PINUS PATULA SUBSPECIES *TECUNUMANII*: THE APPLICATION OF NUMERICAL TECHNIQUES TO SOME PROBLEMS OF ITS TAXONOMY

By P. S. McCARTER* and J. S. BIRKS*

SUMMARY

The problems of distinguishing *Pinus patula* Schiede and Deppe ssp. *tecunumanii* (Eguiluz and Perry) Styles from *P. oocarpa* Schiede in mixed natural stands in Central America prompted this taxonomic investigation which examines relationships within and between provenances of the two taxa. Orthodox taxonomic descriptions are shown to be unsatisfactory in aiding discrimination between them.

A pilot study was planned using 200 trees from five populations of 20 trees from each of the two taxa. Linear discriminant and canonical variable analyses of fifteen needle and cone morphological characters (variables) were carried out. Seven variables were found to contribute significantly to a discriminant function which identified trees as belonging to one or other of the two taxa with only 3% mis-classified. A second discriminant function which used only easily measurable (non-microscopic) variables was calculated; this separated the two taxa with the proportion mis-classified increasing to 9.5%.

Canonical variable analysis using the same variables as in the first discriminant function confirmed the presence of two classes (species) and showed that *P. patula* ssp. *tecunumanii* is a much more variable taxon than *P. oocarpa.*

Data from further provenances of disputed identity were then included in the analyses. These showed that the following provenances in the CFI International Provenance Trials of *P. oocarpa* are in fact *P. patula* ssp. *tecunumanii*: Mountain Pine Ridge, Belize; San Rafael, Yucul and Las Camelias, Nicaragua. Mexican provenances of *P. oocarpa* to which the varietal name *ochoterenae* Martínez is attached are also clearly classified as *P. patula* ssp. *tecunumanii.*

Finally analysis of data from two provenances of *P. patula* are presented. This suggests that the citation of the Tecun Umán Pine as being a subspecies of *P. patula* is correct.

RÉSUMÉ

Des analyses linéaires discriminantes et de variables canoniques employant des combinaisons différentes de caractéristiques morphologiques ont établi une distinction entre *P. oocarpa* Schiede et *P. patula* Schiede et Deppe spp. *tecunumanii* (Eguiluz et Perry) Styles. Les résultats démontrent que plusieurs provenances dans les Essais Internationaux du CFI sur les provenances de *P. oocarpa* sont en fait *P. patula* spp. *tecunumanii.* Celles-ci incluent les provenances de Mountain Pine Ridge (Belize) et de Yucul, San Rafael et Las Camelias (Nicaragua).

RESUMEN

Analisis discriminante lineal y analisis de variables canonicas con combinaciónes diferentes de caracteristicas morfológicos escogio entre *Pinus oocarpa* Schiede y *P. patula* Schiede and Deppe spp. *tecunumanii* (Eguiluz and Perry) Styles. Los resultados mostraron que algunas procedencias, entre ellas Mountain Pine Ridge, Belize; Yucul, San Rafael y Las Camelias, Nicaragua, en los ensayos internacionales de *P. oocarpa*, son realmente *P. patula* spp. *tecunumanii.*

*Department of Forestry, Oxford University, South Parks Road, Oxford, OX1 3RB, England.

Introduction and Taxonomic History

The investigation and collection of seed of known provenances of Central American pine species by Research Staff at the CFI and the results from its subsequent and continuing evaluation in International Provenance Trials have been widely reported (see *e.g.* Kemp, 1973; Greaves, 1980; Gibson, 1982; Stead, 1983). Over the last three years, attention has focussed on a comparatively little known taxon of the closed cone pine group (*sensu* Little and Critchfield, 1969; Barnes and Styles, 1983): *Pinus patula* Schiede and Deppe subspecies *tecunumanii* (Eguiluz and Perry) Styles.

This species was first described by Schwerdtfeger (1953) as *P. tecumumanii* Schwerdtfeger, but since he failed to provide a Latin diagnosis and to designate a holotype, both required by the International Code of Botanical Nomenclature (1983), this name is illegitimate. Other workers considered the taxon to be no more than a deviant form of *P. oocarpa* (Standley and Steyermark, 1958) or a variety of it, *P. oocarpa* var. *tecumumanii* (Aguilar, 1962; Mittak, 1977). Eguiluz and Perry (1983) studied Schwerdtfeger's pine in greater detail in Guatemala and concluded that it was a distinct species. Their specific name (with a slight change of spelling of the epithet) *P. tecunumanii* Eguiluz and Perry, is legitimate. More recently, Styles (1985) has presented evidence to support his long-held view that this taxon is a subspecies and a southerly extension of the natural range of *P. patula*. His citation, *P. patula* ssp. *tecunumanii*, has been used throughout this paper. A full botanical and ecological description of the subspecies can be found in the texts of Eguiluz and Perry (*op. cit.*) and of Styles (1985 and 1986).

Until about 1980, the taxon had been described from only a few sites in upland Guatemala. At around this time, however, it was becoming evident that several provenances of *P. oocarpa* in the International Provenance Trials were performing consistently better than all other provenances at almost every site (Greaves, 1982). Trees from these provenances could often be identified by simple observation of their growth, form and habit. They were reported to be very similar to *P. patula*, having the red flaky papery bark on the upper stem so typical of that species (Gibson, Barnes *pers. comm.*[1]).

It was thus postulated that some of the *P. oocarpa* provenances were in fact Schwerdtfeger's Tecun Umán pine *i.e. P. patula* ssp. *tecunumanii.*

The excellent growth and form of these provenances in trials prompted the intensive programme of exploration and seed collection of *P. patula* ssp. *tecunumanii* in its natural range with the result that the CFI now has seed, resin and botanical specimens from over twenty provenances.

The problem of the identification of *P. patula* ssp. *tecunumanii*

During the exploration and seed collection phases of this work there have been frequent problems with the field identification of the species, especially in distinguishing it from *P. oocarpa* (McCarter, 1984). The problem is not new. Stead (1981) has pointed out that the genus, as a whole, does not easily lend itself to traditional qualitative descriptions which would enable species to be keyed out accurately in terms of, for example, general needle or cone morphology. Even within a fairly limited area many characters are so extremely variable that the ranges of different species overlap considerably. The problem is acute when dealing with closely related species and even more so when there is a likelihood of hybridisation (see *e.g.* Styles *et al.*, 1982). Site quality also plays a role in confusing the situation (McCarter, 1985). *P. oocarpa* on its typical very poor, dry sites and *P. patula* ssp. *tecunumanii* on its more typical fertile moist sites do not present

[1]R. D. Barnes and G. L. Gibson, CFI, South Parks Road, Oxford, OX1 3RB.

identification problems. In mixed stands, however, on sites which are good for *P. oocarpa* and less than optimal for *P. patula* ssp. *tecunumanii* the two taxa can appear, even on close examination, confusingly similar. Occasionally the identity of a pure stand of one or the other can be uncertain.

Using traditional qualitative descriptions, the separation on morphological characters of the two taxa should be a straightforward matter. For example, *P. oocarpa* is reputedly a five-needled species, whilst *P. patula* ssp. *tecunumanii* is mainly four-needled (with a proportion of fascicles with three or five needles). The needles of *P. oocarpa* are described as broad and stiff, with scaly black sheaths whilst those of *P. patula* ssp. *tecunumanii* are slender and pendulous or spreading, with slender smooth sheaths. The bark of *P. oocarpa* is thick, greyish-black and plated; that of *P. patula* ssp. *tecunumanii* is reddish and flaky. Their cones are of different geometry: those of *P. oocarpa* are as broad as they are long, with a flattened base, compared with the narrowly conoidal *P. patula* ssp. *tecunumanii* cones which have a pointed apex and a rounded base (Styles, 1976 and 1985). Nevertheless, trees are often misidentified in the forest because these botanical characteristics are so extremely variable.

The one diagnostic character which is generally accepted as being almost invaribale, is the position of the resin canals in a cross-section of the needle. Almost all *P. oocarpa* needle sections show one or more septal resin canals, unlike almost all *P. patula* ssp. *tecunumanii* needle sections, which have medial resin canals. This characteristic is qualified because occasionally, a needle section of *P. oocarpa* will show no septal resin canals ($<3\%$), and also, much less frequently, a needle section of *P. patula* ssp. *tecunumanii* will have perhaps a single medial resin canal ($<0.2\%$) (McCarter, unpublished data).

Methods for separating the taxa

Given the problems of using these qualitative descriptions to separate the two taxa, it was decided that a numerical approach could be more useful. Such techniques have been successfully used to elucidate taxonomic problems within the genus *Pinus*. As a result of his multivariate study of the *P. chiapensis/P. monticola/P. strobus* group, Andresen (1966) was able to suggest that the former species, originally described as a variety of *P. strobus*, should be elevated to specific rank. The existence of hybrids between *P. caribaea* Mor. var. *hondurensis* (Senecl.) Barr. and Golf. and *P. oocarpa* in natural stands of the species in Honduras was demonstrated by use of canonical correlation analysis (Styles *et al.*, 1982). Stead (1981) made a revision to the *P. pseudostrobus* complex by using a combination of principal components analysis and canonical discriminant analysis.

Measuring the characteristics routinely used by pine taxonomists (about 20 in the above studies) is a lengthy (over two hours per specimen) and often tedious process — especially those which involve microscopic work. Commonsense and the experience of previous workers suggested that, depending on the problem under examination, a much smaller number of characteristics is all that is required to elucidate the problem.

It was thus decided to carry out a pilot study aimed at identifying the characters which in this particular case aided discrimination between *P. oocarpa* and *P. patula* ssp. *tecunumanii*.

Method

For the pilot study, 10 populations of 20 trees each were measured. These populations, together with basic site data are listed in Table 1. The characteristics measured are detailed in Table 2. The needle characteristics were assessed on mature needles, using ten separate fascicles from each tree and the cone characteristics on two fully opened cones. These

Table 1
Basic site data for populations used in pilot study

Population	Country	Computer code	Latitude (° North)	Longitude (° West)	Altitude (m)
P. patula ssp. *tecunumanii*					
Yucul,	Nicaragua	YUCUL	12°55′	85°47′	900
La Paz	Honduras	LAPAZ	14°19′	87°45′	1850
Culmi,	Honduras	CULMI	15°10′	85°20′	600
Villa Santa,	Honduras	VSTEC	14°11′	86°20′	900
Guajiquiro,	Honduras	GUAJI	14°11′	87°50′	2200
P. oocarpa					
San Juan,	Honduras	SANJU	14°24′	88°23′	1300
Villa Santa,	Honduras	VSOOC	14°12′	86°25′	900
La Lagunilla,	Guatemala	LAGUN	14°42′	89°57′	1600
Zamorano,	Honduras	ZAMOR	14°02′	87°03′	1350
Dipilto,	Nicaragua	DIPIL	13°43′	86°32′	1100

Table 2
Morphological characteristics assessed on all needle and cone specimens

Characteristic	Code
Length of needle (cm to nearest mm)	NLTH
Width of needle (mm × 40)	NWTH
Number of needles per fascicle	LVES
Length of sheath (mm to nearest mm)	SHTH
Number of stomatal lines on dorsal surface	SLDO
Number of stomatal lines on ventral surface	SLVE
Number of stomata per 5 mm line on dorsal surface	STOM
Number of marginal serrations per 5 mm	SERR
Number of resin canals (total)	RCAN
Number of septal resin canals	RCSP
Length of cone (cm to nearest mm)	CLTH
Width of cone at widest point (cm to nearest mm)	WTH1
Width of cone at right angles to WTH1 (cm to nearest mm)	WTH2
Width of umbo (mm to nearest 0.5 mm)	UMBO
Width of apophysis (mm to nearest 0.5 mm)	WAPO
Depth of apophysis (mm to nearest 0.5 mm)	DAPO
Length of peduncle (mm to nearest mm)	PEDL

Table 3

Provenance mean values for the needle characteristics

Prov.	NLTH	NWTH	LVES	SHTH	SLDO	SLVE	STOM	SERR	RCAN
LAPAZ	16.4	36.7	4.5	12.6	5.4	7.5	60.3	29.9	2.8
CULMI	18.4	37.0	4.1	10.7	5.7	7.2	54.1	26.3	2.5
VSTEC	18.6	38.0	4.5	13.5	5.8	8.4	54.3	27.6	1.3
YUCUL	17.5	38.6	4.1	13.1	5.3	7.2	52.6	23.1	2.2
GUAJI	16.1	38.2	4.5	14.0	5.9	7.9	58.8	28.1	2.7
SANJU	19.7	41.6	4.8	14.8	5.7	9.1	47.2	21.3	4.3
VSOOC	20.3	38.5	4.7	16.1	5.7	8.7	49.4	22.8	4.0
LAGUN	21.5	38.6	4.9	18.1	5.4	8.5	50.7	23.4	4.4
ZAMOR	21.2	40.3	4.9	17.6	5.5	8.9	45.6	19.9	3.8
DIPIL	20.0	41.8	4.8	16.0	6.5	9.7	47.0	22.0	4.8
S.E. (mean)	6.3	10.1	1.0	5.6	2.6	3.2	12.9	12.7	2.9

Provenance mean values for the cone characteristics

Prov.	CLTH	WTHM	WAPO	DAPO	UMBO	PEDL
LAPAZ	6.5	5.7	11.8	7.3	4.2	2.1
CULMI	5.7	5.5	11.3	7.5	3.7	2.1
VSTEC	6.0	5.7	10.5	6.8	3.6	2.1
YUCUL	5.0	4.9	9.6	6.5	3.7	1.7
GUAJI	6.8	5.2	11.2	7.4	3.8	1.8
SANJU	5.6	5.9	11.0	7.7	3.9	2.3
VSOOC	5.9	5.9	10.7	7.1	3.7	2.4
LAGUN	6.2	6.6	11.8	8.2	4.3	2.1
ZAMOR	6.1	6.6	11.7	7.8	3.7	2.5
DIPIL	6.2	6.0	11.7	7.7	4.2	2.4
S.E. (mean)	3.0	2.3	4.1	3.1	1.4	1.2

are taken routinely from trees from which seed is collected. Tree mean values are used in the analyses as this study was concerned with between tree variation, not within tree variation.

Table 3 shows for each provenance the mean values of the 15 characteristics of interest (to be referred to as variables). The mean value of the two perpendicular cone widths (WTHM) was used because, being highly correlated there was no advantage in using them both. Nor was there any evidence of asymmetry in the cones.

Table 4
Analyses of Variance

Source	d.f.
between provenances	9
between species	1
within species	8
residual	190
Total	199

Mean Sum of Squares and significance level of variance ratjo test

NLTH	NWTH	LVES	SHTH	SLDO
67.6***	62.0***	1.8***	102.5***	2.2**
467.9***	306.0***	10.1***	658.8***	0.6NS
17.6***	31.5***	0.7***	33.0***	2.4**
4.4	10.6	0.1	3.8	0.7

SLVE	STOM	SERR	RCAN	CLTH
13.9***	483.2***	199.7***	25.4***	5.03***
88.2***	3186.4***	1213.8***	186.4***	0.04NS
4.6***	145.2***	72.9***	5.2***	5.65***
1.1	17.7	17.1	0.9	0.98

WTHM	WAPO	DAPO	UMBO	PEDL
5.4***	10.1***	4.8***	1.38***	1.24***
28.6***	10.1***	15.5***	1.17***	6.04***
2.6***	10.1***	3.5***	1.40***	0.64***
0.6	1.8	1.0	0.20	0.15

***$P<.001$ **$.001<P<.01$ *$.01<P<.05$ NS not significant

The multivariate method of analysis selected was the linear discriminant function. A criterion, independent of the measured characteristics, is used to separate the members of the sample into one of two classes. Here the presence or absence of septal resin canals was used to identify a tree as belonging to *P. patula* ssp. *tecunumanii* or *P. oocarpa*. Five populations were *P. oocarpa* and five, *P. patula* ssp. *tecunumanii* (*i.e.* septal resin canals = *P. oocarpa*). Univariate analyses of variance showed highly significant differences both between the two species and between provenances within each species for most variables (Table 4). The discriminant function attempts to reproduce this allocation using the value of Y, a linear combination of some or all of the variables (in Table 2) measured on each member of the sample ($X_1, X_2 \ldots X_{15}$)

$$Y = a_o + a_1X_1 + a_2X_2 + \ldots a_{15}X_{15}$$

In order to discriminate clearly between the classes it is necessary that the mean values of Y for each class are well separated compared with the variation of Y within the classes. The discriminant function is calculated by maximising the ratio of the difference in Y between the classes to the variance of Y within the classes. The constant a_0 is here defined so that the overall mean of Y is O. The rule for allocating individuals to the classes is:

if Y>O individual belongs to class 1
if Y<O individual belongs to class 2

Because the variables were the means of several samples from the same tree, they were regarded as continuous and as having an approximately multivariate normal distribution. There were no missing values.

The objective was to find a discriminant function with a high probability of correctly predicting the species to which a tree belongs, and to identify the variables that made a significant contribution to the discrimination. A further objective was to find a discriminant function that could be used in the forest to help identify a tree. This function would be based on variables that are easily measured in the field *viz.* NLTH, LVES, SHTH, CLTH, WTHM and PEDL. It would not be the optimal discriminant function, but hopefully would identify a tree with a high probability of being correct.

A discriminant function was calculated using the 15 variables; nine variables did not make a significant contribution. Table 5 shows the t-test for the contribution of each variable when the other 14 variables were in the discriminant function.

Table 5
t-values

	Analysis			
Variable	1	2	3	4
NLTH	−1.7NS	−1.4NS		−3.4**
NWTH	−1.4NS			
LVES	−3.0**	−4.0***	−3.5***	−4.4***
SHTH	−4.0***	−3.6***	−5.6***	−4.4***
SLDO	1.0NS			
SLVE	−0.4NS			
STOM	4.1***	6.0***	5.9***	
SERR	−0.1NS			
RCAN	−7.0***	−7.5***	−8.7***	
CLTH	3.4***	3.4***	4.4***	4.9***
WTHM	−2.4**	−2.3*	−2.8**	−4.3***
WAPO	1.6NS			
DAPO	−1.3NS			
UMBO	−0.8NS			
PEDL	−3.2**	−1.8NS	−3.6***	−2.1**

Different combinations of variables produce different linear discriminant functions. The t-value tests the significance of the contribution of each variable to these functions. Analyses 1 and 2 refer to preliminary investigations, analyses 3 and 4 to discriminant functions I and II respectively.

***P<.001 **.001<P<.01 *.01<P<.05 NS not significant

These results show that all the easily measured variables have significant t-values except for NLTH. However, the contribution of a variable to a discriminant function will alter when the calculation is done with a different set of variables. Therefore it is not always necessary to drop a non-significant variable. The discriminant function was recalculated with eight variables, NLTH, LVES, SHTH, STOM, RCAN, CLTH, WTHM and PEDL. The t-values are shown in column 2 of Table 5. NLTH alone is still not significant, and was omitted from the next calculation (column 3).

The discriminant function is:

$$Y = 4.91 - 0.83\,LVES - 0.2\,SHTH + 0.10\,STOM - 0.61\,RCAN + 0.50\,CLTH - 0.42\,WTHM - 0.74\,PEDL \quad \ldots\ldots \text{I}$$

If $Y > 1$ classify the tree as *P. patula* ssp. *tecunumanii*
If $Y < 1$ classify the tree as *P. oocarpa*

Discriminant function I is successful in allocating the trees to the correct species. The number of trees mis-allocated is six (see Table 6). These are the same trees mis-allocated using the discriminant function with 15 variables. The provenances to which the mis-allocated trees belong are shown in Table 7.

The proportion of individuals mis-allocated is smallest for the actual sample used to calculate the discriminant function I. Other samples, identified with this particular discriminant function will generally have a slightly larger proportion of mis-allocated individuals.

Table 6
Allocation to the two taxon by linear discriminant function

Linear discriminant function I

		Final taxon TEC	OOC	Total
Original taxon	TEC	96	3	99
	OOC	3	97	100
	Total	99	100	199

Proportion mis-allocated = 3%

Linear discriminant function II

		Final taxon TEC	OOC	Total
Original taxon	TEC	90	9	99
	OOC	10	90	100
	Total	100	99	199

Proportion mis-allocated = 9.5%

Table 7
The distribution by provenance of trees mis-allocated by the different discriminant functions

	LAPAZ	CULMI	VSTEC	YUCUL	GUAJI	SANJU	VSOOC	LAGUN	ZAMOR	DIPIL	Total
I	1	1	0	0	1	2	1	0	0	0	6
II	1	1	7	0	0	3	3	0	0	4	19

Table 8
The results of the canonical variables analyses

(a) variables used: LVES, SHTH, STOM, RCAN, CLTH, WTHM and PEDL

	Constant	LVES	SHTH	STOM	RCAN	CLTH	WTHM	PEDL
First canonical variable	3.86	−0.64	−0.26	+0.11	−0.47	+0.63	−0.63	−0.71
Second canonical variable	−16.64	+1.90	+0.13	+0.11	+0.24	+0.89	−0.83	−0.44

Provenance mean values of the first two canonical variables

	LAPAZ	CULMI	VSTEC	YUCUL	GUAJI	SANJU	VSOOC	LAGUN	ZAMOR	DIPIL
First canonical variable	2.20	1.95	1.58	1.60	2.33	−1.56	−1.39	−2.11	−2.60	−1.88
Second canonical variable	1.05	−1.44	−0.43	−1.26	1.75	−0.38	0.05	0.73	−0.29	0.27

Mean values of the first two canonical variables for samples from provenances of disputed identity

	MOUNTAIN PINE RIDGE	SAN RAFAEL	LAS CAMELIAS
First canonical variable	1.90	1.24	1.43
Second canonical variable	−2.60	−0.84	0.20

(b) variables used: NLTH, LVES, SHTH, RCAN, CLTH and WTHM

	Constant	NLTH	LVES	SHTH	RCAN	CLTH	WTHM
First canonical variable	13.69	−0.15	−1.10	−0.23	−0.46	+0.69	−0.87
Second canonical variable	−3.08	−0.25	+1.27	+0.16	+0.43	+1.10	−1.42

Provenance mean values of the first two canonical variables

	LAPAZ	CULMI	VSTEC	YUCUL	GUAJI	SANJU	VSOOC	LAGUN	ZAMOR	DIPIL
First canonical variable	1.58	1.96	1.33	1.75	1.95	−1.13	−1.20	−2.57	−2.16	−1.41
Second canonical variable	0.81	−1.31	−0.95	−0.78	2.00	−0.01	0.07	−0.12	−0.43	0.76

Mean values of the first two canonical variables for samples from other provenances

	MOUNTAIN PINE RIDGE	SAN RAFAEL	LAS CAMELIAS	JUQUILA	LLANO DE FLORES	XOXOCOTLA
First canonical variable	2.55	1.69	1.37	2.23	3.37	2.76
Second canonical variable	−1.75	−0.47	0.34	1.24	0.48	−0.46

A canonical variables analysis was carried out using the seven variables, LVES, SHTH, STOM, RCAN, CLTH, WTHM and PEDL, and treating the ten provenances as ten classes. This was to investigate the relationship between the provenances. Canonical variables are linear combinations of the original variables that maximise the variation between classes relative to the variation within classes. The first canonical variable shows the maximum ratio of between to within class variation. Subsequent canonical variables must be uncorrelated with previous ones. The discriminant analysis is a special case of

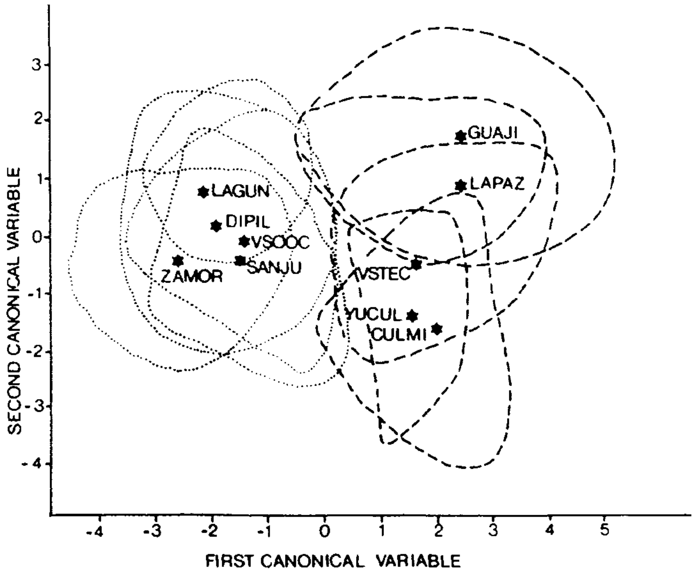

Diagram 1. Plot of canonical variables showing the mean and range of individual trees from each of the ten provenances used in the Pilot Study. Variables used in this analysis were: LVES, SHTH, STOM, RCAN, CLTH, WTHM and PEDL. (........ *P. oocarpa*; -------- *P. patula* ssp. *tecunumanii*).

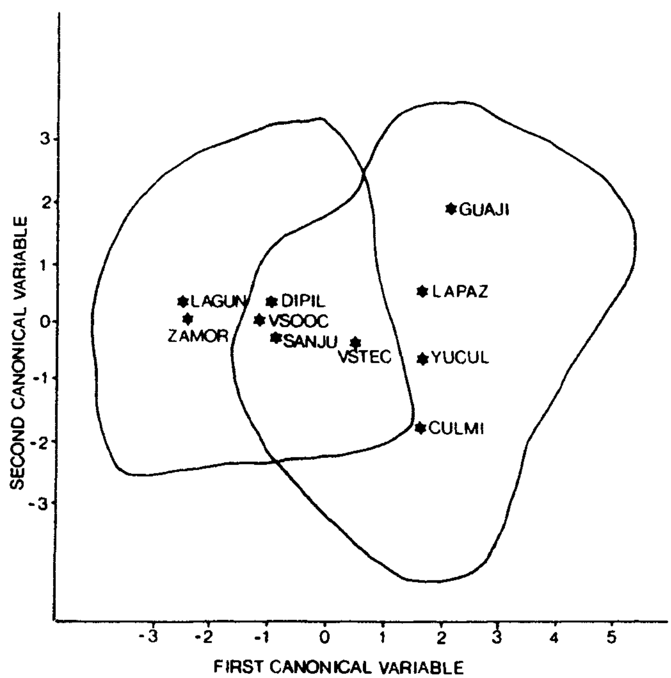

Diagram 2. Plot of canonical variables showing provenance mean values and the ranges of the two taxa. Variables used were: NLTH, LVES, SHTH, CLTH, WTHM and PEDL.

canonical variables analysis when there are only two classes and therefore only one canonical variable, which is the linear discriminant function.

The first canonical variable (Table 8) is very similar to the discriminant function and separates the ten provenances into the two taxa. This confirms that the original criterion for classifying a tree is the correct one.

Diagram 1 is a plot of these canonical variables, showing the mean and the spread of the individual trees for each provenance. There are significant differences between all pairs of provenances except for the following, all of which are *P. oocarpa*:

SANJU-VSOOC, SANJU-DIPIL and VSOOC-DIPIL

All five provenances of *P. oocarpa* are close together and the points for individual trees overlap considerably. The second canonical variable divides the *P. patula* ssp. *tecunumanii* provenances into two groups, VSTEC, YUCUL, CULMI and GUAJI, LAPAZ. This division bears a relationship to the altitudes of the provenances which are given in Table 1. The measurement of seven characteristics (LVES, SHTH, STOM, RCAN, CLTH, WTHM, PEDL) has elucidated the relationships between the original ten provenances.

The other aim of the study was to classify a tree as *P. oocarpa* or *P. patula* ssp. *tecunumanii* using only the six variables NLTH, LVES, SHTH, CLTH, WTHM and PEDL.

The discriminant function II, was calculated using these six variables; all made a significant contribution (Table 5).

$$Y = 13.37 - 0.16\,\mathrm{NLTH} - 1.07\,\mathrm{LVES} - 0.24\,\mathrm{SHTH} + 0.59\,\mathrm{CLTH} - 0.68\,\mathrm{WTHM} - 0.76\,\mathrm{PEDL} \quad \ldots\ldots\ldots\ldots\ldots \text{II}$$

If $Y > 1$ classify the tree as *P. patula* ssp. *tecunumanii*

If $Y < 1$ classify the tree as *P. oocarpa*

The proportion mis-allocated was 9.5%. These are shown in Table 7. A canonical variables analysis was also calculated using these six variables. The plot of the first two canonical variables (Diagram 2) is similar to Diagram 1. The ranges of the individual trees from the two species overlap to a greater extent than in Diagram 1. There are significant differences between all pairs of provenances except for the same three pairs as previously.

This function allows one to make a reasonably accurate attempt at identifying a specimen using easily measured characteristics.

Other provenances of disputed identity

Having demonstrated that the two taxa, *P. oocarpa* and *P. patula* ssp. *tecunumanii* could be satisfactorily separated by the first discriminant function and canonical variable analysis, we next looked at several other provenances of disputed identity.

Greaves (1982) had singled out five provenances in the International Provenance Trials of *P. oocarpa* as showing exceptional promise in terms of vigour, and stem and crown form. One of these was Yucul, which we have already identified as being *P. patula* ssp. *tecunumanii*. The others are: Las Camelias, San Rafael, Mountain Pine Ridge and Jitotol [Jitotil, *sic*].

The provenances of Las Camelias and San Rafael, like Yucul are found in north and central Nicaragua; the sites and phenotype of the trees are very similar to Yucul, and we were expecting them to be identified as the Tecun Umán Pine. Styles (1985) has already stated that they are.

The identity of the provenance from Mountain Pine Ridge, Belize has always been a great deal more uncertain. Hunt (1964) and Lamb (1966) refer to it as *P. oocarpa* var. *ochoterenae* Martínez, whilst Styles (1976) considered it to be typical *P. oocarpa*

Table 9
Basic site data for further provenances examined

Provenance	Country	Latitude (° North)	Longitude (° West)	Altitude (m)
P. patula ssp. *tecunumanii*/*P. oocarpa* var. *ochoterenae*				
Las Camelias,	Nicaragua	13°46′	86°18′	900
San Rafael,	Nicaragua	13°14′	86°08′	1200
Mountain Pine Ridge,	Belize	17°00′	88°55′	700
Jitotol, Chiapas,	Mexico	17°05′	92°30′	1650
Juquila, Oaxaca,	Mexico	16°15′	97°17′	2100
P. patula var. *longepedunculata*				
Llano de Flores, Oaxaca,	Mexico	17°27′	96°29′	2800
P. patula ssp. *patula*				
Xoxocotla, Veracruz,	Mexico	18°40′	97°08′	2550

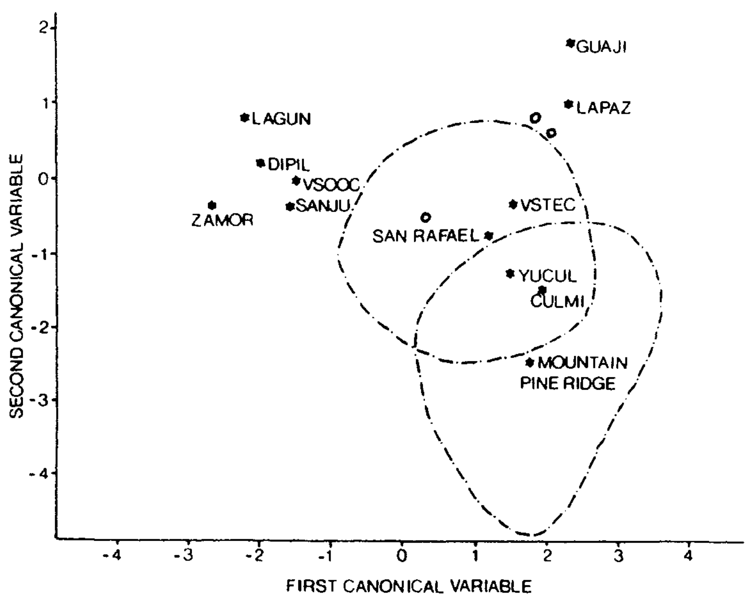

Diagram 3. The canonical variables plot is the same as Diagram 1. Also included are the mean values and ranges of two provenances of disputed identity, Mountain Pine Ridge and San Rafael. The individual tree values for the three available trees from a third provenance, Las Camelias, are also shown. (∘).

as indeed does Dvorak (1985). Wolffsohn (*pers. comm.*[2]) considered that the trees were certainly not typical *P. oocarpa*, and suggested that they were similar, ecologically and silviculturally to the Culmi provenance of '*P. oocarpa*' of eastern Honduras. This we have already demonstrated to be *P. patula* ssp. *tecunumanii*. For Barnes and Gibson (*pers. comm.*[3]), the Mountain Pine Ridge progeny in the International Trials were the most similar to *P. patula* in terms of gross morphology, although they considered it to be quite different from Yucul, in general habit. The results from our analyses would thus be of considerable interest.

No botanical material was available for the Jitotol provenance from Chiapas, Mexico. This is termed *P. oocarpa* var. *ochoterenae* by Mexican foresters and others, although there is also undoubtedly typical *P. oocarpa* at this site. Specimens were available however from another Mexican provenance: Juquila, Oaxaca, which is similarly termed *P. oocarpa*

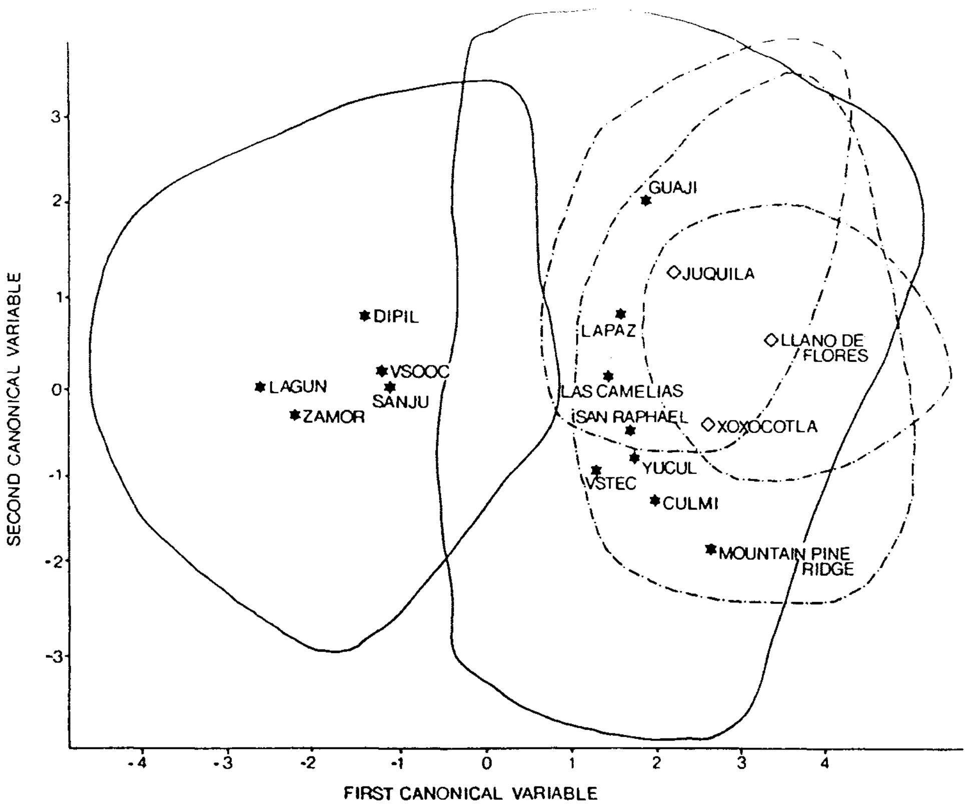

Diagram 4. Plot of canonical variables of all provenances examined. Variables used were: NLTH, SHTH, LVES, RCAN, CLTH and WTHM. This shows the relationships of all the taxa examined to each other. The solid lines delimit the two main taxa, *P. oocarpa* to the left, *P. patula* ssp. *tecunumanii* to the right, and the broken lines (left to right), *P. oocarpa* var. *ochoterenae*, *P. patula* ssp. *patula* and *P. patula* var. *longepedunculata*.

2 A. L. A. Wolffsohn, Escuela Nacional de Ciencias Forestales, Apartado 2, Siguatepeque, Honduras.

3 R. D. Barnes and G. L. Gibson, CFI, South Parks Road, Oxford, OX1 3RB.

var. *ochoterenae.* (Basic site data for all further provenances examined are detailed in Table 9).

The samples from Las Camelias (3 trees), San Rafael (21 trees) and Mountain Pine Ridge (20 trees) were measured. Both discriminant functions I and II classified all the trees as *P. patula* ssp. *tecunumanii.* When the provenance mean values of the canonical variables are plotted (Diagram 3) they are found to lie close to the VSTEC, CULMI and YUCUL group. The sample from Juquila, OAXACA (20 trees) was also clearly identified as *P. patula* ssp. *tecunumanii*, lying between LAPAZ and GUAJI in the plot of the first two canonical variables.

Finally, material was available from two populations of *P. patula*: one typical *P. patula* (20 trees), the other, its variety *longepedunculata* Loock (also 20 trees). We have included plots of the provenance mean values of the canonical variables and of the limits of their variation in Diagram 4. This analysis used the following characteristics: NLTH, SHTH, LVES, RCAN, CLTH and WTHM. (Typical *P. patula* cones are largely sessile and the character PEDL was dropped).

The relationship of our provenances of the Tecun Umán Pine to those populations of *P. patula* would seem to indicate to us that the status which Styles (1985) has suggested for the taxa is correct (*i.e.* its relationship to *P. patula*).

Discussion

The basic problem we have tackled in this study had been one of classification. This has largely been a matter of placing a tree (or a population) into one of two classes: *P. oocarpa* or *P. patula* ssp. *tecunumanii.* That the name of this second class is still a matter of debate does not concern us. Of course there may be more than two classes present: see for example the canonical variable analysis of our five pilot Tecun Uman pine populations. This has demonstrated that two groups are identifiable: GUAJI and LAPAZ, and VSTEC, YUCUL and CULMI. Whether intraspecific variation can account for these differences or not, we leave in the hands of taxonomists.

We have shown that the continuities in the variation patterns of many different morphological characters within the two taxa under study are such that orthodox taxonomic methods of observing phenotype and hence distinguishing genotype are largely unsatisfactory. For those unfamiliar with the complexities and ranges of variation in natural stands of Central American Pines, the evidence that several experienced field foresters, over the period of almost a decade, unknowingly collected seed of *P. patula* ssp. *tecunumanii* along with, or at times, instead of *P. oocarpa* is surely a good indication of the difficulties faced. Nor should the fact that in the trials the two taxa are readily distinguishable be taken as any indication of poor original observation: variation of gross morphological characters of plants grown in exotic locations can and often does bear little resemblance to the variation found in their natural habitats. Rather it underlines the value of such trials in elucidating taxonomic problems.

We have touched briefly on the problem of *P. oocarpa* var. *ochoterenae.* Described by Martínez (1940), from Chiapas, Mexico, the results from our study — although somewhat limited — indicate that this is probably synonymous with *P. patula* ssp. *tecunumanii*, as first described by Schwerdtfeger from Guatemala. Interestingly, Styles (1976) before the present interest in the Tecun Umán Pine suggested that *P. oocarpa* var. *ochoterenae* should be referred to as *P. patula* var. *longepedunculata.*

The entire problem will be much more clearly illuminated when data from the remaining 10–12 populations of this taxon which are available at CFI are included in the analysis.

Conclusions

On the basis of this study the following provenances in the CFI International Provenance Trials of *P. oocarpa* should henceforth be referred to as *P. patula* ssp. *tecunumanii*:

Yucul, Nicaragua
Las Camelias, Nicaragua
San Rafael, Nicaragua
Mountain Pine Ridge, Belize.

It is also likely that the Jitotol provenance from Mexico referred to as *P. oocarpa* var. *ochoterenae* is also *P. patula* ssp. *tecunumanii* although unlike the other four provenances, typical *P. oocarpa* is found in intimate mixture with it, and early seed collections from this site are likely to have included seed from both taxa.

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