

the two species since it has inherited in its shoots the pink colour of *A. spectabilis* and the glabrous character of *A. pindrow*. The segment responsible for pubescence seems to have been removed during the process of segregation. Further, the distribution frequency of the index values shows a strong bimodality between 3,420 m and 3,180 m elevational range and weak bimodalities between 3,690—3,520 m and 3,040—2,900 m. The bimodal distributions show the heterogenous nature of these populations. The strong bimodality at 3,420 m and 3,180 m indicates accumulation of the germ plasm of both the species in this zone. This is evidenced by the presence of a number of trees in this zone which are either pure *A. spectabilis* or *A. pindrow*. It is further of interest that many trees around this zone possess four resin canals in their needles, one median pair (character of *A. pindrow*) and another marginal pair (character of *A. spectabilis*). These trees probably belong to the F₁ generation produced comparatively recently by crossing between the two pure species in this zone. When these individuals backcross to one of their parent species, the co-dominance of the other species in respect to position of the resin canals is removed and the progeny possesses only a single pair of resin canals, the position of which corresponds to the parent species involved in backcrossing. Thus through segregations a mosaic population is created which has been subjected to selection pressure at different altitudinal zones. The successive populations are sympatric at the interfaces and there is no barrier to interbreeding.

Summary

There are two distinct species of *Abies* in the western

Himalayas, a high altitude one *A. spectabilis* and a low altitude one *A. pindrow*; which hybridize freely forming intermediate populations in the middle zones. Analysis of morphological data from individuals along a sample transect through several altitudes, using ANDERSON's method of hybrid-index, revealed introgression. The frequency distribution of the hybrid-index scores showed a strong bimodality in the middle of the distributional range (between 3,420—3,180 m) and indicates the accumulation of the germ plasm of both the species in this zone.

Key words: West Himalayan silver firs, Introgressive hybridization, *Abies pindrow*, *Abies spectabilis*, hybrid index.

Zusammenfassung

Im westlichen Himalaja kommen in Lagen zwischen etwa 2000 und 4000 m vornehmlich zwei Tannenarten vor, in hohen Lagen *Abies spectabilis* (D. DON) SPACH und in tieferen Lagen *Abies pindrow* ROYLE. Die Untersuchung von 15 morphologischen Merkmalen, die stichprobenhaft im Überlappungsgebiet beider Arten erfaßt wurden, läßt auf introgressive Hybridisation schließen.

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Studies of variation in Central American Pines

I. The identity of *Pinus oocarpa* var. *ochoterenai* Martinez

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General Background

International provenance trials organized by the Unit of Tropical Silviculture at the Commonwealth Forestry Institute, Oxford, using *Pinus oocarpa* SCHIEDE as a principal species, were started in 1971 (KEMP, 1973 a, b; F.A.O., 1974). The trials at present involve comparative experiments in nearly 40 tropical countries and are based chiefly on seed collections made from carefully selected populations in the southern parts of the natural range of the species in Central America. Previous to the Oxford trials, most of the seed of this species used in earlier silvicultural studies had been obtained from Mexico. Such early introductions were often of unknown provenance and sometimes incorrectly named.

As an adjunct to the trials, a botanical study of *P. oocarpa* has also been started in order to ascertain its variation over the whole of its natural range and to investigate the tax-

onomic status of the several infra-specific taxa which have been described in the past. The status of those species which are considered doubtfully distinct from it will be examined, as well as the possibility of its hybridization. Since all seed sources of the different provenances issued from Oxford are fully documented and supported by correlated herbarium material and sometimes timber and resin samples, the two aspects of the work taken together will form the basis of a comparative experiment or extensive gene-ecological study of the type carried out by CLAUSEN, KECK and HIESEY (1940) in California using herbaceous plants. Botanical specimens from trees raised in the provenance trial plots throughout the tropics are being collected in order to see how the species behaves and varies in completely new environments outside its area of natural distribution.

In this first paper the identity of the Mexican *Pinus oocarpa* var. *ochoterenai* MARTÍNEZ is discussed, a taxon whose name and identity are already giving rise to a number of problems in the provenance work involving the species.

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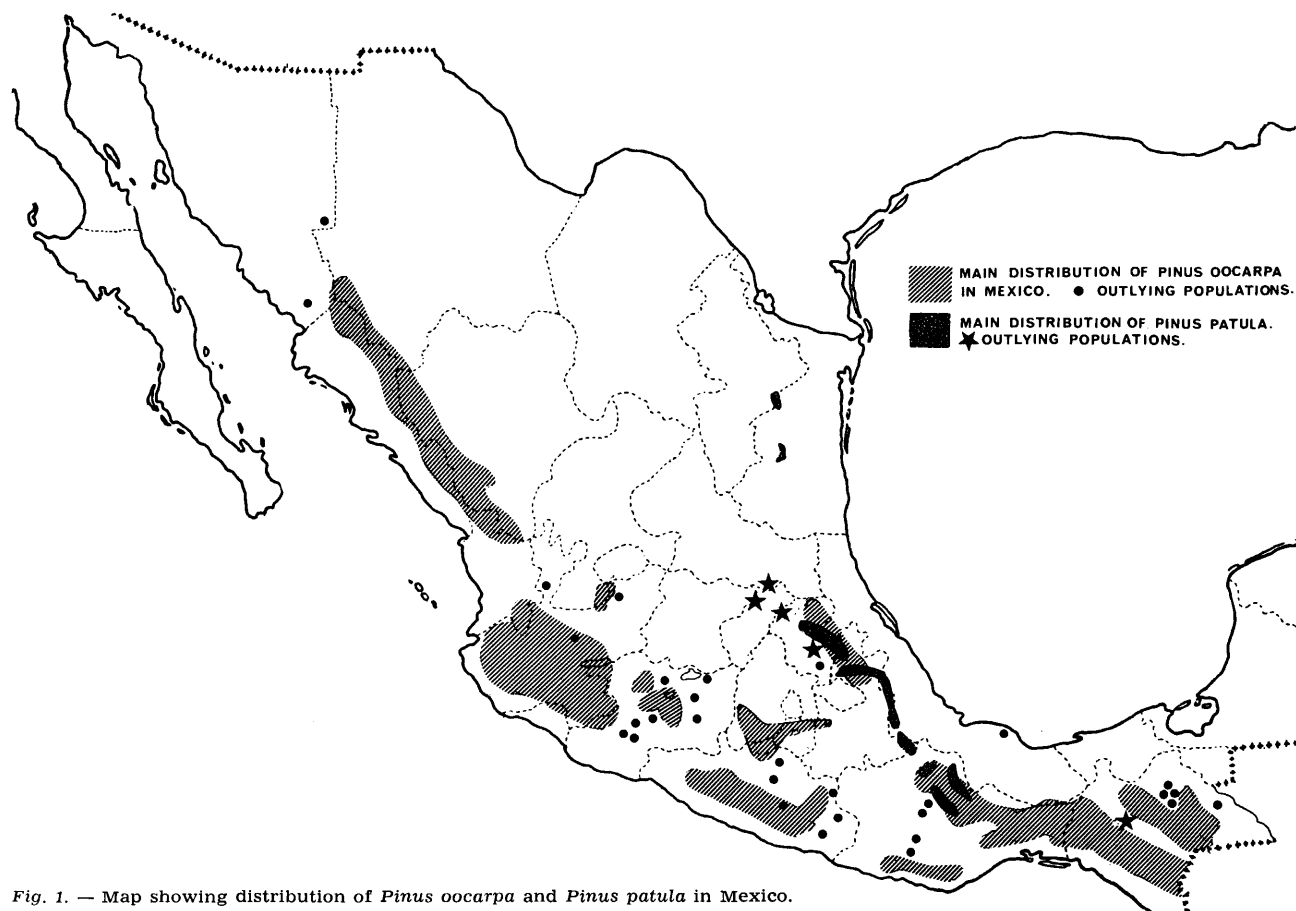


Fig. 1. — Map showing distribution of *Pinus oocarpa* and *Pinus patula* in Mexico.

Introduction

Pinus oocarpa is the most widely distributed and probably the most abundant of the Central American pines, ranging from the north of Mexico (latitude 27° N) in the state of Sonora, to the south of Nicaragua in the Department of León (latitude 12° 40' N). The natural distribution is almost continuous throughout the whole of its range (see Fig. 1 for distribution in northern areas) but small isolated populations, probably relics, occur particularly in Mexico, Belize and Nicaragua. In some countries such as Honduras and Guatemala it forms by far the most important and dominant element in the forest cover (MOLINA, 1964; FAO, 1968), almost always growing in dense stands associated with other pines and a limited number of species of broad-leaved trees, chiefly *Quercus* spp., and herbaceous genera in Melastomataceae and Labiatae. Its ecological requirements have been discussed fully by KEMP (1973 a, b). The species is sub-montane and normally occurs at elevations between 700—2000 m above sea level on a wide range and quality of soil types, very frequently on steep mountain slopes. In Mexico, between Vera Cruz and Ixtepec, trees occur naturally at an altitude of as low as 200 m, and in Guatemala at 250 m (KEMP, 1973 b); however, in Guatemala also, at San Pedro Chiquival, Huehuetenango, others have been found at an altitude of 2450 m. These are exceptional (but see later). The species can survive in very dry areas such as the upper Choluteca Valley, Honduras Republic with an annual rainfall of as low as 650 mm, and in others where up to 1900 mm have been recorded (Department of Zacapa, Guatemala).

²) Some specimens of *P. teocote* SCHIEDE et DEPPE in subsection *Ponderosae* are also difficult to distinguish from the members of this group.

Classification

P. oocarpa is now placed in sub-section *Oocarpae* of the subgenus *Pinus*, (LITTLE and CRITCHFIELD, 1969) which includes among others *P. patula* SCHIEDE et DEPPE, *P. greggii* ENGELM. ex PARL., *P. radiata* D. DON and *P. pringlei* SHAW. The group is a natural one taxonomically and the constituent species are so closely related that they are almost impossible to distinguish in the herbarium when fertile material is not available (LITTLE, 1962)²). Consequently, misidentification of trees in the forest and laboratory is, and has been frequent, especially since several of the species are extremely variable in botanical characters. Needle anatomy is now proving a useful aid in identifying sterile and juvenile material and oleoresin analysis may also prove so in the future.

The section, which occurs chiefly in Mexico, but also in Central America and the Southern United States, is characterized by having needles borne in fascicles of 2—5, with the pedunculate, oblique, female cones persisting on the tree for several years. At maturity the cone-scales open slowly and irregularly to release the seeds. The spring or new shoots are either uni- or multi-nodal, a characteristic which is constant within a species and which is useful for differentiating between species in the field. Shoot apices are, however, frequently lacking from or difficult to see on herbarium specimens. Hybridization among the taxa within the group is well known (CRITCHFIELD, 1967).

Variation

As a forest tree and in its botanical characters *P. oocarpa* is an extremely variable species. When well-grown, as in some areas of Guatemala it can reach an average height of 35 m (with exceptional specimens up to 55 m tall) producing a tree of magnificent form with a straight bole and small crown. In some other parts of the range (particularly the

drier lowland areas of Mexico) it forms a small, poorly-shaped, bushy tree with a crooked and twisted bole and a large crown of many lateral branches. Variation in botanical features is exemplified by the enormous differences in size and shape of the mature female cone and its constituent scales, which occur even on a single tree; in the form, habit and texture of the foliage and in the length of the needles and their number per fascicle (see below).

Although *P. oocarpa* has been studied in considerable detail in Mexico (MARTÍNEZ, 1948; FAO, 1962) there has until recently been very little known about its distribution and variation in Central America. Separate descriptive accounts of it appear in the more recent floras and monographs (STANDLEY and RECORD, 1936; LOOCK, 1950; STANDLEY and STEYERMARK, 1958; AGUILAR, 1961; FAO, 1962; MOLINA, 1964) but there has been no overall synthesis of its botanical features covering the whole of its natural range on a monographic scale. Its geographical distribution has still to be adequately mapped. These aspects will be considered fully in a later paper.

Attempts to accommodate the variation so far have been made by SHAW (1909) and MARTÍNEZ (1940, 1948) but both studied the species in the northern part of the range only. The former has described a short-needled form (*P. oocarpa* var. *microphylla* SHAW) from the Mexican States of Sinaloa, Nayarit and Jalisco whilst Martínez has described three further varieties, again all from Mexico: — *P. oocarpa* var. *trifoliata*, which now appears to be a very wide-spread taxon, but of dubious taxonomic status, has needles predominantly in fascicles of three instead of the usual five; an ill-defined taxon *P. oocarpa* var. *manzanoi* occurs in the State of Hidalgo which is distinguished from the type by a number of minor morphological features; the important and highly interesting *P. oocarpa* var. *ochoterrenai* from the southern state of Chiapas, which forms the subject of this paper. A further incorrectly described species occurs in Guatemala (*P. tecumumanii* SCHWEDTJE. nom. illegit.) (SCHWEDTJEGER, 1953) which is considered by some authors to be related to *P. oocarpa*. Its status is still very uncertain and research on it is proceeding.

In its botanical characters typical *P. oocarpa*, as described by SCHIEDE (1838) is a five-needled pine (see Fig. 2 (a) and 3 (b)), although fascicles each with 3, 4, 5 or very rarely 6 needles can occur on individual specimens. (STYLES, in press.). The needles, which vary in length from 12–28 cm, are coarse and thick, up to 1.5 mm in width. They are generally held stiffly erect on the tree or they may be

spreading; they are never truly pendulous. Usually the foliage is light, shining green, often tufted at the ends of the branchlets. The shape of the female cone is very characteristic. When closed it tends to be more or less symmetrically ovoid to broadly ovoid-conical ("broadly egg-shaped"). When mature, the scales open widely to give it the appearance of a rosette, the basal scales remaining flat to form a slightly asymmetric base. The cone is extremely variable in size, ranging from 2.5–11.5 cm in length and up to 9.75 cm in breadth. Because the cone is usually rather broad relative to its length, the ratio l/b is a useful taxonomic character for distinguishing it from related species. The cone scales are generally thick, flat or slightly convex, with a flat apophysis, dorsal umbo and very short, deciduous prickle. The cones are borne on stiff peduncles up to 3.5 cm long, in groups of up to three, but never in clusters (see Fig. 4 (a–c)).

The needle of *P. oocarpa* is very distinctive in its internal anatomy when seen in cross section. Such sections reveal 3–8 resin ducts which are almost always septal, i.e. they abut on to both the hypoderm and endoderm layers of the leaf (see Fig. 5 (a) and (b)). In a few very rare instances some resin canals are entirely internal or external (JÄHRIG, 1963). My own research reveals that this character is reasonably constant for the species and a valuable one for distinguishing it from related species, as a large number of sections of leaves have now been made from specimens collected throughout the range.

The Status of *Pinus oocarpa* var. *ochoterrenai* Martínez

This is probably the most important and widely-known of all the infraspecific taxa described by MARTÍNEZ within *P. oocarpa*. The name is now frequently quoted in forestry literature, especially that concerning provenance trials of *P. oocarpa*. But almost all authors mention that its exact taxonomic status appears uncertain and somewhat of a mystery (ABELL, 1970; POYNTON, 1975). It is all the more interesting since provenances bearing this name are claimed to have superior growth characteristics when grown in trials. *P. oocarpa* var. *ochoterrenai* was first described by MARTÍNEZ in 1940, with his own collection numbers 3624 (Coapilla) and 2145, 3564 (San Cristóbal de las Casas) as types. These specimens were collected from Chiapas in southern Mexico.

The botanical characters by which MARTÍNEZ separates this variety from the typical form are given below in Table 1, but he gives no details of the habit of the tree or any information about its ecology.

Table 1. — A comparison of the botanical characters of *P. oocarpa* (typical) and *P. oocarpa* var. *ochoterrenai* (after MARTÍNEZ).

Botanical character	<i>P. oocarpa</i> (typical)	<i>P. oocarpa</i> var. <i>ochoterrenai</i>
No. of leaves per fascicle	generally 5, rarely 3 or 4	mainly 3 or 4, rarely 5
Colour and form of leaves	bright green; coarse, stiff	yellowish-green, very slender
Form, shape and colour of mature ♀ cone	very woody, broadly and shortly ovoid to globular; yellowish-green to grey	weakly woody: narrowly ovoid; dark yellowish-brown to reddish
Position of apiculus on the umbo of cone scale	apiculus directed towards the base of the cone	apiculus directed towards the apex of the cone
No. of cone scales and type of umbo	few, regular, thick; with a smooth umbo	numerous, irregular, thin, with a flat, rugose umbo
Position of resin canals in leaf	septal	medial

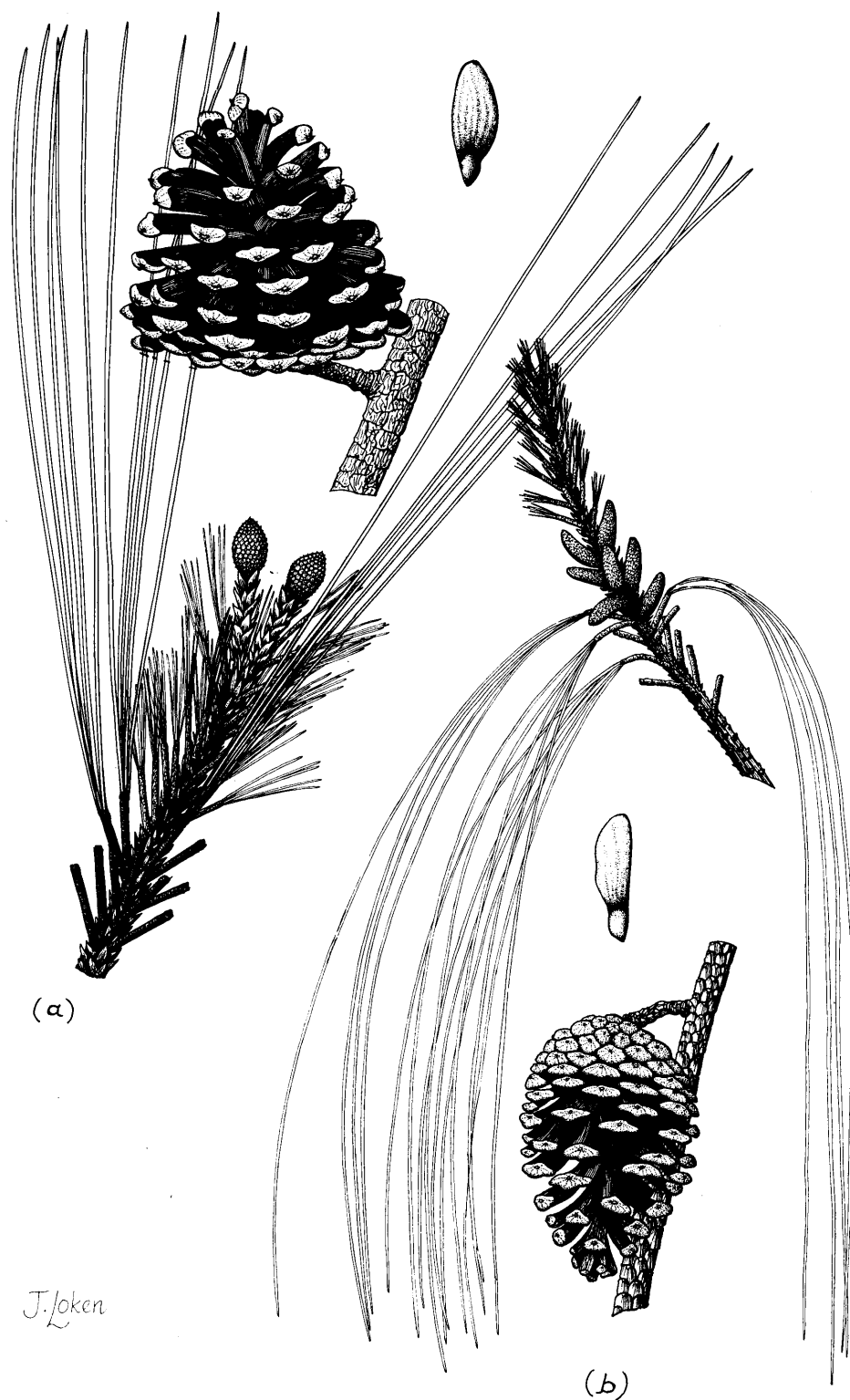


Fig. 2. — (a) *Pinus oocarpa* (typical): Habit; female cones ($\times 1$) and seed ($\times 2$). All from STYLES 35 (Mexico). (b) *Pinus patula* var. *longipedunculata*: Habit, female cone ($\times 1$) and seed ($\times 2$). All from STYLES 113 (Mexico).

The small population of this variety of *P. oocarpa* (as understood by MARTÍNEZ), now appears to have a very limited distribution in the southern Mexican state of Chiapas, and is confined to a restricted area in the neighbourhood of San Cristóbal de las Casas ($16^{\circ} 45' N$, $92^{\circ} 38' W$). The area lies within the Pine-Oak forest vegetation zone of the central plateau of the Chiapas Highlands (BREEDLOVE, 1973)

which predominates between 1300 and 2600 m altitude. The commonest associated trees here are oaks, (*Quercus* spp.) and several species of pine — *P. oaxacana* MIROV, *P. pseudostrobus* LINDL., *P. ayacahuite* EHRENB. and the typical form of *P. oocarpa*. Thus the variety and the type would appear to be completely sympatric in their distributions in this area.



Fig. 3. — (a) *Pinus oocarpa* var. *ochoterenai*: Habit, female cone ($\times 1$) and seed ($\times 2$). All from STYLES 119 (Mexico). (b) *Pinus oocarpa* (forma): Habit, female cone ($\times 1$) and seed ($\times 2$). All from STYLES 158 (Belize).

Field studies

There are very few specimens of Martínez's variety extant in major herbaria and its ecology and distribution have been little studied since it was first described (see FAO, 1962; PINEDA *et al.*, 1973). In order to obtain more botanical material and ecological information, two visits were made to southern Mexico in 1972 and 1974; studies were carried out in the neighbourhood of San Cristóbal de las Casas and in natural forest along the Pan American Highway south-eastwards to Comitán (Chiapas). This is mostly at an altitude of approximately 2600 m and from

where the tree has been recorded by previous collectors. Soils in the area are relatively deep and the luxuriant undergrowth and varied second storey shrub layer suggest that a higher annual rainfall occurs, probably in the region of 1300–1500 mm. Scattered trees agreeing with the description of Martínez were located as well as others of typical *P. oocarpa*; in some localities the two taxa were growing together in close proximity. This is the highest altitude at which typical *P. oocarpa* has ever been encountered anywhere over its entire range and the trees were of very poor form, with crooked boles and heavily branched

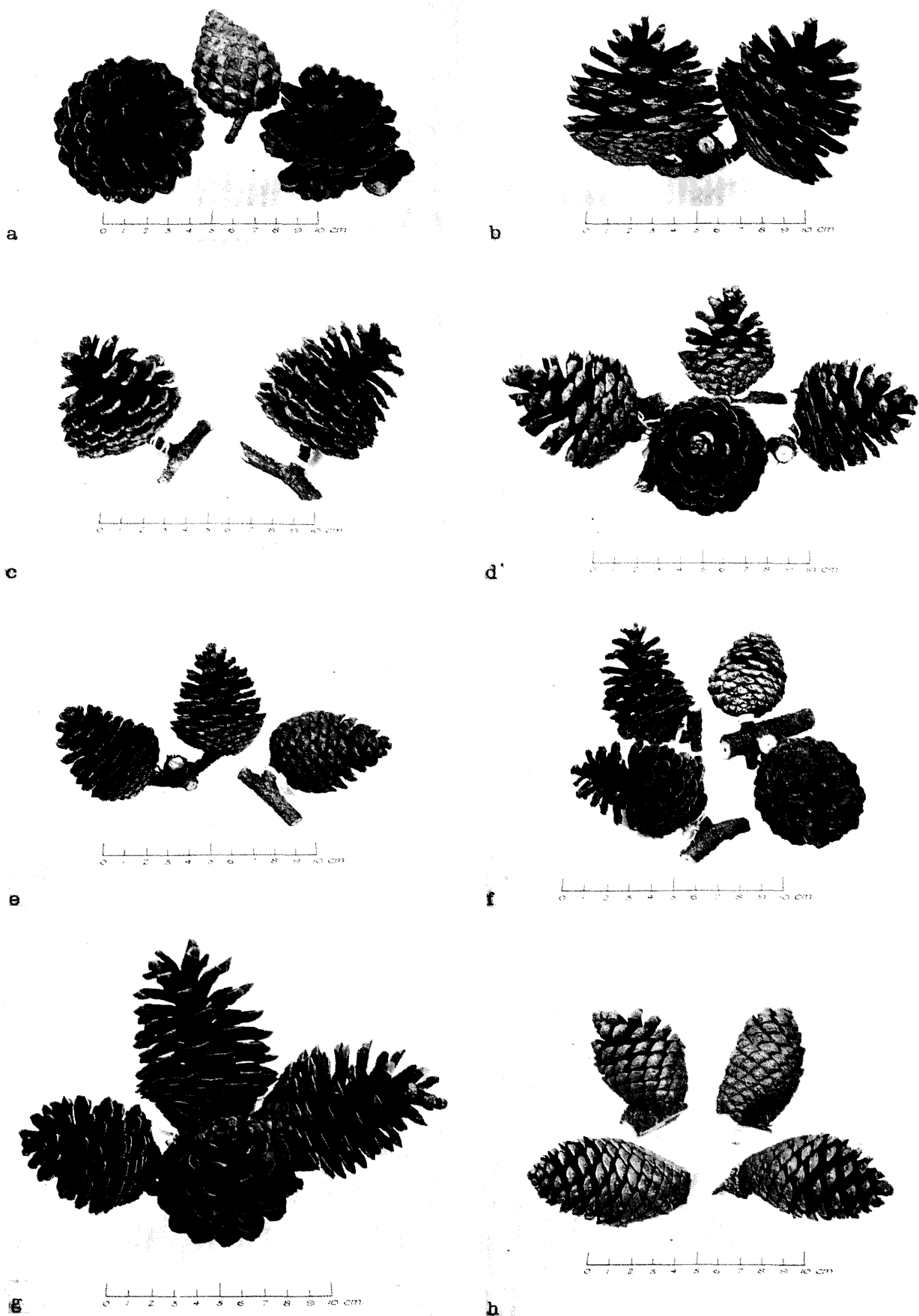


Fig. 4. — Mature female cones. a. *Pinus oocarpa*, STYLES 112, Chiapas, Mexico. b. *Pinus oocarpa* STYLES 107, Chiapas, Mexico. c. *Pinus oocarpa*, STYLES 109, Chiapas, Mexico. d., e. *Pinus oocarpa* var. *ochoterenai*, STYLES 119, Chiapas, Mexico. f. *Pinus patula* var. *longipedunculata*, STYLES 113, Oaxaca, Mexico. g. *Pinus patula* (typical), SAYLOR s.n., Puebla, Mexico. h. *Pinus patula*, without collector, cult. S. Africa.

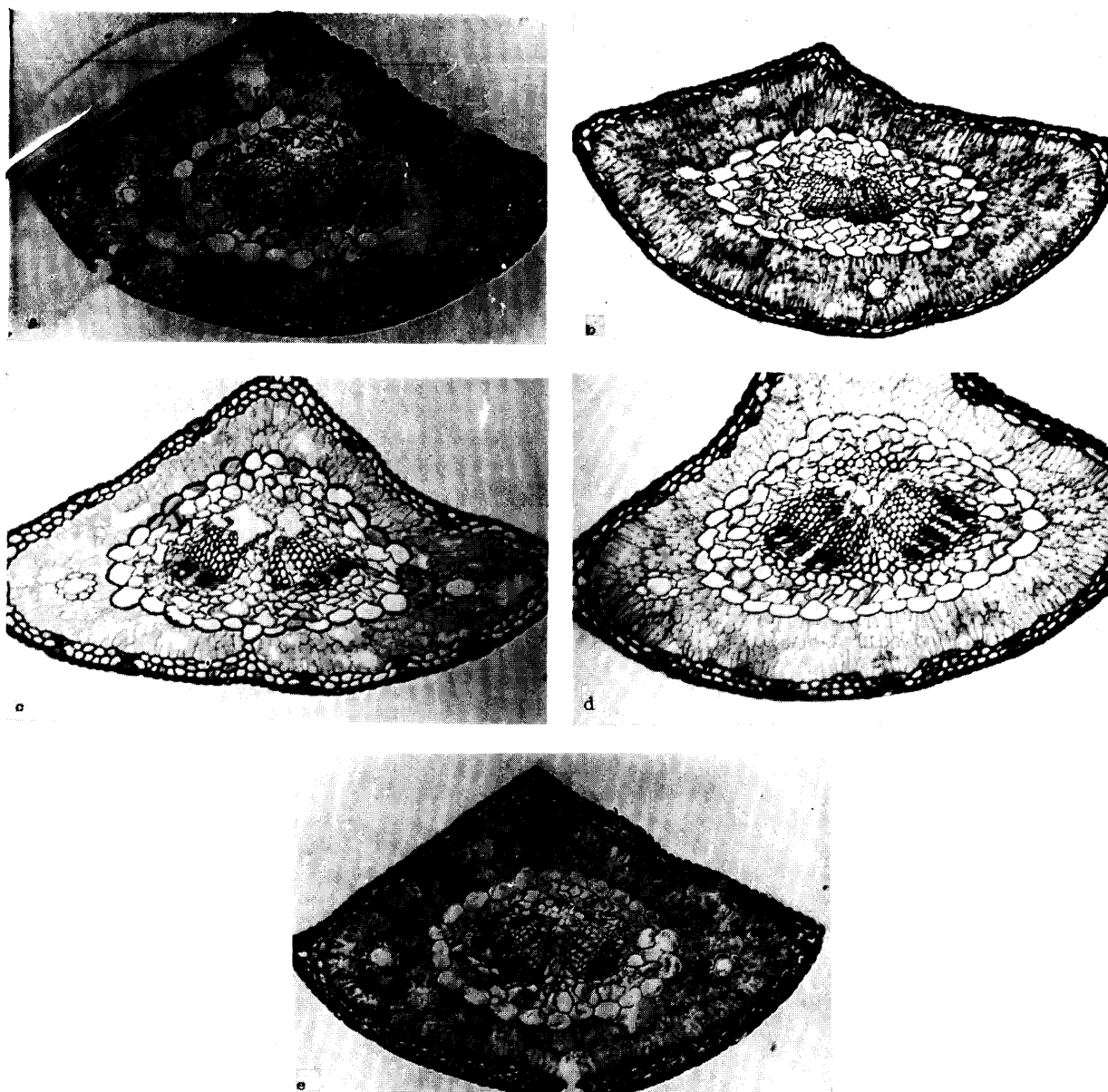


Fig. 5. — Cross sections of needles. a. *P. oocarpa*, STYLES 115 ($\times 170$), Mexico. b. *P. oocarpa*, STYLES 27 ($\times 170$), Honduras. c. *P. patula* var. *ochoterenai* ($\times 170$), LITTLE 17957, Mexico. d. *P. patula* var. *longipedunculata* ($\times 130$), STYLES 113, Mexico. e. *P. patula*, STYLES 44 ($\times 170$), Mexico.

crowns. Trees of *P. oocarpa* var. *ochoterenai* were, on the other hand, magnificent with straight boles up to 30 m tall and several whorls of arching lateral branches, forming a light crown. The bark was quite different from the typical species being rich reddish-brown in the upper part of the bole, scaling in papery plates towards the base. The trees completely lacked the thick, greyish-black, deeply furrowed bark so characteristic of typical *P. oocarpa* with which it was growing. The foliage was also striking: instead of the coarse, more or less erect, bright green needles borne in fascicles of 5 (almost 96% in the typical species), the needles of *P. oocarpa* var. *ochoterenai* were distinctly pendulous, very slender (less than 1 mm wide), soft and yellowish green in colour. The majority of the fascicles were of 4 (75%) rather than 5 (15%) needles, and a smaller percentage (10%) with only 3 needles was also found (see Fig. 3 (a)). Most of the young branches were also distinctly glaucous, a feature I have never previously noticed in *P. oocarpa*. The mature female cones were completely atypical of *P. oocarpa*, being narrowly conical to oblong-conical, instead

of shortly ovoid to broadly ovoid-conical. Furthermore they were on average much smaller (from 5–9 cm instead of up to 11.0 cm, and less broad). The scales were also less woody and did not appear to open so fully to form the flattened rosette characteristic of *P. oocarpa*. The cones were all pedunculate — the stalks varying from 1.5 cm–2.5 cm in length (see Fig. 4 (d) and (e)).

When I attempted to identify specimens collected from these trees using the key to Mexican pines devised by LITTLE (1962) I arrived in every case to a conclusion that they belonged to a form of the closely related, but quite distinct, *P. patula* var. *longipedunculata* and not to *P. oocarpa*. This latter taxon is known so far only from Oaxaca and adjacent state to the north of Chiapas.

P. patula var. *longipedunculata* was established by LOOCK (in MARTÍNEZ, 1948) and trees belonging to the variety were found in the mountains of Rancho Benito Juárez, Oaxaca, S. Mexico, at an altitude of between 2500–3000 m. This was the most southerly extension of the species then known. Associated species were *P. ayacahuite*, *P. pseudo-*

strobis and *Quercus* spp. The trees differ from the type mainly in the size of the cones, being smaller (5–8 cm instead of up to 10 cm or more), with comparatively weak scales which open relatively quickly (i.e. do not remain closed for such a long period). The cones also possess peduncles with the stalk ranging up to 3.0 cm in length, whereas in the typical form they are sessile or sub-sessile (see Fig. 4 (g), (h)). The leaves are typically slender, soft, flexible and pendulous, in fascicles of 3, 4 and 5.

On a visit to this locality in Oaxaca, I immediately noticed its very close ecological similarity to the Chiapas forest and was struck by the luxuriance and richness of the understorey vegetation and by the few dominant species which were common to both. The altitude was recorded as approximately 2700 m.

These trees thus seem to agree phenotypically in all botanical characters with those placed by MARTÍNEZ under *P. oocarpa* var. *ochoterenai* (see Fig. 2 (b)), more especially in their pedunculate, conical cones and their slender, pendulous needles. Straight cylindrical boles and reddish-brown bark were common to trees in both populations, as well as the predominant occurrence of 4-needled fascicles in the foliage. Cross sections of the needles of trees from both populations also differed from the typical form of *P. oocarpa* in possessing medial rather than septal resin canals (see Fig. 5 (c–e)). Cytological examination of root-tip mitoses of both revealed the expected chromosome number of $2n = 24$, although differences in karyotype have not yet been investigated (STYLES and KHOSLA, 1975).³

BARRETT (1972), in his detailed study of the species, has shown that in the northern part of its range *P. patula* is predominantly a 3-needled pine (up to 97% of fascicles), whereas in the south the percentage of fascicles with 4 (up to 52%) and 5 (up to 5%) needles greatly increases. This is especially noticeable in provenances collected in Oaxaca (S. Mexico), named by him *P. patula* var. *longipedunculata*. This particular character has a tendency towards a clinal distribution with the Chiapas population thus showing a similar tendency towards 4-needled fascicles. BARRETT is of the opinion however (and I am in full agreement with him), that Looock's variety is not worthy of separate identity, since trees bearing pedunculate to sub-sessile cones occur scattered throughout the range of the species and even within a single locality. The other morphological characters mentioned by Looock are too variable to be of any diagnostic value taxonomically.

I can only surmise that MARTÍNEZ wrongly classified the Chiapas specimens because they were so far south of the then known natural range of *P. patula* (see Fig. 1). At that time (1940), the Oaxaca populations of *P. patula*, with their atypical cones and needle number, had not yet been discovered.

I am therefore proposing here that these two taxa should be formally combined and that from henceforth the Chiapas trees previously placed by MARTÍNEZ in *P. oocarpa* var. *ochoterenai* should be referred to *P. patula*.

The full nomenclatural citation should be: —

Pinus patula SCHIEDE et DEPPE, in SCHLECHT. and CHAM., *Linnaea* 6: 354 (1831).

³ It should be noted that *P. oocarpa* and *P. patula* hybridize readily. Hybrids have occurred naturally between plantation trees in S. Africa (Un. S. Afric. Ann. Rep. Dept. For., 1956, 1958, 1959) and CRITCHFIELD (1967) reports abundant viable seed set from artificial crosses made between them at Placerville, California. It is almost certain that the two species hybridize in Chiapas where they grow in mixed populations. Some atypical specimens identified as *P. oocarpa* in herbarium collections may in fact represent hybrids.

Syn *P. oocarpa* var. *ochoterenai* MARTÍNEZ, in Anal., Inst. Biol. Mex. 9 (1): 65 (1940).

P. patula var. *longipedunculata* (longepedunculata) Looock ex MARTÍNEZ, Los pinos mexicanos: 333 (1948).

This was suggested earlier by STYLES (in Wormald, 1975). The view that the two taxa are the same thing and thus conspecific is supported by CRITCHFIELD and LITTLE (1966) who also tentatively considered *P. patula* var. *longipedunculata* Looock to be taxonomically identical with *P. oocarpa* var. *ochoterenai*. Furthermore B. HALBERG,⁴ a forest botanist, who has lived in Chiapas for many years, states (in litt.) „I have seen many variations of the lowland (below 1500 m) *P. oocarpa* and cannot accept the San Cristóbal pine as a variety of it; it is too erect, symmetrical of crown and different in bark and leaves. On the contrary, I would find it quite acceptable to consider it as a variety of *P. patula* which it resembles in many characters, as well as in elevation and humid habitat.“ R. J. POYNTON⁵ also tells me (in litt.) that young trees grown from a collection of seed made by Hodgson at 8,500 ft (c. 2,590 m) at El Tapanal, Oaxaca, and named originally as *P. oocarpa* var. *ochoterenai* have the appearance of *P. patula* rather than *P. oocarpa*. This seems to be a case of the original collector taking *P. patula* var. *longipedunculata* for the variety of *P. oocarpa*, possibly after following book descriptions and keys.

My very detailed botanical studies so far indicate that *P. patula* does not occur south of the Chiapas highlands, but there is, however, another, as yet incorrectly described species, *P. tecumumanii* SCHWEDT-FEGER (nom. illegit.) (SCHWEDT-FEGER, 1953) from Guatemala which requires investigation. I have not seen any botanical specimens of it, but trees given this name occur in the more humid areas of the Departments of Baja Verapaz, Totonicapán and Huehuetenango, at altitudes of between 1900 and 2700 m. Associated species are *P. pseudostrobus* and *P. ayacahuite*. The trees are said to resemble those of *P. oocarpa* but differ in being of superior form, with rich reddish-brown bark and slender, drooping foliage. The needles are in bundles of 3, 4 and 5. The female cones are described by the author as narrowly conical to oblong, greyish-yellow in colour, and varying from 4 to 7 cm in length. From this description it seems that we could be dealing with yet another disjunct population of *P. patula* which will be a further extension of its natural range into Central America. It may also prove to be the same tree to which SHAW refers (1909). A study of *P. tecumumanii* will be undertaken as soon as botanical material becomes available, especially since STANDLEY and STEYERMARK (1958) considered it, with some doubt, as either a variety *P. oocarpa*, or a possible hybrid between *P. oocarpa* and *P. pseudostrobus*.

Provenance Trials

As far as I can trace, only one seed collection which may possibly be of MARTÍNEZ's variety has been attempted for provenance work. This was made by MORTENSON who collected seed of what he called *P. oocarpa* var. *ochoterenai* (E.A.A.F.R.O. No. 1527) and of typical *P. oocarpa* at Jitotil [Jitotol], Chiapas (see MORTENSON, 1969) at an altitude of 1730 m. A further collection of "high altitude" (2,500 m.a.s.l.) "var. *ochoterenai*" was also made at San Cristóbal de las Casas (E.A.A.F.R.O. No. 1526). Seed of these provenances was subsequently distributed under E.A.A.F.R.O. seed-lot

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numbers and now forms the bases of trials in several tropical countries notably E. Africa and Australia.

MORTENSON unfortunately obtained no botanical voucher specimens when he made his seed collections so that the exact and unequivocal identification of the parent material of his seedlots E.A.A.F.R.O. Nos. 1526 and 1527 cannot be checked. Photographs of the parent trees taken by MORTENSON which are now kept at E.A.A.F.R.O. Headquarters in Nairobi, strongly recall the habit of *P. patula*. Interesting evidence has, however, already emerged from one of the trials, supporting my view, that his *P. oocarpa* var. *ochoterenai* is almost certainly conspecific with *Pinus patula*. NIKLES (1974, in litt.⁹) states, "A most surprising finding is that E.A.A.F.R.O. No. 1527 is, next to Belize, the most impressive material in the study, [in Queensland, Australia] clearly superior to other introductions from Chiapas. Lot 1527 has unusual morphology — the trees look somewhat like *P. patula*". The habit of even young trees of this species is very characteristic and completely different from that of *P. oocarpa*.

Nomenclature

The name *P. oocarpa* var. *ochoterenai* has unfortunately been used incorrectly for provenances originating outside the natural range of the taxon in Chiapas. Both HUNT (1962) and LAMB (1966) use it for typical *P. oocarpa* from Belize, and MORTENSON (1969), MOLFINO and VAIRETTI (1972) and GOUDET (1974) have used it for seed originating from Honduras Republic. MORTENSON (loc. cit.), LOOCK (1950) and MIROV (1967) also claim that it occurs in Guatemala. ABELL (1970) in Zambia, on the other hand, refers to it for seed which was obtained from the north-western state of Jalisco in Mexico, whereas McDONALD (1971) in Kenya uses this name for seed originating both from Belize and the state of Oaxaca (Mexico); the latter has hitherto been outside the supposed known geographical range of the variety in Mexico.

Indeed, the varietal name *ochoterenai* seems to be used more or less indiscriminately among commercial seed collectors for any Central American provenance of *P. oocarpa* which they believe to be superior to var. *typica* as a seed source for plantations (GULDAGER and GREENWOOD, 1973). For instance, MARTIN (1971) states "...la variété *ochoterenai* est très supérieur à toutes les autres, et si l'approvisionnement en graines était satisfaisant, on pourrait envisager de ne faire des extensions industrielles qu'à partir de cette variété, qui peut être plantée à écartement plus large." The seed used in the trials cited by MARTIN was obtained from Belize and Honduras Republic!

The situation in South Africa regarding nomenclature seems to be equally confused. POYNTRON (1975) stated that seed of the variety was obtained from Honduras Republic in 1934 and that trees grown from it in arboretum plots display, unlike the typical species collected in Mexico, excellent form and a fast rate of growth. They even bear comparison with *P. caribaea* var. *caribaea* and *P. caribaea* var. *bahamensis*, at present among the most promising taxa for plantation work in S. Africa.

Nearly all the trials of *P. oocarpa* so far show that provenances from the southern part of its range in Central America are superior in growth and form to the Mexican, at least in the early stages.

The identification of all provenances of doubtful nomenclature at present grown in provenance trials can be check-

ed at Oxford when the trees reach the cone-bearing stage.

As trees of the southern populations of *P. patula* are of such excellent form, it is suggested that seed collections should be made from them for use in provenance trials and to confirm the suggestions made in this paper.

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Summary

Botanical and ecological studies as well as evidence from albeit young provenance trials support the view that the variety *ochoterenai* of *Pinus oocarpa* originally described from S. Mexico by MARTÍNEZ, is synonymous with a form of *P. patula* SCHIEDE et DEPPE. This now considerably extends the natural range of the latter species. The varietal name "*ochoterenai*" has unfortunately been wrongly applied to other forms of *P. oocarpa* in Central America which has given rise to considerable nomenclatural confusion both in the literature and in the work on provenance trials involving this species. It should no longer be used in connection with any trials involving *P. oocarpa*. It is recommended that seeds of the southern population of *P. patula* should be collected from authentically named trees and grown in trials in order to confirm the proposition outlined above.

Key words: *Pinus oocarpa* SCHIEDE, *Pinus oocarpa* var. *ochoterenai* MARTÍNEZ, *Pinus patula* SCHIEDE et DEPPE, variation of morphological characters, classification and nomenclature.

Zusammenfassung

Botanische und ökologische Studien in jüngeren Provenienzversuchen haben ergeben, daß *Pinus oocarpa* var. *ochoterenai* MARTÍNEZ, die in Süd-Mexiko natürlich vorkommt, wahrscheinlich als Form von *Pinus patula* SCHIEDE et DEPPE anzusehen ist. Dies würde zur Folge haben, daß das natürliche Verbreitungsgebiet von *Pinus patula* als beträchtlich größer anzusehen wäre als bisher. Auf Grund der Untersuchungsergebnisse sollte der Name *ochoterenai* in Zukunft nicht mehr mit dem Artnamen *P. oocarpa* in Zusammenhang gebracht werden.

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Geographic Variation in *Quercus rubra* in North Central United States Plantations¹⁾

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Introduction

Cooperative provenance testing of northern red oak (*Quercus rubra* L.) was initiated in 1962 by the state agricultural experiment stations in the North Central region of the U.S.A. The primary objectives are: (1) to identify genetic variation in important traits and also possible response interactions between geographic origin and planting locality; (2) to make seed source recommendations for the establishment of genetically-improved plantations of red oak in the North Central region.

Methods

Seed was collected from an average of 8 trees per geographic origin (provenance). Collection localities were distributed over most of the species range, except for the southernmost areas (Fig. 1). Earlier, trials in Ohio had indicated that extreme southern population samples of *Q. rubra* were not winter-hardy in the North Central region of the U.S.A.

Three successive seed years were required to complete the collections. At the time, long-term storage methods had not been developed for red oak. Therefore, each year's col-

lections were sown in the Ohio Division of Forestry's Green Springs nursery soon after receipt in the autumn. Thus there were three successive years' nursery stock.

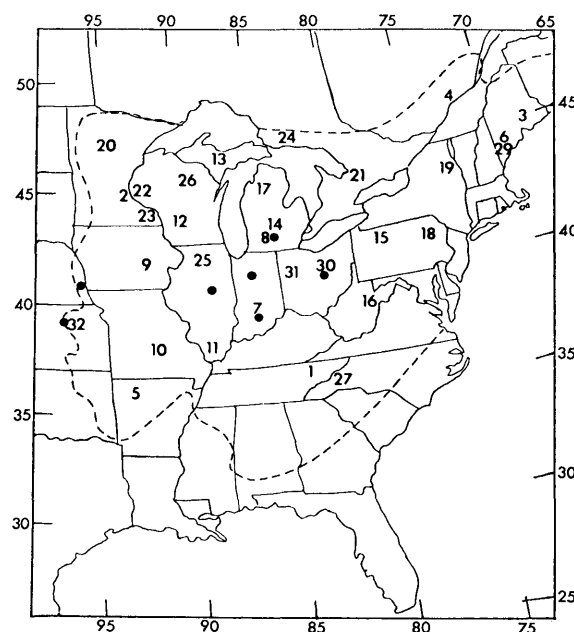


Fig. 1. — Red oak seed collection localities (numbers), experimental plantation localities (dots), and limits of the species distribution (broken line, from LITTLE 1949).

¹⁾ North Central Regional Project NC-99, Cooperative State Research Service, U.S. Dept. of Agriculture. Approved for publication as OARDC Journal Paper No. 156-76.

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