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SLASH PINE (*PINUS ELLIOTTII*), INCLUDING SOUTH FLORIDA SLASH PINE

Nomenclature and Description

by

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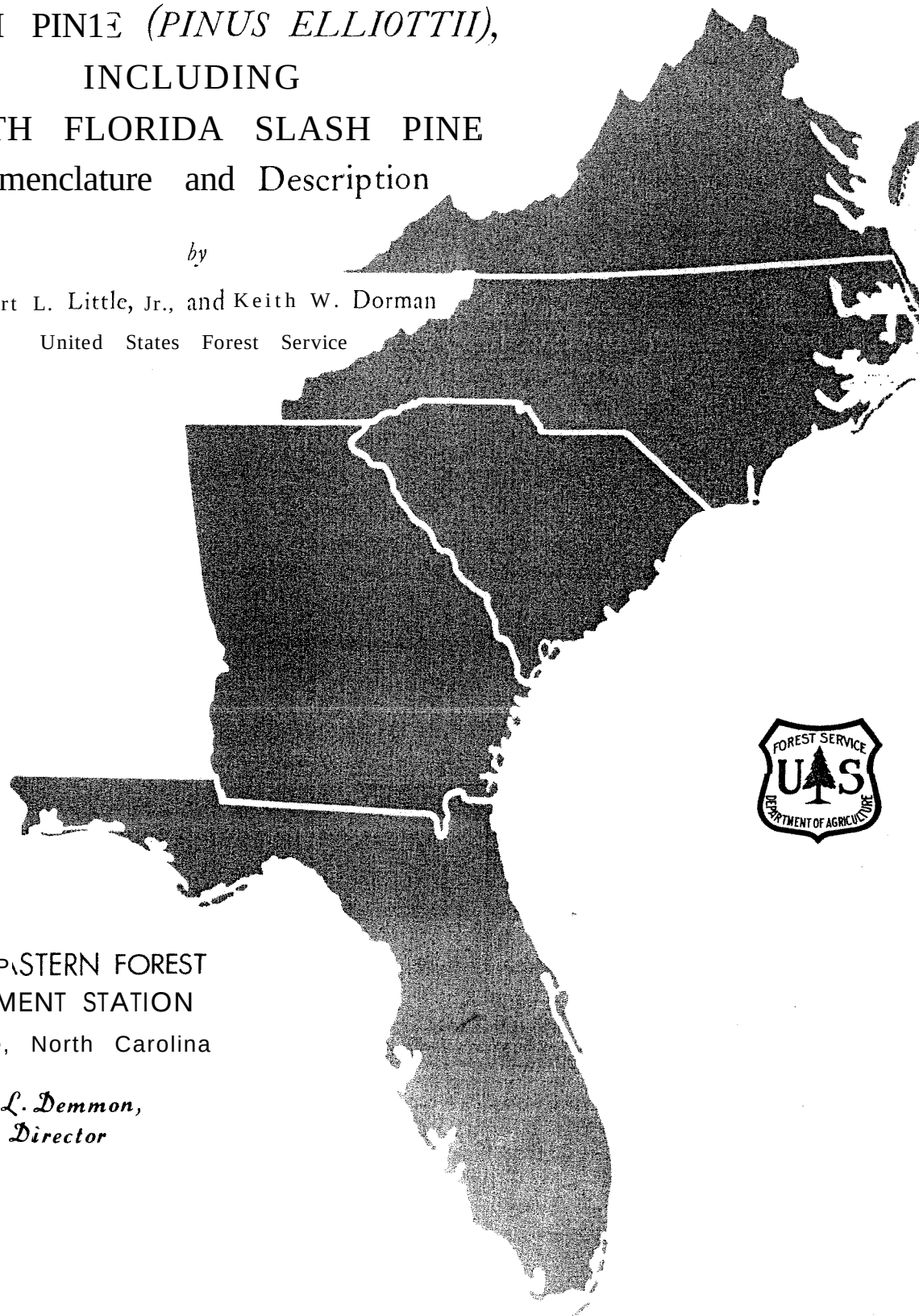
United States Forest Service



SOUTHEASTERN FOREST EXPERIMENT STATION

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SLASH PINE (PINUS ELLIOTTII), INCLUDING SOUTH FLORIDA SLASH PINE, NOMENCLATURE AND DESCRIPTION

by

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INTRODUCTION

Slash pine (*Pinus elliottii* Engelm.), including its variation South Florida slash pine recently distinguished as a new botanical variety, has been known by several different scientific names. As a result, the common name slash pine is more precise and clearer than scientific names. The slash pine of southern Florida differs from typical slash pine in a few characters important in forestry, such as seedling, wood, and resin production. A study of the botanical nomenclature and geographic variations of this valuable tree species is therefore appropriate.[2]

This species is one of the most important pines in southeastern United States for lumber, pulpwood, and naval stores (Mattoon, 1940). It is widely and successfully grown in forest plantations, and more than 200 million young slash pines are being planted in 1954 on more than 200,000 acres in eight southern states.

Many botanists and most foresters, including the United States Forest Service, have applied the name *Pinus caribaea* Morelet to slash pine throughout its range. Others have restricted this name to the variation in southern Florida and regard the widespread familiar slash pine as a separate species, *P. elliottii* Engelm. or also *P. palustris* Mill., the latter name usually applied to longleaf pine. The distinguished American dendrologist Charles S.

1/ Respectively, forester (dendrology), United States Forest Service, Washington, D. C., and forester (research administration), Southeastern Forest Experiment Station, United States Forest Service, Macon, Georgia.

2/ A summary of this study with formal description of the new botanical variety has been published by Little and Dorman, Journal of Forestry 50(12): 918-923, December 1952.

Sargent used at different times these four specific names for slash pine: P. elliottii, P. cubensis, P. heterophylla, and P. caribaea.

The name P. caribaea is given also to pines of West Indies and Central America. Some differences between these pines of tropical climates and pines in the United States bearing the same name have been observed in experimental plantings in the United States and in plantations in South Africa. A precise nomenclature of these native and exotic pines is particularly important in planting programs.

For some years foresters have known the variation of slash pine in southern Florida which has a grasslike, almost stemless seedling stage, an irregular spreading crown, and very heavy wood with thick summer-wood, and which is not worked for oleoresin. South Florida slash pine, the only common pine south of Lake Okeechobee, occupies about 1,750,000 acres of commercial forest lands. Most of this area has been cut over, and much needs artificial reforestation. Preliminary attempts to grow nursery stock from northern Florida were not successful. Questions about the name of the south Florida variation have come to the United States Forest Service from time to time. Therefore; we have been requested to make a taxonomic study of these pines.

Our studies show that among the hard pines with shiny brown cones generally classified as Pinus caribaea Morelet are three different geographically separated populations or taxonomic entities (taxa). Because of significant differences, these three kinds of pines should be recognized by foresters as distinct in forest management, in utilization, and in planting, especially in areas removed from the natural ranges.

Two botanical species will be distinguished in this report, P. caribaea Morelet, Caribbean pine, with tropical distribution in West Indies and Central America, and P. elliottii Engelm., slash pine, in southeastern United States. The latter is subdivided into two varieties, P. elliottii var. elliottii, typical slash pine, ranging along the warm temperate coastal plain from South Carolina to central Florida and eastern Louisiana, and a new variety P. elliottii var, densa, South Florida slash pine, in subtropical southern Florida and coasts of central Florida. Throughout the following report these variations will be designated accordingly, except where references are made to different usage of names by other authors.

HISTORY OF NOMENCLATURE

Histories of the confused nomenclature applied to typical slash pine (Pinus elliottii var. elliottii) in the United States, to South Florida slash pine (P. elliottii var. densa), and to Caribbean pine (P. caribaea) outside the United States in West Indies and Central America are summarized here. This review will serve to define the scientific names applied to these pines by the principal botanical specialists at different times in the past since first recognition, and to indicate the correct scientific names under the International Code of Botanical Nomenclature. Only the more important references, such as publications containing new names, monographs, regional floras, and tree manuals or lists, are mentioned.

SLASHPINE (TYPICAL)

For typical slash pine (P. elliottii var. elliottii) the six following scientific names are reviewed in the approximate order of their adoption: P. taeda var. heterophylla, P. elliottii, P. cubensis, P. heterophylla, P. caribaea, and P. palustris.

Pinus taeda var. heterophylla

Stephen Elliott (1816-24) in 1824 was the first botanist to distinguish slash pine, naming it a variety of loblolly pine, Pinus taeda, var. heterophylla. In his Sketch of the Botany of South-Carolina and Georgia (2: 636,1824), he described this new variety as follows:

"Along the marshes near the mouths of the fresh-water rivers, (at least in Georgia) this pine is very common. It is frequently called the smooth-bark Loblolly Pine. It becomes occasionally a very large tree; its bark is as smooth as that of P. Palustris but in longer scales; it has more sap-wood than any of our pines, and its leaves I have found in some instances by twos and threes indiscriminately mingled even on the old branches."

Thus, Elliott's variety of Georgia marshes was named from its variable leaves in both 2's and 3's, instead of in 3's in P. taeda, and was further characterized by its smooth bark. Elliott's herbarium, which is preserved in the Charleston Museum, Charleston, S. C., contains no specimen of this pine, according to the list of his type specimens by Weatherby (1942). One of us has also examined Elliott's herbarium and confirmed the absence of a type.

Slash pine was unknown to earlier botanists before Elliott, and likewise was not distinguished from loblolly pine or longleaf pine by botanists in the half century that followed. According to Harper (1928, p. 157; 1943, p. 204, 206), previous to the 1870's the turpentine pines of the South were generally regarded as all longleaf pines. Then botanists began to recognize another pine growing chiefly in branch swamps, in some places called "slashes," which became known as slash pine.

Pinus elliottii

About 1872, J. H. Mellichamp, a physician of Bluffton, S. C., rediscovered slash pine. In a revision of the genus Pinus, George Engelmann (1880, pp. 186-190, pl. 1-3) published a detailed description of the new species P. elliottii, well illustrated with three excellent plates and based largely upon Mellichamp's copious specimens and notes. This new species honored Stephen Elliott, whose earlier variety, P. taeda var. heterophylla, was cited as a synonym. The local name blue pine, from the purplish bark, and the name slush-pine, credited to Sargent, were mentioned. According to Sargent, this was "by far the handsomest of all the southern pines." Engelmann recorded the range from near Charleston, S. C!., to south Florida and west to Mobile, Ala. He stated that this species was closely allied to P. cubensis and might prove to be a geographical variety. As no specimen collected by Elliott has been located, the name P. elliottii is to be associated with Mellichamp's many specimens now found in different herbaria, particularly those at Missouri Botanical Garden examined by Engelmann.

Pinus elliottii Engelm. appeared as nomen nudutn without description in an earlier list of trees of the United States in 1876 by Vasey (Cat. Forest Trees U. S. 30. 1876; U. S. Dept. Agr. Rpt. Comm. Agr. 1875: 178. 1876) and also in another list in 1880 by Sargent (1880, p. 74), who remarked, "A large tree, probably often confounded with P. taeda." Chapman (1883, p. 650) took up this name in the supplement of his Flora.

The name P. elliottii was short lived and was united with P. cubensis in 1884 by Sargent, as noted below. Then, after the names P. heterophylla and P. caribaea were adopted in turn for typical slash pine, Small (1913a, p. 33) in 1913 revived P. elliottii Engelm. for the northern variation while retaining P. caribaea for slash pine of southern Florida. However, Small (1933, pp. 3-5) later rejected P. elliottii in favor of P. palustris, as explained under that name.

A few authors have continued to use P. elliottii. Coker and Totten (1934, pp. 19-22) were unable to agree with Small's interpretation. They accepted P. elliottii as the single species of slash pine from Miami, Fla., northward; but admitted that P. caribaea may get into the Florida Keys, out of the range covered by their book. West and Arnold (1946, pp. 3, 6) retained P. elliottii as slash pine for the northern variation as a distinct species from P. caribaea as Caribbean pine for the south Florida variation.

Pinus cubensis

In 1884 Sargent (1884, pp. 202, 520-523, map) accepted Pinus cubensis Griseb., with slash pine as the first of four common names and reduced P. elliottii Engelm. to synonymy. He stated that A. H. Curtiss' specimens from the Florida Keys connected the forms of South Carolina, Georgia, and northern Florida with the West Indian tree and that this was the only species of pine in southern Florida. The range was extended west to southeastern Louisiana but was confined to near the coast and not beyond 50 or 60 miles inland. The map of Florida showing the distribution of the pine forests (opposite p. 522 and dated 1881) indicated the inland forests as P. palustris and forests of P. cubensis only along the coasts. This map, one of the first of slash pine, is of special interest as showing remarkably well the distribution of South Florida slash pine in southern Florida and northward along both coasts, though the variety does not extend as far north on the east coast as mapped and the range in western Florida west of Cedar Keys is not this variety. Typical slash pine as it occurs mixed with longleaf pine across central and northern Florida was not distinguished from the latter.

However, studies by George Russell Shaw and others about a half century ago showed that P. cubensis Griseb. is a species of eastern Cuba and is different from pines of southeastern United States. Since that time P. cubensis has disappeared from usage in this country. Fernald and Schubert (1948, pp. 183-186) alone among recent authors referred the slash pine of southeastern United States to P. cubensis Griseb.

Pinus heterophylla

Following an old "American Code" rule that priority began with publication as a variety, Sudworth in 1893 reinstated Elliott's oldest, varietal name as Pinus heterophylla (Ell.) Sudw. (Torrey Bot. Club Bul. 20: 45. 1893; U. S. Dept. Agr. Rpt. Secy. Agr. 1892: 329. 1893) to replace P. cubensis Griseb. He regarded the mainland and insular pines as one species and used the common name Cuban pine. Mohr (1897) adopted Sudworth's name in his monograph of the southern pines and noted the occurrence also in Cuba and Honduras, but his map (pl. 3) omitted southern Florida from the range. P. heterophylla was further used by Sudworth (Nomencl. Arbor. Fl. U. S., U. S. Dept. Agr. Div. Forestry Bul. 14: 31. 1897) and was adopted also by Sargent in his Silva of North America (1891-1902, 11: 157-159, pls. 591-592. 1897).

However, this binomial had been published twice before in 1849 for two other species. Under present rules P. heterophylla (Ell.) Sudw. dates from 1893 and besides lacking priority must be rejected as a later homonym.

Small (1903, p. 28) adopted the name P. heterophylla (Ell.) Sudw. for a pine listed between P. taeda L. and P. serotina Michx. and in addition to slash pine, P. elliotti? Engelm., with the following distribution: "Sandy swamps, near the coast, Ga. and S. C.--It produces the palest bark and the

softest wood of our pines and has the most restricted range." No pine with this name or range has been distinguished by recent authors, though P. heterophylla was afterwards retained by Small (1933, p. 5). Shaw (1914, p. 72) referred P. heterophylla Small, not Sudw., to synonymy under P. taeda L. We found only four sheets in a folder of P. heterophylla "as to name" at the New York Botanical Garden, two of which were sterile. Small's own specimen (J. K. Small, June 15-18, 1895; NY) from Brunswick, Glynn Co., Georgia, with immature cones is P. serotina Michx., according to examination of needle anatomy and as originally labeled. Another specimen with immature cones from the same county (R. M. Harper 1537; NY) apparently is the same. A specimen from Miami, Fla., labeled "P. heterophylla in part" (J. K. Small and G. V. Nash Oct. 27--Nov. 13, 1901; NY) is P. elliottii var densa. Thus, P. heterophylla sensu Small was not the s&e as Elliott's variety of that name but was P. serotina Michx. in part.

Pinus caribaea

Present usage of Pinus caribaea Morelet (1855) for the slash pine of southeastern United States as a species occurring also in Cuba, Bahama Islands, and Central America follows the conservative monograph by Shaw (1914, p. 70). Morelet's name for a pine at Isle of Pines appeared in an obscure publication and had been overlooked until mentioned by Shaw (1904b). He combined P. elliottii Engelm. and P. bahamensis Griseb., described from Bahama Islands, under the older name P. caribaea.

Sargent (1905, pp. 18-19, fig. 18; 1926, pp. 15-16, fig. 17), who had previously used three other specific names for slash pine, *then* adopted a fourth, P. caribaea. Most authors have likewise accepted P. caribaea.

Britton and Shafer (1908, pp. 35-37, fig. 27-28) adopted P. caribaea, Their photograph of slash pine in south Florida apparently is South Florida slash pine.

However, as noted below, several American authors have restricted P. caribaea in the United States to south Florida, the variation here called South Florida slash pine, and have retained P. elliotti Engelm. for slash pine.

Pinus palustris

Adding to the confusion,. Small (1933, pp. 3-5) adopted for slash pine Pinus palustris Mill., the name generally applied to longleaf pine, for which he took up P. australis Michx. f. A few others, such as Van Dersal (1938, pp. 187, 191) and De Vall (1941, pp. 121-132), followed Small's last change *in* nomenclature.

Little (1948, pp. 457-458) maintained P. palustris for the longleaf pine and further rejected P. australis as nomenclaturally superfluous when

published. Fernald and Schubert (1948, pp. 181-186) and Fernald (1948, pp. 241-249) rejected P. palustris as "hopelessly indefinite" and adopted P. australis for longleaf pine.. It seems simplest to retain P. palustris for longleaf pine, the oldest name established in usage, pending settlement of this controversial question. P. palustris sensu Small, for slash pine, apparently is a misapplication of-the name.

SLASH PINE IN SOUTH FLORIDA

Several American authors have restricted the name Pinus caribaea in the United States to the pine of south Florida and have regarded the familiar, more widespread slash pine of northern Florida and beyond as a different species P. elliottii. However, none heretofore has suggested that South Florida-slash pine differs from both P. caribaea and typical P. elliottii. Thus, no separate specific or varietal name has been given to this pine. A summary of principal authors distinguishing this variation follows:

That Engelmann (1880, p. 187) included South Florida slash pine unrecognized in his new species P. elliottii was indicated by his quotation from A. P. Garber, "the most common pine in South Florida..."

One of the first to recognize the existence of the two kinds of slash pine in Florida was Eugene A. Smith (1884), whose early map and notes have been cited by Harper (1928, p. 157). Smith's (1884, map opposite p. 187) agricultural map of Florida dated 1880 is somewhat like that of Florida showing the pine forests by Sargent (1884, map opposite p. 522) dated 1881, and mentioned above under P. cubensis. Both were in different volumes of the reports of the 10th United States Census of 1880. However, Smith's, really a vegetation map, was more detailed and like Sargent's map showed pitch or Cuban pine in south Florida and northward along both coasts, the range of South Florida slash pine, but also farther north. After discussing the longleaf pine region, Smith (p. 205) wrote under pitch pine: "The pitch pine grows all along the Gulf coast, and has been designated as Pinus Elliottii Engelmann, in the northern portion of its area of occurrence, while southward it is named Pinus Cubensis Grisebach, by Professor Sargent, who considers it identical- the Cuban pine." Smith credited to Sargent records of pine along the coasts of northern Florida now known to be typical slash pine, but Sargent then had P. elliottii as a synonym of P. cubensis. The change in forests from longleaf pine to pitch or Cuban pine south of latitude 27° was noted by Smith (p. 207), who quoted a similar earlier observation by Col. J. L. Williams in a book, Territory of Florida, published in 1837.

In 1901 Rowlee (1903) made a field study of the pines of south Florida

Cuba, and Isle of Pines. He concluded that the pine of south Florida, which he called P. heterophylla (the name then applied to slash pine), was not identical with Cuban pines known as P. cubensis Griseb. but had very different cones. However, he did not enumerate the differences and did not separate the pine of south Florida from that northward. Rowlee's observations were not checked by others until confirmed independently by our own field studies a half century later.

Small (1913a, p. 33), known for the numerous slight variations he distinguished among the southeastern plants, was another to recognize early that typical slash pine and South Florida slash pine are distinct, -though the differences he reported have not been confirmed by others. The former was listed as P. elliottii Engelm., blue or swamp pine, distributed as far south as the Everglade region. The latter as P. caribaea Morelet, slash pine, was distributed in "southern peninsular Florida, and some of the lower keys and near the coast to Georgia and Mississippi. Also in the Bahamas and Cuba." He retained also P. heterophylla (Ell.) Sudw., pond or slash pine, in swampy soil near the coast in South Carolina and Georgia.

In his handbook on Florida trees published the same year, Small (1913b, p. 2) accepted the same two species and stated the Florida range of P. caribaea as follows: The SLASH-PINE grows in dry sand close to most of the coast line of Florida, and on rock on the Everglade Keys, the lower Florida Keys and a few of the upper keys. P. caribaea as Caribbean-pine without P. elliottii was further listed by Small in two local floras of southern-Florida, Flora of Miami (1913c, p. 2) and Flora of the Florida Keys (1913d, p. 2).

In 1914, Roland M. Harper (1914, p. 361) who has made numerous important studies of the trees and other plants of southeastern United States during the past half century, published notes on the distribution and properties of South Florida slash pine, which are quoted in full in the following paragraphs. He recorded P. elliottii as slash pine south in Florida to about latitude 27° Lake Okeechobee. Two photographs taken in 1909 accompanied the following notes.

"Our southernmost conifer, Pinus Caribaea, seems to have no distinctive common name in general use. (It has been called 'Cuban pine' by several writers on forestry in recent years, but that name would be more appropriate for Pinus Cubensis, a species confined to eastern Cuba.) It is abundant in South Florida, and may extend along the coast to Georgia and Mississippi, though this point has not yet been determined beyond question. It is said to occur also in the Bahamas, western Cuba, the Isle of Pines, and British Honduras. It grows in pure stands, like the long-leaf, and south of the Caloosahatchee River it is almost the only pine, and more abundant than all other trees combined. It is confined to low regions within 100 feet af sea-level, and the saw-palmetto is usually the most conspicuous feature of the undergrowth (in Florida, but not in the tropics, for this palmetto does not grow farther south).

"It grows mostly in sandy soil north of Miami, and on limestone rock south of there, where sand is scarce. Although it occupies the driest soils within its range (quite unlike its *near* relative P. Elliott%), the country where it grows is so low that there is usually water within two or three feet of the surface. The climate is subtropical, with no snow and little frost, and the summers are much wetter than the winters.

"This species withstands fire about as well as P. palustris and P. Elliottii do, or perhaps even better, and is exposed to-it as often.

"Its wood is similar to that of the long-leaf pine, except that it is more resinous and brittle, and therefore is not used much for lumber except locally where there is no other pine within easy reach. The gum does not flow readily, and consequently very little turpentine is obtained from this species; but it is not unlikely that the increasing scarcity of long-leaf pine may before long bring about the invention of some method for utilizing P. Caribaea as a profitable source of naval stores. The range of this species lies almost entirely south of the cotton crop, but the soil or rock in which it grows is being planted extensively to grape-fruit, mangoes, avocadoes, and other tropical fruits."

The Florida Forest Service in a mimeographed news release entitled "Forest Service studies slash pine" and dated October 15, 1934, described for the first time the distinctive grasslike seedlings of slash pine grown from south Florida seed. These grasslike seedlings were contrasted with the normal seedlings from seed collected in north Florida grown in the same nursery at Olustee. According to the release, it was planned to establish plantings of the' two side by side in various parts of the State to continue observations of their growth habits, to settle the question of whether or not they were two distinct species, and to determine whether the faster growing variation could be planted commercially in places occupied by the slower growing variation. Two significant paragraphs of this news release, quoted below, are almost identical with a quotation published by De Vall (1941, p. 129), credited to a letter from T. W. Young:

"During the past spring [1934], Mr. D. J. Weddell, of the Florida Forest Service, noted that the seedlings in certain beds at the State nursery were markedly different from those about them--even though they were on identical soil and had received the same care, fertilizer, watering, et cetera. An investigation of the records showed the seed used in these Particular beds were collected in the vicinity of Highlands Hammock by the boys of the C.C.C. camp at Sebring.

"Measurements taken on August 28 [1934] by the present nurseryman, Mr. T. W. Young, show that the average height of the trees grown from the south Florida seed is about three and a third inches as compared with more than'seven and a half inches for those grown from seed collected in north Florida. In addition, the seedlings grown from seed collected in the southern part of the State have developed a stem of only about three inches, terminating in a cluster of needles very *similar to* those of a longleaf pine

seedling. The north Florida seedlings have needles from near the ground to the tip of the stem, growing in a well distributed manner without bunching."

Apparently *most* of the plantations mentioned in the news release are no longer in existence. De Vall cited one plantation of southern seedlings in northern Florida with nearly 100 percent mortality.

One of the most detailed investigations of the two variations of slash pine in Florida was made by Wilbur B. De Vall (1941, 1945), now at Alabama Polytechnic Institute, while with the University of Florida and afterwards U. S. Forest Service. Unfortunately, much of his work, including maps and distribution records, remained unpublished in a thesis.3/

In an article condensed from his thesis, De Vall (1941) checked the taxonomic characters used by Small (1933) to separate the two related pines and followed the latter's final nomenclature. He made a 1200 mile field trip along both coasts of Florida, collecting specimens in each county. Differences in cones mentioned by Small, such as shape, proportions, length, and curvature of prickles, were found to be unreliable. He reported for South Florida slash pine as P. caribaea the number of resin ducts in needle cross section to be 4 to 9, in contrast to 2 or occasionally 3 cited by Harlow (1931) for "slash pine." The grasslike seedling with very short thickened stem in the southern variation was contrasted with the normal, spindly seedling with pencillike stem in the northern variation. The distribution of the southern variation was in the form of a widely spread "Y" extending from Big Pine Key north in Florida near the coasts. South Florida slash pine was not used for naval stores because it did not produce the flow of gum of the more northern pines.

Later De Vall (1945) published a key to the species of native Florida pines, in which these two pines were separated according to the number of resin ducts of the needle, 2 or 3 in typical slash pine and 4 to 9 (average 7) in South Florida slash pine.

The common pine of south Florida and the keys was listed as P. caribaea, slash pine, by Buswell (1945, p. 12).

West and Arnold (1.946, pp. 3, 6) distinguished two species, P. caribaea Morelet as Caribbean pine for southern Florida slash pine and P. elliotti Engelm. as slash pine for the northern variation. They illustrated the differences in seedlings and published perhaps the first drawing of the grasslike seedling with large tap root of the former. However, they admitted that there was little to distinguish mature trees in general appearance and did not illustrate the cone and foliage of the former. Resin ducts in needles

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3/ De Vall, Wilbur B. The taxonomic status and ecological variations of certain southern pines. 125pp., illus. M. S. thesis, Univ. Fla., 1941. (Typewritten)

of the former were reported to be more abundant (5 to 10) than in the latter (3 to 4).

Harlow and Harrar (1950, p. 96) noted that there appeared to be two geographic forms of P. caribaea, which some authors recognized as separate species.

Several studies, mostly unpublished, of South Florida slash pine have been made by personnel of the United States Forest Service. Shortly after the grasslike seedling was discovered by the Florida Forest Service in 1934, Frank Heyward, of the U. S. Forest Service, on November 3, 1934, made a photograph of seedlings of the common and south Florida varieties of slash pine at the Florida Forest Service Nursery at Olustee, Florida. The short, thick-stem seedlings of South Florida slash pine are in strong contrast to the taller, slender-stem seedlings of local origin. On April 23, 1935, he took several pictures of forests of the southern variation 20 miles south of Ft. Meyers, Lee County.

Wilbur B. De Vall, while employed by the U. S. Forest Service, in 1945 sent specimens of South Florida slash pine to the Forest Service Herbarium. The drawing (fig. 1) by Leta Hughey, was made at that time from one of his fresh specimens.

Year-old seedlings of Pinus caribaea from Cuban and British Honduran seed sown in Texas in 1929 were much less frost-resistant than stock from Florida seed, the Woody-Plant Seed Manual (U. S. Dept. Agr., Forest Service 1948, p. 264) reported in a summary of climatic races among the pines. However, according to some botanists more than one species was included.

In response to inquiries about the confused nomenclature of southern pines, Little (1948, pp. 457-458) published a note maintaining P. palustris Mill. for longleaf pine instead of slash pine. He noted that P. caribaea apparently was the oldest available name for slash pine and indicated thedesirability for additional field study to determine whether the more northern variation merited specific segregation as P. elliottii Engelm.

CARIBBEAN PINE IN WEST INDIES

The earliest known scientific name given to the pines in this study was P. caribaea Morelet (Rev. Hort. Côte d'Or 1: 105. 1851; not seen), for which Caribbean pine is the English equivalent. Morelet's name was overlooked by botanists for about a half century and was not listed in Index Kewensis. The original publication apparently is rare, and no copy is available in the United States. Four years later the name P. caribaea Morelet (Soc. Hist. Nat. Dépt. Moselle Bul. 7: 100. 1855) was again published, also in an obscure, overlooked article, which we have examined at the Library of Congress. Discovery of the second article was reported by

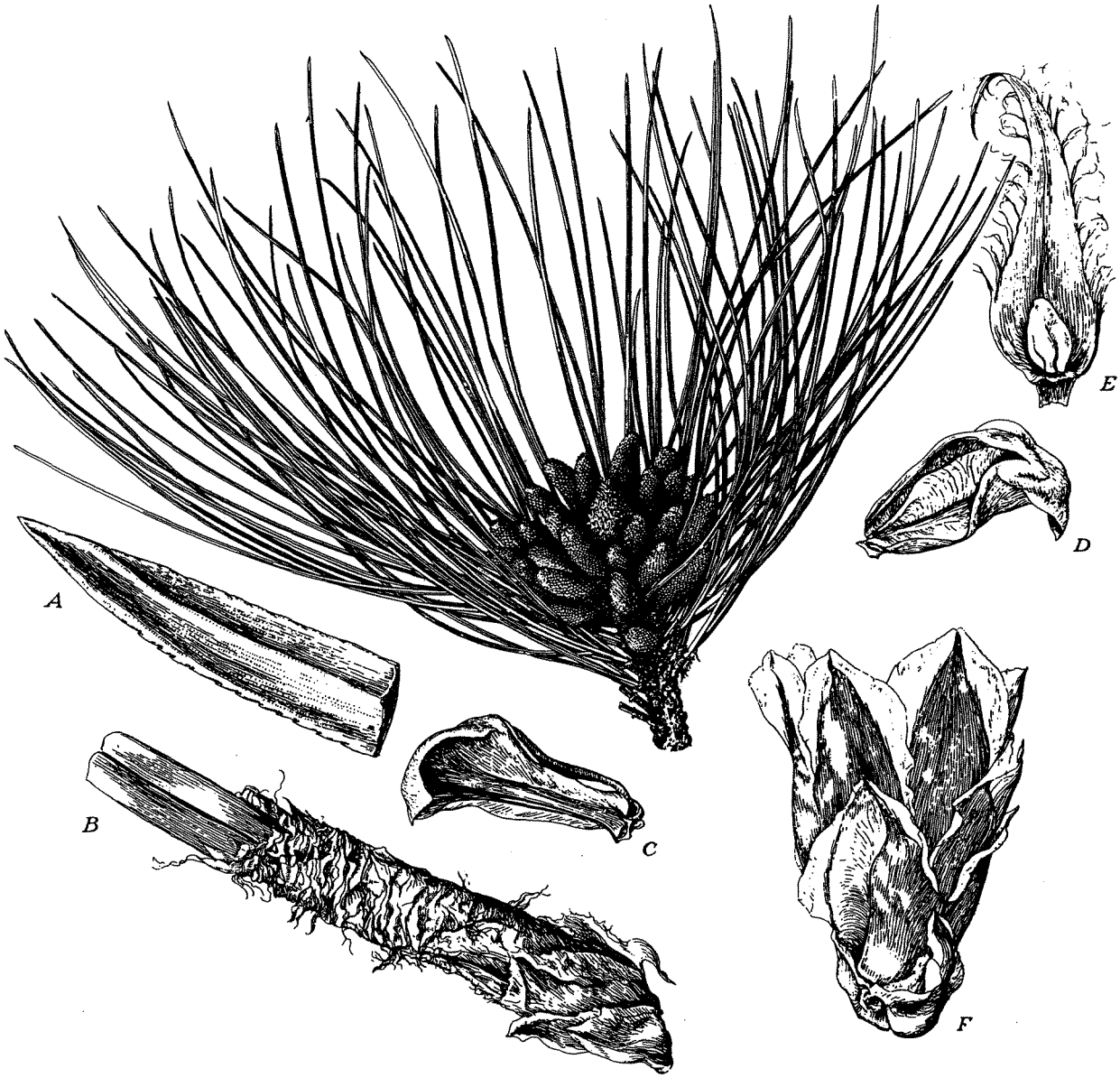


Fig. 1. --Drawings of South Florida slash pine from fresh specimen collected in Martin County, Florida, by W. B. De Vall, Jan. 23, 1945. Upper center, leafy twig with male cones or strobili before opening to shed pollen, almost ½x. A-F, details about 9x. A, apex of needle. B, sheath at base of fascicle of needles. C,D, microsporophylls with two opened pollen sacs. E, bud scale. F, bracts at base of strobilus. Drawing by Leta Hughey, U.S.D.A.

Shaw (1904a), who quoted the Latin diagnoses of this and another new species of pine. Afterwards, Shaw (1904b, pp. 52, 70) cited Morelet's first publication of the two names.

Morelet's (1855) second article described two new species of pines from Isle of Pines, P. tropicalis and P. caribaea, and included Latin and French descriptions of both. He noted the unexpected occurrence of pines at sea level in the tropics and gave appropriate geographic specific names. Oddly enough, the generic name Pinus was not published anywhere in the 4-page French article but was abbreviated to "P." before the two new names. However, the French word "pins" appeared in the title, the locality in Latin and French-Spanish as "insula Pinorum" and "l'île de Pinos" and the Spanish common name of P. caribaea as "pino blanco."

If Morelet preserved specimens of his two new species, the types have not been found in any large herbarium or cited by others. However, his descriptions of the only two species of pines at Isle of Pines are clear. As the island was named from the *forests* of *pines,* these *trees* are sufficiently common that various botanists including one of us have collected authentic specimens (topotypes) of both species at the type locality. The identity of the name P. caribaea with a pine growing at Isle of Pines is unquestioned.

Pinus caribaea Morelet is important because as the oldest name it must be adopted. Further, if the species is divided, that name must be retained for Morelet's pine, that is, the pine growing on Isle of Pines (International Code of Botanical Nomenclature, Art. 63. 1952).

Because of the rarity of Morelet's publications on pines, further notes may be worthy of record. Arthur Morelet, or Chevalier [Pierre Marie] Arthur Morelet (1809-1892), of France, was known principally as a malacologist but also collected plants and published a few papers on conifers. Starting late in 1846, he made a voyage to Cuba, Central America, and Yucatan, and explored the Maya ruins there while collecting plant and animal specimens. He published in French a detailed 2-volume account of his travels (Morelet, 1857), with a map showing that his route did not include the United States. One-volume translations of his explorations in Central America later were published in English in 1871 and in German in 1872. Two articles by him in 1849 and 1851 contained Latin diagnoses of 150 new species of mollusks collected on that trip. A brief biographic note in the valuable card file by J. H. Barnhart at the New York Botanical Garden listed five short biographic references.

August H. R.Grisebach (1864, p. 503) gave the name Pinus bahamensis Griseb. to cones without foliage from Bahama Islands. Another name by the same author, P. cubensis Griseb. (Amer. Acad. Arts Sci. Mem., new ser., 8: 530. 1863) was originally given to specimens collected by Charles Wright in eastern Cuba. For a time it was applied indiscriminately to Cuban pines (Engelmann, 1880, p. 185) and also to slash pine of southeastern United

States, as reported above. Sargent (1891-1902 ; 11: 158. 1897) included West Indies in the range of P. heterophylla, the name then applied to slash pine.

Rowlee (1903) in his field study of the pines of southern Florida, Cuba, and Isle of Pines in 1901 noted differences among the pines referred to P. cubensis Griseb. As already mentioned, he regarded the pine of southern Florida as a different species, P. heterophylla. At Isle of Pines in addition to P. cubensis he distinguished a new species, P. recurvata Rowlee (1903, p. 107), named from the recurved scales of the open cones. He noted in these Antillean tropical pines the increase in density and relative amount of summerwood in the annual ring, with increased weight per cubic foot and greater hardness of wood. Later authors have reduced P. recurvata to synonymy under P. caribaea Morelet, the older name not known at that time.

Shaw visited Isle of Pines and Cuba in 1903 and recorded the occurrence of P. heterophylla Sudw. at the former locality and raised to specific rank a variety of Grisebach as P. terthrocarpa (Wright) Shaw (in Sarg., Trees Shrubs 1: 149, pl. 75. 1903; 1: 213. 1905). In his illustrated account of the pines of Cuba (Shaw 1904a) he adopted P. bahamensis Griseb. for the former, but shortly afterwards his attention was called to Morelet's two earlier overlooked names. Accordingly Shaw (1904b) took up the names now in use, P. caribaea Morelet instead of P. bahamensis and P. tropicalis Morelet for P. terthrocarpa.

Coker (1905, p. 203, pl. 25, fig. 2) listed the pine of the Bahama Islands as P. bahamensis Griseb. but noted that it resembled P. taeda and was then thought to be identical with P. elliottii Engelm. from Florida.

In a flora of Isle of Pines based upon his collections in October 1916, Jennings (1917) listed both P. caribaea and P. tropicalis.

Britton and Millspaugh (1920, pp. vi, 461) recorded a single species of pine in Bahama Islands, P. caribaea Morelet (P. bahamensis Griseb.), It forms extensive forests on the Great Bahama, Abaco, Andros, and New Providence Islands and occurs also some distance southeastward on North Caicos and Pine Cay of the Caicos Islands but is absent from the other islands. A recent description of the pine forests of P. caribaea in the Bahamas is by Kellogg (1951).

Florin (1933), studying the coniferous specimens collected by E. L. Ekman in the West Indies, accepted P. caribaea Morelet in the broad sense as a species of West Indies, southeastern United States, and Central America. He described and illustrated the leaf anatomy also.

Roig y Mesa (1928, pp. 571-574, pl. 37; 1945, pp. 548-550) published for P. caribaea and two other native Cuban pines botanical descriptions, distribution data, and economic notes. The common names "pino macho" in Cuba and "pino amarillo" in Isle of Pines were listed for this species, and

southeastern United States was listed in the range. P. caribaea was included by Fors (1937, p. 85) in his publication on Cuban woods.

The most recent detailed taxonomic account of the pines of Cuba is by J. P. Carabia (1941). He recognized four native species of pines: P. occidentalis Swartz and P. cubensis Griseb. in mountains of eastern Cuba, the former also in Dominican Republic and Haiti; and P. tropicalis Morelet and P. caribaea Morelet, both in Pinar del Rio in western Cuba and in Isle of Pines. The distribution of the last was given also as southeastern United States, Bahamas, Honduras, and Guatemala. In the key, P. caribaea was listed as having 3 needles, rarely 4, in a fascicle. Led;; (1946, pp. 71-72) in his Flora de Cuba likewise accepted the same four species.

The pine forests of Cuba and Isle of Pines and distribution of pine species have been discussed in articles on the vegetation of these islands by Marie-Victorin and León (1942-1944) and Seifriz (1943). The ranges of these pines in Cuba were mapped also by Marie-Victorin and León (1942, p. 81, fig. 41).

CARIBBEAN PINE IN CENTRAL AMERICA

Forests of Pinus caribaea, Caribbean pine, along the Atlantic slope in Central America have been described and photographed by botanists and foresters in various publications, several of which may be cited here. Identification of the species as the same as P. caribaea of the West Indies has been almost unanimous by recent authors. -Under the name Cuban pine, Record and Hess (1943, p. 18, map 3), among others, mapped the range of P. caribaea in the broad *sense* in southeastern United States, West Indies, and Central America, showing the occurrence in Mexico, British Honduras, Guatemala, Honduras, and Nicaragua.

Pinus hondurensis Séneclauze (Conif. 126. 1867), an obscure, unindexed name hitherto overlooked, may be the first scientific name given to this pine in Central America. In 1867 Adrien Séneclauze, a French horticulturist, published this name in a book on the cultivated conifers in his horticultural establishment. P. hondurensis was a pine grown in France from seed received from Honduras in 1854. We are indebted to I. M. Johnston and Albert G. Johnson, of Harvard University, for bringing this old name to our attention and for furnishing a copy of Séneclauze's description in French, which we quote:

"Pinus Hondurensis C. S.
"Pin de Honduras

"Feuilles réunies par 3, 4, quelquefois même par 5, 6, dans la même gaine, ténues, triquètres, lisses, d'un beau vert tendu luisant, tres-inégales, souvent tortuenses, longues de 12-22 centimetres. Gaines

membraneuses, brun clair, lisses et luisantes. Longues de 10-20 millimètres. Coussinets peu saillants, longuement décurrents. Écorce d'un bronze clair, brillant, profondement sillonnée par la décurrence de coussinets.

"Belle espèce, rustique. Recue en 1854."

This description of pines growing in a commercial establishment agrees fairly well with P. caribaea but lacks the important details of cones for positive identification. Probably the trees had not yet borne cones. It is doubtful if specimens are available. Record (1927, p. 33) and Standley (1930a, pp. 25-26) listed only three species of Pinus from Honduras, P. caribaea, P. oocarpa Schiede, and P. pseudostrobus Lindl. Paul J. Shank has informed us by letter that P. ayacahuite Ehrenb., a 5-needle soft pine, also occurs in mountains of that country. P. caribaea is common at lower elevations down to sea level and would be the species most likely collected first.

In the first comprehensive flora of Central America by Hemsley (1879-1888); 3: 186-189. 1882-1886), no pine corresponding to P. caribaea or from the Atlantic Coast of Central America was mentioned. Sargent (1891-1902; 11: 158. 1897) adopting the name P. heterophylla for a species of southeastern United States, mentioned highlands of Central America in the range. Probably present usage of P. caribaea follows the generic monograph by Shaw (1914, p. 72), who recorded this species from Honduras and Guatemala.

Standley (1930a, p. 198) in his flora of the Yucatán Peninsula in Mexico mentioned that no pines from that region were available but that pines presumably of P. caribaea, which is common in nearby regions, were reported from near the border of British Honduras. Many plant species of British Honduras have not yet been collected in the adjacent but poorly known Mexican territory of Quintana Roo. P. caribaea was not included in the monograph of the pines of Mexico by Martínez (1945, 1948). In a letter he informed us that it may be expected in Quintana Roo but that he had seen no specimen from there.

The pine forests of British Honduras were described by Standley and Record (1936, pp. 20, 33, 45, 67, illus.), who regarded the common pine, P. caribaea, as the same as slash pine of southern Florida,. Lundell (1940, p. 36, pl. 2-4, 1945, pp. 270-272, map) has published additional data on these pine lands, including a vegetation map. Tests of properties of the wood of P. caribaea, with the trade name British Honduras pitch pine, by Richard Gordon Bateson, were reported in a forest products research publication of Great Britain, Department of Scientific and Industrial Research (1937).

Standley (1941, p. 3) noted that P. caribaea, as Cuban pine in Guatemala, was confined to the Atlantic Coast area in the eastern part, chiefly in the Department of Izabal. In their report on the forests of

Guatemala, Holdridge, Lamb, and Mason (1950, pp. 16, 27, map) recorded P. caribaea, pino, from the subtropical moist forest at low elevations in northern and eastern parts of the country, including the southeastern part of Petén.

In Honduras, Record (1927, p. 33) and Standley (1930b, p. 25) listed P. caribaea, with the common names "ocote," "pino ocote," and "pinavete," as one of three native species of pines.

Fahnestock and Garratt (1938) recorded the distribution of P. caribaea, as Nicaraguan pine, in Nicaragua in the northeastern part-chiefly from Rio Prinzapolca south to Rio Grande, the southern limit of commercial range of the species. They also made tests of the properties of the wood. More recently the pine forests of P. caribaea in Nicaragua have been described further and mapped by the Food and Agriculture Organization mission to Nicaragua (Food and Agriculture Organization, 1950, pp. 48-52, map).

Recently Loock (1949, pp. 61-62, fig. 2) considered the British Honduran pine as altogether different from P. caribaea of the United States and renamed the former P. hondurensis L-51, p. 210, pl. on p. 209). This new name, which is identical with the much older name by Seneclauze, is discussed below under P. caribaea. Loock listed differences in seedlings, leaves, needle anatomy, cones, and seeds and reported that in plantations in Natal, South Africa, pines from British Honduras seed grew about one and a half times as fast as pines from seed from Georgia. The scientific name P. caribaea has been applied to pines cultivated in Australia, as well as to plantations in South Africa from seed collected in southeastern United States, Cuba, and British Honduras.

OUR INVESTIGATIONS OF PINUS CARIBAEA AND P. ELLIOTTII

Our studies of these pines have included field observations and collection of specimens, examination of herbarium specimens and fresh material, and a check of the nomenclature. In January 1951 we made an extended field trip over the range of slash pine in southeastern United States, collecting specimens in South Carolina, Georgia, Florida, Alabama, and Mississippi, all the States where this pine is native except Louisiana. That was the best time of year to obtain male and female strobili at pollination, year-old cones, and opened mature cones. We traveled through Florida along the western part from Pensacola eastward, down the west coast, to Key West, and north along the east coast in studying the variations of slash pine, particularly South Florida slash pine. The senior author made a brief side trip to Isle of Pines to study *Pinus caribaea* Morelet at the type locality and to collect authentic specimens.

At the Harrison Experimental Forest, near Gulfport, Miss., we examined the experimental plantings of young pines from Mississippi, northern Florida, south Florida, Cuba, and British Honduras, made by the Division of Forest Pathology, U. S. Department of Agriculture. Near La Belle, Fla., we studied extensive forests of South Florida slash pine of the Atlantic Land and Improvement Company in Hendry and Collier Counties.

In September 1952 we revisited southern Florida, making additional observations. The senior author has examined the herbarium specimens of *Pinus caribaea* and *P. elliottii* in herbaria of the United States National Museum (U. S. National Herbarium, in the lists of specimens abbreviated to US) and New York Botanical Garden (NY), and material of P. *caribaea* from West Indies and Central America kindly lent by the Chicago Natural History Museum (F). We also studied the material in the University of Florida herbarium. In addition to our own collections, personnel of the U. S. Forest Service has furnished fresh material. These specimens have been deposited in the Forest Service Herbarium (USFS) at Washington, D. C.

The results of our investigations are presented in the formal taxonomic treatment which follows. Among the hard pines with shiny brown cones generally classified as *Pinus caribaea* Morelet, three different geographically separated populations or taxonomic entities (taxa) merit distinct botanical names. The available scientific names here accepted for these three groups have been reviewed under history of nomenclature. In the subsequent discussion the more important characters upon which the classification is based are further described.

TAXONOMIC TREATMENT

Pinus caribaea and P. elliottii are closely related species, belonging to subgenus Diploxylon, the hard pines, and to Section Australes, which is typified by Pinus palustris Mill. (P. australis Michx. f.), longleaf pine. The species in this section are found in southeastern United States, West Indies, Mexico, and Central America, though specialists have not agreed upon the exact limits of the section or upon all the species to be placed in it.

Under the widely followed classification of the genus Pinus by Shaw (1914), the group Australes contains besides P. occidentalis Swartz from West Indies, P. ponderosa Laws. from western North America, and other species from Mexico and Central America, and the following related species in southeastern United States: P. palustris Mill. (longleaf pine), P. caribaea Morelet (including P. elliottii, slash pine), P. taeda L. (loblolly pine), P. echinata Mili. (shortleaf pine), and P. glabra Walt. (spruce pine).

Pilger (1926) in a slightly different, later classification of the genus Pinus retained in Section Australes 6 species, P. palustris, P. caribaea (including P. elliottii), P. occidentalis Swartz of the West Indies, P. oocarpa Schiede of Mexico and Central America, and two other Mexican species.

The related native species may be readily distinguished by reference to botanical manuals and tree handbooks. De Vall (1940, 1945) has enumerated the differences between slash pine and longleaf pine. P. caribaea and P. elliottii are separated from other related pines partly by their shiny iight brown cones. The mature unopened cones with the shiny exposed, thickened ends (apophyses) of the cone scales appear as if varnished.

The key which follows mentions the more obvious differences between P. caribaea and P. elliottii and varieties. Additional distinguishing characteristics are given in the formal botanical descriptions and in table 1.

Key to Pinus caribaea and P. elliottii and varieties:

A. Needles in fascicles of 3 (sometimes 4 or 5 on young trees); cones usually small (5-10 cm. long), with small weak prickles less than 1 mm. long; seeds narrowly ovoid, about twice as long as broad, averaging less than 6 mm. long, wings usually remaining attached--Pinus caribaea Morelet, Caribbean pine.

AA. Needles in fascicles of 2 and 3; cones usually larger (7-14 cm. long), with stout prickles 1-2 mm. long; seeds ovoid, less than twice as long as broad, averaging 7 mm. long,

wings becoming detached--Pinus elliottii Engelm., slash pine.-B

B. Needles in fascicles of 2 and 3; seedling normal with erect, slender, pencillike stem--Pinus elliottii var. elliottii, slash pine (typical).

BB. Needles in fascicles of 2 (infrequently 3); seedling with grasslike, almost stemless stage with very short stem, many crowded needles, and thick taproot--Pinus elliottii var. densa Little & Dorman, South Florida slash pine.

PINUS CARIBAEA Morelet — Caribbean pine

Pinus caribaea Morelet, Rev. Hort. C&e d'Or 1: 105. 1851 (not seen). Morelet, Soc. Hist. Nat. Dépt. Moselle Bul. 7: 100. 1855. Morelet ex Shaw, Gard. Chron., Ser. 3, 36: 98. 1904.
Pinus bahamensis Griseb., Fl. Brit. West Ind. Is. 503. 1864.
Pinus hondurensis Séneclauze, Conif. 126. 1867.
Pinus recurvata Rowlee, Torrey Bot. Club Bul. 30: 107. 1903.
Pinus hondurensis Loock, So. Africa Forestry Assn. Jour. 18: fig. 2 opposite p. 60. 1949; nomen nudum.
Pinus hondurensis Loock, Union So. Africa Dept. Forestry Bul. 35: 210, pl. on p. 209. 1951.

Medium-sized to large tree about 15-30 m. (50-100 ft.) tall and 30-100 cm, (12-40 in.) in trunk diameter, multinodal, with broad, rounded or irregular crown of irregular ascending branches. Bark on small trees thick, rough, furrowed, gray, on large trees becoming fissured into large, flattened squarish plates, reddish brown and separating off in thin layers.

Buds composed of many linear acuminate, white-ciliate, reddish brown scales; old scales on twig becoming recurved, gray, and broken. Leafy twigs 5-12 mm. in diameter, orange brown when young, becoming brown to gray brown, rough and scaly. Leaves needlelike, crowded and spreading at ends of twigs and remaining attached about 2 years, in fascicles of 3 (sometimes 4 or 5 on young trees, very rarely 2), mostly 15-25 cm. long, 1.5 cm. or less broad, rigid, serrulate, dark or yellowish green, slightly shiny, with stomata in whitish lines on all surfaces; resin ducts 2-8, internal *or rarely* 1 medial; hypoderm biform, thick, of 3 to 5 layers of cells; sheaths 10-12 mm. long, light brown, becoming brown to blackish, persistent (fig. 2).

Strobili appearing before the new leaves, in January or February, when pollination occurs. Male strobili many, sessile in short, crowded clusters near ends of twigs mostly in lower part of crown, cylindrical, 20-32 mm. long, 5 mm. broad, with 12-18 ovate, scarious margined, reddish brown bracts at base. Femalestrobili mostly in upper part of crown, appearing near apex of elongating twigs but becoming lateral, 2-4 (1-8) in a whorl and 1-3 whorls formed in a year. Year-old cones (conelets) erect to

Fig. 2. --Caribbean pine (Pinus caribaea Mor.) from Isle of Pines. At the top, twig with three whorls of year-old cones and female cones at pollination. Below, twig with male cones at pollination.

reflexed on scaly stalks l-l.5 cm. long, ellipsoidal, 1.5-2 cm. long and 1 cm. broad, the shiny tan scales with a minute prickle.

Mature cones (fig. 3) usually reflexed, symmetrical, 5-10 (4-E) cm. long, when closed conical, more than twice as long as broad, and 2.5-3.5 cm. in diameter, when open cylindrical to ovoid and 3.5-6 cm. in diameter, usually deciduous (in some areas persistent a year or more). Cone scales reflexed or wide spreading, thin, flat, dark chocolate brown on inner surfaces; apophysis with a transverse ridge, tan and shiny; umbo small, slightly raised, gray, ending in an inconspicuous small straight weak prickle less than 1 mm. long.

Seeds narrowly ovoid, about twice as long as broad, pointed at both ends, j-angled; averaging less than 6 mm. long, 3 mm. wide, and 2 mm. thick; usually light colored, mottled gray or light brown; with a membranous brown wing less than 20 mm. long, usually remaining attached.

Seedling normal, with erect, slender, pencillike stem. Cotyledons usually 6 or 7 (4-9).

Wood hard and heavy, with annual rings, formed in a frostless tropical climate with dry winter season, and with broad summerwood.

There is a small cone race at Pine Cay, Caicos Islands, in southeastern Bahamas, some distance from the large islands to the northwest having pines. The cones on specimens from Pine Cay are only 4-6.5 cm. long. However, specimens with large cones 8-9 cm. long have been collected on North Caicos, also in the Caicos group.

As previously mentioned, Loock (1951, p. 210, pl. on p. 209) has proposed the new species P. hondurensis Loock for the segregate pine of British Honduras and Guatemala and probably also Cuba identified as P. caribaea, because it differed from a pine of the latter name from Georgia and Florida in southeastern United States. Though we have not had the opportunity of inspecting the Central American pine in the field, many herbarium specimens including topotypes of P. hondurensis Loock from Stann Creek, British Honduras, as well as published descriptions and photographs by Loock and others, have been available for study. We concur that the Central American pine is specifically different from slash pine of southeastern United States but are unable to separate the former botanically from the West Indian pine, P. caribaea. Thus, P. hondurensis Loock is a synonym of P. caribaea as well as a homonym and perhaps also synonym of P. hondurensis Séneclauze and cannot be maintained. It is the pine of-southeastern United States instead, which requires a change in name to P. elliottii Engelm. under the International Code of Botanical nomenclature.

Since many tropical plant species are common to Central America and Cuba, the occurrence of a tropical species of pine in both not too

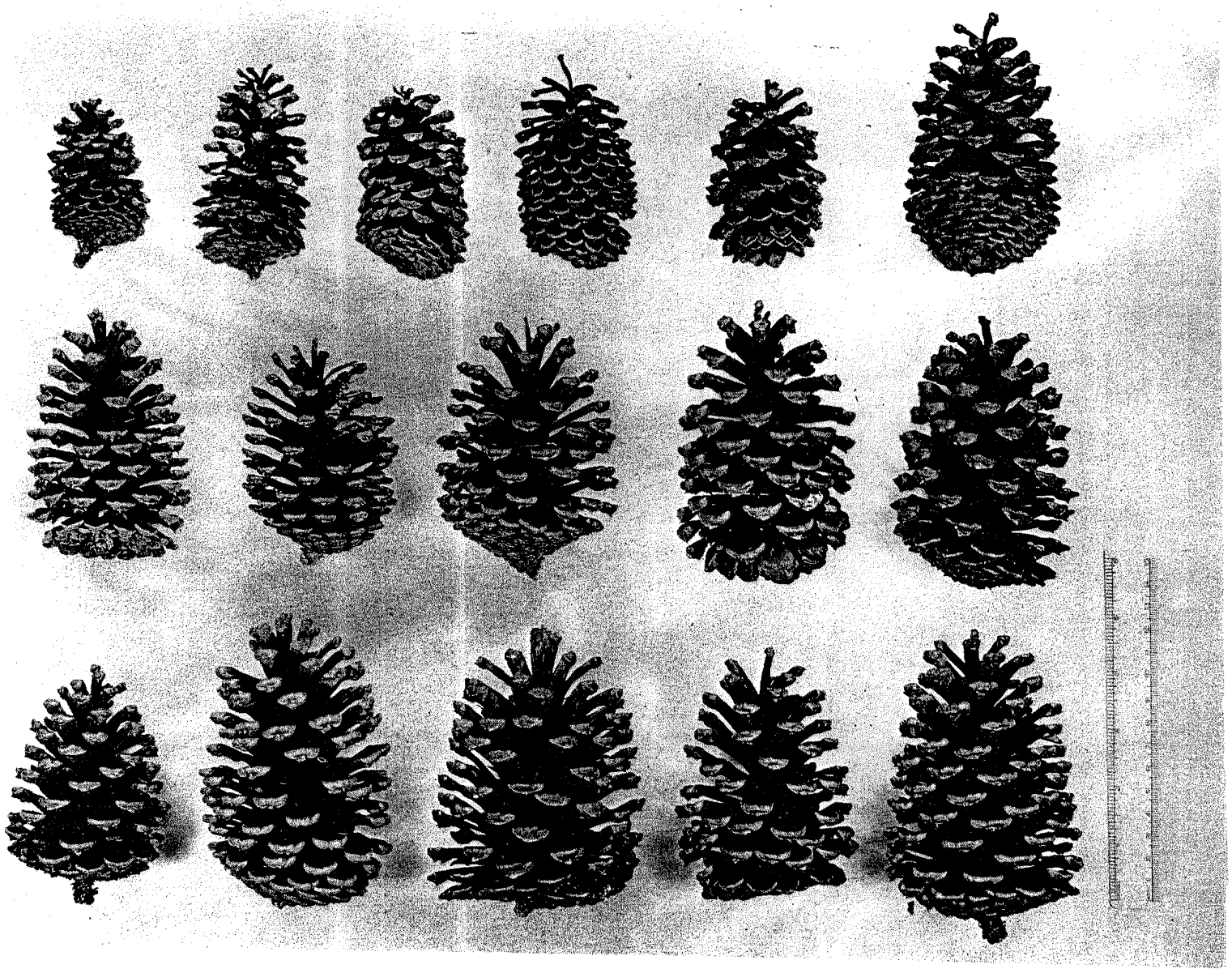


Fig. 3.--Cones of Pinus caribaea and P. elliottii. Top row, first two cones at left are Caribbean pine from Isle of Pines (collection numbers, Little 14047, 14051). Other cones in top row and middle row are South Florida slash pine (Little and Dorman 14042, -43, -54, -24, -25, -33, -59, -60, -61). Those in the bottom row are typical slash pine (Little and Dorman 14010, -21, -68, -73, -75).

distant regions is not unexpected. However, future studies in plantations may reveal minor differences in growth and the existence of different races. Loock has noted the reported occurrence of races in British Honduras. Our studies indicate'that seedlings from British Honduras are tall and slender with many juvenile leaves and that the number of resin ducts in the needles (table 2) is commonly slightly lower in British Honduras (2-5) than in the West Indies (3-8).

Though it was discovered at Isle of Pines, this pine is uncommon there and appears to be decreasing in numbers. The common pine for which the island was named is P. tropicalis Morelet, tropical pine, also described from there. Photographs taken at Isle of Pines show differences in seedlings, saplings, and trees of both species (figs. 4, 5). Pinus tropicalis

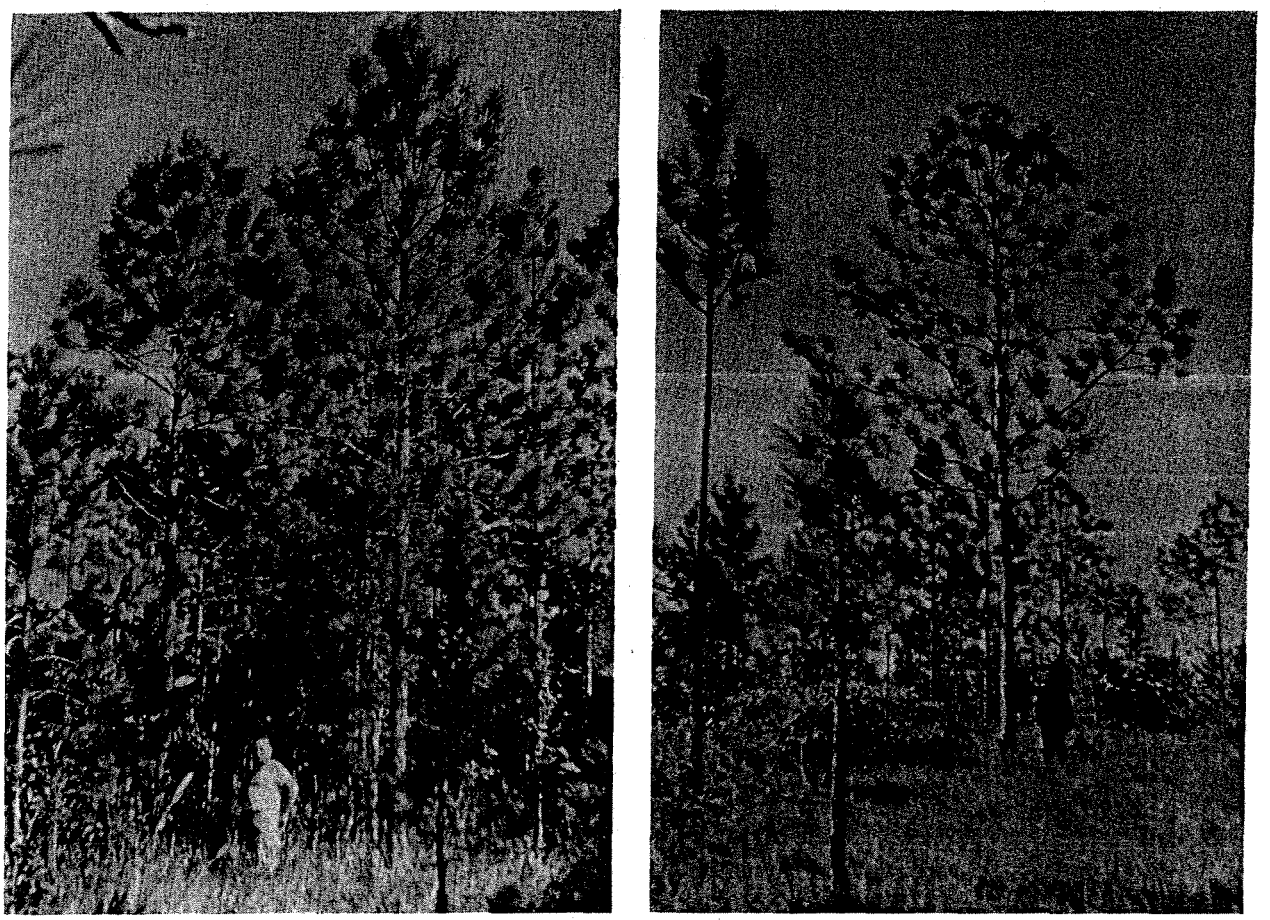


Fig. 4.--At the left, Caribbean pine at Isle of Pines, the type locality, showing saplings and trees with branches not in whorls. At the right, larger tree of Caribbean pine 35 feet high and 8 inches d.b.h. at Isle of Pines. At left foreground are two saplings of tropical pine.

Fig. 5. --At the left, tropical pine (Pinus tropicalis) at Isle of Pines, the type locality, showing an unbranched sapling and trees with whorled branches. At the right, trees, of tropical pine at Isle of Fines, distinguished by their whorled branches.

is readily distinguished by its grasslike seedling stage, needles in 2's and often longer, and smaller cones without prickles. A uninodal pine, it forms one whorl of branches a year and is recognized by the regular, whorled branching. Occasional saplings have few branches or are unbranched (fig. 5).

Range--West Indies and Central America. Bahama Islands (six or more, namely, Grand or Great Bahama Is., Great Abaco Is., New Providence Is., and Andros Is. at northwestern end; North Caicos Is. and Pine Cay in Caicos Is. at southeastern end; absent from most of Bahama Is.). Western Cuba, in province of Pinar del Rio. Isle of Pines. Atlantic slope of Central America in British Honduras, eastern Guatemala, northern Honduras, and northeastern Nicaragua. Perhaps also in southeastern Quintana Roo, Mexico.

Representative specimens of P. caribaea Morelet examined:

BAHAMA IS. Great Bahama Is., Eight Mile Rocks, N. L. Britton and C. F. Millspaugh 2469 (US, NY). Great Abaco Is., Marsh Harbor, L. J. K. Brace 1634 (NY). New Providence Is., 3½ mi. S. of Nassau, A. E. Wight 75 (NY, F). Andros Is., Nicholl's town, L. J. K. Brace 6895 (NY, F--2 sheets with pencillike seedlings); near Lisbon Creek, Mangrove Cay, J. K. Small and J. J. Carter 8497 (US, NY, F). Caicos Is., North Caicos, Bellemont, C. F. Millspaugh and C. M. Millspaugh 9187 (NY, F); Pine Cay, P. Wilson 7694 (NY, F).

CUBA. Pinar del Río, Guane to Mantaua, J. A. Shafer 11209 (us, NY, F); Los Palacios to Herradura, J. A. Shafer 11697 (US, NY); San Diego de los Banos, N. L. Britton, F. S. Earle, and C. S. Gager 6766 (us, NY): Pan de Cajalbana, Bros. León and Charles 4935 (NY); Vinales, E. P. Killip 13559 (US).

ISLE OF PINES (CUBA). (Type locality of P. caribaea Morelet.) S. W. of Vivijagua, 0. E. Jennings 82 (NY); 15 mi. W. S. W. of Nueva Gerona, E. L. Little, Jr., 14047 (US, USFS).

MEXICO. Quintana Roo. Reported but apparently not yet collected. No specimens at US, NY, F.

BRITISH HONDURAS. Stann Creek District (type locality of P. hondurensis Loock), 6 mi., Stann Creek Ry., W. A. Sehipp 386 (NY, F). Belize District, Belize, H. C. Kluge in May 1920 (US, NY). Honey Camp, C. L. Lundell 677 (US, F). El Cayo District, Mountain Pine Ridge, H. H. Bartlett 11934 (US, Maskall Pine Ridge, P. H. Gentle 1130 (NY, F).

GUATEMALA. District of Pete;, La Libertad, C. L. Lundell 2846 (US, F). Dept. Alta Verapax, Secaquim, W. R. Maxon and R. Hay 3141 (NY). Dept. Izabal, near Cristina, J. A. Steyermark 38416 (US, F).

HONDURAS. Dept. Yoro, near Coyoles, T. G. Yuncker, J. M. Koepper, and K. A. Wagner 8182 (US, NY, F). Dept. Cortes, near Agua Azul, L. 0. Williams and A. Molina R. 11315 (F). Dept. Morazán, Quebrada de Santa Clara, near Río Yeguare, P. C. Standley and L. 0. Williams 1288 (F). San Pedro Sula, W. N. Bangham 317 (US, F). Near Olanchito, S. J. Record and H. Kuylen in Feb. 1927 (US).

NICARAGUA. Sisin, on Segovia River about 50 mi. inland from Cape Gracias, R. G. Robinson, Oct. 1, 1943 (US).

PINUS ELLIOTTII Engelm. slash pine

Pinus elliottii Engelm., Acad. Sci. St. Louis Trans. 4: 186, pl. 1-3. 1880; also reprinted as folio.

Pinus palustris Mill. (Gard. Dict. Ed. 8, Pinus No. 14. 1768) was adopted by Small (1933, pp. 4-5) and a few other authors for this species. However, that name generally has been accepted for longleaf pine, though more recently rejected by others as indefinite, and apparently does not apply to slash pine.

This species honors Stephen Elliott, South Carolina botanist, who first distinguished slash pine as a botanical variety of loblolly pine, Pinus taeda var. heterophylla Ell., in his Sketch of the Botany of South-Carolina and Georgia (1816-24). Though no type specimen was designated, Engelmann's original description was based largely upon numerous -specimens collected by J. H. Mellichamp at Bluffton, S. C., and deposited in several herbaria. Rolla M. Tyron, Jr., of the Missouri Botanical Garden, has informed us that the herbarium of that institution contains 39 sheets, representing various stages and parts, collected by Mellichamp between 1872 and 1880 and labeled P. elliottii by Engelmann. Identity of the description, plates, and specimens with slash pine is unquestioned. The generalized specific description which follows includes both varieties.

Small to large trees about 8-30 m. (25-100 ft.) tall and 20-100 cm. (8-40 in.) in trunk diameter, multinodal, with narrow or broad crown. Bark on small trees thick, rough, furrowed, gray; on large trees becoming fissured into large, flattened, squarish plates, orange or reddish brown and separating off along thin purplish layers.

Winter buds about 12 mm. long and 6 mm. in diameter, composed of many linear acuminate, white-ciliate, reddish brown scales, elongating in early spring to form scaly, candlelike twigs almost 1 cm. in diameter; old scales on twig becoming recurved, gray, and broken. Leafy twigs stout, 10-12 mm. in diameter, orange brown when young, becoming brown to gray brown, rough and scaly. Leaves needlelike, crowded and spreading at ends of twigs and remaining attached about 2 years, in fascicles of 2 and 3, mostly 18-25 (30) cm. long, 1.5 mm. broad, rigid, serrulate, dark green, slightly shiny, with stomata in whitish lines on all surfaces; resin ducts 2-9 (11), internal or sometimes 1 or 2 (rarely 4) medial; hypoderm biform, thin to thick, of 2-4 layers of cells; sheaths 12-15 mm. long, light brown, becoming gray, persistent.

Strobili appearing before the new leaves, in January or February, when pollination occurs. Male strobili many, sessile in short, crowded clusters near ends of twigs mostly in lower part of crown, cylindrical, 3-6 cm. long, 5-7 mm. broad, dark purple, with about 11 or 12 ovate, scarious margined, reddish brown bracts at base. Female strobili mostly in upper part of crown, appearing near apex of elongating twigs but becoming

lateral, l-3 (sometimes 5 or more) in a whorl and 1 or sometimes 2 (rarely 3) whorls formed in a year. At pollination, female strobili erect on stout brownish scaly stalks 15 mm. long, ellipsoidal, 11-13 mm. long and 6 mm. wide, pinkish to pale purple, the scales with minute pale green points about .5 mm. long; after pollination becoming darker and reddish purple. Year-old *cones (conelets)* erect, spreading, or reflexed on scaly stalks 1-1.5 cm. long, ellipsoidal, 15-22 mm. long and 10-15 mm. broad, the shiny tan scales with raised, pointed umbo and with a stout prickle.

Mature cones spreading *or* reflexed, symmetrical, mostly 6-14 cm. long, when closed conicalto narrowly ovoid, mostly more than twice as long as broad, and 3-5 cm. in diameter, when open ovoid to cylindrical and 4-10 cm. in diameter, deciduous. Cone scales spreading or slightly reflexed, thin, flat, dark chocolate brown on inner surfaces; apophysis with a transverse ridge, tan to brown, shiny; umbo raised, gray or tan, ending in a stout gray prickle 1-2 mm. long, straight *or* slightly incurved or recurved.

Seeds ovoid, less than twice as long as broad, pointed at lower end, and slightly 3-angled; averaging about 7 mm. long, 4 mm. wide, and 3 mm. thick; blackish or mottled gray; with a membranous wing 15-30 (35) mm. long, light to dark brown, becoming detached.

Seedling normal or in a variety grasslike and almost stemless. Cotyledons usually 7 *or 8 (5-10).*

Wood heavy to very heavy and hard.

Range--Southeastern United States, Coastal Plain from southern South Carolina to southern Florida and eastern Louisiana.

PINUS ELLIOTTII Engelm. var. ELLIOTT11 slash pine (typical)

Pinus taeda L. var. heterophylla Ell., Sketch Bot. S.-C. Ga. 2: 636. 1824.
Pinus elliottii Engelm. ex Vasey, Cat. Forest Trees U. S. 30. 1876; U. S. Commr. Agr. Rpt. 1875: 178. 1876; nomen nudum.
Pinus elliottii Engelm. ex Sarg., Cat. Forest Trees No. Amer. 74. 1880; nomen nudum.
Pinus elliottii Engelm., Acad. Sci. St. Louis Trans. 4: 186, pl. l-3. 1880; also reprinted as folio.
Pinus heterophylla (Ell.) Sudw., Torrey Bot, Club Bul. 20: 45. 1893. Non P. heterophylla K. Koch, Linnaea 22: 295. 1849. Non P. heterophylla Presl, Epim. Bot. 236. 1849.

The new name Pinus elliottii var. elliottii conforms to a change in the International Code of Botanical Nomenclature (Art. 35) made in 1950. When a new variety is published, the original element of a species automatically becomes the typical variety with specific epithet repeated. However,

in ordinary usage by foresters where this typical, widespread, more northern variety clearly is meant, the shorter name Pinus elliottii or slash pine should suffice as heretofore.

Large tree about 15-30 m. (50-100 ft.) tall and 60-100 cm. (24-40 in.) in trunk diameter, with erect straight axis and narrow pointed crown. Leaves in fascicles of 2 and 3; resin ducts 2-8 (9), internal or sometimes 1 or 2 medial; hypoderm biform, thin, of 2 (sometimes 3) layers of cells (fig. 6).

Mature cones mostly 9-14 cm. long, when closed mostly conical, mostly more than twice as long as broad, and (3) 4-5 cm. in diameter, when open ovoid and (5) 6-10 cm. in diameter (fig. 3). Cone scales spreading.

Seedling normal, with erect, slender, pencillike stem.

Wood representative of southern yellow pines, with normal proportions of springwood and summerwood, relatively heavy.

Snow, Dorman, and Schopmeyer (1943) have photographed the early stages of female strobili of typical slash pine. Coker and Totten (1934, p. 21) illustrated year-old cones of P. elliottii, showing erect, spreading, and reflexed cone stalks all from the-same tree. The degree of curvature of the stalks possibly may depend partly upon the position of the twig in relation to gravity. J. H. Mellichamp, of Bluffton, S. C., found two trees which produced bisexual strobili and distributed specimens with this abnormality. At the upper ends of some male strobili were female strobili. Sargent (1891-1902; 11: 4. 1897) mentioned these bisexual cones, which also have been observed in other species.

Range--Southeastern United States, Coastal Plain in southern South Carolina (from Berkeley County southward), southeastern and southern Georgia, northern, western, and central Florida south to Lake Okeechobee, southern Alabama, southern Mississippi, and southeastern Louisiana (west to Tangipahoa Parish).

Representative specimens of Pinus elliottii Engelm. var. elliottii examined:

SOUTH CAROLINA. Berkeley Co., Francis Marion National Forest, 8 mi. S. of Jamestown, E. L. Little, Jr., and J. W. Wood 14327 (US, USFS). -Hampton co., 7 mi. N. of Estill, E. L. Little. Jr., and K. W. Dorman 14074 (US., USFS). Beaufort Co., Bluffton, J. H. Mellichamp in June 1871, 1875, 1876, 1881, 1893, and 1894 (the last one with bisexual strobili; all at US); J. H. Mellichamp in 1872, 1873, 1876, 1878, 1879 (all at NY).

GEORGIA. Chatham Co., near Montgomery, R. M. Harper 1822 (US). Emanuel Co., near Oak Grove, E. J. Palmer 38275 (US, NY). Long Co., 4 mi. NW of Ludowici, E. L. Little, Jr., and K. W. Dorman 14073 (US, FS). Coffee co., near Douglas, R. M. Harper 2046 (US).

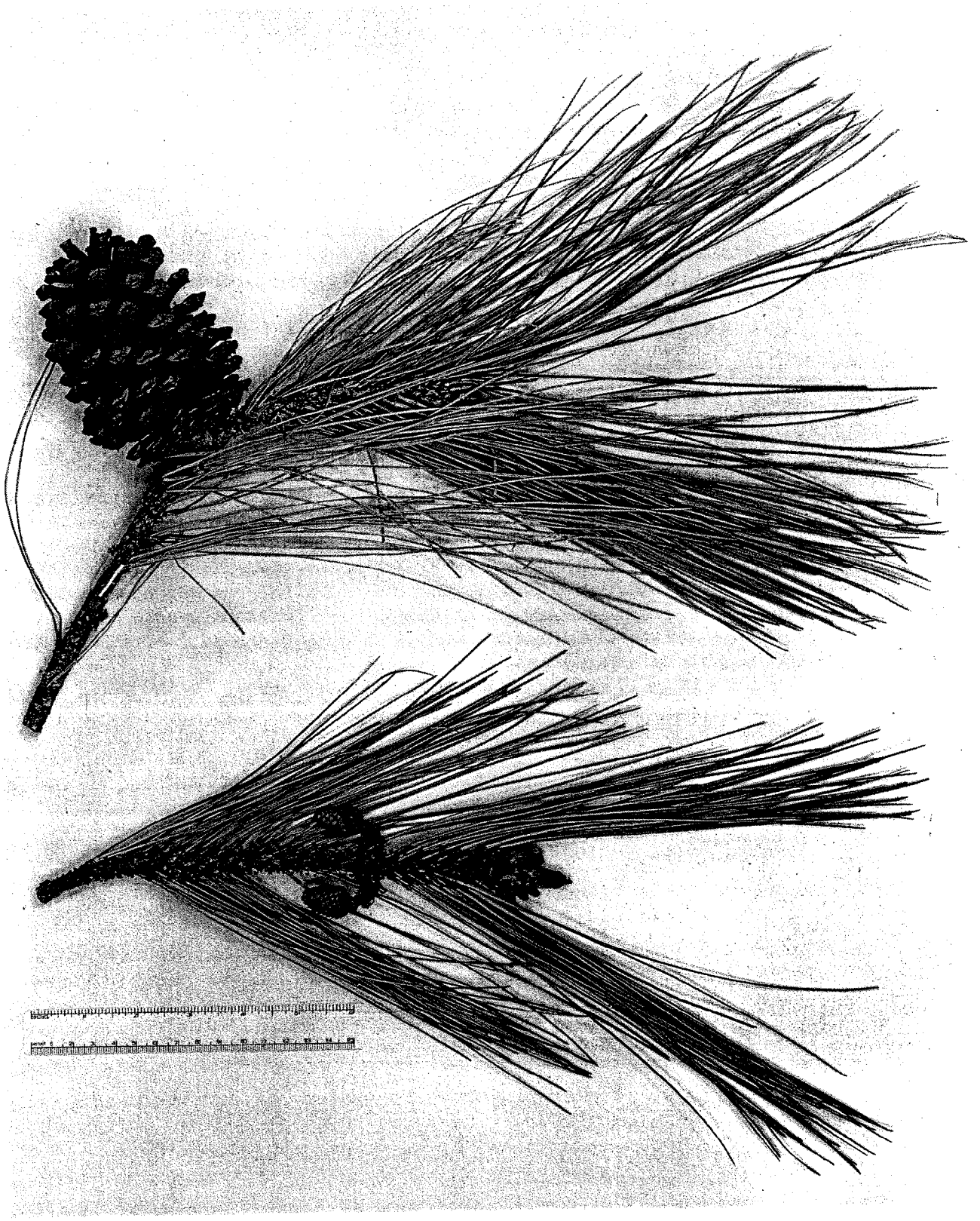


Fig. 6.--Slash pine (Pinus elliottii var. elliottii). At the top, twig with mature cone, Alachua County, Florida. Below, twig with year-old cones and immature male cone, Hampton County, South Carolina.

ALABAMA. Escambia Co., 16 mi. E. of Brew-ton, E. L. Little, Jr., and K. W. Dorman 14004 (US, FS). Mobile Co., Mobile, C. Mohr, Feb. 2, 1880 (us).

MISSISSIPPI. Harrison Co., Mississippi City, E. L. Little, Jr., and K. W. Dorman 14010 (US, USFS).

LOUISIANA. Washington Parish, W. R. Mattoon in May 1917 (NY). St. Tammany Parish, W. R. Mattoon in May 1917 (NY). Tangipahoa Parish, W. R. Mattoon in May 1917 (NY).

FLORIDA. Duval Co., Jacksonville, A. H. Curtiss 2651 (US). Baker co., Olustee, A. H. Antonie and L. G. Elfer 8367 (N. Y. State Coll. Forestry Project I, distributed with wood samples, US). Alachua Co., Phifer, 10 mi. SE of Gainesville, E. L. Little, Jr., and K. W. Dorman 14063 (US, USFS). Levy Co., 5 mi. S. of Lebanon Station, E. L. Little, Jr., and K. W. Dorman 14021 (US, FS). Franklin Co., St. Vincent Is., Biological Survey, Nov. 13, 1911 (us).

PZNUS ELLZOTTZZ Engelm, var. *DENS,4* Little and Dorman South Florida slash pine

Pinus elliottii Engelm. var. densa Little and Dorman, Jour. Forestry 50:921, figs. 1, 2. 1952.

A varietate typica differt statu juvene graminiforme cum caule perbreve, foliis multis densis, hypocotyle densissima, et radice primario denso; etiam foliis plerumque 2 in fasciculo, anatomia foliorum cum hypodermide densa biforme in 3- vel 4-seriebus cellularum, et ligno ponderoso duro cum parte aestivale densissima.

Differs from the typical variety in its grasslike seedling stage, with very short stem, many crowded needles, very thick hypocotyl, and thick tap root; also in its leaves mostly 2 in a fascicle, in its needle anatomy with thick biform hypoderm of 3 or 4 layers of cells, and in its very heavy hardwood with very thick summerwood.

The specific epithet densa, dense, refers to the dense, very heavy, hardwood with very thick summerwood; also to the grasslike seedlings with crowded needles, very thick hypocotyl, and thick taproot, and to the thick hypoderm of the needles.

Medium-sized or small (to large) tree 8 to 26 m. (25-85 ft.) tall and 20-50 cm. (8-20 in,) in trunk diameter, maximum size 31 m. (100 ft.) and 107 cm. (42 in.), with axis often forking into large branches and with irregular, flat-topped and spreading, open crown. Leaves in fascicles of 2 (infrequently 3); resin ducts 3-9 (11), internal or sometimes 1 or 2 (rarely 3 or 4) medial; hypoderm biform, thick, of 3 or 4 (2-5) layers of cells (fig. 7).

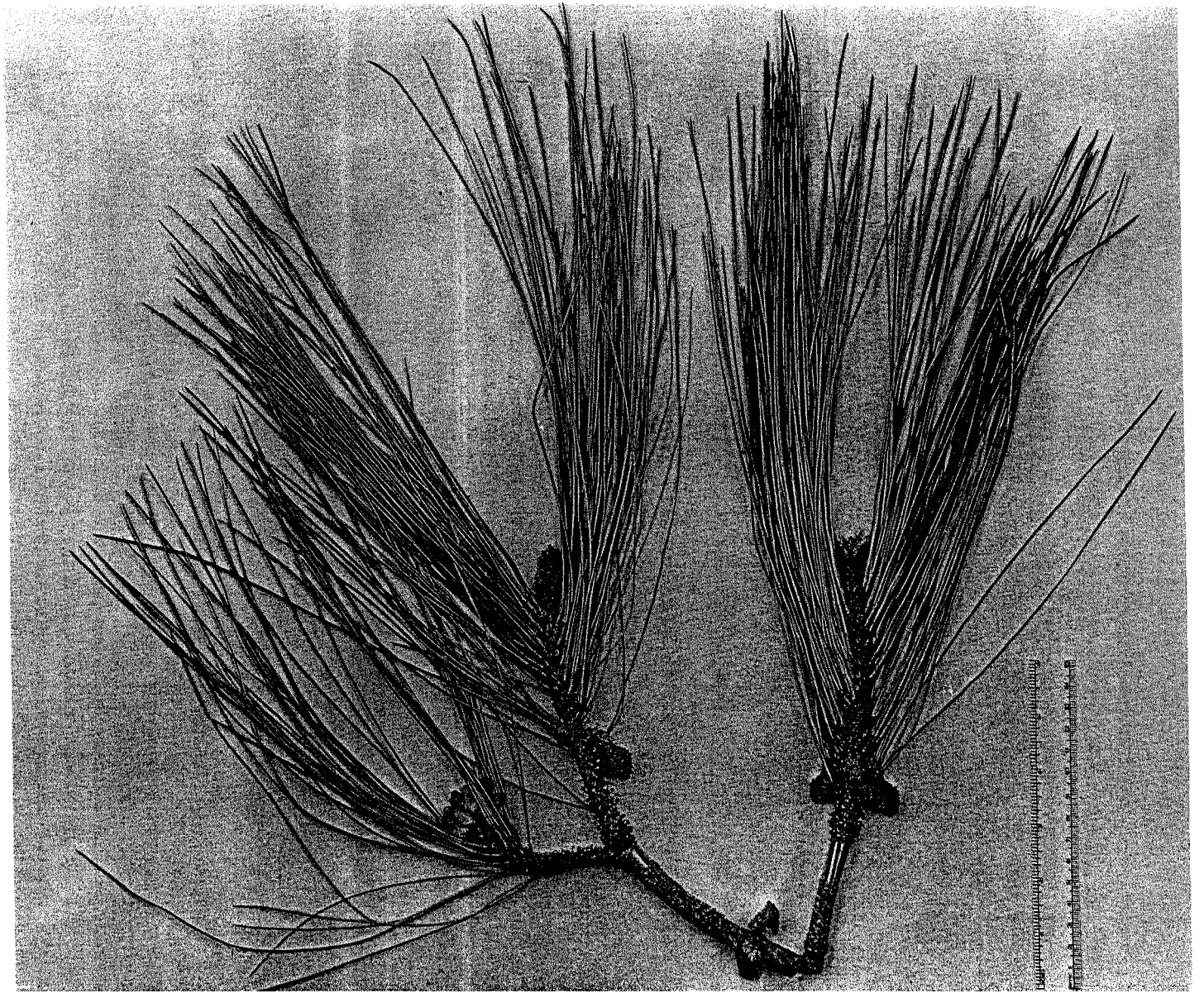


Fig. 7. --South Florida slash pine (*Pinus elliottii* var. *densa*). At the left, twig with young male cones. At the right, twig with year-old cones and female buds. This is the type collection from Hendry County, Florida. (Rule is 15 cm., or 6in., long.)

Mature cones mostly (5) 7-12 cm. long, when closed conical to narrowly ovoid, mostly more than twice as long as broad, and (3) 3.5-5 cm. in diameter, when open ovoid to cylindrical and (4) 6-8.5 cm. in diameter (fig. 3). Cone scales spreading to slightly reflexed.

Seedling with a grasslike, almost stemless stage like that of longleaf pine (P. palustris Mill.) for about 2 to 6 years. The many needles are crowded-on the very short stem. Below is a very thick structure with rather thick bark, mostly hypocotyl, becoming 1.5-3 cm. in diameter and 3-h cm. long and tapering into the thickened tap root.

Wood with very thick summerwood, very heavy and hard. Sapwood pale light brown or yellowish; heartwood reddish brown.

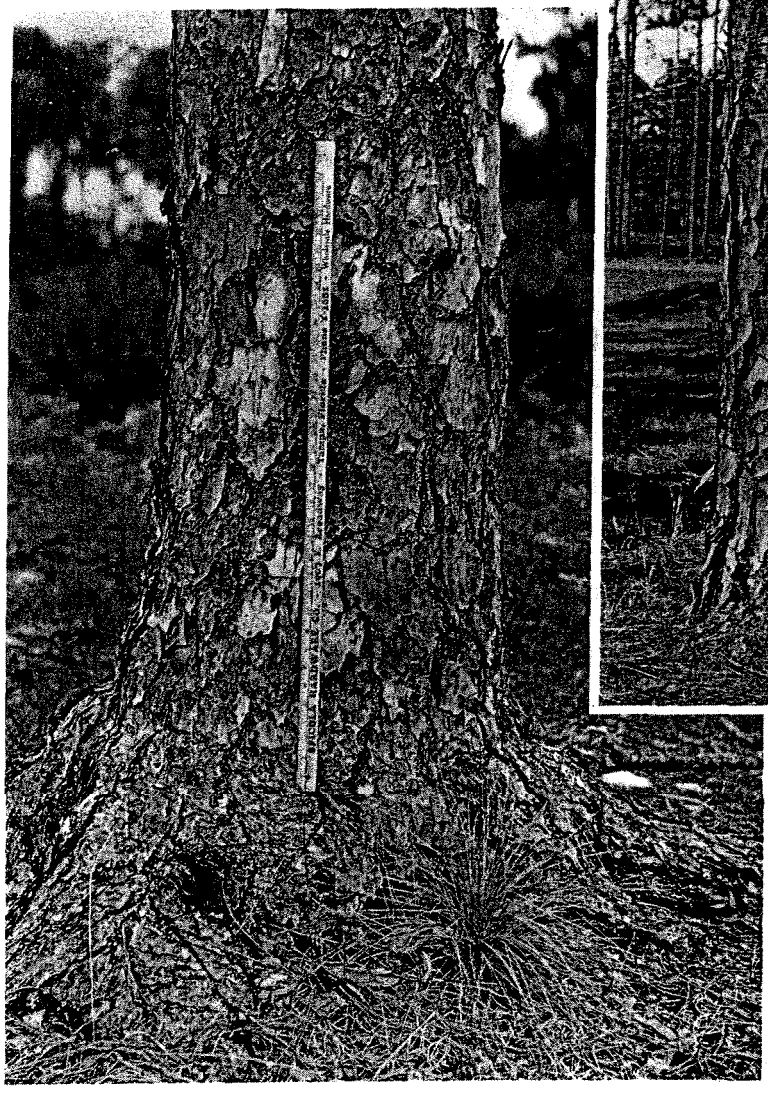
On the virgin flatwoods in Hendry and Collier counties, Florida, average height of mature trees is 55 feet with a range of usually 35 to 85 feet and maximum of 100 feet. Average age is 80 years, but age of mature trees exceeds 100 years. Large trees growing in those flatwoods often have a pronounced swelling at the base of the trunk (fig. 8). At Big Pine Key mature trees on the exposed limestone outcrops are only 15 to 25 feet tall and less than 6 inches in trunk diameter (fig. 9).

Rapidly growing saplings sometimes are unbranched and lack lateral branches for relatively long portions of their height and have longer, slightly curving and drooping needles and large buds with whitish scales. These plants resemble longleaf pines, and like the grasslike seedlings, suggest a relationship.

Cones from a few localities in southern Florida (Big Pine Key in Monroe County and places in Dade, Broward, and Lee counties) are smaller, (5) 6-8.5 cm. long, when open are cylindrical and 4-5 cm. in diameter, and have many crowded, slightly reflexed *cone* scales which expose their inner surfaces and give a dark chocolate brown color and cylindrical shape to the opened cone. Though these small cylindrical open cones seem different, no morphological differences were observed. The cylindrical shape is a result of the cone scales being widely opened and spreading downward. Normally cone scales toward the apex of a cone are less widely spreading and give a gradually narrowed, pointed shape to the opened cone. Large cones of this variety seldom have reflexed cones except at the base (fig. 3).

The name Pinus caribaea (sensu Small) was applied to pines of south Florida by Small (1913a, 1913b, 1913c, 1913d, 1933), Harper (1914), De Vall (1941, 1945), and West and Arnold (1946).

Range--Known only from Florida; southern part and northward along both coasts in central part. Southern Florida from Lower Florida Keys (Big Pine Key, Little Pine Key, No Name Key, Cudjoe Key, Ramrod Key, Big Torch Key, Middle Torch Key, and Howe Key; not on other Lower Keys or



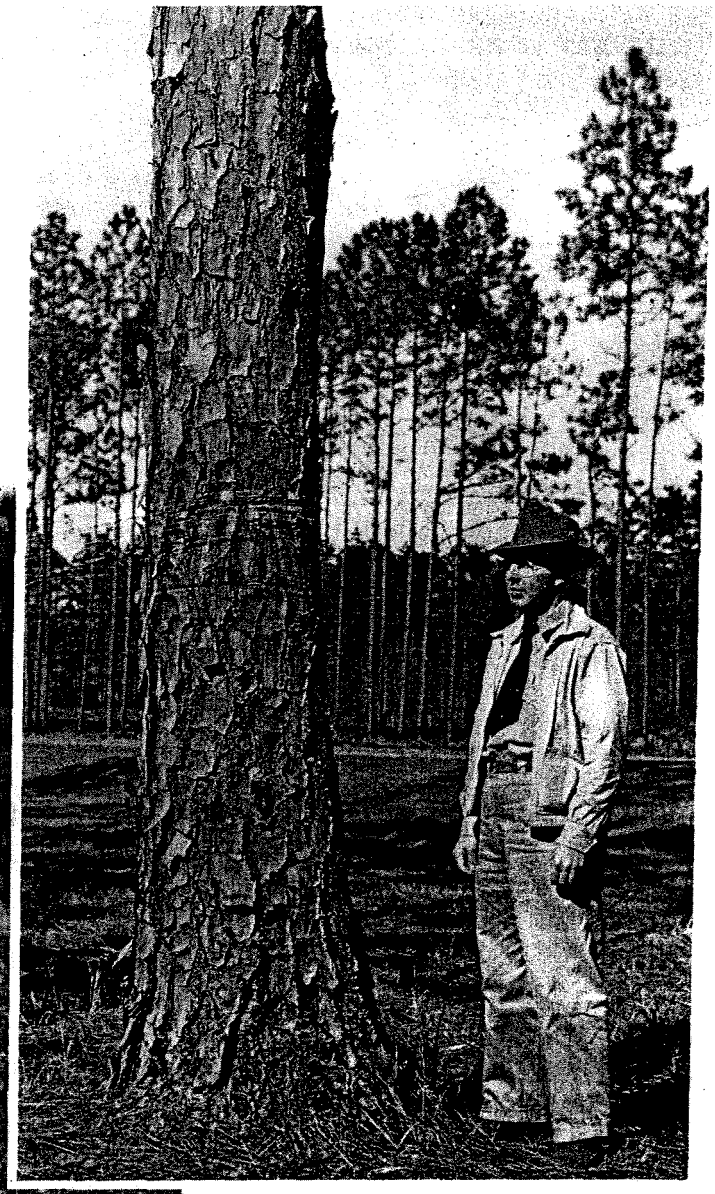


Fig. 8.--On the left, trunk of 18-inch South Florida slash pine showing swollen base occurring on some trees. On the right, trunk of 19-inch slash pine in northern Florida showing bark of large flat plates bordered by deep gray furrows.

Fig. 9.--At Big Pine Key, 31 miles from Key West, South Florida slash pine trees are short and grow very slowly. These trees are growing in a few inches of soil over limestone rock.

Upper Keys) north to Lake Okeechobee, northward in a narrow strip along Atlantic Coast to Volusia County and northward in a narrow strip along Gulf Coast to Levy County.

Representative specimens of Pinus elliottii Engelm. var. densa Little and Dorman examined:

FLORIDA. Volusia Co., 4 mi. S. of New Smyrna, E. L. Little, Jr., and K. W. Dorman 14062 (US, USFS). Brevard Co., Cocoa, A. S. Rhoads 8323 (N. Y. State Coll. Forestry Project I, distributed with wood samples, US). Martin CO.) 6 mi. SE of Stuart, E. L. Little, Jr., and K. W. Dorman 14058 (US, LJSFS). Broward Co., Pompano, E. L. Little, Jr., and K. W. Dorman 14053 (US, USFS). Dade Co., Miami, H. N. Moldenke 491 (US, NY); 10 mi. N. of Homestead, E. L. Little, Jr., and K. W. Dorman 14042 (US, USFS). Monroe Co.,

Little Pine Key, K. Small, J. J. Carter, and G. K. Small 3635 (NY): Big Pine Key, E. L. Little, Jr., and K. W. Dorman 14043 (US, USFS). Collier Co., 1 mi. N. of Corkscrew, E. L. Little, Jr., and K. W. Dorman 14026 (US, USFS). Hendry Co., 20 mi. SE. of La Belle, Sec. 4 T. 45 S., R. 31 E., E. L. Little, Jr., and K. W. Dorman 14033 (US--TYPE: NY, F, USFS, Univ. Fla.). Lee Co., Ft. Myers, J. P. Standley 135 (US, NY). De Soto Co., 9 mi. SE. of Arcadia, E. L. Little, Jr., and K. W. Dorman 14025 (US, USFS). Pasco Co., 9 mi. SW. of Weekiwachee Springs, E. L. Little, Jr., and K. W. Dorman 14024 (US, USFS).

A few authors have indicated the range of South Florida slash pine as extending northward in a narrow strip along the coasts to Georgia and Mississippi. These records may be traced back to the early maps of pine forests of Florida by Sargent (1884) and Smith (1884) and to P. caribaea as used by Small (1933). Harper (1943, pp. 204, 206) regarded the identification of the commonest pine of the coast strip of Alabama as still somewhat problematical. He accepted two species for the coast strip, P. caribaea on Dauphin Island and in a narrow belt along the coast and P. elliottii farther inland.

However, we have no records of South Florida slash pine from outside of Florida. Our collection from the Gulf shore at Mississippi City, Miss., listed above, is typical slash pine. Another specimen also cited, from St. Vincent Is., Franklin Co., Fla., off the Gulf Coast of western Florida, was identified by needle anatomy as the northern variety. Possibly some pines in exposed sites along the coast may have an irregular or stunted form like that of the southern variety. It would be desirable to examine seedlings for more positive identification.

Over most of its range in south Florida, P. elliottii var. densa is the only native pine and forms pure forests or-is scattered in grasslands. Northward along the coasts it overlaps with P. clausa (Chapm.) Vasey, sand pine, which extends into south Florida on coastal sand dunes. In the interior of central Florida from Lake Okeechobee northward, it is replaced by P. palustris and P. elliottii var. elliottii. Thus, P. elliottii var. densa is the southernmost native pine and only subtropical pine in the United States.

The climate within the range of P. elliottii var. densa is subtropical (tropical on the Lower Florida Keys). Rainfall is about 40 to 60 inches annually, and there is a six months dry winter period. The altitudinal range is from about 5 to 50 feet or more above sea level. Nearly all of southern Florida has an elevation less than 25 feet above sea level, according to Davis (1943, fig. 26).

The vegetation of these pine lands of south Florida has been described at length by Harper (1928) and Davis (1943). The latter has also mapped the pine forests in detail. Two types of forests of P. elliottii var. densa are distinguished, the pine flatwoods and the rockland

pine forests, both on relatively dry sites. The former is widespread on the sandy lowland plains or flat lands, often calcareous. The latter occurs on ridges of Miami oolite (limestone) of Pleistocene age south and southwest of Miami to Homestead and beyond and also on Big Pine Key and adjacent keys. In many places very little soil is present, and the rough, jagged "dogtooth" limestone weathered by solution in falling rain water without frost action outcrops at the surface.

Statistical information on the forests of South Florida slash pine is contained in a U. S. Forest Service forestry survey publication by J. F. McCormack (1950). This report covers the ten southern counties of the State, from Lake Okeechobee southward, where the pines are South Florida slash pine except for small quantities of longleaf pine at the northern end and sand pine along the coasts. The commercial forest area of the pine type in southern Florida in 1949 was 1,755,500 acres, of which four-fifths was poorly stocked or unstocked and only 33,700 acres in saw-timber stands. The net volume of sawtimber in pine was 434,300,000 board feet. Owing to cutting operations, the volume of pine sawtimber here was reduced 54 percent in the 13-year interval between forest surveys in 1936 and 1949. These virgin stands in Collier, Hendry, Lee, and Charlotte counties, being scattered and less accessible, were among the last to be cut over in the State, and a small part has not yet been cut. This area also contains commercially important forests of bald cypress (*Taxodium distichum* (L.) Rich.).

The entire area occupied by this newly described variety of pine is very young geologically, having been covered by ocean waters at various times as late as interglacial stages of the Pleiostocene epoch (Cooke, 1939, 1945; Davis, 1943, pp. 58-75). This topic is further discussed under relationships and history of *P. elliottii* and *P. caribaea*.

The principal differences between the two varieties of slash pine, *P. elliottii*, are summarized in table 1. As ranges of the two varieties are distinct, identification can be made readily from the location of the specimen or wild tree. In the field, the seedlings, whether with normal, pencillike stems or with a grasslike, almost stemless stage, are the most reliable characters. Differences in shape and size of mature trees are usually obvious. Herbarium specimens can be identified by the thickness of hypoderm of needles, as shown in microscopic examination of needle cross section. Some specimens of South Florida slash pine are readily distinguished by the small cones with reflexed cone scales.

Table 1. --Principal differences between the two varieties of slash pine, *Pinus elliottii* Engelm.

Item	Slash pine (typical) *P. elliottii* var. *elliottii*	South Florida slash pine *P. elliottii* var. *densa*
Seedling	Normal with erect, slender, pencillike stem.	Grasslike, almost stemless stage like that of *P. palustris*, with very short stem, many crowded needles, very thick hypocotyl, and thick tap root.
Leaves	Needles in fascicles of 2 and 3.	Needles in fascicles of 2 (infrequently 3).
Needle anatomy	Hypoderm biform, thin of 2 (sometimes 3) layers of cells.	Hypoderm biform, thick, of 3 or 4 (sometimes 2 or 5) layers of cells.
Cones	Opened cones ovoid, with spreading cone scales.	Opened cones ovoid to cylindrical, with spreading to slightly reflexed cone scales.
Size	Large tree.	Medium-sized or small (to large) tree.
Shape of tree	Erect straight axis and narrow pointed crown.	Axis often forking into large branches and with irregular, flat-topped and spreading, open crown.
Wood	Wood relatively heavy, with normal proportions of spring and summerwood.	Wood very heavy and hard, with very thick summerwood.
Oleoresin	Flows readily and important commercially.	Not harvested commercially from living trees.
Range	Southeastern United States, Coastal Plain from southern South Carolina to central Florida (Lake Okeechobee) and southeastern Louisiana.	Florida only, south Florida north to Lake Okeechobee and northward along coasts in central part to Volusia and Levy counties.
Habitat	Moist soil of swamps and ponds, but also on drier sites.	Dry sites on sandy flat lands and limestone outcrops.

DISTRIBUTION MAP

The ranges of *Pinus caribaea* and the two varieties of *Pinus elliottii* are summarized in the distribution map (fig. 10). This map has been compiled from various sources, including herbarium specimens and published floras, published distribution maps, and vegetation maps of political units previously cited.

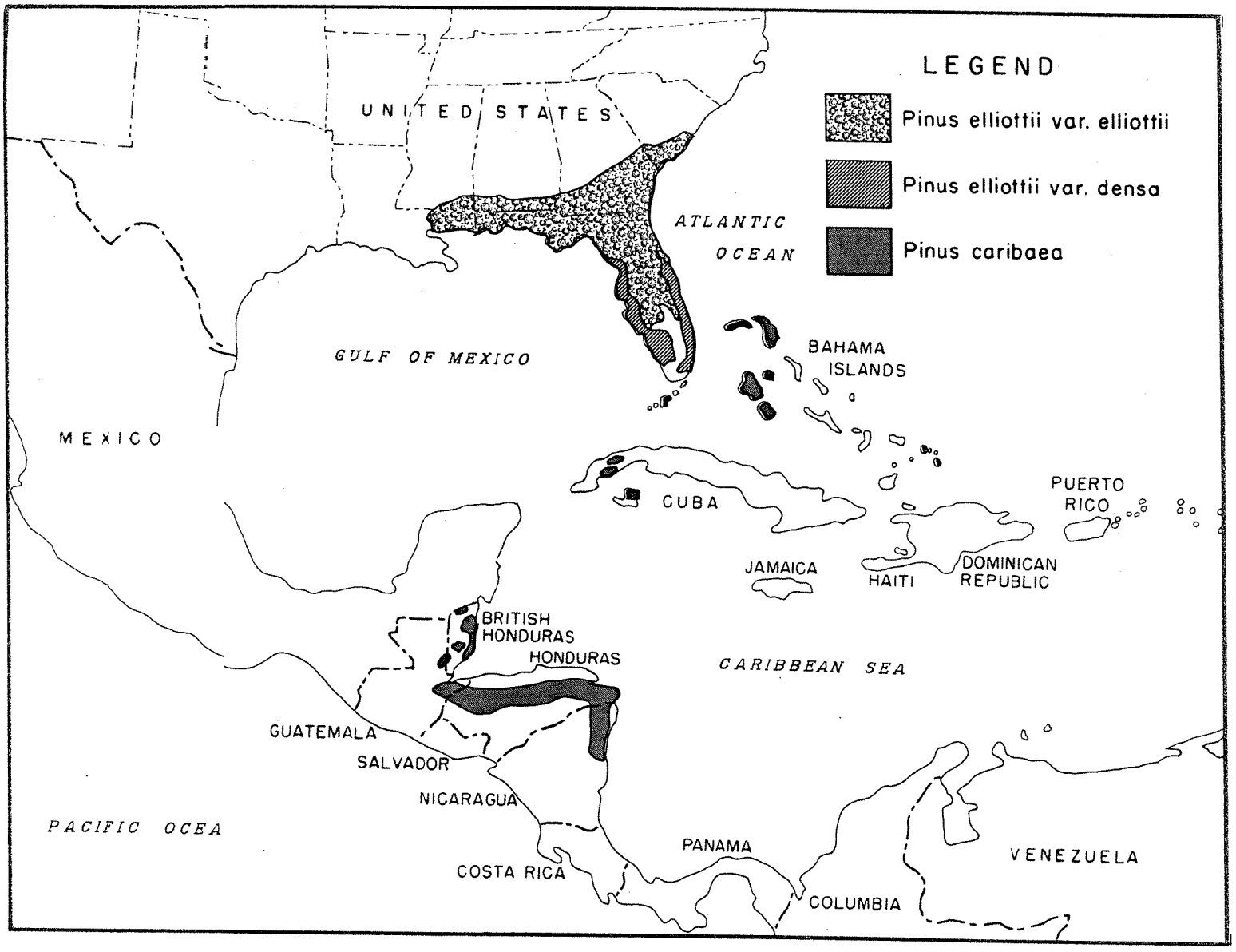
Three variations are distinguished within the limits formerly mapped by some authors as a single species. The broad limits including West Indies, and Central America as well as southeastern United States were shown as *P. caribaea* in maps by Record and Hess (1943, map 3 on p. 18, as Cuban pine) and by Harlow and Harrar (1950, p. 5, fig. 2). The general limits of slash pine within the United States have been indicated on several published distribution maps of that species.

SEEDS

Differences in seeds, such as size, are among the more obvious characters distinguishing the two species *P. caribaea* and *P. elliottii*. Loock (1951) reported that seeds of *P. caribaea* sent from British Honduras to Southrica were considerably smaller and of much lighter color than seeds received from the United States under the same name. Seeds from British Honduras also had shorter wings which usually remained attached. We have independently observed these differences in seeds when examining samples kindly supplied by the Government foresters of Cuba and British Honduras. As the seeds of the two species are so dissimilar, it seems odd that these pines have been retained together under the same name so long. However, taxonomists probably had no occasion to examine quantities of seeds for planting purposes.

Seeds of *P. elliottii* are larger, averaging about 7 mm. long, 4 mm. wide, and 3 mm. thick; broader, less than twice as long as broad, pointed at lower end, ovoid and slightly 3-angled; in part darker, blackish or mottled gray; usually with longer wing 15 to 30 mm. long, which becomes detached. In contrast, seeds of *P. caribaea* from Cuba and British Honduras are smaller, averaging less than 6 mm. long, 3 mm. wide, and 2 mm. thick; narrower, about twice as long as broad, narrowly ovoid, pointed at both ends, and 3-angled; usually light colored, mottled gray or light brown; usually with shorter wing less than 20 mm. long, which usually remains attached unless broken off in seed cleaning.

Length of wing probably is correlated with size of cone, averaging shorter in seeds from south Florida than in samples northward. In 2 samples from British Honduras the wings mostly were detached or detachable. Seed


LEGEND
Pinus elliottii var. elliottii
Pinus elliottii var. densa
Pinus caribaea
UNITED STATES
ATLANTIC OCEAN
GULF OF MEXICO
BAHAMA ISLANDS
MEXICO
CUBA
PUERTO RICO
JAMAICA
HAITI
DOMINICAN REPUBLIC
BRITISH HONDURAS
HONDURAS
CARIBBEAN SEA
GUATEMALA
SALVADOR
NICARAGUA
PACIFIC OCEA
COSTA RICA
PANAMA
COLUMBIA
VENEZUELA

color is variable, as some seeds from British Honduras were dark gray and blackish, and seeds from south Florida were mottled gray.

Wakeley (1951, p. 501, table-28) has given for slash pine (P. elliottii var. elliottii) figures on length and width of seeds, both means and range of samples (not smallest or largest individual seeds), based upon large numbers of samples used in planting. Lengths of seeds averaged .28 in. with range of .24 to .32 in. (7 mm. and 6-8 mm.), and widths averaged .18 in. with range of .16 to .22 in. (4.6 mm. and 4.0-5.6 mm,). In contrast Loock (1951) stated that the seeds from British Honduras seldom exceeded 3/16in. (.19 in. or 4.8 mm.) in length. These differences in seed size are greater than in our approximate measurements of a few samples.

The following publication, which has not been available, indicates that seeds have been used in identification of pines: Uyeki, Homiki. The seeds of the genus Pinus as an aid to the identification of species, Suigen, Korea, Agr. and For. Col. Bul. 2. 1927.

SEEDLINGS

Slight differences in average cotyledon numbers of seedlings may occur among the pines studied. Engelmann (1880, pp. 174, 186) in his revision of the genus Pinus observed variations in cotyledon numbers among the different species. In the original description of P. elliottii he listed 6-9 cotyledons, usually 8. Butts and Buchholz (1940) recorded cotyledon numbers in various species of conifers based upon counts of embryos. For P. caaibaea, origin not stated, their count of 82 embryos gave 5-10 cotyledons; mean 7.73.

In growing seedlings in cans of soil, we observed slight variations in average numbers of cotyledons among samples from different places. Accordingly, cotyledon counts of germinating seedlings were made. A sample of P. elliottii var. elliottii from De Soto National Forest in southern Mississippi based upon a count of 25 seedlings gave 6-9 cotyledons with mean 7.36. Another from Clinch Co., Ga., of 50 seedlings had 5-10 cotyledons with mean of 7.72, almost identical with numbers reported by Butts and Buchholz. One lot of 50 seedlings of P. elliottii var. densa from Hendry Co., Fla., showed 5-8 cotyledons, mean 6.76.

Seedlings of P. caribaea had slightly smaller averages. A sample from Cuba of 100 seedlings gave 4-8 cotyledons, mean 5.90, and another from Cuba of 50 seedlings 4-8 cotyledons, mean 5.96. A lot from British Honduras of 100 seedlings had 4-9, mean 6.58.

Of course, these six small samples are inconclusive, but they suggest that average cotyledon number is highest in P. elliottii var. elliottii,

slightly lower in var. densa and lower still in P. caribaea. However, as the extreme numbers are nearly the same, the ranges overlapping, and the averages only slightly different, cotyledon numbers would not be useful in identification.

One of the most distinctive characteristics of South Florida slash pine (P. elliottii var. densa) is its grasslike, almost stemless seedling stage resembling that of longleaf pine (P. palustris). In longleaf pine the seedling passes through a resistant grass stage and for 2 to 10 years remains almost stemless with a large tuft of very long grasslike needles (Wahlenberg, 1946, pp. 58-59, 86-99). Earlier references to the grasslike seedling of South Florida slash pine have already been reviewed.

Seedlings of South Florida slash pine grown from seed at the Harrison Experimental Forest in southern Mississippi retained their grasslike seedling stage. Similarly, seedlings of typical slash pine from northern Florida planted near La Belle, in south Florida, had typical, slender, pencillike stems. Thus, the grasslike seedling form is inherited (figs. 11, 12).

Fig. 11: Four strains of pine after 2 years planted at Harrison Experimental Forest in southern Mississippi. On the left, pine of Cuban origin (Pinus caribaea); left foreground, South Florida (Pinus elliottii var. densa); right foreground, northern Florida (Pinus elliottii var. elliottii); far right, local Mississippi strain (Pinus elliottii var. elliottii). The typical slow growth and bushy form of the South Florida slash pine is readily apparent. The pines of Cuban and South Florida origin have been severely injured by freezing since the picture was taken.

Fig. 12. --At the left, slash pine of northern Florida origin planted in Hendry County, in southern Florida. It shows the typical slender form and rapid height growth of pines in northern Florid-a and none of the characteristics of South Florida slash pine. The seedling is 3 years old and it is 33 inches tall. The stem is 5/8 inch in diameter at the base. At the right, 2-year-old seedlings of South Florida slash pine 6 to 15 inches tail, naturally seeded in Hendry County, Florida.

Grasslike seedlings of South Florida slash pine are shown in figure 13, and seedlings of Caribbean pine and slash pine with pencillike stems in figures 13 and 14. The very thick structure below the needles is largely hypocotyl. In pine seedlings the hypocotyl is the transition region between stem and root, located below the cotyledons and afterwards below the fascicles of leaves, which are borne from stems. It becomes 1.5-3 cm. in diameter over a length of 3-4 cm. and tapers into the thickened tap root. The unusual thickening is mostly dead outer bark but includes some. inner bark and wood. After height growth is begun the

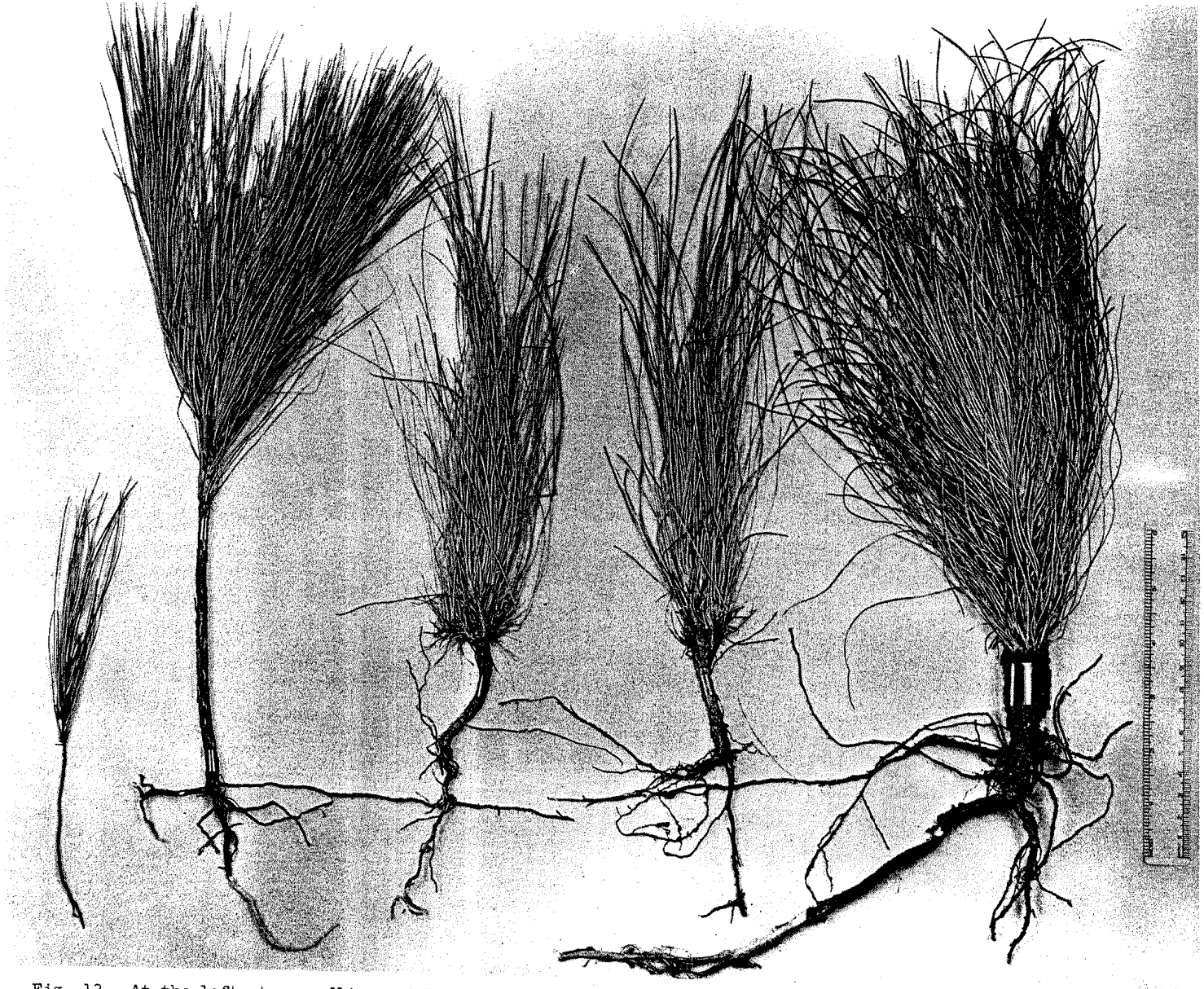


Fig. 13.--At the left, two seedlings of Pinus caribaea, Caribbean pine, from Isle of Pines, and on the right, three seedlings of Pinus elliottii var. densa, South Florida slash pine, from Hendry County, Florida, showing typical form.

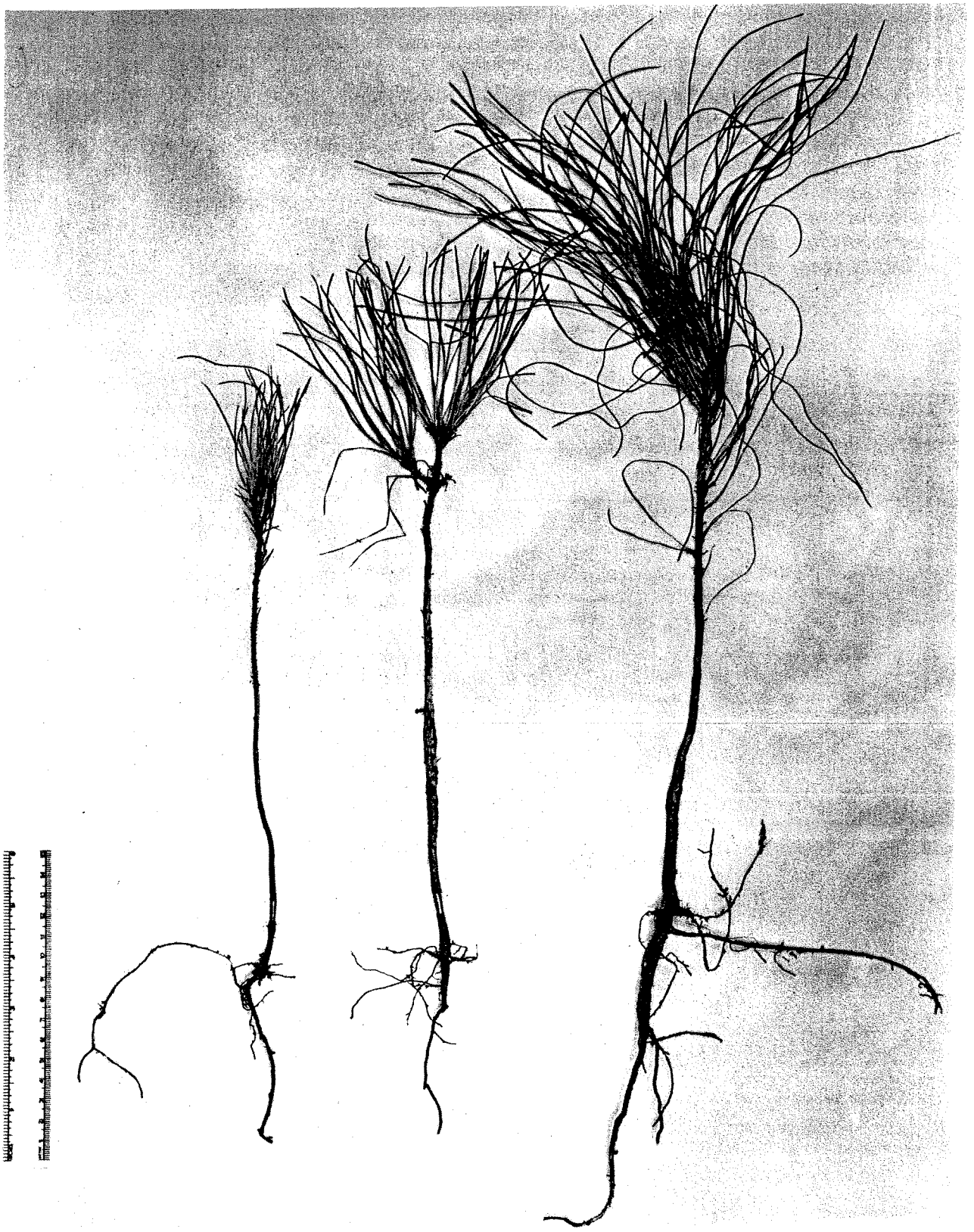


Fig. 14.--Three seedlings of Pinus elliottii var. elliottii, slash pine from Baker County in northern Florida. These seedlings have slender stems typical of the variety.

'seedlings resemble those of slash pine from northern Florida (fig. 15). Prominent long horizontal lateral roots develop from the tap root.

These grasslike seedlings, like those of longleaf pine, apparently are resistant to fire, being adapted in their low growth, thick insulating bark, and stored food in the enlarged portion. Foresters of the Atlantic Land and Improvement Company reported that in preliminary tests of nursery grown stock of typical slash pine and wildling stock of South Florida slash pine together near La Belle in southern Florida, the latter were more resistant to fire in that area of annual burning by cattlemen. It is interesting to note that South Florida slash pine, like longleaf pine, grows on dry sites subject to frequent burning and where the resistant grasslike

Fig. 15.--Dense reproduction of South Florida slash pine in a recently logged area in Hendry County, Florida.

seedling is an adaptation of survival value. In contrast, typical slash pine with normal, pencillike seedlings is characteristic of moister sites with infrequent fires.

Pinus caribaea Morelet has a normal seedling with pencillike stem, as we verified at the type locality, Isle of Pines. However, P. tropicalis Morelet, the more common species described by the same author from the same type locality, does have a grasslike stemless seedling (fig. 16,17). Seedlings of these two species were seen growing naturally side by side at Isle of Pines (fig. 18). In Pinar del Río, western Cuba, where both species

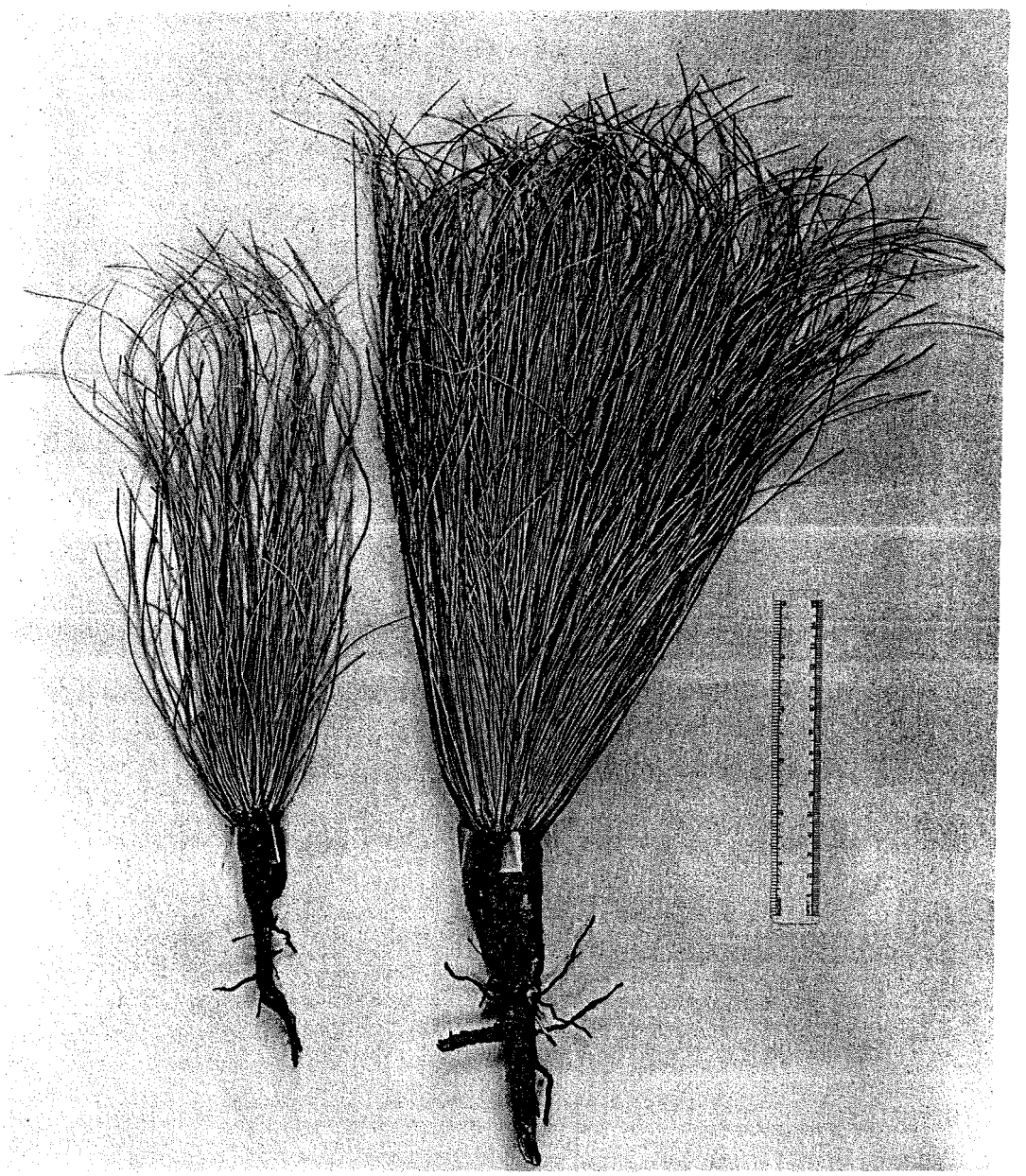


Fig. 16.--Seedlings of Pinus tropicalis from Isle of Pines. Seedlings of this species have an almost stemless form, similar to that of South Florida slash pine.

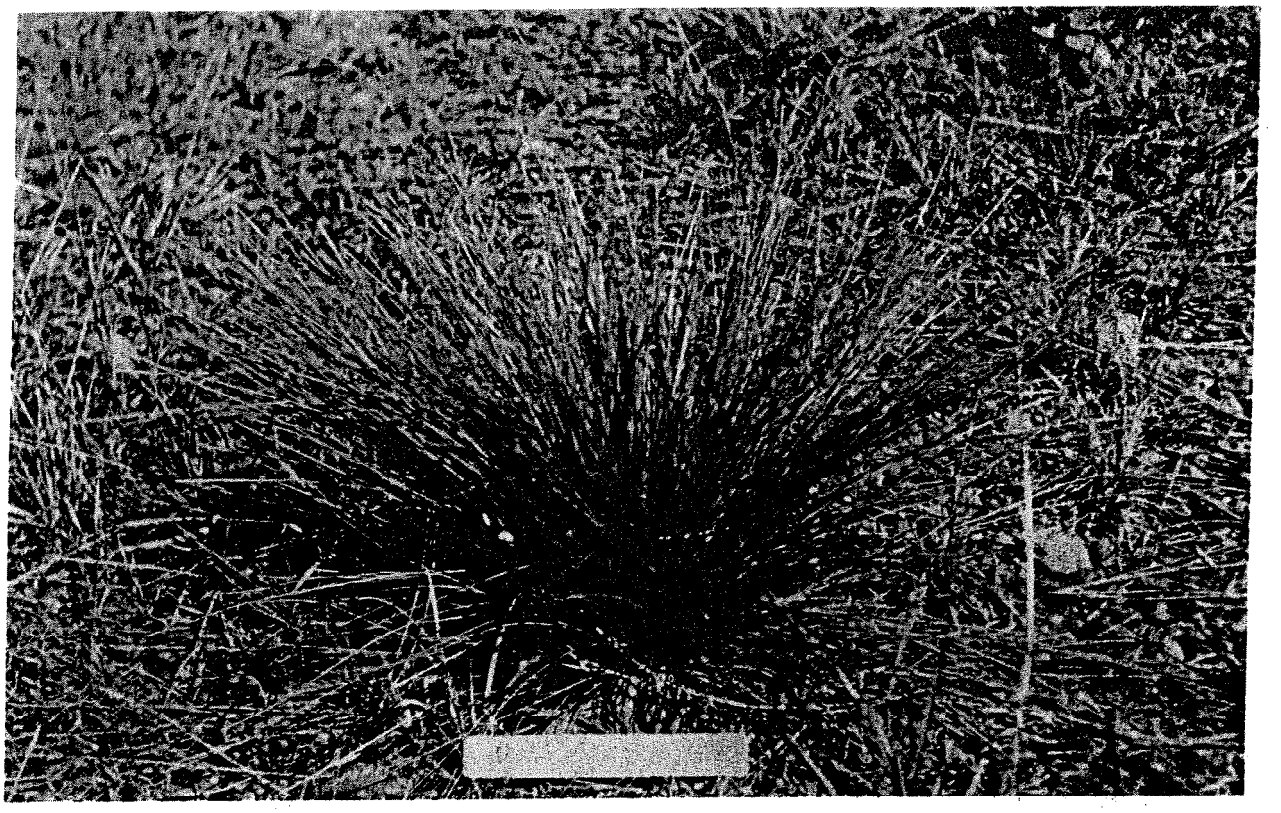


Fig. 17.--Grasslike seedling stage of tropical pine at Isle of Pines. Diameter at base is $1\frac{1}{2}$ inches across the thick bar. (Rule is 15 cm., or 6 inches, long.)

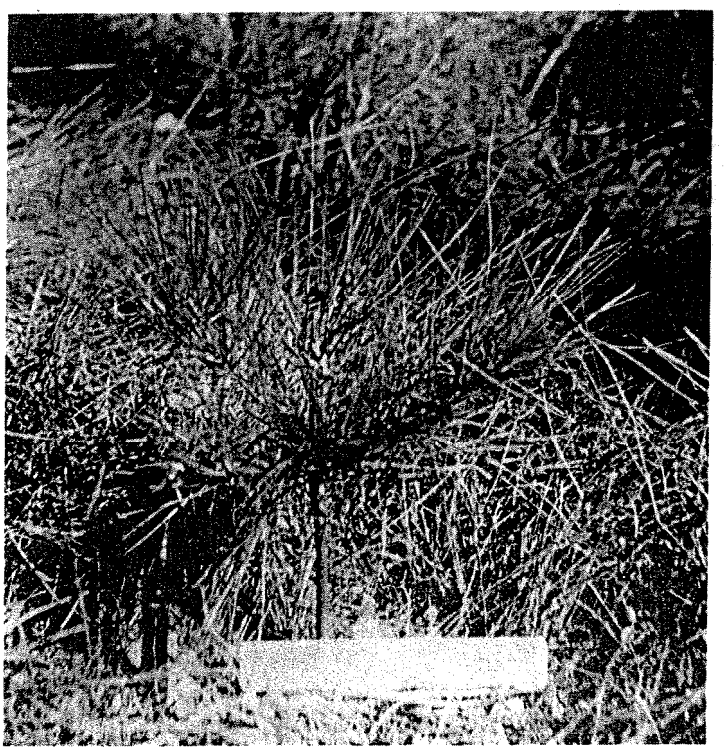


Fig. 18. --Seedling of Caribbean pine at Isle of Pines less than 1 foot high, with pencillike stem $\frac{1}{4}$ inch in diameter at base. (Rule is 15 cm., or 6 inches, long.)

are also native, the same differences in seedlings occur. Alberto J. Fors kindly has sent us one seedling of each species from Cuba verifying these characteristics. Incidentally, P. tropicalis, which has the resistant, grasslike seedlings is much more common than P. caribaea on both islands, and the latter is becoming scarcer.

A. C. Shaw, who recently visited Bahama Islands and collected material of P. caribaea for us there, states that on Great Bahama and Great Abaco Islands east of Florida the pine seedlings are normal and not stemless. Two herbarium specimens of seedlings from Andros, Bahama Is. (L. J. K. Brace 6875; F) likewise have normal, pencillike stems.

In British Honduras, Paul J. Shank reports that seedlings of P. caribaea also are normal. Loock (1951) noted that seedlings from British Honduras seed grown in South Africa were more slender and tender than those of seed from the United States. The former had yellowish brown stems and light green foliage and the latter purplish stems and dark green leaves. At Harrison Experimental Forest in southern Mississippi we observed year-old seedlings from British Honduras seed in a seedbed. (They were killed by cold weather soon afterwards.) These seedlings were unusually tall and slender and peculiar in having only the blue green juvenile leaves rather' than some needles in bundles. Seedlings from Cuba of the same age were not available for comparison and may not be similar to those from British Honduras.

This character of delayed height growth in the seedling stage apparently has developed independently in species of pines in other regions. Apache pine, P. engelmannii Carr. (P. latifolia Sarg.), of southwestern United States-and adjacent Mexico has a grasslike seedling stage as shown by Righter and Duffield (1951). The Institute of Forest Genetics, U. S. Forest Service, at Placerville, Calif., reports finding grasslike seedlings also in P. montezumae Lamb., P. pseudostrobusl . , and P. michoacana Martínez of Mexico and in an Asiatic species, P. merkusii De Vriese, and has lent us herbarium specimens of nursery grown seedlings of some of these.

NEEDLE ANATOMY

Differences in microscopic anatomy of needles, as well as the number of needles in a fascicle, have been employed by botanists as supplementary characters in the classification and identification of species of Pinus. Though most species of the genus have a more or less constant number, P. elliottii is a noteworthy exception. It and the earlier variety, P. taeda var. heterophylla, both were originally described as having the leaves in 2's and 3's. Engelmann (1880, p. 188) recorded in P. elliottii that leaves of young trees are more frequently in 2's and in older ones as often in 3's.

In South Florida slash pine the needles are predominantly in 2's (infrequently 3). It was unexpected to find at Isle of Pines, the type locality, needles of P. caribaea uniformly in 3's, as botanists had regarded the two as the same. There is a sharp separation and an abrupt difference in needle number between the 2-needle pine of southern Florida and its 3-needle relative in Bahama Islands, Cuba, and Isle of Pines.

shaw (1914, p. 4) noted that in species having a variable number of needles, the number of needles in a fascicle is in some degree dependent on climatic conditions, the smaller number occurring in colder regions. For P. caribaea in the broad sense he listed 2 and 3 leaves in a fascicle or more in the southern range. However, in P. elliottii segregated from the former the smaller number of needles is commoner southward in the warmer climate.

De Vall (1941, 1945) and West and Arnold (1946) used the number of resin ducts (or resin canals) in needles as a means of distinguishing the two variations of slash pine in Florida. Accordingly, we have studied needle anatomy of P. caribaea and the varieties of P. elliottii in a search for further means of distinguishing these closely related pines.

Several investigators have made detailed studies of microscopic anatomy of needles in the genus Pinus and have published keys for identification of species based upon needle characters. Following earlier European and American workers, Shaw (1914, pp. 2-7, pl. 2) in his monograph of this genus described the leaf anatomy, including tissues and variations, of pines and prepared a sketch of the needle cross section for each species.

Keys to species of Pinus based upon needle anatomy have been prepared .in different parts of the world, such as by Doi and Morikawa (1929) in Japan, Harlow (1931) in the United States, and by Sutherland (1934) in New Zealand. The first had drawings showing variations in characters and the other two were well illustrated by photomicrographs of each species. These useful keys indicate that needle anatomy is more or less constant for a species even when cultivated in some other part of the world, such as New Zealand, where this genus is not native. Harlow's (1931) illustrated key is helpful for identification of sterile or poor material of Pinus.

Nevertheless, leaf anatomy is of minor importance and supplementary value in the identification of trees. Trees are large plants with many variations in gross structure available for classification. Characters used to separate species of trees should be preservable on herbarium specimens, though of course other features, such as bark, may be employed in the field. If two populations of trees differ only in microscopic details, such as leaf anatomy, wood anatomy, or chromosome numbers, they would be placed by taxonomists under the same scientific name. For example, two pines differing only in number of resin ducts in the needles would be considered the same for practical purposes. Differences of needle anatomy of pines are useful in identification when constantly associated with differences in gross morphology. Even then, the tedious microscopic examination required to observe

these minute details is seldom employed except in identification of incomplete or sterile specimens.

Perhaps the most detailed study of variations in microscopic needle anatomy within a single species of Pinus is that by Weidman (1939, pp. 868-870, pls. 1-3), of the U. S. Forest Service, on Pinus ponderosa. Because of similarities in needle structure and in geographical races, it is particularly significant in our study. Pines from seed from 10 western States were grown together in experimental progeny plots in northern Idaho and analyzed after 25 years as to racial variations. J. H. Ramskill, of the University of Montana, made detailed examinations of microscopic needle anatomy both of pines from these plots and of pines from each parent locality. Two structures were found to vary in pines from regions with different climates. For example, needles from Siskiyou, southwestern Oregon, in the North Pacific region with a mild, humid climate had a biform hypoderm (the tissue just inside the epidermis or outermost layer) of 1 layer of thin-walled cells and 1 or 2 layers of thick-walled cells and stomata not depressed or *sunken.* At the other extreme, needles from Ashley, northeastern Utah, in the interior Central Plateau region with a severe, drier climate had a biform hypoderm of 1 layer of thin-walled cells and 2 to 4 layers of thick-walled cells and stomata deeply depressed corresponding to 'the number of layers of cells in the hypoderm. Similar variations were found in relative thickness of walls in inner rows of hypoderm cells and percentage of thick-walled cells in inner hypoderm rows, the pines from a mild climate having mostly thin cell walls and few thick-walled cells and those from severe climates having practically all the cells with thick to very thick cell walls. Moreover, these variations were retained by the progenies in the new habitat and were regarded as inherited. A minor exception was that progenies *from* some interior regions grown under a less vigorous climate had fewer layers of hypoderm cells and slightly less stomatal depression than pines at the parent localities.

Stover (1944) studied variationsin leaf structure of Pinus contorta Dougl. and two other conifers in different habitats of Medicine Bow Mountains in Wyoming. He observed a greater number of hypoderm cells in leaves from xeric habitats than in leaves from mesic habitats.

De Vall (1941, pp. 126-128) examined the number of resin ducts in needles of South Florida slash pine, which he listed as P. caribaea. He noted that Harlow (1931, pl. 10, fig. 2) had illustrated-for slash pine (as P. caribaea) 2 internal resin ducts and mentioned an occasional additional medial resin duct. In 40 samples of 2-needle fascicles of South Florida slash pine from 15 Florida counties, De Vall found the number of resin ducts to vary from 4 to 9, except that 2 specimens from the northern part of the range had 3. According to his unpublished thesis, De Vall also examined specimens of typical slash pine from more than 10 localities in northern and western Florida and reported the number of resin ducts to be commonly 3 to 5, infrequently 2 and rarely more than 5. In a key to the species of native Florida pines; De Vall (1945) separated these variations on the

basis of number of resin ducts, 2 or 3 in typical slash pine and 4 to 9 (average 7) in South Florida slash pine. He noted that the number is shown by the resin droplets visible with a hand lens on the cut surface made with a razor or sharp knife.

West and Arnold (1946, p. 3) similarly mentioned number of resin ducts as a means of separating these two pines in Florida, the number in 2-needle fascicles being more abundant (5 to 10) in South Florida slash pine than in typical slash pine (3 to 4).

In the original description of P. elliottii, based largely upon specimens from South Carolina and therefore the typical slash pine, Engelmann (1880, p. 189, pl. 1, figs. 4-7) illustrated 4 leaf sections, 2 binate leaves with 9 and 5 resin ducts, respectively, and 2 ternate leaves with 8 and 4 resin ducts each. According to his explanation of figures, "the ducts are wide or small, few or many, in these specimens, varying from 4 to 9." Sargent (1891-1902; 11: 157, pl. 591, fig. 11. 1897) recorded the number of resin ducts in P. heterophylla as 4 to 6 (4 illustrated in fig. 11) and indicated that there was usually a single layer of thick-walled cells in the hypoderm.

Doi and Morikawa (1929, pp. 175-176) in their key described for P. caribaea 2 *or 3 needles,* resin ducts 3 to 5, and hypoderm partly of 1 layer and partly 2 layers and biform. Sutherland (1934, figs. 21, 22) published photomicrographs of cross sections of a ternate needle with 4 internal resin ducts and a binate needle with 2 internal and 2 medial resin ducts, both with biform hypoderm of 2 layers of cells. She noted (p. 522) that in P. caribaea the fundamental structure of needles does not differ in the 2- and 3-needle bundles. These descriptions and figures represent typical slash pine.

Harlow (1931, pl. 10, fig. 2) published for P. caribaea a photomicrograph of a binate leaf of typical slash pine with 2 internal resin ducts and biform hypoderm of 2 layers of cells and mentioned occasionally an additional medial resin duct and 3 layers of cells in the hypoderm. However, as he recorded a range from 2 to 10 (or more) resin ducts in needles within a species for 11 other species, number of resin ducts obviously is of limited value in identification. Harlow and Harrar (1937, fig, 35) illustrated a ternate leaf with 4 resin ducts (3 internal *and 1* medial) and thin biform hypoderm of 2 layers.

Florin (1933, p. 4, pl. 2, figs. 11, 12) studied needle anatomy in monographing the conifers of the West Indies from E. L. Ekman's collections. He described the needle anatomy of P. caribaea interpreted in the broad sense as having 2 to 4 resin ducts, always internal, and the hypoderm biform with 2 to 4 layers of thick-walled cells. The two photomicrographs showed a binate leaf and a ternate leaf, both with 4 resin ducts and with a thickened hypoderm of about 2 or 3 layers of thick-walled cells. These illustrations, further identified from the citation of the locality of the

specimen, Miami, Fla., (H. N. Moldenke 491) were of South Florida slash pine.

Recently Loock (1951, figs. E-G on p. 214) has published photomicrographs of needle cross sections from British Honduras described as a new species, P. hondurensis, 2 ternate leaves showing 4 and 3 internal resin ducts, respectively, and hypoderm of 4 or 5 layers of cells. For contrast he illustrated a binate needle from Florida as P. caribaea with 7 internal resin ducts and 2 medial, which is identifiable from the thin hypoderm of 2 layers of cells as typical slash pine. In the text he noted that the internal structure of leaves of the two was very similar except that the former had 2 to 4, usually 3 or 4, internal -resin ducts and the latter 2 to 9 internal ducts with 1 or 2 not quite internal.

We have examined microscop-ically needle cross sections of representative specimens from throughout the range of P. caribaea and P. elliottii. Fresh material has been studied of our collections of P. elliottii var. elliottii from five States, of P. elliottii var. densa from variousplaces in southern Florida and northward, and of P. caribaea from the type locality at Isle of Pines. Additional herbarium specimens of P. caribaea from different localities in Bahama Islands, western Cuba, British Honduras, Guatemala, Honduras, and *Nicaragua* have been sectioned.

Important material from cultivated plants *grown* outside the natural range or at localities away from the source of seed has been supplied by personnel of the U. S. Forest Service. From the Eddy Arboretum, Institute of Forest Genetics, Placerville, Calif., came fresh specimens of trees growing from seeds from British Honduras, Mississippi, and northern Florida. From the Harrison Experimental Forest near Gulfport, Miss., we received tree material, the seed of which came from South Carolina, Georgia, and Louisiana, as well as specimens from the experiment by the Division of Forest Pathology, Plant Industry, Soils, and Agricultural Engineering, of 3-year-old pines from Mississippi, northern Florida, southern Florida, and Cuba.

Cross sections were cut from needles about midway between base and apex. Both binate and ternate needles were examined, as some specimens, particularly those of P. caribaea, were of only the latter. Our observations confirmed those of Sutherland that needle structure in 2- and j-needle fascicles is similar. Dried needles were softened by soaking cut pieces in hot water. The cross sections were cut freehand with a razor blade by placing the bundle on a cork held by a finger and cutting against the finger nail, which was gradually moved backward. The thinner sections were then mounted in water and examined under low power of the compound microscope. This simple method of preparing temporary mounts of freehand sections proved adequate for *our* taxonomic study.

The *results* of our examinations of *cross* sections of pine needles are summarized in tables 2 and 3. The principal variations in tissues studied because of possible value in identification were the number and

Table 2.--Resin ducts and hypoderm layers in pine needles in different regions

Species or variety	Region	Localities	Total resin ducts	Medial resin ducts	Hypoderm layers
		Number			
Pinus elliottii var. *elliottii*	Southeastern United States	10	1/2-8 (9)	0 (1-2)	2 (3)
Pinus elliottii var. *densa*	South and central Florida	12	3-9 (11)	0 (1-4)	3-4 (2, 5)
Pinus caribaea (all regions)	West Indies and Central America	28	2-8	0 (1)	3-5 (2)
Pinus caribaea	Isle of Pines	2	3-6	0 (1)	3-5
Pinus caribaea	Western Cuba	3	5-6	0	3-5
Pinus caribaea	Bahama Islands	8	3-8	0 (1)	3-5
Pinus caribaea	British Honduras	7	2-5	0	3-5 (2)
Pinus caribaea	Guatemala	3	2-4	0	3-4 (2)
Pinus caribaea	Honduras	4	2-5	0	3-4 (2)
Pinus caribaea	Nicaragua	1	2-3	0	3 (2-4)

1/ Figure in parenthesis indicates number rarely observed.

position of the resin ducts and the number of layers of cells in the hypoderm.

In these pines the resin ducts of the needles are internal; that is, their bordering cells are inside the mesophyll, or green tissue, and touch the endodermis layer. Or, 1 or 2 (rarely 3 or 4) of the total number of resin ducts may be medial; that is, more or less centrally located within the mesophyll, or green tissue, as indicated in table 2. In the pines studied, the hypoderm, or tissue just inside the epidermis, is biform.; that is, with an outer layer of thin-walled cells and 1 to 4 inner layers of thick-walled cells.

Table 2 shows great range in total number of resin ducts within the same taxonomic entity. P. elliottii var. elliottii has 2 to 8 (rarely 9); P. elliottii var. densa has 3 to 9 (rarely 10 or 11); and P. caribaea 2 to 8. Thus, number of resin ducts cannot be used as a means of separating the two varieties of P. elliottii, as suggested by De Vall (1941, 1945) and West and Arnold (1946).

The number of resin ducts is variable, even among needles on the same twig. On material from one tree of P. elliottii var. elliottii from near Lake City, Fla., needles with 5, 6, 7, 8, and 9 resin ducts were examined.

However, we have observed another microscopic character, thickness of the hypoderm of needles, by which nearly all specimens of the three pine variations studied can be identified. The number of layers of cells in the hypoderm, as shown in needle cross section, is given in the last column of table 2. These figures all include the thin-walled cells, uniformly a single outer layer in these pines, and the thick-walled cells in 1 to 4 inner layers.

P. elliottii var. elliottii is readily identified and distinguished from the-other two variations by the thin hypoderm of only 2 (infrequently 3) layers, the outer layer of thin-walled cells and the inner one of thick-walled cells. P. elliottii var. densa has a thick hypoderm of 3 or 4 (infrequently 2 or 5) layers, of which all except the outermost layer are of thick-walled cells. P. caribaea also has a thick hypoderm of 3 to 5 (infrequently 2) layers, of which all but one are of thick-walled cells. The last generally is distinguishable from P. elliottii var. densa by the slightly thicker hypoderm, at least in places.

The thinnest hypoderm was found in P. elliottii var. elliottii, which grows in a humid, warm temperate climate, thickened hypoderm in P. elliottii var. densa, which grows in a subtropical climate with dry winters, and thicker hypoderm in P. caribaea, which grows in a tropical climate with a long dormant dry season. If thickness of hypoderm is correlated with climatic differences, as found by Weidman (1939) in P. ponderosa, then in

Table 3. --Resin ducts and hypoderm layers in needles of cultivated pines

Location and species or variety	Source of seed	Localities	Total resin ducts	Medial resin ducts	Hypoderm layers
		Number			
Institute of Forest Genetics, Placerville, Calif.:					
Pinus elliottii var. *elliottii*	Miss.	1	4-5	1/0 (1)	2
Pinus elliottii var. *elliottii*	No. Fla.	1	5-7	1-2 (3)	2 (3)
Pinus caribaea (2 trees)	Brit. Honduras	1	4-9	0-2 (3)	3-2
Harrison Expt. Forest, near Gulfport, Miss.:					
Pinus elliottii var. *elliottii*	s. c.	1	2	0	2
Pinus elliottii var. *elliottii*	Georgia	2	2-4	0 (1)	2 (3)
Pinus elliottii var. *elliottii*	La.	1	2	0	2
Harrison Expt. Forest, near Gulfport, Miss. :2/					
Pinus elliottii var. *elliottii*	Miss.	1	2-4	0 (1)	2
Pinus elliottii var. *elliottii*	No. Fla.	1	2-5	0-1	2
Pinus elliottii var. *densa*	So. Fla.	1	2-4	0 (1-2)	2 (3)
Pinus caribaea	Cuba	1	2-3	0	2-3
Near La Belle, Fla.:3/					
Pinus elliottii var.- *elliottii*	No. Fla.	1	2-5	0-1 (2)	2
Hillsborough State Park, Fla.: 4/					
Pinus elliottii var. *elliottii*	Fla.	1	4-7	0-1 (2)	2
Pinus elliottii var. *densa*	So. Fla.	1	4-6	0-1 (2)	2-3 (4)

1/ Figure in parenthesis indicates number rarely observed.
2/ From a j-year-old plantation established by the Division of Forest Pathology; each sample was composed of needles from 3 plants.
3/ From a j-year-old plantation of the Atlantic Land and Improvement Co.; the-sample was from 5 plants.
4/ From a plantation about 17 years old.

these subtropical and tropical pines, it apparently is associated with a dormant dry season.

There is some relationship between thickness of the hypoderm and the position of the stomata in rows on the surfaces of the needles. Where the hypoderm is thin, the stomata are near the surface, and where the hypoderm is thick, the stomata commonly are sunken, their depth in the stomatal grooves corresponding roughly to the thickness of the hypoderm.

These pines, being hard pines (subgenus Diploxylon), have two vascular bundles in the needles, which are located close together. In some of the cross sections of P. caribaea the two vascular bundles are almost united, and in a few there is essentially only one vascular bundle.

The amount of thick-walled cells, or sclerenchyma cells, within the endodermis and around the vascular bundles varies considerably and apparently is not of taxonomic value in the pines studied. These thick-walled cells are arranged in 1 or 2 or more layers above and below the vascular bundles and sometimes also between them or often are absent. In P. elliottii *var.* elliottii these thick-walled cells are usually absent or sometimes in a layer, and in P. elliottii var. densa they vary from 0 to 1 or 2 layers. The thick-walled cells within the endodermis are more common and more conspicuous in P. caribaea, usually in 1 to 3 layers above and below the vascular bundles and often between. Doi and Morikawa (1929, pp. 152-153) and Harlow (1931, p. 13) noted that the occurrence of these thick-walled cells is variable and not of taxonomic value in most species.

The material examined from cultivated *trees grown* outside the natural ranges is inadequate to indicate whether thickness of hypoderm in the needles varies under different environmental conditions. Table 3 summarizes the data obtained from needle cross sections of pines grown at the Eddy Arboretum, Institute of Forest Genetics, Placerville, Calif., at Harrison Experimental Forest, near Gulfport, Miss., from near La Belle, Fla., and at Hillsborough State Park, Fla. Trees of P. elliottii var. elliottii retained the'ir thin hypoderm when grown at Placerville, Calif., and near Gulfport, Miss., which is within the natural range. However, two trees of P. caribaea from British Honduras seed grown at Placerville, Calif., had hypoderm of intermediate thickness, or only slightly thickened, of mostly 3 layers (partly 2).

In the experiment at Harrison Experimental Forest, near Gulfport, Miss., needles from 3 plants each of 3-year-old pines from 4 geographic sources were examined. The 2 lots (1 local) of P. elliottii var. elliottii had characteristic thin hypoderm. The grasslike, almost stemless seedlings of P. elliottii var. densa from seed from southern Florida had needles mostly with thin hypoderm of 2 layers, though a few needles had 3 layers in part. The j-year-old pines of P. caribaea from Cuban seed (already killed by cold weather) had a slightly thickened hypoderm of 2 and partly 3 layers, less than in mature trees in Cuba. These young pines from Cuban seed did have many more thick-walled cells inside the endodermis of the needles (mostly 2 layers above and below the vascular bundles) than did the other pines in the experiment.

For comparison, needles of a similar grasslike, almost stemless seedling of P. palustris growing naturally near the experiment in Mississippi were examined. These needles also had the hypoderm only slightly thickened, partly 2 and 3 layers, while needles of mature trees of that species have a thick hypoderm of 3 to 6 layers of cells. Apparently the needles of grass-like seedlings on the ground have the hypoderm less developed than needles of mature trees. It will be interesting to examine needles of P. elliottii var. densa at this experiment in Mississippi after the plants have become large trees. Incidentally, the needle anatomy of P. elliottii var. densa is rather similar to that of the related species P. paiustris. Both have thickened hypoderm, but the hypoderm of the latter, 3 to 6 layers of cells, generally is thicker, at least in places. Possibly P.'elliottii var. densa obtained genes for the thickened hypoderm as well as the grasslike seedlings from If. palustris or from a common ancestor. Three-year-old seedlings of Pinus elliottii var. elliottii from northern Florida seed source grown near La Belle, Fla., had the thin hypoderm of 2 layers of cells characteristic of this variety. However, seedlings in general do not develop a thickened hypoderm comparable to that found in needles of mature trees.

Inquiries about plantations of the two varieties of Pinus elliottii growing side by side, including those projected by the Florida Forest Service in 1934, were made. Specimens submitted from these plantations at Hillsborough State Park, Fla., about 17 years old showed the differences in hypoderm thickness. Plantations of slash pine about the same age at Highlands Hammock State Park near Sebring, Fla., were visited. This locality was the source of the seed of South Florida slash pine from which the grass-like seedlings were first observed in nurseries in 1934. However, in the absence of records, the seed source was uncertain. The needles examined had thin or only slightly thickened hypoderms.

Plantations of Pinus elliottii var. densa in northern Florida were sought. Pine specimens from Austin Cary Memorial Forest near Gainesville, Fla., reported to be from southern Florida seed, had needle anatomy with thin hypoderm like the northern variety.

Specimens from near Olustee, Fla., reported to be from southern Florida seeds, were examined also. Needles from one plantation showed a slightly thickened hypoderm of 2 or 3 layers of cells, indicating a possible southern Florida origin. However, samples from another planting said to be from southern seed agreed with the northern variety in the thin hypoderm.

Future studies of older plantations of the two varieties of Pinus elliottii and Pinus earibaea may show whether the differences observed in thickness of needle hypoderm of wild trees are constant or in part correlated with environmental conditions. The thicker hypoderm tissues are found southward in habitats progressively more xeric. If later shown to be variable, the thickness of needle hypoderm would not be a reliable character for identification of planted pines.

SHAPEOFTREE

One characteristic of South Florida slash pine not shown in specimens and not easily described is the distinctive shape of the crown of mature trees. Mature trees of the virgin forests lack the straight axis or leader characteristic of most pines and other conifers but have a forked axis and an irregular, spreading crown, often slightly flat-topped. Photographs (figs. 19, 20, 21, 22) illustrate the shape, which possibly is related to climatic conditions or to more open forests on poor sites and which might not be associated with hereditary differences. The trunks of large trees in flatwoods of Hendry County often have a swollen base (fig. 8).

Shaw (1914, pl. 29, fig. 255) under P. caribaea sketched the habit of a tree which apparently was P. elliottii var. elliottii, as a tree of P. palustris in the background was included for comparison. This spreading typical slash pine tree had a forked axis and broad open crown with several large, ascending to nearly horizontal branches. Pinus caribaea in British Honduras and Guatemala has a rounded open crown, according to published photographs (Lundell, 1940, pls. 2-4; Loock, 1951).

Mature trees of South Florida slash pine average somewhat shorter than corresponding trees of typical slash pine. However, the height of typical slash pine trees gradually becomes 20 feet less on poorer sites from northern Florida south to central Florida also.

Near the southern limit of longleaf pine (P. palustris Mill.), in central Florida north of Lake Okeechobee, trees of that species also have an irregular spreading crown. While passing through Wauchula, Hardee County, we observed short longleaf pines with bushy spreading tops scattered in the grasslands of grass and dwarf palmettos.

J. Cecil King, of Lake Wales, Fla., sent to the Forest Service Herbarium in 1951 specimens of this form of longleaf pine from central Florida which in a few ways is like South Florida slash pine. This variation was found by him all over Polk County and at Plant City, Hillsborough County, near the southern limit of longleaf pine at Lake Okeechobee. The variation has needles mostly in 3's but sometimes in bundles of 4 or 5 and relatively long, 30-38 cm. He reports other differences: slightly smaller size and shorter, irregular spreading crown and crooked trunk, bark gray black, instead of reddish brown, wood dark yellow orange instead of pale yellow, resin with different odor, and cones slightly larger (15-18 cm. long) than typical longleaf pine in that area, The variation is confined to flatwoods, while typical longleaf pine grows on the hill6 as well as flatwoods.

These differences mostly are minor and insufficient to merit recognition of a botanical variety. As already noted, variations in numbers of needles occur in some other pines, which generally have a larger number southward in warmer climates. This variation of longleaf pine parallels

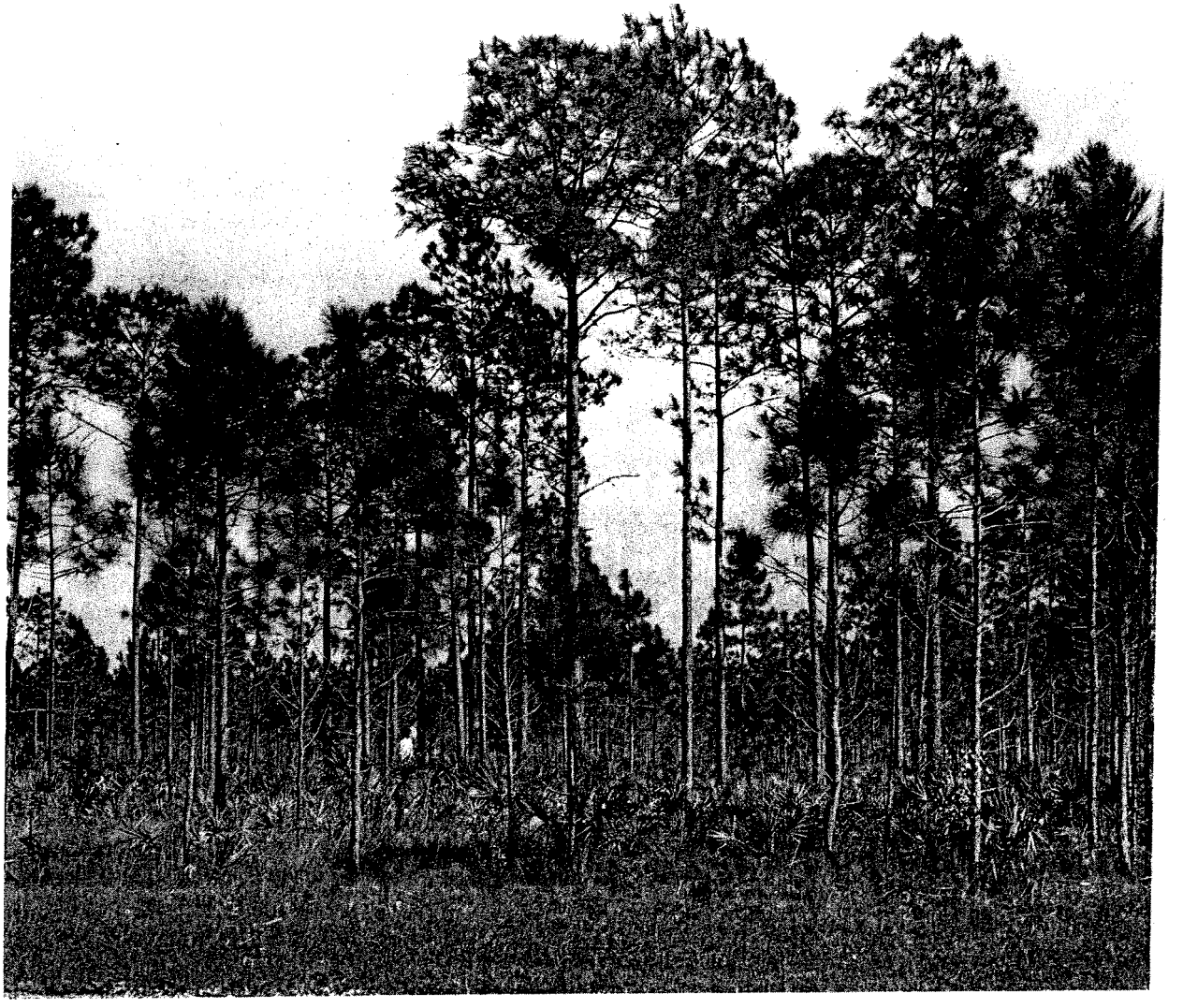
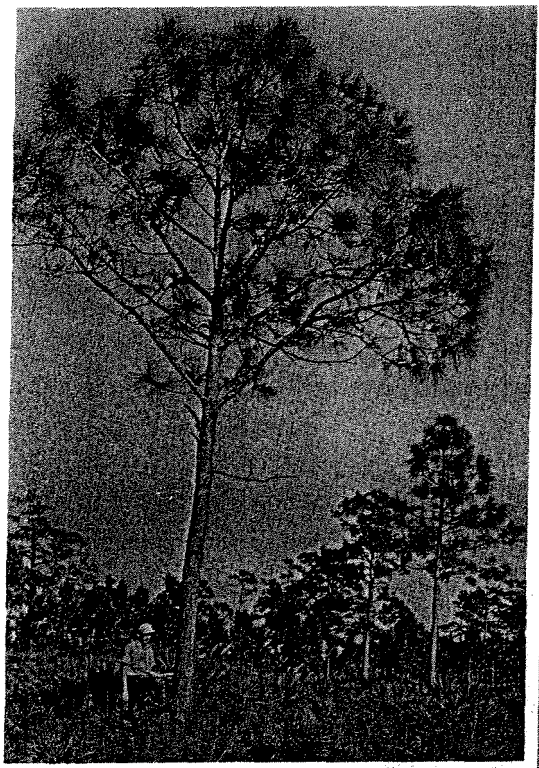


Fig. lg.--Stand of South Florida slash pine on limestone outcrop in Dade County, Florida. The older trees are developing flat-topped crowns.



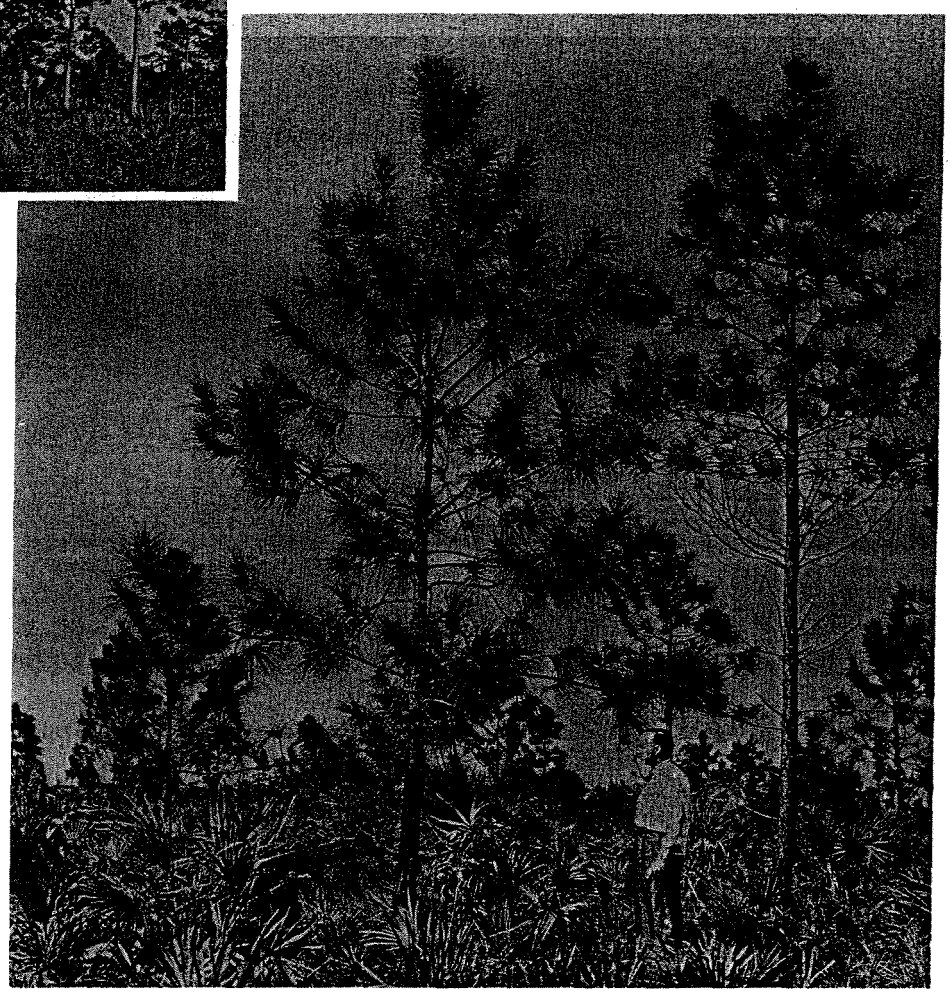


Fig. 20.--Young South Florida slash pine show different branching habit. In the foreground of the picture on the left, in Hendry Co., is a 27-year-old tree, 9 inches in diameter and 25 feet tall. It is beginning to show the typical broad and flat-topped crown. In the background is a slender-crowned tree that is 20-years old, 5 inches in diameter, and 20 feet tall. In the picture on the right, 20-foot trees, 4 inches in diameter, differ in length of branch. They are growing on very thin soil on a limestone outcrop in Dade County.

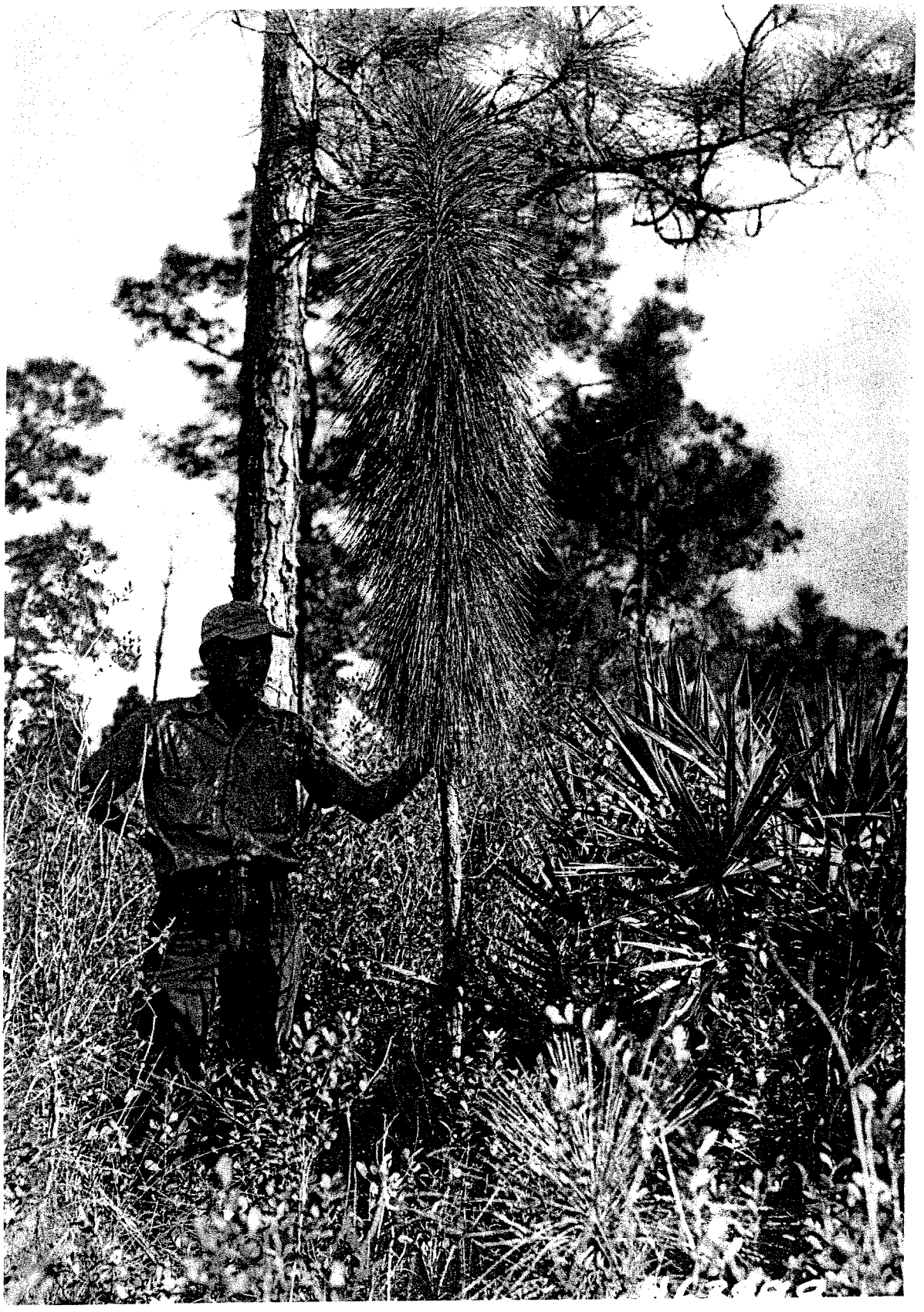


Fig. 21.--Some saplings of South Florida slash pine have few side branches. In this picture from Hendry County, the unusual sapling is 10 feet tall and unbranched.

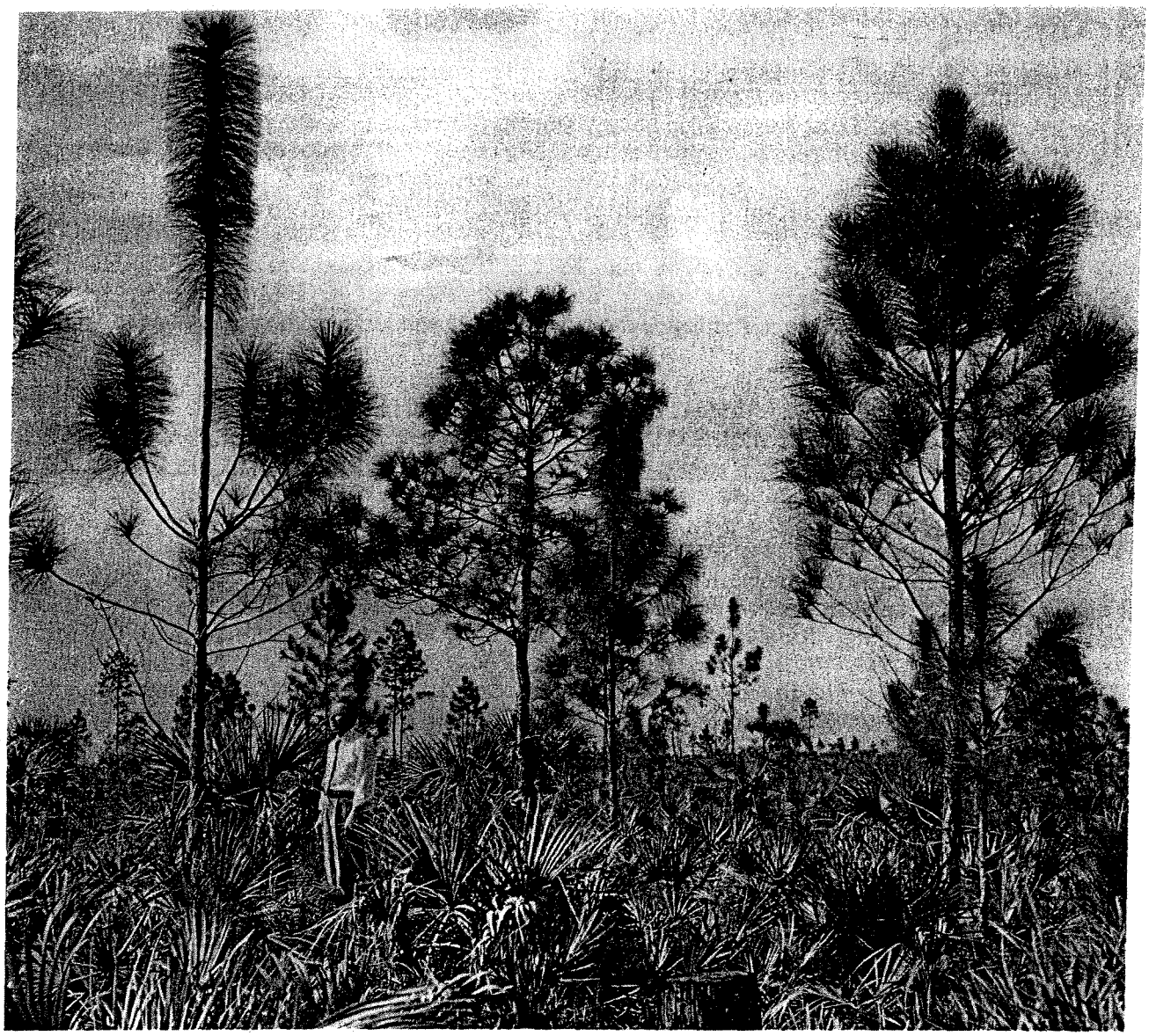


Fig. 22. --South Florida slash pine, Dade County, Florida. Note unusual shape of sapling at left.

that of slash pine in occurring at the southern limit of the species in subtropical Florida and in the irregular shape of the trees.

WOOD

The wood of Pinus elliottii var. densa, which is marketed as longleaf yellow pine, differs from that of all other pines of southeastern United States in its greater proportion of summerwood, its greater hardness, and its greater density or specific gravity. However, the wood of this variety has no anatomical structural differences from that of P. elliottii

var. elliottii or other species of the southern yellow pine group, according to examination by the Forest Products Laboratory of samples from Hendry County in southern Florida. In fact, the different species of the southern yellow pine group cannot be separated on the basis of wood alone, with the exception of longleaf pine when the pith is present and the position of the sample in the tree is known (Wahlenberg, 1946, p. 15, fig. 3).

Related tropical pines in the West Indies and Central America have similar hard, dense woods. As early as 1903 Rowlee (1903) observed great density and large amount of summerwood in the Antillean tropical pines.

It is not known whether these wood properties of P. elliottii var. densa are correlated with hereditary characteristics of this variety or a result of the environmental conditions, such as the subtropical, less humid climate. In time, tests of wood from trees of this variety and of P. elliottii var. elliottii planted together in both northern and southern Florida should reveal the answer.

Differences in mechanical properties of the wood of the two varieties are indicated in tests made at the Forest Products Laboratory of shipments from different localities and reported by Markwardt and Wilson (1935, table 21). Shipment 752, from Dade County, was the only one from southern Florida within the range of var. densa, while shipment 314 from Nassau County and shipment 1063 from Columbia County were from the northern border of Florida and shipment 1059 from St. Tammany Parish, La., all within the range of var. elliottii. These tests gave a specific gravity of dry wood of var. densa as .717, the highest value of any of the native pines, and of var. elliottii, .569 to .662. South Florida slash pine has a specific gravity about one-third greater than other southern pines. The higher portion of dense summerwood adds weight, hardness, and strength.

Detailed tests of the physical properties of wood of South Florida slash pine from Hendry County, south Florida, were made by Harry W. Cyphers, Jr.[4] He concluded that this variety possesses physical properties which, in general, are superior to those of the northern slash pine and associated species and is suitable for use as a high-quality timber product. His tests indicated that the wood should be highly suitable for construction and building materials, including high class structural timber, stringers, joists, and ties. Also, he thought it might be quite useful in car construction for sills, siding, roofing, and decking, and in low grade of lumber for boxes and crating. Other suggested uses were for railroad ties, paving blocks, flooring, and planing mill products.

The wood from lumbering operations of the Atlantic Land and Improvement Co,, La Belle, Fla., is used chiefly for structural timbers and

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4/ Cyphers, Harry W., Jr. Pertinent physical properties of slash pine wood from the Florida Everglades. 26 pp., illus. Master of Forestry thesis, School of Forestry, Duke Univ., Durham, N. C. 1950. (Typewritten)

also for lumber. Wall panels of the company's local office made from this lumber are attractive because of the reddish brown heartwood. South Florida slash pine is harvested also for pulpwood.

An investigation of the creosote treating characteristics of South Florida slash pine was made by Verne F. Bliss. 5/ He found the wood to be receptive to preservative with creosote oil.

The wood of P. caribaea formed under frostless tropical climates of West Indies and Central America has annual rings. Growth is not continuous, but there is a dormant period probably correlated with a dry season. In January 1951 at the type locality on Isle of Pines the grass around the pines was observed to be dead. Stumps showed annual rings of wood.

In Central America the formation of additional growth rings of wood each year apparently is characteristic and may serve to distinguish wood of P. caribaea from that of P. elliottii. Fahnestock and Garrett (1938) noted these differences. In timbers from Nicaragua they observed that the growth rings consisted of several bands of early and late wood, usually two or more narrow preliminary late-wood bands and a final wider band. Loock (1951) mentioned for British Honduras the clearly defined growth rings with dense bands of summerwood and one or more narrow secondary rings of dense wood commonly present in the late wood. He added that the secondary rings and stratified late wood are a diagnostic feature of pines growing under subtropical to tropical conditions.

OLEORESIN

A minor difference between the two varieties of P. elliottii previously noted is that trees of South Florida slash pine are not worked commercially for resin, apparently because the resin flows poorly. South Florida is not included in the map, gum-naval-stores productivity zones, prepared by the Forest Survey, Southern Forest Experiment Station, and published by Ostrom (1945).

However, pieces of old heartwood and stumps, or retort wood, of South Florida slash pine are gathered in lumbering operations in Hendry and Collier counties and shipped to mills for resin production by steam distillation plants. Sargent (1884, p. 202) reported that turpentine was occasionally manufactured in south Florida from this pine. *Harper*

5/ Bliss, Verne F. A study of the effective penetration of creosote oil in the wood of slash pine from south Florida. Unpublished Master of Forestry thesis, School of Forestry, Duke Univ., Durham, N. C. 1949. (Typewritten. Not seen.)

(1914, p. 361) stated that the gum does not flow readily and that very little turpentine was obtained from this pine. He predicted invention of some method for utilizing this pine profitably for naval stores.

Preliminary analyses by the Maval Stores Station, Olustee, Fla., of turpentines of the two varieties of slash pine have not revealed significant differences in density, refractive index, or optical rotation.

Islip and Mathews (1950) analyzed oleoresin from P. caribaea in British Honduras and found it normal, the turpentine oil of good quality, and the rosin similar in character to commercial American rosin. Paul J. Shank reports that resin of P. caribaea is harvested commercially in Honduras and consumed locally. In Cuba, according to Albert J. Fors, resin is not obtained from P. caribaea because there are not enough pines of suitable diameter.

DISEASE RESISTANCE

The two varieties of P. elliottii and P. caribaea from Cuba all differ markedly in resistance to the fusiform rust of southern pines caused by Cronartium fusiforme (Pk.) Hedgc. and Hunt, according to preliminary investigations made by the Division of Forest Pathology, Bureau of Plant Industry, Soils, and Agricultural Engineering, U. S. Department of Agriculture, in cooperation with the Forest Service. These young experimental plantings made by Paul V. Siggers and others of the Division of Forest Pathology on the Harrison Experimental Forest in southern Mississippi were also a source of specimens for our study of needle anatomy.

A preliminary report of results by the Division of Forest Pathology is summarized in the following quotation from the annual report of the Southern Forest Experiment Station (1950, p. 59).

"A native 'south Florida' strain of slash pine and one from Cuba showed striking rust resistance and susceptibility, respectively, in geographic seed source plantings. In a south Mississippi planting, for instance, the infections after 2 years in the field are 4 percent (south Florida) and 66 percent (Cuba), as compared to 20 and 24 percent for north Florida and Mississippi strains. The south Florida strain differed greatly in growth characteristics and appearance from all other collections of slash pine within the United States. A number of these other native strains, in several plantings ranging from 3 to 7 years old, have not yet revealed any marked differences in rust resistance."

RELATIONSHIPS OF PINUS ELLIOTT11 AND P. CARIBAEA

Though the origin and history of Pinus elliottii, P. caribaea, and related species are not known, some evidence on the relationships of these pines may be obtained from studies of botanical classification, present distribution of species and floras, plant migration, geological history, and other sources.

As shown by botanical characteristics, most of the species of pines of southeastern United States and West Indies are closely related, and, as previously stated, most were placed by Shaw (1914) in his group Australes. P. tropicalis Morelet has some characters suggesting affinities with this group, though placed by Shaw in his group Lariciones, all Old World species except *two.*

Florin (1933, p. 17) accepting P. caribaea in its broadest sense, concluded from the present distribution that this species possessed a larger, more or less connecting area before the Pliocene epoch but became cut up in Pliocene and in more recent times has not been able to spread in the West Indies.

As defined here, P. caribaea has most of its area in Central America but is present also in Isle of Pines, western Cuba, and four of the larger Bahama Islands at the northwestern part of the group and on two of the Caicos Islands at the southeastern end but not on many small islands. Its range is greater than that of the other three West Indian pines; none of which occurs on the Bahama Islands or in Central America. In western Cuba and Isle of Pines it is considerably less common than P. tropicalis, which is endemic to these two islands. The larger, disjunct distribution of P. caribaea suggests a relatively great age.

Pinus elliottii var. elliottii, of continuous distribution on the Coastal Plain from South Carolina to Florida and Louisiana, apparently is of more recent origin, while P. elliottii var. densa occupies a relatively new habitat on the southern Florida lowland and is probably very young in comparison.

The nearest points of ranges of P. caribaea and P. elliottii var. densa are not between the *Lower* Florida Keys and western-Cuba but between Palm Beach, Fla., and Great Bahama Island, a distance of about 60 miles across deep water. As the closest forests of P. elliottii var. elliottii are a slightly farther distance to the northwest, the temperate and tropical extreme variations are separated there by only about 150 miles.

The main problem is the disjunct occurrence of P. caribaea in both West Indies and Central America. It is not known in which direction migration may have occurred. The occurrence of P. caribaea on six or more of the Bahama Islands and the absence of the other three species of Cuban

pines from all those islands suggest either a more rapid rate of migration or a greater age for the first and indicate also that migration of pines across bodies of water is slow and irregular. According to numbers of widely distributed plant species, the flora of the West Indies is related to that of northern South America (where pines are absent), to that of Central America, and to a much lesser extent to south Florida.

In analyzing the plant affinities between Cuba and neighboring countries, Seifriz (1943, pp. 385-387) noted that Cuba is 140 miles from Florida and 125 miles from Yucatán, yet its flora is primarily South American but separated by 600 miles of water. He cited four routes for plant migration by Yucatán, Florida, Lesser Antilles, and over water from Venezuela and agents, such as hurricanes, birds, and natural rafts (drifting logs). He mentioned pine and oak, neither tropical, as suggesting migration from the United States, citing *Quercus virginiana* Mill., live oak of southeastern United States, as also found in western Cuba and *P. caribaea* as common in Florida. Though he concluded that the major portion of Cuba's plant life came from the south, there were strong ties with southern North America through Mexico or Florida. He noted that Isle of Pines was a part of western Cuba geologically, ecologically, and floristically; that there had been recent submergence, and that emergence of about 50 feet would unite the two.

Many interesting disjunct distributions of species of eastern United States in the highlands of Mexico and Central America have been reported by Sharp (1946) and others. *Pinus strobus* L., eastern white pine, has been found in southern Mexico by Martínez (1939) and later in Guatemala.

Some plant migration in the West Indies, chiefly of beach plants, doubtless has occurred by means of ocean currents, as shown by the detailed studies of Guppy (1917). Winds, particularly hurricanes from the southeast, may have aided dispersal to the United States. Migrating birds may have distributed seeds of some kinds to islands. During the long geological periods since the genus *Pinus* appeared, some migrations by slow and irregular steps obviously have occurred.

Inasmuch as pine pollen is transported long distances in quantities by the wind, migration across water gaps by gene infiltration into a closely related species by means of wind-borne pollen is a possibility. Transport by wind would be from the West Indies to Florida and Central America. Incidentally, the pollen of all three variations of pines studied was found to be indistinguishable in size and shape.

Bermuda, a small isolated volcanic island about 700 miles northeast of the Bahama Islands and 400 miles southeast of North Carolina, has an impoverished flora of seed plants. Britton (1918, pp. vii-viii) noted that nearly all the native species of seed plants inhabit the West Indies or southern Florida or both and concluded that they originated from seeds or other parts transported from the North American mainland or West Indies by

wind, ocean currents, and birds. There are no pines, and the only native conifer is the endemic Bermuda juniper, Juniper& bermudiana L., the most abundant and characteristic tree of Bermuda. It is related to J. barbadensis L. (J. lucayana Britton), of the northern Bahama Islands-and Cuba. Britton (1918, p. 410) suggested that the former might have originated from the latter by a seed transported by a migratory bird and differentiation through long isolation. Similarly, the Azores Islands, located 800 miles off the coast of Portugal, have a juniper (J. oxycedrus) regarded by some as a distinct variety, but no pine (Guppy, 1917, pp. 409-410, 430-432). Obviously, migration of pines is limited by large bodies of water except through pollen.

Direct information on P. earibaea and P. elliottii from the fossil record is lacking. For example, Hollick (1924) found no fossil gymnosperms in a study of the fossil flora of the West Indies. Pinus, *a very* old *genus* geologically, was in eastern United States throughout the Cretaceous and Tertiary. The present species of the genus in Florida probably date from Pleistocene and invaded Florida from higher areas northward which remained land during the Pleistocene submergences.

As students of plant and animal distribution often explain irregular present distribution of species and floras partly on the basis of former land connections, land bridges, or continental drift, evidence from historical geology may be reviewed. Campbell (1940) concluded that peninsular Florida has been submerged throughout most of its geological history between land masses of southeastern United States and the Greater Antilles and that only since the beginning of the Pliocene epoch has this area been part of North America. During the Pleistocene epoch there were various fluctuations of sea level in Florida controlled by alternate accumulation and melting of the polar and subpolar ice caps. The levels were lowest during maximum extent of ice sheets and highest when the ice melted.

Cooke (1939, 1945) has discussed further the oscillations of sea level in the four main ice ages of the Pleistocene epoch and noted that the accumulation and wasting of the continental ice caps would account for variations of perhaps two or three hundred feet. He published maps of the shore line of Florida at different stages, showing in the glacial stages the mainland including the Florida Keys and in interglacial stages southern Florida submerged. The most recent shore line, Pamlico, which was preceded by a fall of about 60 feet below the present shore, was about 25 feet above present sea level and probably represents the mid-Wisconsin recession. All of Florida south of Lake Okeechobee was then submerged except an island in the vicinity of La Belle and Immokalee. Afterwards there was an undetermined lower sea level and a rise to the present sea level (and probably still continuing) with the melting of the Wisconsin ice cap.

Schuchert's (1935) detailed reference on the historical geology of the Antillean-Caribbean region included southeastern United States and Central America as well as the West Indies. He concluded that Florida probably

was never connected with Cuba or Bahama Islands. His maps indicated land connections between Central America and the Greater Antilles from Honduras and Nicaragua to Jamaica and Hispaniola both in lower Oligocene and from upper Miocene to lower Pliocene. Isle of Pines 60 miles south of Cuba was connected with Cuba in Pleistocene time and became separated very late in Pleiostocene or recent time.

Woodson (1940), citing Schuchert, noted the existence of a "core" of Central America highlands of Guatemala, Honduras, and northeastern Nicaragua, which had had no major submergence since at least Middle Carboniferous, and another "core" in the highlands of interior British Honduras and adjacent Pete/n, exposed since Cretaceous. These old land masses served as centers of survival of geologically old species and migration outward.

Of exceedingly great interest to this study as well as to numerous other investigations are the recent natural radiocarbon measurements by Kulp, Feely, and Tryon (1951), and others. By the carbon 14 method of age determination discovered by W. F. Libby and others, they dated two samples from Bermuda associated with recent fluctuations in ocean level. A fossil "cedar" log (doubtless Juniperus bermudiana L., mentioned previously) dredged from a harbor at Bermuda was found to have an age of 11,500 ± 700 years. The sample is representative of a widespread "cedar" forest now lying under 10 to 30 feet of water and 10 to 20 feet of mud and killed presumably by rise in sea level at the end of the last, or Wisconsin, glacial period. This age determination concurs with others from North America and Europe in placing the termination of the last glacial period as about 11,000 years ago.

A sample of Bermuda peat obtained from the same dredging but stratigraphically above the "cedar" forest was dated as 6,900 ± 150 years old and suggests slow rate of sea level rise equivalent to rate of retreat of the Wisconsin continental glacier. This peat sample representing a higher water stage indicates that the time for the complete melting of the ice sheet must have been about 6,000 years.

These figures date the fluctuations in sea level already cited from geological evidence. Thus, as recently as about 11,000 years ago, the ocean surface was perhaps 60 feet lower than now because of removal and storage of water in continental ice sheets. At that time the Florida Keys, now separated by shallow water less than 17 feet deep, were joined northward to the mainland, and the coastal zone now occupied by South Florida slash pine was much broader. Also, western Cuba and Isle of Pines, now 60 miles distant, were connected, and their pine forests of P. tropicalis and P. caribaea probably were continuous. However, then and now, Florida was separated from the nearest Bahama Islands and Cuba by the deep Florida Straits, through which the Gulf Stream passes.

Though Central America and the Greater Antilles were separated by deep water during interglacial stages, the water gap was much narrower than at present. Then migration by seeds or pollen would have been less difficult than now.

Pinus elliottii var. densa with an altitudinal range from about 5 to 50 feet or more above sea level, mostly less than 25 feet, obviously has been greatly affected by the fluctuating sea levels of the Pleistocene epoch. Its entire area is very young geologically, having been covered by ocean waters in the interglacial stages and the area up to 25 feet, nearly all the present range, was submerged by the Pamlico sea as recently as the mid-Wisconsin recession (Davis, 1943, pp. 58-75, fig. 26). This botanical variety of obviously recent origin thus has become established on a newly exposed habitat which moved with alternating stages of submergence. Likewise, the pine forests of P. caribaea on the mostly low Bahama Islands are younger than the last interglacial stage.

As the Florida Keys were connected with the mainland during the stages of glaciation, the range of this new variety probably became continuous to Big Pine Key and remained so until somewhat less than 11,000 years ago. Then, as in the case of the juniper at Bermuda, the lower forests were submerged, and the trees may have migrated to slightly higher levels above the rising *shore* line.

A similar migration of trees and other plants northward across Canada has occurred following melting of the last ice sheet and increase in temperatures. These migrations have also included plants at great distances southward, and are still in progress. For example, Mattoon (1936) and others have reported that typical slash pine is naturally migrating northward in southeastern United States. It is hardy and produces seed when planted moderate distances north of the natural range.

This study revealed unexpected relationship and some apparent gene interchange among three pines of separate ranges, P. palustris, P. elliottii var. densa, and P. tropicalis. All three have a grasslike almost stemless seedling stage, while other pines of southeastern United States and West Indies do not, so far as known. Vigorous saplings of the latter two pines often are without lateral branches and bear long, slightly curving and drooping needles, and have large buds with whitish scales, as in P. palustris. The first two have similar leaf anatomy also.

Chemical analyses of the oleoresins may reveal additional relationships. Mirov (1948) summarized results from various studies of different species of Pinus but had no data on the new variety nor of samples from widely separated localities, such as within the range of P. caribaea.

SUMMARY

Evidence from field and herbarium studies, as well as experimental plantings, shows that among the hard pines with shiny brown cones generally classified as Pinus caribaea Morelet there can be distinguished three different geographically separated populations or taxonomic entities (taxa) meriting distinct botanical names.

Pinus caribaea Morelet, Caribbean pine, in the narrow sense, is a tropical species of the West Indies and Central America. Its range is Bahama Islands (six or more islands), western Cuba, Isle of Pines, and Atlantic slope of Central America in British Honduras, eastern Guatemala, northern Honduras, and northeastern Nicaragua, and perhaps also in southeastern Quintana Roo, Mexico. It is characterized by needles in fascicles of 3 (sometimes 4 or 5 on young trees); cones usually small (5-10 cm. long), with small weak prickles less than 1 mm. long; seeds narrowly ovoid, about twice as long as broad, averaging less than 6 mm. long, wings usually remaining attached.

Pinus elliottii Engelm., slash pine, a name already used by some authors, is adopted for a closely related species including the two entities in southeastern United States as botanical varieties. It is characterized by needles in fascicles of 2 and 3; cones usually larger (6-14 cm. long), with stoutprickles 1-2 mm. long; seeds ovoid, less than twice as long as broad, averaging 7 mm. long, wings becoming detached.

Pinus elliottii var. elliottii, slash pine (typical), the familiar and commerically important slash pine, is widely distributed along the warm, temperate Coastal Plain from southern South Carolina to central Florida and west to eastern Louisiana. It has needles in fascicles of 2 and 3 and normal seedlings with erect, slender, pencillike stems.

Pinus elliottii var. densa Little & Dorman, South Florida slash pine, has been published as a new variety for the entity restricted to subtropical south Florida north to Lake Okeechobee and northward along both coasts in central part to Volusia and Levy counties. It has needles in fascicles of 2 (infrequently 3); seedling with grasslike, almost stemless stage with very short stem, many crowded needles, and thick tap root. The trees are generally medium-sized or small, with axis often forking into large branches, and with irregular, flat-topped and spreading, open crown. The wood is very heavy and hard, with very thick summerwood. The resin flows poorly and is not harvested commercially.

Nearly all specimens of the three named entities can be identified by the number of layers of cells in the hypoderm of the needle cross section. P. elliottii var. elliottii has a thin hypoderm of only 2 (infrequently 3) layers. P. elliottii var. densa has a thick hypoderm of 3 or 4 (infrequently

2 or 5) layers. P. caribaea has a slightly thicker hypoderm of 3 to 5 (infrequently 2) layers. Number of resin ducts in the needle cross section varies greatly and cannot be used in identification.

Pinus hondurensis Loock, recently proposed as a new species for the segregate pine of British Honduras and Guatemala and probably also Cuba, is reduced to a synonym of P. caribaea. It is also a homonym and perhaps also synonym of an obscure older name, P. hondurensis Séneclauze.

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