxonomic affinity of provenances within newly formed clusters. The most closely related provenances are those within the smallest ellipse, inside of the smallest rectangle. In cluster 1, subgroup (a), Guajiquiro and Huixtan are most closely related. Las Trancas shows the most affinity to Guajiquiro and Huixtan. Pachoc is most closely related to Las Trancas, Guajiquiro and Huixtan. The distances between subgroups and between clusters are not drawn to scale. The taxon name next to each provenance are those used by field foresters. The name above each cluster is that which is suggested by the authors.

than (c). The morphological variation among *P. tecunumanii* subgroups was not significantly different as detected by the sensitivity of our analysis but most likely explains the continued perception by some foresters that more than one taxon is present. The subtle morphological likenesses found within groups of *Pinus tecunumanii* provenances appear to be the result of adaptation to specific ecological niches through natural selection. These groups of *P. tecunumanii* may have further been influenced by differing degrees of introgression with *P. oocarpa* at the high elevations, especially in the eastern part of its range. Additional taxonomic studies that include monoterpene analysis and genetic (DNA) research are needed to better understand the evolutionaly history of these subgroups.

Morphologically the variant *patula* provenances, Juquila and Tlacuache, (cluster 4) were distinguishable from trees in other clusters by their narrow cone width (35 mm) and percent medial and internal resin canals (see Table 3). Examination of the pair wise comparisons of taxa in Table 3 suggests that Juquila and Tlacuache were most closely related to, but distinctly different from, *P. patula* var. *longipedunculata*, and most distantly related to *P. tecunumanii.* Subsequent to the analysis of our original data, a second inspection of the Tlacuache area revealed groups of several trees that resembled the var. *longipedunculata* much more closely than those trees used in our study. It appears that there may be two closely related taxonomic entities in the closed-cone pine group on this mountain, a var. *longipedunculata* and a variant of it. At least five additional populations of trees similar to those seen at Juquila and Tlacuache have been reported in the same mountain chain (Sierra Madre del Sur) in the state of Guerrero (Donahue 1990). More taxonomic studies are needed to determine the relationship between Juquila and Tlacuache and trees of apparent similar morphology in Guerrero, and the relationship between these populations in the Sierra Madre del Sur and *P. patula* var. *longipedunculata* in other locations in southern Mexico. The classification of Juquila and at least one group of trees in Tlacuache as a variant of *P. patula* is still subject to further study but our results suggest that trees from these provenances cannot be considered to be *P. tecunumanii.*

The confusion in taxonomic classification of closed cone pines in southern Mexico is the result of thousands of generations of introgression and, in some instances, is exacerbated by the fact that collectors have utilized different methods of sampling and based results on different sample sizes. The trees chosen by CAMCORE in this study were selected on the phenotypic qualities of stem straightness and volume. Collections based on morphological traits traditionally used by forest taxonomists like peduncle length, cone width etc. rather than on economically important traits, may change the provenance composition of individual clusters and interpretation of results. In this study, we believe that the effects of the sampling method did not alter the results. After the analysis of the data, we realized that the Napite site sampled by CAMCORE and the Tierra Negra site studied by Mr. Perry (who selected specimens as part of a botanical study) (Fig. 3.) actually represented different trees at the same location collected in different years. Botanical samples from both collections grouped together in subsection (d) of cluster 1 (Fig. 5).

Had we forced the analysis to provide only two clusters, which is essentially what McCarter and Birks (1985) did when they formed discriminant functions for *P. patula* ssp. *tecunumanii* and *P. oocarpa*, the *P. tecunumanii, P. patula* vars. *patula* and *longipedunculata* and variant *patula* provenances in our study would have been combined together as one taxon. However, the normalized root mean square distances between these four clusters in our analysis were found to be statistically different and suggested that broader grouping (fewer clusters) would be inappropriate.

Even though our data suggest that *P. oocarpa* var. *ochoterenae* and *P. tecunumanii* represent the same taxonomic entity in Chiapas, Mexico, such a finding did not always correlate well with our field observations. For example, the fissured grey bark and wide bark plates (rather than smooth reddish bark with small plates), observed on trees selected at Jitotol suggested a relationship much closer to Martinez's *P. oocarpa* var. *ochoterenae* than *P. tecunumanii*. However, similarities in external and internal needle morphology with Central American *P. tecunumanii* caused botanical samples from Jitotol to be clustered with provenances from that region. The assessment of bark characteristics (color, size of bark plates, percent of the main stem with smooth vs. rough bark etc.), in addition to the morphological traits that are commonly used in taxonomic analysis, may be useful to better delineate differences between closely related taxa in the region. Bark characteristics have seldom been used in any taxonomic analysis of these closed cone pines.

It appears that the northern and western range of *P. tecunumanii* in Mexico only includes the state of Chiapas. *Pinus tecunumanii* does not appear to be west of the Isthmus of Tehuantepec in eastern Oaxaca. The Isthmus has always been considered the physical barrier that separates the pine forests of Mexico from Central America because of its unique climate and low elevation. *Pinus tecunumanii* from the highlands of Chiapas and Central America is related to *P. patula* west and north of the Isthmus but has undergone evolutionary changes that warrant its taxonomic separation.

Conclusions

Morphological study of botanical samples from 29 locations in southern Mexico and Central America of what was locally known as *P. tecunumanii*, *P. oocarpa* var. *ochoterenae*, and *P. patula* var. *longipedunculata* were subjected to cluster analysis. Results indicated that the *P. oocarpa* var. *ochoterenae* from Chiapas was statistically indistinguishable from *P. tecunumanii* in Central America and it was suggested that all provenances be called *P. tecunumanii*. However, two provenance of locally known *P. oocarpa* var. *ochoterenae* from western Oaxaca, Juquila and Tlacuache, were found to be significantly different from *P. tecunumanii* and *P. patula* var. *longipedunculata*. Results suggest that several closely related taxa do exist in southern Mexico, but that their delineation will vary among taxonomists as long as methods of sampling, the characters analyzed, and sample sizes differ.

Within *P. tecunumanii*, morphologically similar groups of provenances were identified. Close geographic proximity of provenances subjected to similar natural selection pressures probably explain these morphological likenesses. Additional morphologic studies should include bark characteristics.

No. *P. tecunumanii* was found to occur in Oaxaca, Mexico. Based on our results, the northern and western limits of *P. tecunumanii* in Mexico is the state of Chiapas.

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Notes

1. Mr. Jesse P. Perry, Jr., 306 North Front St., Hertford, NC 27944.
2. Martinez (1940) originally described *P. oocarpa* var. *ochoterenae* from botanical samples

that he collected near San Cristobal de las Casas and Coapilla, Chiapas. The area near San Cristobal is called San Jose. Loock (in Martinez, 1948) collected samples of *P. patula* var. *longipedunculata* in the mountains of Rancho Benito Juarez, Oaxaca, in a place known locally as Cuajimaloyas. Schwerdtfeger (1953) collected specimens of *P. tecunumanii* in San Jeronimo and Pachoc, Guatemala as well as several other locations. Trees from the provenances of San Jeronimo, Pachoc, Cuajimaloyas, and San Jose are also included as part of this taxonomic study.

References

Donahue, J. K. 1990. Closed-cone pine explorations in the State of Guerrero, Mexico. CAMCORE Technical Note, No. 4. North Carolina State University. 1 p.

Dvorak, W. S. 1985. One-year provenance/progeny tests results of *Pinus tecunumanii* from Guatemala established in Brazil and Colombia. Comm. For. Review 64(1): 57—65.

——. 1986. Provenance progeny testing of *Pinus tecunumanii*. In: Proceedings of joint meeting of working parties on breeding theory, progeny testing, seed orchards. Williamsburg, Va, pp. 299—309.

Eguiluz, T. and J. P. Perry. 1983. *Pinus tecunumanii*: una especie nueva de Guatemala. Ciencia Forestal: 8(4): 3—22.

——. 1986. Taxonomic Relationships of *Pinus tecunumanii* from Guatemala. Comm. For. Review 65(4): 303—314.

Loock, E. E. M. 1950. The pines of Mexico and British Honduras. Department Agric. Bull., No. 26. South Africa. 244 pp.

Martinez, M. 1940. Pinaceas Mexicanas. Descripcion de algunas especies y varidades nuevas. Anal. Inst Biol. 11: 57—73.

——. 1948. *Los Pinos Mexicanos*. Segunda Edicion. Mexico City, Mexico 361 pp.

McCarter, P. S. and J. S. Birks. 1985. *Pinus patula* subspecies *tecunumanii*; The application of numerical techniques to some problems of its taxonomy. Comm. For. Review. 64(2). 117—132.

Statistical Analysis System. 1985. SAS User's Guide: Statistics, 5th edition. 956 pp.

Schwerdtfeger, F. 1953. Informe al Gobierno de Guatemala sobre la Entomolgia Forestal de Guatemala. Vol. I. Los Pinos de Guatemala. Informe FAO/ETAP. No. 202, Rome, Italy, 58 pp.

Styles, B. T. 1985. The identity of Schwerdtfeger's Central American Pine. Forest Genetic Resources Information, No. 13. Food and Agriculture Organization, Rome., pp. 47—51.

——. 1976. Studies in variation in Central American pines I. The identity of *Pinus oocarpa* var. *ochoterenae* Martinez. *Silvae Gen.* 25(3—4). pp. 109—117.

——. and P. S. McCarter. 1988. The botany, ecology and conservation status of *Pinus patula* ssp. *tecunumanii* in the Republic of Honduras. Oxford Forestry Institute, Dept. of Plant Sciences. University of Oxford, UK. 34 pp.

Appendix 1. Provenance means and their standard errors ( ). The codes for the morphological traits are presented in the text of the paper.

Species	Provenance	Morphological characteristics							
		CLENG (mm)	CWIDT (mm)	PLENG (mm)	NUMFAS	NLENG (mm)	PMED (%)	PINT (%)	PSEP (%)
PAT	Rosario	70.3 (3.4)	52.1 (1.8)	1.9 (0.5)	3.2 (0.1)	222 (5.4)	91.7 (4.3)	8.3 (4.3)	0.0 (0.0)
PAT	Corralitla	62.1 (3.4)	40.9 (2.7)	2.4 (0.5)	3.2 (0.1)	222 (5.5)	89.8 (7.4)	8.5 (5.8)	2.0 (1.8)
PAT	Huayacoctla	84.0 (3.9)	54.4 (2.7)	1.9 (0.4)	3.2 (0.1)	209 (8.8)	89.8 (7.4)	8.5 (5.8)	2.0 (1.8)
PAT	Papalo	80.3 (2.6)	41.8 (2.5)	2.3 (0.9)	3.4 (0.1)	221 (5.8)	90.8 (5.4)	9.2 (5.4)	0.0 (0.0)
VPA	Tlacuache	54.4 (2.9)	35.0 (1.9)	9.5 (1.8)	4.5 (0.1)	175 (6.4)	29.6 (12.2)	70.4 (12.2)	0.0 (0.0)
VPA	Juquila	58.7 (2.3)	35.3 (1.4)	10.0 (0.9)	4.5 (0.1)	184 (3.1)	40.6 (8.6)	59.4 (8.6)	0.0 (0.0)
LPA	Ixtlan	75.1 (3.9)	41.9 (1.5)	6.8 (1.2)	3.6 (0.2)	210 (6.9)	82.3 (7.4)	17.8 (7.4)	0.0 (0.0)
LPA	Manzanal	65.8 (3.5)	40.3 (2.5)	10.5 (0.7)	4.4 (0.2)	195 (3.3)	73.1 (8.4)	26.8 (8.4)	0.0 (0.0)
LPA	Cuajimoloyas	63.8 (3.2)	45.1 (2.0)	8.4 (1.5)	3.7 (0.2)	202 (6.9)	72.6 (7.0)	24.8 (7.0)	0.0 (0.0)
OOC	Nejapa	50.9 (1.6)	57.9 (3.6)	17.5 (0.6)	4.4 (0.2)	190 (8.9)	19.3 (7.4)	20.4 (5.8)	60.3 (4.1)
TEC	Jitotol	58.4 (3.0)	42.9 (1.7)	11.2 (1.2)	4.2 (0.1)	182 (4.1)	94.5 (2.1)	5.5 (2.1)	0.0 (0.0)
TEC	Piedrecitas	60.4 (3.8)	41.4 (1.7)	12.0 (0.5)	4.2 (0.2)	187 (3.9)	98.3 (1.1)	1.7 (1.1)	0.0 (0.0)
TEC	San Jose	56.1 (3.4)	41.8 (1.7)	10.7 (1.6)	4.1 (0.1)	183 (6.3)	93.9 (2.9)	5.3 (2.5)	0.0 (0.0)
TEC	R. Nuevo	67.2 (3.3)	47.7 (3.3)	11.8 (1.2)	4.1 (1.2)	178 (3.3)	93.6 (1.9)	6.4 (1.9)	0.0 (0.0)
TEC	Teopisco	55.4 (2.7)	49.7 (1.8)	10.5 (0.8)	4.1 (0.1)	183 (6.5)	98.6 (1.4)	1.4 (1.4)	0.0 (0.0)
TEC	Huixtan	63.7 (1.9)	46.8 (1.0)	13.6 (0.5)	3.8 (0.2)	166 (4.4)	91.2 (4.3)	8.8 (1.4)	0.0 (0.0)
TEC	Chanal	74.7 (2.6)	44.8 (1.8)	13.6 (1.2)	3.8 (0.2)	183 (3.7)	93.4 (1.6)	1.6 (1.6)	0.0 (0.0)
TEC	Chempil	60.1 (3.8)	48.2 (3.0)	12.1 (1.9)	4.3 (0.2)	177 (5.8)	91.6 (2.1)	8.2 (2.2)	0.0 (0.0)
TEC	Ocosingo	66.8 (3.7)	50.4 (2.4)	12.5 (2.0)	4.4 (0.2)	199 (6.8)	97.3 (1.8)	2.8 (1.8)	0.0 (0.0)
TEC	Napite	67.5 (3.2)	51.0 (2.4)	12.8 (1.0)	3.7 (0.1)	175 (5.7)	95.0 (3.4)	5.0 (3.4)	0.0 (0.0)

Appendix 1. *(Continued)*

Species	Provenance	Morphological characteristics							
		CLENG (mm)	CWIDT (mm)	PLENG (mm)	NUMFAS	NLENG (mm)	PMED (%)	PINT (%)	PSEP (%)
TEC	T. Negra	67.3 (6.8)	50.6 (4.7)	11.2 (0.6)	4.1 (0.1)	185 (5.7)	96.3 (2.5)	3.7 (2.5)	0.0 (0.0)
TEC	Montebello	51.0 (2.3)	45.4 (1.2)	14.4 (1.2)	3.9 (0.1)	189 (5.2)	88.6 (2.6)	9.8 (3.2)	0.0 (0.0)
TEC	Carrizal	58.3 (9.4)	46.8 (1.9)	12.4 (1.4)	4.1 (0.1)	185 (4.3)	93.2 (5.2)	1.6 (1.6)	0.0 (0.0)
TEC	Pachoc	53.8 (1.9)	43.5 (2.3)	9.0 (0.6)	4.8 (0.1)	170 (5.7)	84.3 (4.3)	15.6 (4.3)	0.0 (0.0)
TEC	San Jeronimo	60.3 (4.8)	46.3 (2.8)	11.1 (1.0)	4.4 (0.1)	191 (6.7)	92.3 (2.2)	2.2 (1.3)	4.5 (4.5)
TEC	San Vicente	56.0 (4.7)	43.9 (3.1)	12.3 (0.6)	4.3 (0.1)	185 (6.4)	81.5 (3.5)	10.9 (3.3)	4.0 (2.1)
TEC	San Lorenzo	52.9 (2.2)	41.8 (3.4)	11.5 (0.6)	4.3 (0.2)	196 (7.3)	83.3 (7.1)	10.0 (5.2)	1.2 (1.2)
TEC	S. Jose Pinula	53.5 (1.8)	41.6 (1.9)	14.4 (1.2)	4.3 (0.1)	197 (10.7)	94.1 (2.2)	2.8 (1.8)	0.0 (0.0)
TEC	La Soledad	64.5 (2.4)	43.1 (1.8)	15.0 (1.2)	4.3 (0.1)	197 (3.8)	84.0 (3.2)	13.5 (2.8)	3.2 (1.4)
TEC	Metapal	57.8 (4.2)	42.2 (4.1)	14.6 (1.1)	4.3 (0.1)	176 (6.7)	90.6 (4.3)	9.4 (4.3)	0.0 (0.0)
TEC	Las Trancas	59.2 (3.2)	45.9 (2.3)	16.3 (1.3)	4.5 (0.1)	161 (5.4)	88.5 (5.5)	11.5 (5.6)	0.0 (0.0)
TEC	Guajiquiro	62.8 (7.7)	50.0 (5.5)	14.0 (2.5)	4.5 (0.1)	163 (6.2)	93.8 (2.8)	6.2 (2.8)	0.0 (0.0)