A STUDY OF VARIATION AND TAXONOMY OF THE *PINUS PSEUDOSTROBUS* COMPLEX

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SUMMARY

Taxonomic problems have caused some confusion in the International Provenance Trials of the *Pinus pseudostrobus* complex organized by the Commonwealth Forestry Institute (CFI). A study of variation and taxonomy of the Pseudostrobus group was recently completed at the CFI and this paper summarizes the work done. Principal Components Analysis and Canonical Discriminant Analysis were used to examine data from range wide collections. It was discovered that there are three well defined species in the group *P. pseudostrobus* Lindl., *P. maximinoi* H.E. Moore (the correct name for *P. tenuifolia* Benth.) and *P. douglasiana* Martinez. The very variable *P.pseudostrobus* was found to have two infraspecific taxa *P. pseudostrobus* subsp. *apulcensis* (Lindl.) Stead and *P. pseudostrobus* var. *oaxacana* (Mirov) Harrison. Analysis of voucher specimens and results from a CFI trial in Honduras indicate that seed lots of two species, *P. pseudostrobus* and *P. maximinoi*, have been included in the trials. The correct names for all the seed lots included in trials are given in a table.

RESUMEN

Problemas taxonómicos han causado una cierta confusión en los ensayos internacionales de procedencia del complejo *Pinus pseudostrobus*, organizados por el Instituto Forestal de la Mancomunidad (CFI). Un estudio de variación y taxonomia del grupo Pseudostrobus fue recién completado en el Instituto, y este papel presenta un resumen del trabajo hecho. Se utilizarón análysis de componentes principales y análysis discriminante canonical en un examen de datos procedentes de muestras colectadas en la distribución geográfica entera. Se descubrió que existen tres especies bien definidas en el grupo; *P. pseudostrobus* Lindl., *P. maximinoi* H.E. Moore (el nombre correcto de *P. tenuifolia* Benth.) y *P. douglasiana* Martinez. Se encontró que el muy variable *P. pseudostrobus* tiene dos taxa infra-especificas, *P. pseudostrobus subespecie acapulcensis* (Lindl.) Stead y *P. pseudostrobus var. oaxacana* (Mirov) Harrison. Análysis de muestras de referencia y resultados de un ensayo CFI en Honduras indican que se han incluido en los ensayos lotes de semillas de dos especies, *P. pseudostrobus* y *P. maximinoi*. Se dan en un cuadro los nombres correctos de todos los lotes de semillas incluidos en ensayos.

Introduction

The Commonwealth Forestry Institute (CFI) has for more than 15 years been coordinating the exploration, collection and evaluation of Central American Pines. The work has concentrated on *Pinus caribaea* Mor. and *P. oocarpa* Schiede and more recently a complex designated *P. pseudostrobus* Lindl. (in which *P. tenuifolia* Benth.) has been included. The details of the project have been reported previously in this Review (Kemp, 1973; Greaves 1981). (1981)).

A study of the variation and taxonomy of the *P. pseudostrobus* complex has recently been completed at the CFI. The results will be recorded in detail in two

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papers dealing with the methods of analysis employed and the taxonomic conclusions respectively. The purpose of this article is to communicate the results of the study in outline and in particular the name changes which affect the provenance seed collections included in the CFI trials.

Taxonomic Background

The views of Martinez (1945, 1948) were taken as a working taxonomy at the beginning of the study. He refers to the Pseudostrobus group which contains three species, *Pinus pseudostrobus* Lindl., *P. tenuifolia* Benth. and *P. douglasiana* Martinez. *P. pseudostrobus* is a very varible species and various attempts have been made to clarify that variation. Martinez accepts the following infraspecific categories:–

P. pseudostrobus var. *oaxacana* Martinez
P. pseudostrobus var. *apulcensis* (Lindl.) Martinez
P. pseudostrobus var. *coatepecensis* Martinez
P. pseudostrobus var. *estevezii* Martinez
P. pseudostrobus f. *protuberans* (Roezl) Martinez

A map of the distribution of this group is shown in Figure 1.

The taxonomic picture is not completely straightforward. In a publication on the geographic distribution of pines by Critchfield and Little (1966), *P. pseudostrobus* and *P. tenuifolia* are treated as synonymous, and referred to as "*P. pseudostrobus*, including the doubtfully distinct *P. tenuifolia* Benth . . .". In the same publication *P. douglasiana* is mapped together with *P. pseudostrobus*. Critchfield (pers. comm.) visited Michoacán, Mexico where *P. pseudostrobus* (including *P. tenuifolia*) and *P. douglasiana* occur together, and he was unable

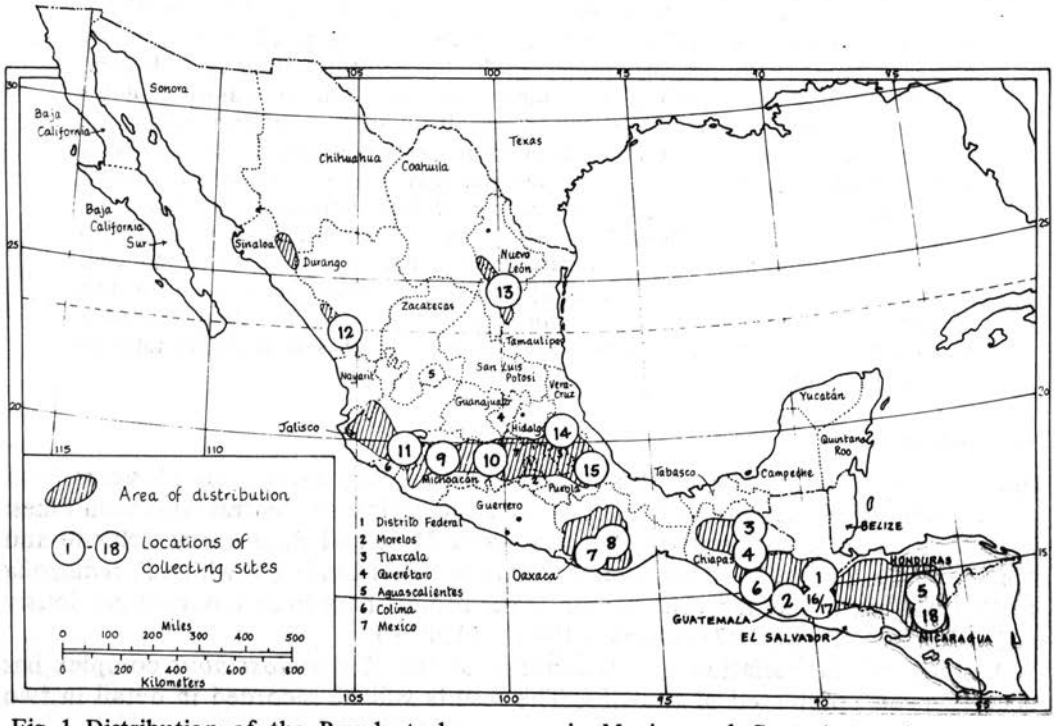


Fig. 1 Distribution of the Pseudostrobus group in Mexico and Central America. (Adapted from Critchfield and Little (1966).)

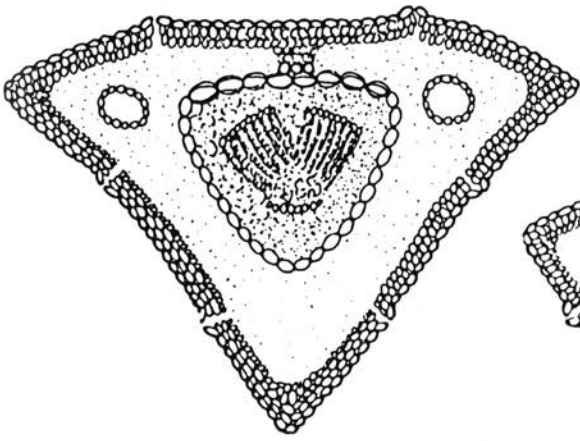


Fig. 2(a)

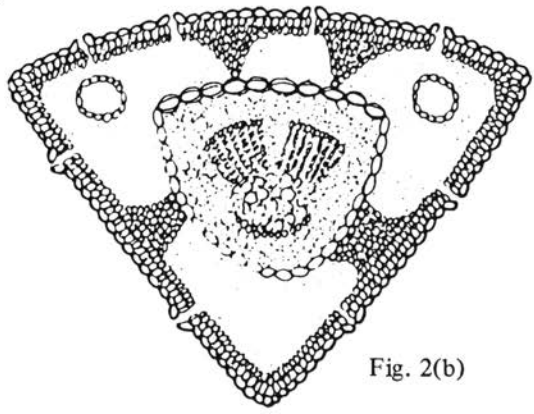


Fig. 2(b)

Fig. 2 (a) Needle section of *P. maximinoi* from Ocxingo, Chiapas, Mexico (Stead and Styles 324) showing one intrusion. Magnification is about 90.
(b) Needle section of *P. douglasiana* from Urua an, Michoacan, Mexico (Stead and Styles 549) showing four intrusions. Magnification is about 80.

to make definite identifications. In some areas of forest he was unsure whether there were three separate taxa present, or one very variable taxon. This view is summarized in Coyne and Critchfield (1974).

In Central America some investigators have treated *P. pseudostrobus* and *P. tenuifolia* as separate species (Schwerdtfeger (1953), Aguilar (1961)) whilst others have considered them to be synonymous and referred to them using the older name *i.e. P. pseudostrobus* (Standley and Steyermark (1958), Molina (1964)).

The CFI adopted the designation *P. pseudostrobus* (including *P. tenuifolia*) to describe the material used in the trial programme. The trials were organized in cooperation with the Instituto Nacional de Investigaciones Forestales (INIF), Mexico who follow the work of Martinez, and accept the three separate species in the Pseudostrobus group. Cooperation between the CFI and INIF required a standardized taxonomy and this study was initiated to solve the various problems involved.

Analyses and Conclusions

Complex patterns of variation are found in the genus *Pinus* and a numerical approach was adopted in an attempt to clarify the patterns found in the Pseudostrobus group. Population collections of approximately 25 trees each were made at 18 different sites throughout the range, and the material was assessed for 20 characters of the gross morphology, micromorphology and internal needle anatomy. These data were analysed using a combination of Principal Components Analysis (PCA) and Canonical Discriminants Analysis (CDA). PCA was used to demonstrate patterns of variation and suggest possible groupings of individuals into taxa. CDA was used to examine the relationship between groups, the most suitable characters

for separating groups, and the success with which groups had been formed.

The analyses revealed that the three species in the Pseudostrobus group can be distinguished fairly easily if a large range of characters is considered, particularly characters of the internal anatomy of the needles (see Figure 2).

It was found that in the southern part of the range of the group, southern Mexico and Central America, only *P. pseudostrobus* and *P. tenuifolia* are found, and that these two can be quite clearly identified. Confusion existed in the north-western part of the range where it was found that *P. pseudostrobus* and *P. douglasiana* grow in close association, and resemble each other in field characters. Furthermore, *P. pseudostrobus* in this part of the range looks very like *P. tenuifolia* in overall morphology.

The confusion found in the field can be resolved by a close examination of sets of characters only observable in the laboratory. Particularly it was found that the intrusions of the leaf hypoderm across the chlorenchyma to the endoderm, is a good character for distinguishing *P. tenuifolia* and *P. douglasiana* from *P. pseudostrobus* (see Figure 2). This character is variable within *P. tenuifolia*, as described by Shaw (1909), but PCA revealed a constant clinal pattern of increasing frequency of intrusions, moving from the southern part of the range to the north. Typically in Honduras and Nicaragua intrusions are infrequent, averaging less than one per needle, in southern Mexico and Guatemala needles have an average of one or two intrusions per needle, and further north, *e.g.* Michoacán, Mexico, an average of three intrusions per needle. Thus in the north-western part of the range where *P. pseudostrobus* often resembles *P. tenuifolia*, identification can be made fairly accurately on the presence or absence of intrusions.

It was found that *P. douglasiana* does not have more intrusions than *P. tenuifolia* as was suggested by Martinez, at least in that part of their ranges where they overlap. Both species here have typically three intrusions per needle. They can be distinguished, however, on the basis of the longer, coarser needles and wider, more robust cones of *P. douglasiana*.

If *P. tenuifolia* is accepted as a separate species then a different name must be used. H.E. Moore (1966) pointed out that the name *P. tenuifolia* used by Bentham in 1842, is a later homonym and is therefore illegitimate. The binomial *P. tenuifolia* had already been published in 1796 by Salisbury (actually used to describe the well known *P. strobus* L.). Moore proposed the name *P. maximinoi* to describe *P. tenuifolia* Benth. in recognition of the contribution by Prof. Maximino Martinez to the taxonomy of Mexican pines.

The same methods of analysis were used to examine patterns of variation within *P. pseudostrobus*. A PCA of data from specimens throughout the range of *P. pseudostrobus* revealed no clear cut divisions within it. On the basis of this analysis it was decided that there were no taxonomic groupings within *P. pseudostrobus* worthy of specific rank.

One sub-group, comprised of most of the specimens representing *P. pseudostrobus* var. *apulcensis*, *P. pseudostrobus* var. *estevezii* and *P. pseudostrobus* var. *coatepecensis*, was partially separated out and proved to have a separate identity when tested using CDA. This group is well defined geographically and ecologically. It is restricted to north-eastern Mexico where it grows on drier sites with sparse associated vegetation. It has been given the rank of subspecies and should be called *P. pseudostrobus* subsp. *apulcensis* (Lindl.) Stead.

Numerous individuals included in the PCA had been labelled at collection *P. pseudostrobus* var. *oaxacana*. These did not group together in the analysis nor did they show any distinct geographical or ecological identity. Despite the

conspicuous nature of the apophysis which characterizes this taxon it is only worthy of varietal rank.

Material of *P. pseudostrobus* f. *protuberans* was examined and found to be typical of *P. pseudostrobus* (*P. pseudostrobus* subsp. *pseudostrobus*).

Therefore on the basis of the results of this study the taxa within the Pseudostrobus group are as follows:–

P. pseudostrobus Lindl.
  P. pseudostrobus subsp. *apulcensis* (Lindl.) Stead
  P. pseudostrobus var. *oaxacana* (Mirov) Harrison
P. maximinoi H.E. Moore
P. douglasiana Martinez

Material collected for the study and taken on loan from several herbaria was used to prepare accurate distribution maps. (See Figs. 3, 4, 5 and 6).

CFI International Provenance Trials

The species of the Pseudostrobus group were amongst the first to be tested as exotics. Various trials and plantation projects indicated their potential and the possible rewards from selection and breeding work. This information is best summarized by Poynton (1979). Seed collections were started by the CFI in the early 1970's in Central America and at about the same time by INIF in Mexico. An agreement was made that there should be a joint CFI/INIF programme for distribution of seed for trials. INIF took charge of the distribution of seed to

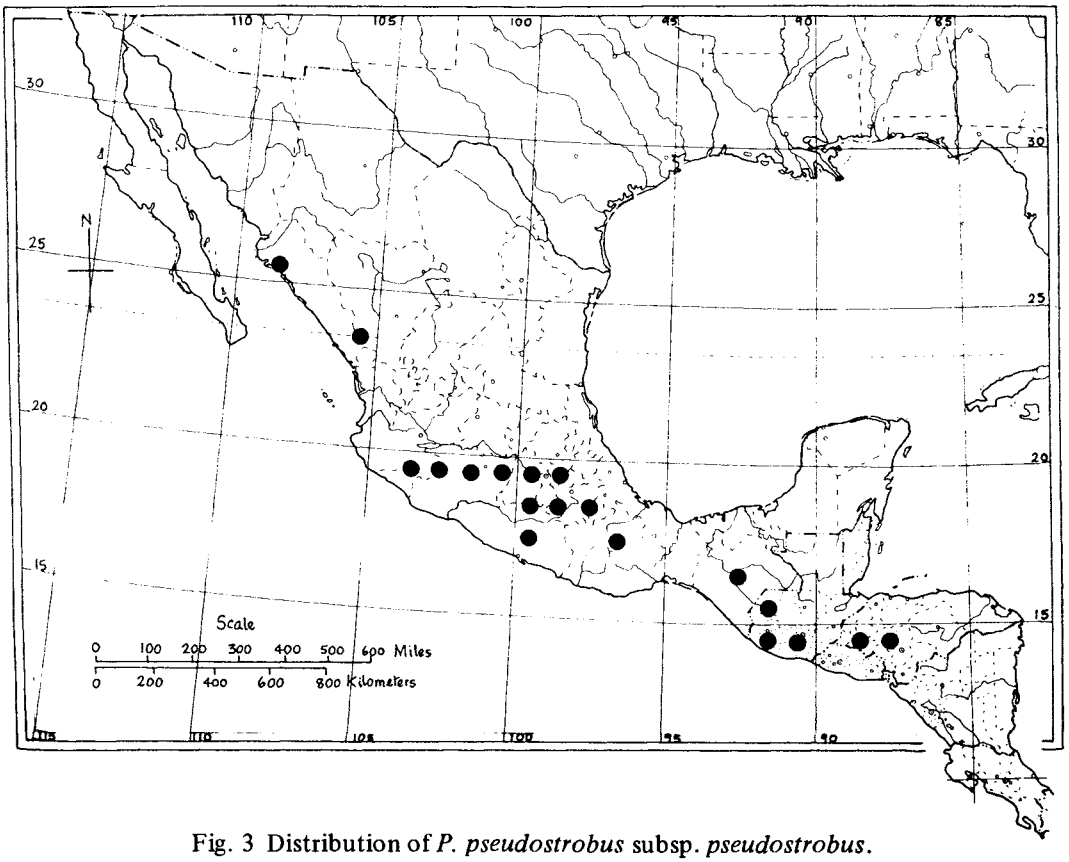


Fig. 3 Distribution of *P. pseudostrobus* subsp. *pseudostrobus*.

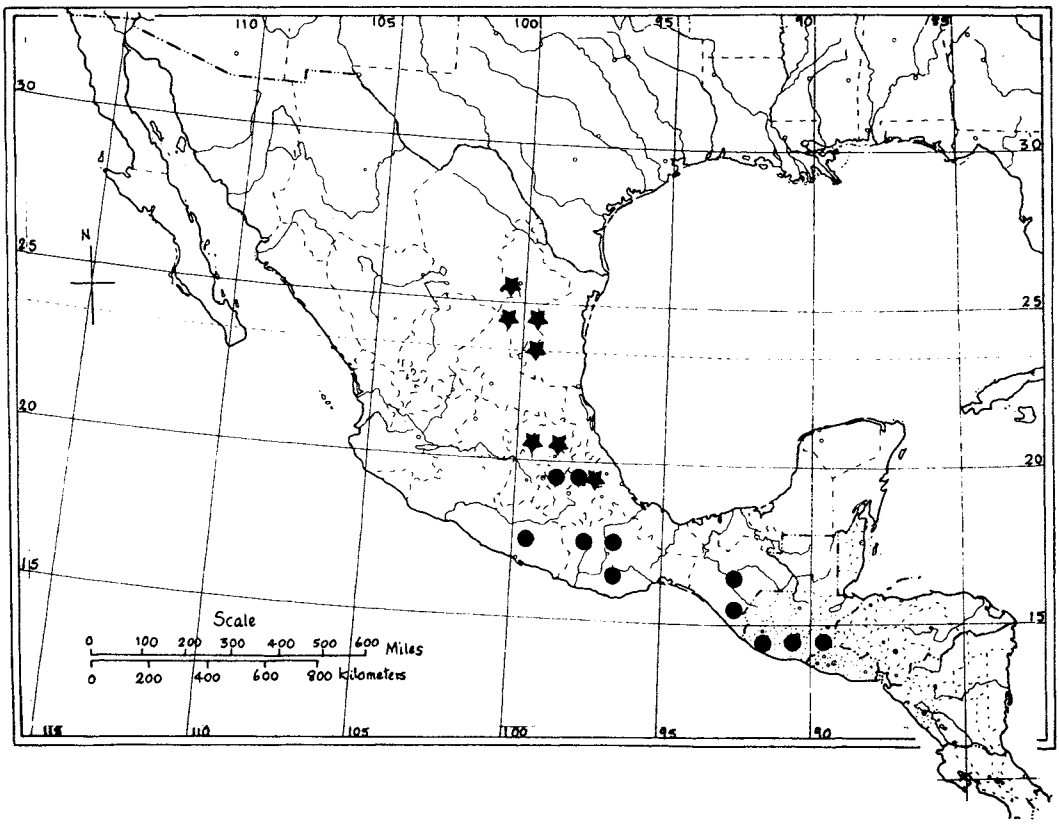


Fig. 4 Distribution of *P. pseudostrobus* subsp. *apulcensis* ★ and *P. pseudostrobus* var *oaxacana* ●.

countries in Latin America and the CFI distribution of seed to Africa and the Asia and Pacific regions.

A complete list of the provenance collections accumulated for trials is given in Table 1.

The majority of seed distributions were made in 1976 but several have been made subsequently. The list of countries which have received seed for trials is as follows:–

Australia, Brazil, Burma, China, Colombia, Ecuador, Haiti, Honduras, India, Indonesia, Japan, Madagascar, Mexico, Morocco, Mozambique, Nepal, Pakistan, Papua New Guinea, Peru, Philippines, South Africa, Tanzania, Thailand, Zaire, Zimbabwe.

It is hoped that such a wide ranging and well defined set of seed collections established in a variety of conditions will give a good indication of the potential of *P. pseudostrobus* (including *P. tenuifolia*) as an exotic and suggest which might be the best seed sources under different conditions.

Some of the trials are now three or four years old. Some early results have been collected and published *e.g.* Thailand (Thailand Pine Improvement Centre, 1978), Honduras (Houkal, 1980 and in press) and South Africa (van der Sijde, in press).

A study of voucher specimens collected with each provenance seed collection indicated that all except one of the seed lots called *P. pseudostrobus* (including

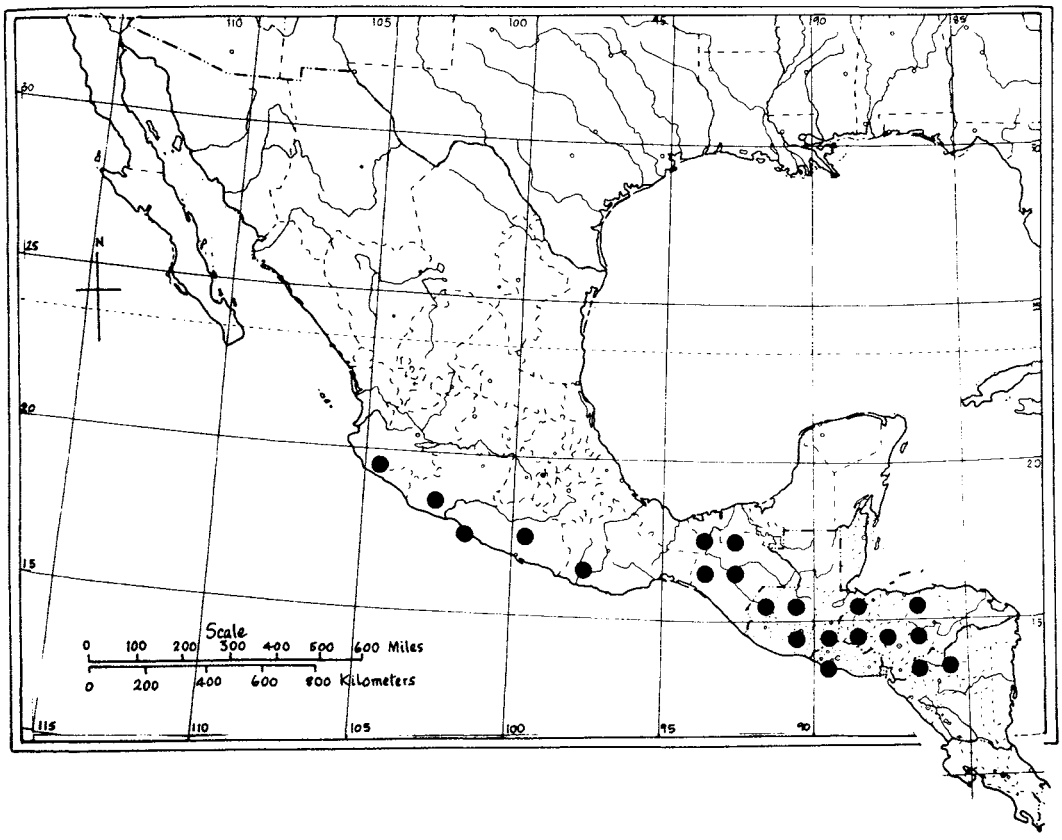


Fig. 5 Distribution of *P. maximinoi*.

P. tenuifolia) at the time of collection by the CFI should now be called *P. maximinoi* according to the results of this taxonomic study. Voucher specimens for the Mexican collections have not been examined but it is most likely that these are of *P. pseudostrobus*. Evidence for this conclusion was obtained from provenance trials results (see below).

The most detailed results available so far are for the trials in Honduras. Information on the provenances included, the nursery procedure and early field performance are given in Houkal (1980 and in press). It is too early in this experiment to make any significant forestry conclusions but results so far are interesting taxonomically.

A visit to one of the trial sites in Honduras was made during the course of this work. It was not necessary to take any detailed measurements to reveal that, as discussed by Houkal (in press), the trial was comprised of provenances representing two distinct taxa.

One group of provenances from Nicaragua, Honduras and including one from Guatemala (San Juan Sacatepequez, K63) showed a phenotype with a symmetrical crown of fine branches, with fine buds, covered by long, thin needles which tend to droop. The second group of provenances from Mexico and Guatemala (Tecpán, K75) had a long, thick, branchless leader, thicker buds and longer coarser needles than the first group. All of the provenances showed reasonable survival but there

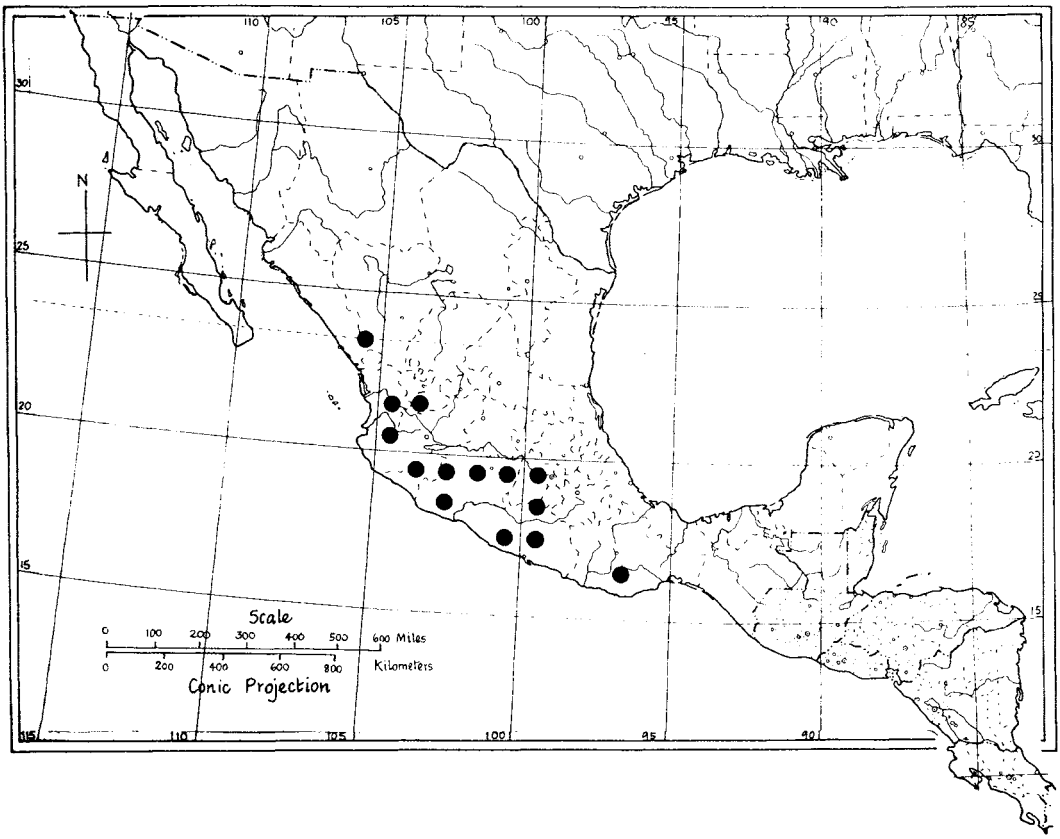
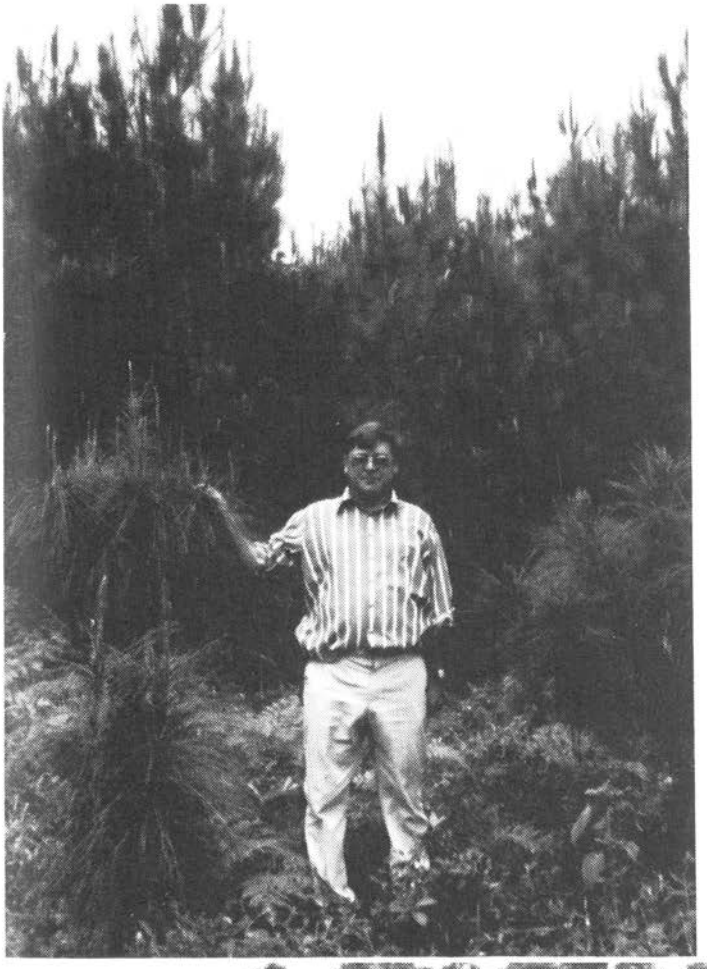


Fig. 6 Distribution of *P. douglasiana*.

was a noticeable difference in height growth. Trees from the first group of provenances listed above, were all much taller than those from the second group. The photographs taken during this visit demonstrate the differences found (see Photographs 1 and 2). It is apparent from these observations that the provenance seed collections made by the CFI and INIF include representatives from two taxa, *P. maximinoi* and *P. pseudostrobus*, which are showing considerable differences in growth and form when planted together in one trial.

Based on the results of this morphological study and the field trial all the CFI provenance collections from Nicaragua and Honduras are determined to be *P. maximinoi* along with collection K63 from San Juan Sacatepequez in Guatemala. All the INIF collections plus CFI collection K75 from Tecpán, Guatemala represent *P. pseudostrobus*. The definitive determinations for all the provenances are given in Table 1.

In the absence of voucher specimens or adult material from trees grown in trials it is impossible to determine whether collections called *P. pseudostrobus* might be further placed in an infraspecific category *i.e. P. pseudostrobus* subsp. *apulcensis* or *P. pseudostrobus* var. *oaxacana* but as most of the Mexican collections are from Hidalgo, Puebla and Oaxaca this is likely. Indeed the seed lots numbered INIF 429, 438 and 500 were called *P. pseudostrobus* var. *oaxacana*, and lots numbered INIF 459 and 495 were called *P. pseudostrobus* var. *apulcensis*, by the Mexican collectors.



Photograph 1 CFI trial in Honduras. In the foreground *P. pseudostrobus* (INIF 500) and in the background *P. tenuifolia* (= *P. maximinoi*).

Photograph 2 CFI trial in Honduras. In the foreground *P. pseudostrobus* (K75, INIF 438, INIF 343) and in the background *P. tenuifolia* (= *P. maximinoi*) (K150). In the distance is a natural stand of *P. tenuifolia* (= *P. maximinoi*).

Close scrutiny of the *P. pseudostrobus* plots particularly those from Michoacán, at the trial in Honduras, did not reveal any evidence that seed of *P. douglasiana* had been erroneously included with *P. pseudostrobus*.

TABLE 1 Seed collections of *P. pseudostrobus* (including *P. tenuifolia*) in CFI trials.

Collector's No.	*Seed Store No.*	*Country*	*Site*	*Latitude Longitude*	*Altitude m*	*Mean annual rainfall mm*	*Number of trees in collection*	*Definitive Identification*
K95	13/73	Nicaragua	Volcan Yali	13° 15'N 86° 11'W	1,400	1,500	54	*P. maximinoi*
K105	9/74	"	"	"	"	"	–	"
K50	28/71	Nicaragua	Rafael	13° 12'N 86° 06'W	1,200	1,500	–	*P. maximinoi*
K131	4/76	Nicaragua	Dipilto	13° 43'N 86° 30'W	1,100	1,200	120	*P. maximinoi*
K132	7/76	Nicaragua	Jinotega	13° 02'N 85° 59'W	1,450	1,360	18	*P. maximinoi*
K149	27/77	"	"	"	"	"	19	"
K133	8/76	Nicaragua	Dantali	13° 08'N 85° 57'W	1,050	1,360	60	*P. maximinoi*
K172	37/78	"	"	"	"	"	28	"
K104	2/74	Honduras	Loma de Ochoa	14° 48'N 87° 30'W	1,200	1,400	55	*P. maximinoi*
K119	10/75	Honduras	Cofradia	14° 00'N 87° 06'W	1,300	948	40	*P. maximinoi*
K77	11/72	Honduras	Tatumbla	14° 02'N 87° 05'W	1,600	1,300	–	*P. maximinoi*
K121	20/75	Honduras	La Fortuna	14° 10'N 86° 35'W	1,250	1,298	38	*P. maximinoi*
K122	21/75	Honduras	El Cedro	13° 48'N 86° 35'W	1,100	1,074	40	*P. maximinoi*
K150	30/77	Honduras	Dulce Nombre	14° 52'N 88° 49'W	1,200	1,670	73	*P. maximinoi*
K75	10/72	Guatemala	Tecpán	14° 50'N 91° 05'W	2,200	1,600	–	*P. pseudostrobus*
K63	42/71	Guatemala	San Juan Sacatepequez	14° 43'N 90° 40'W	1,800	1,500	–	*P. maximinoi*
K51	18/73	Guatemala	Jalapa	14° 42'N 89° 57'W	1,300	1,000	–	*P. maximinoi*
INIF 343	–	Mexico	Nogales, Jacala, Hidalgo	20° 59'N 99° 14'W	2,250		–	*P. pseudostrobus*
INIF 429	–	Mexico	Tlaxiaco, Oaxaca	17° 20'N 97° 40'W	2,200	1,003	–	*P. pseudostrobus*
INIF 438	–	Mexico	Boca del Perro, Tlaxiaco, Oaxaca	17° 21'N 97° 40'W	2,000	1,003	–	*P. pseudostrobus*
INIF 459	–	Mexico	San Salvador el Seco, Puebla	19° 01'N 97° 06'W	2,400		–	*P. pseudostrobus*
INIF 476	–	Mexico	Angahuan, near Uruapan, Michoacán	19° 30'N 102° 14'W	1,780	790	–	*P. pseudostrobus*
INIF 485	–	Mexico	Uruapan, Michoacan	19° 31'N 102° 06'W	1,634	790	–	*P. pseudostrobus*
INIF 495	–	Mexico	Minas Viejas, Zimapan -Jacala, Hidalgo	21° 11'N 99° 00'W	2,000		–	*P. pseudostrobus*
INIF 500	–	Mexico	San Vicente Lachixio, Sola de Vega, Oaxaca	16° 29'N 97° 05'W	2,200	833	–	*P. pseudostrobus*
INIF 501	–	Mexico	San Pedro el Alto, Zimatlán, Oaxaca	16° 45'N 96° 45'W	2,600	833	–	*P. pseudostrobus*

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