

THE UPLAND PINE FORESTS OF NICARAGUA

A Study in Cultural Plant Geography

BY
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PREFACE

There is a frequent correlation between actual vegetation and remote human occupations. The rate of succession towards the original forest community, the establishment and maintenance of certain plant communities and the dominance of certain species, can in many cases be attributed to past human interventions, some of them dating several centuries back.

GERARDO BUDOWSKI

THIS IS A STUDY in cultural plant geography,¹ a study concerned with the relation of human activities to the occurrence and distribution of the genus *Pinus* in Nicaragua—the area of the southern geographical terminus of the genus in the Western Hemisphere.

In the humid tropics, the climatic climax vegetation is a mixed forest containing a great variety of species; the nature of any other type of plant community is largely determined by the selective effects of nonclimatic conditions, especially edaphic factors but also human activities such as forest clearing, grazing, and burning. Students of both man and vegetation have been giving increasing attention to the correlation between the existence of many tropical savannas and grasslands and burning by man. There has been much less concern, however, for the possible correlation between fire and tropical forest communities dominated by a single woody species; such a relation has been suggested, for example, for certain casuarina forests in the East Indies, eucalyptus forests in northeastern Australia, teak forests in Burma and Thailand, oak forests in Central America, and pine forests in Southeast Asia and Middle America.

Species of the genus *Pinus* extend well into tropical latitudes in the Western Hemisphere. On the Caribbean coast of Nicaragua near Bluefields, a *Pinus caribaea*-grassland association extends to 12°10' N. latitude (fig. 1), and in the northwestern highland area known as the Segovias, discontinuous stands of pine, mainly *Pinus oocarpa*, extend south of Matagalpa to 12°45' N. Studies of the ecology of the lowland pine savannas of eastern Nicaragua have previously been made by James J. Parsons (1955b), B. W. Taylor (1959a), and Jeffrey Radley (1960), but the upland pine forests (fig. 3) have received little attention in the literature.²

Most pine species readily invade open sites and thus may be part of an early successional stage rather than a climax plant community. Pine seeds are known to germinate best in exposed mineral soil, and young seedlings of many species, including *P. oocarpa* and *P. caribaea* in Nicaragua, are intolerant of shade. How then can the Nicaraguan pines, all of which occur in the warm and humid climates of elevations below 5,000 feet, compete with much faster growing tropical plant species so successfully that they form large and pure stands?

My observations indicate that in highland Nicaragua, pines grow mainly on sites with thin soils and acidic parent materials, in an area having a long history of human settlement which involved forest destruction, periodic burning, and

¹ The term "cultural plant geography" has been proposed by William C. Robison (1958: 286) "... as a designation for the study of vegetation changes resulting from man's occupancy of the earth..."

² For brief discussions of the highland pines see Taylor (1959b:207-209) and Food and Agricultural Organization (1950:48-52).

soil erosion; however, regardless of soil conditions, the upland pines seem incapable of competing successfully—except, possibly, in localized “natural habitats”—with broadleaf vegetation for a long period of time without the aid of at least occasional fires.

In this study climatic, edaphic, and biotic relationships as well as economic and historical human factors are examined to provide a basis for understanding the biogeography of the upland pine forests of Nicaragua. Special attention is given to the role of fire as an ecologic agent. Relief, parent rock materials, soils, climate, and vegetation are considered in some detail, primarily as they relate to the distribution of the pines, but also as they relate to settlement and land-use practices in the pine area.

It is important to point out that the physical and cultural geography of the interior of Nicaragua is very poorly known; consequently, this study is in many ways a reconnaissance. For most of Nicaragua there is need for basic research in all fields of the physical and social sciences.

The field work for this study was carried out in the period from January to September, 1957, under a Buenos Aires Convention Fellowship awarded by the Institute of International Education. The fellowship was administered in Nicaragua by the United States Information Service under Mr. Thomas Thoman and by the Ministry of Education in Managua.

I wish to express my indebtedness to Dr. B. W. Taylor, plant ecologist for the Food and Agricultural Organization Mission in Nicaragua, for his very valuable help with vegetation and soils; the Inter-American Geodetic Survey under Captain Billy Pendergast in Managua for provision of maps and aerial photographs; the personnel of the Servicio Técnico de Agrícola de Nicaragua, a joint Point Four-Nicaraguan program in agriculture; the many others in Managua who provided data, general assistance, and contacts with people in the field; Doña Celia Guillén de Herrera of Ocotal, the beloved teacher of children, who knows the history, folklore, and landscape of the Segovias as does no other living person; and finally to all the people of the Segovias who gave me their hospitality, friendship, and knowledge of their land.

Grateful acknowledgment is made to the professors of the University of California who have guided the preparation of this study: James J. Parsons for his helpful criticism, suggestions, and encouragement during the entire period of field work, research, and writing; N. T. Mirov, a plant physiologist with a great knowledge of, as well as affection for, the genus *Pinus*; Edward C. Stone, who has a broad background in forest ecology; and Carl O. Sauer, who first turned my interests toward Latin America and “man’s role in changing the face of the earth.”

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CHAPTER I

THE GENUS *PINUS* IN THE TROPICS

OF EXISTING CONIFERS, the genus *Pinus* is not only the most economically valuable group, but is also one of the oldest and most widespread. Fossil pines that date back to the Jurassic have been found, and in the Cretaceous, pines were common throughout northern latitudes. During the Tertiary and after, pine species evolved that were adapted to a wide variety of environmental conditions: secondary centers of diversification arose in south-central China and central Mexico, from which tropically acclimated pine species eventually migrated southward almost as far as the equator in Sumatra¹ in the Old World and to central Nicaragua in the New World. Of the 94 pine species listed by Mirov (1961) for the world, the greatest number occur in central Mexico, where there are at least 33 distinct species; southward, in Middle America, the number decreases rapidly to 10 in Chiapas, 8 in Guatemala, 5 in Honduras, and only 3 in Nicaragua. Three pine species are recognized in the Caribbean islands.

The distribution of pines in Middle America and the southern United States is shown in figure 1.² For Chiapas in southern Mexico, the Central American countries, and the Caribbean islands, the known species, 13 in all, are indicated in table 1.

All Central American pine species except *P. caribaea* occur in Mexico, and their distribution suggests that they originated there. These pines may not have migrated southward into Central America until relatively late in geologic history because the Isthmus of Tehuantepec either was under water or existed only as a low, narrow land bridge during most of the Tertiary. *P. caribaea*, the most widely dispersed of the Middle American pines, shows a very close affinity with the pines of the southeastern United States, and its dispersal may have been by both Caribbean and Gulf Coast routes. Land bridges, such as one that probably joined the Antilles and Honduras in the late Miocene-early Pliocene, might account for the discontinuous distribution of *P. caribaea*. That *P. caribaea* can migrate across sea barriers, however, is evidenced by its scattered occurrence in the Bahamas, which emerged during or after the Pleistocene and have never been joined to one another or to the mainland. For some pines, then, it is not necessary to postulate land bridges to explain dispersals.³

¹ A statement by U Aung Din (1958:121) claiming that *P. merkusii* occurs below the equator naturally in Sumatra, Java, and Borneo has not been substantiated. Buys, Japling, and Fernandes (1928:5) mention reports of pines (*P. merkusii*) on Mt. Kerintji in Sumatra two degrees south of the equator, but say that such occurrence is doubtful. The late H. H. Bartlett, in a letter to N. T. Mirov at the University of California (1955), says he knows of no pine on Kerintji and suggests a possible confusion with *Casuarina sumatrana*.

² The main sources for the distribution of pines in the Caribbean area shown on figure 1 are as follows: Shantz and Zen, 1936: fig. 2 (southern United States); Leopold, 1959: fig. 6 (Mexico); Miranda, 1952: [20a] (Chiapas); Standley and Steyermark, 1945: 277 (Guatemala); Lauer, 1959: abb. 2, and Servicio Forestal de Honduras, unpublished sketch map (Honduras); Great Britain, Colonial Office, 1959: veg. map sheets 1, 2 (British Honduras); Radley, 1960: fig. 18 (east coast of Nicaragua and Honduras); Taylor, 1959b, and Donovan (interior Nicaragua); Lauer, 1954: [46a] (El Salvador); Waibel, 1943: pl. 1 (Cuba and the Isle of Pines); Holdridge, 1947: pl. 6, and Street, 1960: map 5 (Haiti); Ciferri, 1952: [326a] (Dominican Republic); and Kellogg, 1951: 795 (Bahama Islands).

³ Although pine seeds are not generally carried far by the wind, even when winged, pine pollen in quantities is transported long distances by wind, and "infiltration" of genes of one

In the Caribbean area the distribution of pines is rather unusual. Although *P. caribaea* occurs both on the islands and the mainland, *P. occidentalis* and *P. tropicalis* are restricted to Cuba and Hispaniola. *P. occidentalis* grows from the coastal zone to 10,000 feet above sea level, possibly the greatest range of any pine species. Most stands occur on the ancient rocks of eastern Cuba and southern Hispaniola, where the species may be the relict of a very early introduction. *P. occidentalis* is a member of the group *Australes*, which includes *P. palustris*

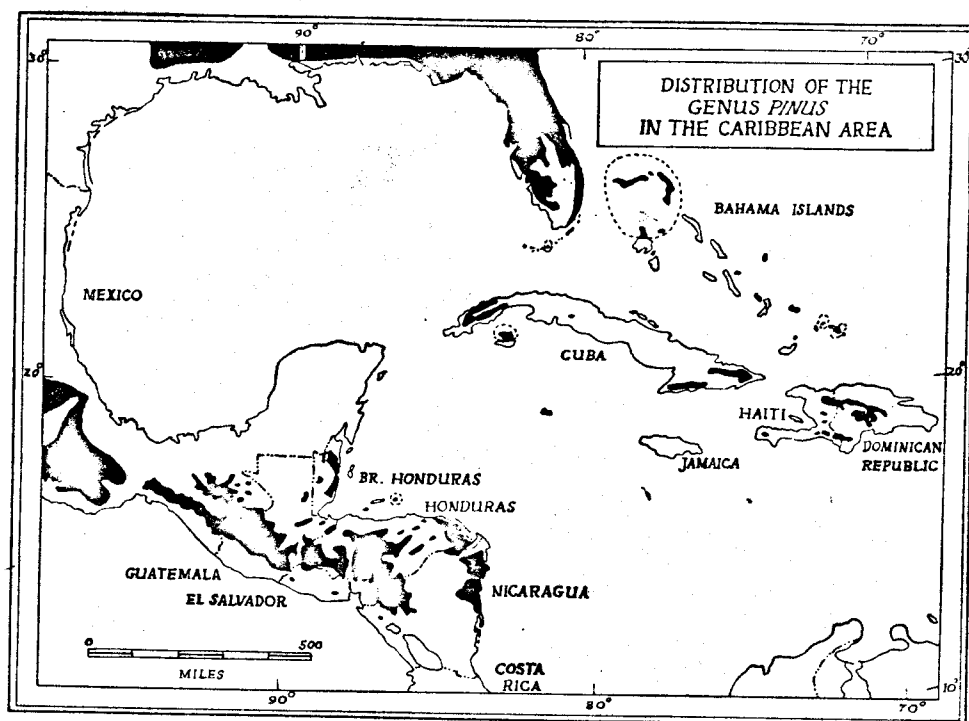


Fig. 1. The distribution of the genus *Pinus* in the Caribbean area.

(longleaf pine) and *P. elliottii* (slash pine) of the southern United States, many of the Central American pines, and *P. caribaea*. *P. tropicalis* occurs only in lowland savannas in western Cuba and the Isle of Pines, areas that have been above the sea only since the Pleistocene. Curiously, *P. tropicalis* is a member of the group *Lariciones*, most species of which are found in Asia, including tropical Southeast Asia. The fact that there are no pines on either Puerto Rico or Jamaica is not readily explained; apparently *P. caribaea* does not grow naturally on Jamaica and other Caribbean islands because edaphic conditions are unsuitable (Asprey and Robbins, 1953:369).

A few pine species also extend into tropical latitudes in the Old World. *P. insularis*, *P. khasya*, and *P. merkusii* are found in Assam, Thailand, Burma, and

species across water gaps into other species is possible. Migrating birds undoubtedly help distribute seeds to islands. The relationships of *P. caribaea* to the other Caribbean pines and to the pines of the southeastern United States, with speculations on origins and history, are discussed by Little and Dorman (1954). See also Asprey and Robbins (1953:369), who suggest a post-Tertiary over-water migration of *P. caribaea* from Yucatan to western Cuba.

the Philippines, at elevations ranging from a few hundred to several thousand feet; the pine in Sumatra is *P. merkusii*. Scattered reports (Bor, 1938:130; Lizardo, 1955:218; and van Steenis, 1949:lxv) indicate that most, if not all, of the south Asiatic pine forests, like those of tropical America, are subject to frequent ground fires, and that ecological relationships are similar in the two areas.

Not only is the genus *Pinus* restricted to the Northern Hemisphere, but few of the other Northern Hemisphere conifers extend very far into the Southern Hemisphere. *Libocedrus* is probably the only North American coniferous genus

TABLE 1
SPECIES OF *PINUS* IN CHIAPAS, CENTRAL AMERICA, AND THE CARIBBEAN ISLANDS

Species of <i>Pinus</i>	Locations									
	Chiapas	Guatemala	British Honduras	Honduras	El Salvador	Nicaragua	Cuba	Isla of Pines	Hispaniola	Bahama Islands
<i>P. ayacahuite</i>	×	×	..	×
<i>P. hartwegii</i>	×	×
<i>P. montezumae</i>	×	×	..	×
<i>P. oocarpa</i>	×	×	..	×	×	×
<i>P. oaxacana</i>	×
<i>P. pseudostrobus</i>	×	×	..	×	×	×
<i>P. rudis</i>	×	×
<i>P. strobus</i> , var. <i>chiapensis</i>	×	×
<i>P. tenuifolia</i>	×	×
<i>P. teocote</i>	×
<i>P. caribaea</i>	×	×	×	..	×	×	×	..	×
<i>P. tropicalis</i>	×	×
<i>P. occidentalis</i>	×	..	×	..

that occurs farther south than *Pinus*.⁴ In the New World, *Abies* and *Taxus* apparently terminate in the Lake Yojoa area of central Honduras; *Cupressus* occurs as far south as El Salvador (Lötschert, 1955:76); and the last stands of *Pinus* are those of *P. caribaea* near Bluefields on the east coast of Nicaragua (Radley, 1960:164). Likewise, few of the southern Hemisphere conifers extend north of the equator. The only exception in the New World is *Podocarpus*, which reaches into Mexico and Cuba. It is believed that the southern conifers have been separated from the northern conifers since the late Paleozoic (Li, 1953:260).

Although pines cover large areas in the tropical latitudes of Middle America, many of the stands are at high elevations where the climate is temperate or cold.⁵ As temperature drops and the frost period lengthens with increase in altitude, the number of plant species decreases and growth is slower—conditions comparable to those of the natural habitats of pines in northern latitudes. The pine forests con-

⁴ *Libocarpus*, however, occurs in western North America, South America, China, Formosa, New Guinea, New Zealand, and New Caledonia. In the Old World, *Juniperus* is found in the area of Lake Nyassa in East Africa, and *Taxus* has been reported in Celebes.

⁵ Climatic zones used here are based on the classification given by E. E. M. Loock (1950:20), whereby a mean annual temperature of over 75°F is tropical; 67–75°F, subtropical; 50–67°F, temperate; and below 50°F, very cold.

sidered in this study as tropical, and which consequently are largely dependent upon nonclimatic conditions that restrict mixed broadleaf competition, are those growing below the lowest level of frost, which is probably above 6,000 feet in most of Central America.* All of the pines in Nicaragua and many large pine stands elsewhere in Central America occur below 6,000 feet.

The occurrence of the genus *Pinus* in Middle America is seldom, if ever, pre-

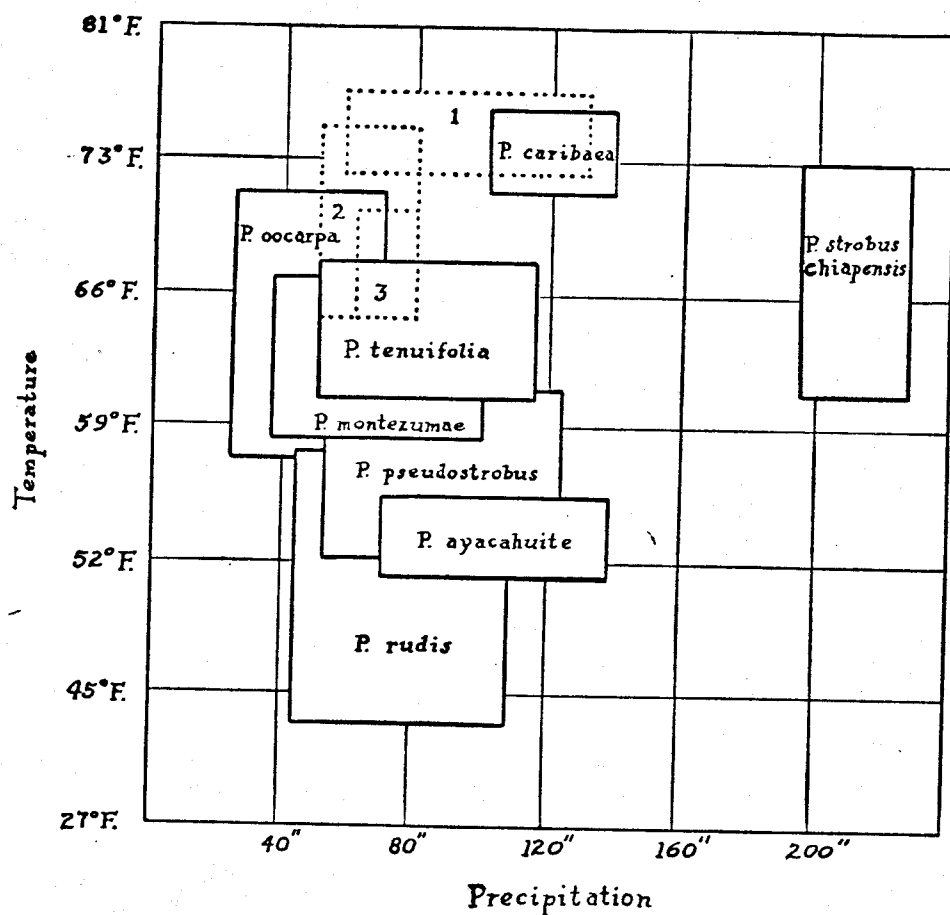


Fig. 2. Climatic ranges of the pine species in Guatemala and Nicaragua. The approximate ranges of the Guatemalan species are shown by solid lines; the Nicaraguan species are shown by dotted lines: 1. *P. caribaea*; 2. *P. oocarpa*; 3. *P. pseudostrobus*. Source for Guatemalan pines: Schwerdtfeger, 1953: fig. 138.

vented by climate. Pines grow where temperatures range from tropical to cold and precipitation from 35 to over 120 inches annually.

Each species, of course, occurs within characteristic temperature and precipitation ranges (fig. 2), although varieties and ecotypes may vary somewhat from

* Loock (1950:38) extends the subtropical zone in southern Mexico to 6,000 feet, below which frost is very rare. L. R. Holdridge (1947:20) locates a continuous frost line in southern Haiti at 6,000 feet, but with some frosts as low as 5,300 feet in depressions.

the norm of the species. For example, north of Nicaragua *P. pseudostrobus* grows from 6,000 to 10,000 feet above sea level, but in Nicaragua, only from 3,500 to 5,000 feet. Pines also show great variation in their tolerance for soil and drainage conditions. The growth of any pine species in a given area, however, is only partly accounted for by climatic and edaphic conditions; plant competition and inhibition, the history of the evolution and dispersal of the species, and the activities of man also help to account for the presence or absence of a species.

CHAPTER II

THE PHYSICAL GEOGRAPHY OF THE SEGOVIAN UPLANDS OF NICARAGUA

NICARAGUA, THE LARGEST COUNTRY of Central America (1957), comprises three basic physical units: (1) the Caribbean lowlands, composed mainly of Pleistocene and recent marine sediments or reworked river sediments; (2) the Pacific coastal region, which comprises the depressions of Lake Managua and Lake Nicaragua, a chain of young volcanoes surrounded by extensive ash plains, the Managua-Carazo volcanic plateau, and scattered residual hills west of the lakes; and (3) the central mountain region of old Mesozoic-Paleozoic basement rocks intruded and partly overlain by Tertiary volcanic materials. The area of this study falls within the northwest portion of the central mountain region.

RELIEF

The pine forests of western Nicaragua are confined to that part of the country known historically as "Las Segovias,"¹ an upland area ranging from 1,500 to 5,500 feet elevation located between Lake Managua and the border of Honduras, and embracing the present Departments of Nueva Segovia, Madriz, Estelí, and the settled western parts of Jinotega and Matagalpa (fig. 3). Since pines are scattered throughout the Segovias, the terms "pine uplands" and "Segovias" will be used here synonymously. East of the pine forests and the frontier of settlement on the eastern edge of the Segovias extend vast unpopulated tracts of little-explored tropical forest and high mountains.

The lowest break in the Central American mountain system north of the valley of the Río San Juan, which forms part of the boundary between Costa Rica and Nicaragua, is at the headwaters of the Río Grande de Matagalpa. This break is 2,000 feet above sea level near the town of Matagalpa and descends to only 1,000 feet near Muy Muy, 30 miles to the southeast. The mountains in Nicaragua north of the Río Grande form the Segovian group, and those to the south form the Chontales group (Cordillera Chontaleña). The two areas differ markedly in topography, geology, and flora, and are also historically and culturally distinct. The southern group is essentially a rolling plateau with a few high peaks and ridge crests, in sharp contrast to the more rugged Segovian mountains. Pre-Tertiary rocks, with a few minor exceptions, do not occur in Nicaragua south of the Río Grande, but ancient granitic and metamorphic rocks are widespread to the north. Thus this river seems a satisfactory dividing line between the two main Central American mountain systems. These systems have been described by Charles Schuchert (1935:364) as "(1) the greater, northern Central American (or Guatemalan) system; and (2) the volcanic Pliocene-Pleistocene (or Costa Rican) system,

¹The place name "Segovia" was applied to the pine upland area of Nicaragua in 1536 by Rodrigo de Contreras, governor of Nicaragua, who was reminded of his own pine-forested home in Segovia, Spain (Guillén de Herrera, 1945:38). The expression "Segovian mountains" is used here as a general topographic term for the entire mountain system of northern Nicaragua; however, "Segovias" will be used in the more popular sense to mean that part of the northern highlands originally occupied by the Spaniards.

²Very little of the northern Nicaraguan highlands had ever been mapped in detail before aerial surveying was initiated by the Inter-American Geodetic Survey in the Segovias in 1937.

bordering Honduras, whose divides form the international boundary,³ are known as the Montes de Dipilto, Montes de Jalapa, and Montes de Colón. This connected group of ranges is separated from the high and broad Cordillera Isabella to the south by the valley of the Río Coco, the longest river in Central America; the Cordillera Isabella in turn is separated from the Cordillera de Darién by the Río Tuma; and the Cordillera de Darién is separated from the Chontales mountains by the Río Grande de Matagalpa (fig. 4). These east-west-trending cordilleras with their many spurs are the main mountain ranges of Nicaragua; the highest peaks are Kilambé (elev 6,440 ft) and Saslaya (elev 6,560 ft) in the forest-covered Cordillera Isabella. The highlands gradually play out toward the Atlantic Coast, giving way to a low, rolling, stream-dissected surface. To the west, near Limay and El Sauce, the Segovian mountains drop abruptly onto the young alluvial and volcanic ash plains of León and Chinandega.

The Río Grande de Matagalpa, whose source is near the town of Matagalpa, passes across the two largest plains in the Segovias, the Llano de Olama around Muy Muy and the Llano de Sebaco between Darío and Sebaco. The low elevations, 1,000 to 1,800 feet above sea level, and the dry climates of both plains have probably helped block the southward advancement of the genus *Pinus*. Smaller plains or wide valleys occur north of the town of Estelí, around Limay, and north of Jinotega (recent alluvium and Tertiary sediments on fig. 5). In the Segovias, the only level terrain having pines is the Llanos de Totecacinte, a mountain-rimmed grassland situated between Jalapa and Totecacinte in the Department of Nueva Segovia. With this latter major exception, the pine stands of the Segovias are on mountain slopes where drainage is good and soils are generally thin.

The pine uplands extend approximately 100 miles from north to south and 75 miles from east to west. Of this 7,500-square-mile area, only a little more than 600 square miles are covered by pine forests (Taylor, 1959b:210), three-fourths of which are in the mountains of the Department of Nueva Segovia. Nevertheless, the scattered pine stands give a distinctive character to the landscape of the Segovias.

PARENT MATERIALS

The geology of the Nicaraguan highlands is probably the least studied in all Central America,⁴ but enough is known to divide the mountains of the Segovias into three major lithologic units (fig. 5). The ranges bordering Honduras in the Department of Nueva Segovia are granitic; the other mountains in the Department south to the Río Coco consist of metamorphic rocks, primarily schist; and most of the remainder of the pine upland area consists of Tertiary volcanic materials, predominately andesitic.

³ The position of the eastern two-thirds of the Honduran-Nicaraguan boundary, long in dispute, has been under arbitration by the International Court since 1957. The boundary shown on the maps in this study, from just north of Totecacinte eastward along the drainage divide between the Río Coco and the Río Aguan, is based on Nicaragua's claim as of 1957. Honduras, however, claims a boundary along the Río Coco to the Río Poteca in Nueva Segovia.

⁴ Most geologic maps of Central America, such as Roberts and Irving, (1957: pl. 1), are based mainly on the work of Karl Sapper (1937). Since 1955, surveys have been made in Nicaragua by a team of Italian geologists led by Dr. Tito Lagana; much of their work has been in the Segovias. See the *Boletín del Servicio Geológico Nacional de Nicaragua* (Nicaragua, 1957).

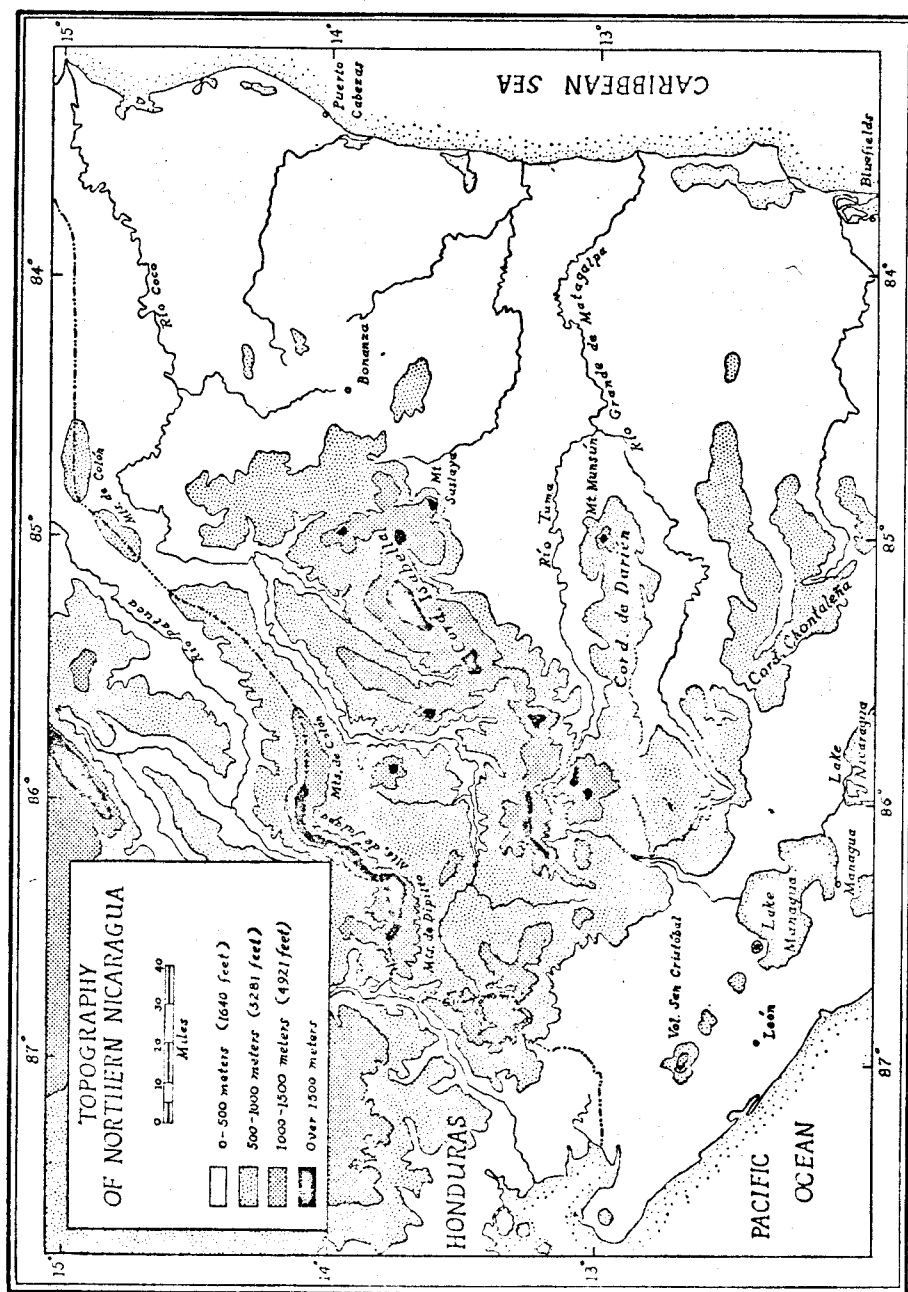


Fig. 4. Topography of northern Nicaragua. Source: Tugueigalpa sheet. American Geographical Society, 1:1,000,000, 1942.

Soil, vegetation, and agriculture are all strongly influenced by the silica content of parent materials. In the wet tropics, siliceous (acidic) rocks such as granite, schist, rhyolite, and some andesites and porphyries usually produce sandy soils and gravels when decomposed and eroded; fine-grained basic rocks low in silica, such as basalt, break down readily into clays. In the pine uplands of Nicaragua, pines generally grow on soils formed from coarse-grained acidic parent materials, especially granite and schist.

The coarse granite of the Honduran border ranges was probably intruded into surrounding metamorphic rocks⁵ at the end of the Paleozoic. The heavily forested eastern extension of the Montes de Colón is geologically unexplored, but the granitic core probably continues. A few granitic outcrops also occur further south, one east of Telpaneca and others in the Cordillera Isabella. The most extensive pine forests of Nicaragua grow on slopes of deeply weathered granite in the Montes de Dipilto and Montes de Jalapa; agriculturally, the coarse soils of these mountains support only inferior forage and some poor coffee plantings in areas of broadleaf forest at high elevations.

At the foot of the Montes de Dipilto, from Mozonte to Totecacinte and south to the Río Coco, lies a rolling surface on which streams have apparently been rejuvenated by upwarping. The ravines expose schists, which abut against the granite in the border ranges. Pines are scattered throughout this area; but, being readily accessible, many of the stands have been logged off (pl. 30, *b*). At the base of the mountains there are a few pines on a deep belt of unconsolidated sediments from a former east-west-trending stream course. The widened northeast extension of this belt is the seasonally flooded Llanos de Totecacinte. The soils of this plain are mainly peaty loam; however, the soils of the margins contain considerable quartz gravel washed down from adjacent granitic slopes, and on these margins, stands of both *P. oocarpa* and *P. caribaea* are found.

In eastern Nueva Segovia and eastern Madriz there are a number of discontinuous metamorphic mountain segments, each with a series of pine-forested ridges 3,500 to 4,500 feet in elevation. The most prominent of these are east of Jalapa, north and east of Telpaneca, and in the vicinities of Murra and Quilalí. Although these ranges are composed mainly of schist, small amounts of quartz (pl. 21, *a*), quartzite, and gneiss are present, and outcrops of black marble occur in several places just north of the road from Ocotal to Jalapa.

Quartz veins, often bearing gold and silver, are common in both the granites and the schists of Nueva Segovia, and have been extensively mined since Conquest times, if not earlier. Mining has been primarily responsible for the early and continued settlement of a large number of towns in Nueva Segovia, including Ciudad Antigua, Jalapa, Jicaro, Telpaneca, and Mozonte. Towns such as Quilalí, Dipilto, Macuelizo, and Murra, which were founded in the nineteenth century, also originally grew up around mines; others such as Ocotal and San Fernando (pl. 29, *a*), have been supported by stream-terrace agriculture and scattered coffee plantings. All mining operations have been abandoned in Nueva Segovia, many quite recently,

⁵ The metamorphic rocks of Nueva Segovia have not been dated, but are very likely the oldest rocks in Nicaragua and part of the geologic nucleus of Central America, which has long stood above the sea. Schuchert (1935:318) considered corresponding metamorphisms in Chiapas, Guatemala, and Honduras to be middle Paleozoic or older.

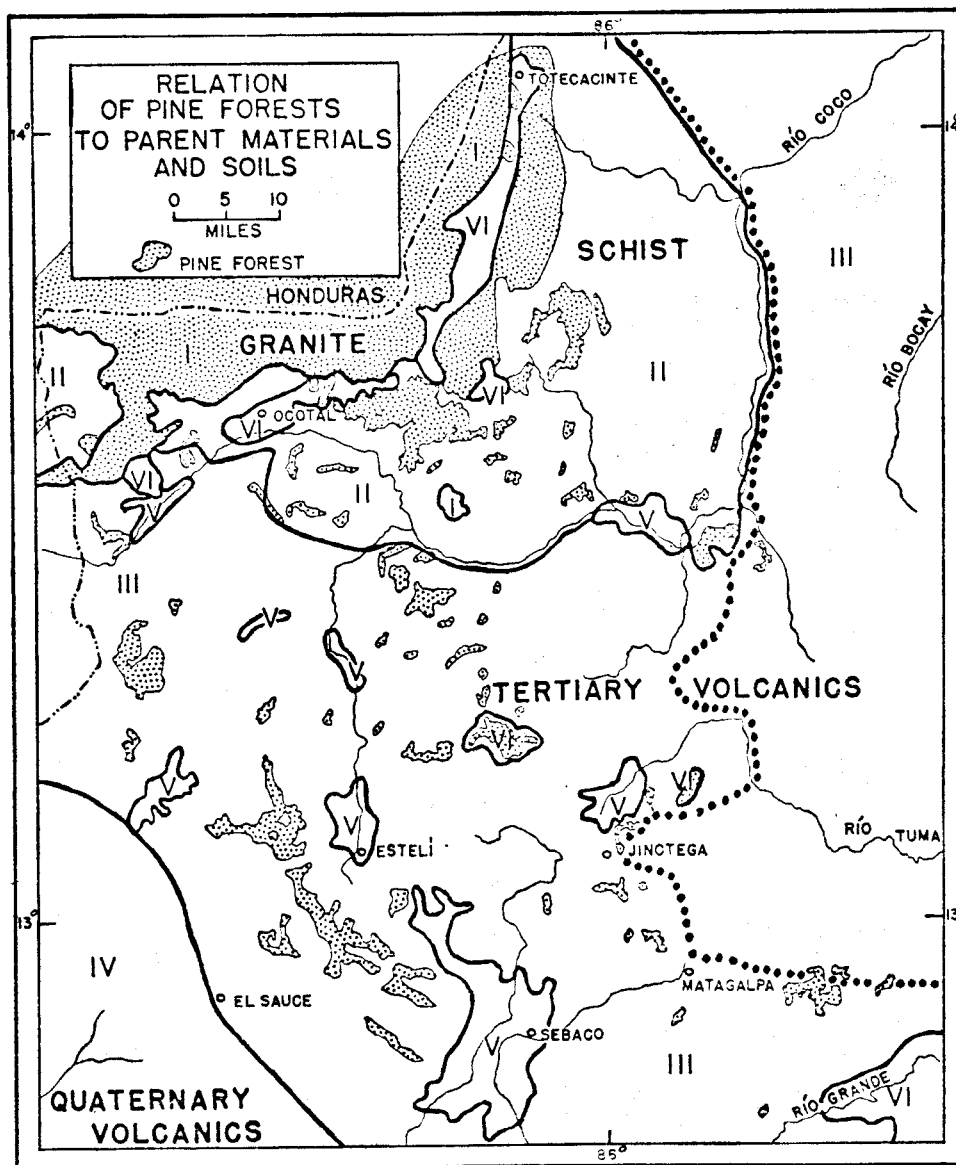


Fig. 5. Relation of pine forests to parent materials and soils. I, Granite; II, Metamorphics (mainly schist); III, Tertiary volcanics; IV, Quaternary volcanics (mainly ash); V, Recent alluvium (mainly black clay); VI, Tertiary sediments. The dotted line indicates the approximate boundary between shallow upland soils (west) and deep tropical brown and reddish-brown latosols (east). East of the line, rainfall is over 70 inches annually and the vegetation is rain forest; to the west vegetation is mainly secondary deciduous forest, scrub savanna, and pine forest. Main source: Taylor, 1959b.

and such settlements as Murra and Macuelizo have as a result nearly become ghost towns.

South and east of the Río Coco and west of Ocotal, almost all of the older rocks of the pine uplands were covered by volcanic materials during the intense eruptive activity of the late Tertiary. Pines are very scattered in the southern Segovias, and where patches do occur they are usually on soils formed from acidic volcanic rocks such as rhyolite, dacite, porphyry, feldspar andesite, and andesite porphyry. I have also observed a few pines on soils derived from basic andesite in the Department of Estelí, and from conglomerate, breccia, tuff, and kaolinized rocks in the Departments of Madriz and Jinotega.

Extending eastward from the towns of Matagalpa and Jinotega are the high and sparsely settled Cordilleras of Darién and Isabella; rainfall is heavy, and dense tropical forest covers the slopes. Andesite is the most common rock in the cordilleras. Basalt, rhyolite, and various porphyries are also present, and there have been a few reports of older granitic and metamorphic rocks in the Cordillera Isabella; quartz veins, again a source of exploitable gold, often occur in the andesite. In contrast, basalt rather than andesite seems to predominate to the south in the Chontales mountains. The easternmost upland pines are found on the southern slopes of the Cordillera de Darién a few miles east of Matagalpa, often on andesite porphyry.

West of the section of the Inter-American Highway which runs from the Honduran border to Darío, there is a series of low, dissected plateau surfaces (Mesetas de Estelí) formed by Pliocene lava flows. Between the lava plateaus and the cordilleras are the Llano de Sebaco and the Llano de Olama and, in central Madriz and western Jinotega, several elevated mature surfaces, some flat, some hilly. Stands of pine are found on some of the peaks and ridges associated with the lava plateaus, but seldom on the plateaus; in those places where the mature surfaces of Madriz and Jinotega support scattered pines, the parent material is a mixture of conglomerate and loosely consolidated river or lake sediments, including bands of diatomaceous earth.

The region west of the cordilleras, including Nueva Segovia, is the driest part of the Segovias and has the densest population and the oldest permanent settlement. These western uplands are a deforested and seriously eroded cattle-range country, permanent agriculture and the major settlements being limited to the larger plains and valleys; the existing pine forests are mainly on ridge tops.

A small amount of ash from Pleistocene and recent eruptions in the Marrabios chain of volcanoes near the Pacific Coast may have fallen in the valleys and plains of the western pine uplands; however, the prevailing winds are from the northeast, and most falling ash has been and still is being deposited to the south and west of the active coastal volcanoes.* Fall of volcanic ash is, of course, very important to agriculture because, in general, soils formed from young volcanic parent materials are much more productive than those formed from older, considerably weathered, volcanic rocks. The presence of young volcanic soils is responsible for the great fertility of the Plains of León and Chinandega, and is undoubtedly a major reason

*The role of wind currents in distributing volcanic ash and the effects of the distribution on population density in Nicaragua have been described by Sapper (1902).

for the concentration of population on the Pacific lowlands and on the volcanic plateau just south of Managua; in marked contrast is the relatively sparse population of the Segovias and the near absence of population in the eastern mountains and plains. Dense populations in the highlands of Central America are usually found in areas where volcanic activity has been recent, as in Costa Rica and Guatemala. In northern Nicaragua, Pleistocene and later vulcanism has been confined mainly, if not entirely, to the Pacific coast area west of a line passing from a few miles southwest of Limay and El Sauce (fig. 5) to the northeast corner of Lake Nicaragua. No pine forests exist in this young volcanic region, with one isolated exception—on the adjacent volcanoes San Cristóbal and Casita north of León (fig. 4).

The distribution of pines in the northern highlands of Nicaragua does show a relation to certain parent materials. The largest stands of pine are on soils formed from granitic rocks and schist in the Department of Nueva Segovia, and the scattered stands further south grow on soils formed from volcanic parent materials that generally have a high silica content, such as andesite porphyry and rhyolite. A striking example of the relation of pines to acidie rocks is a small stand of *P. caribaea* growing in eroded sandy soil on a hill (elev 1,300 ft) composed of rhyolite between the pine uplands and the pine savannas of the Atlantic coast, about 8 miles west of Constanacia (a Bonanza mine) near Ocotal (pine) Falls some 40 to 50 miles inland from the coastal pine savannas. The surrounding vegetation is broadleaf evergreen forest.

It is not unusual for a pine species to show a close relation to certain types of soils and parent materials, especially acidie rocks,⁷ but the nature of the physiological response is often unclear.

CLIMATE

The climate of most of the central highlands of Nicaragua is tropical, winter-dry "savanna," or *Aw* according to the Köppen classification. Scattered areas of *C* climate occur at cooler elevations, above about 4,000 feet: *Cf* climate in the eastern cordilleras and a dryer *Cw* climate in the western mountains. Very few climatic data for the pine upland area are available. Annual precipitation averages and approximate 50- and 80-inch isohyets are shown in figure 6, monthly rainfall figures for representative stations are given in table 2,⁸ and mean monthly temperatures for Somoto are given in table 3.

In Central America, rainfall is highest east of the interior highlands, where the northeasterly trade winds bring moisture from the Caribbean most of the year, and lowest on the leeward, Pacific side of the central highlands. In the western uplands

⁷ H. J. Lutz (1958:81) has stressed the frequent relationship of less exacting tree species, including pines, to acidie rocks high in silica and low in plagioclase and ferromagnesium minerals, which produce poor soils deficient in soluble salts and having coarse texture and good drainage.

⁸ Most of the rainfall figures shown on figure 6 and in table 2 are from records kept since 1952 by the Río Tuma Hydroelectric Project Survey. The data for Ocotal, Grecia, Cacamuya, and Danlí were obtained from private individuals and are also for a very short time span. The Neptune Gold Mining Company is the source for Bonanza. The only record of any duration, Finca Pataste, 1915-1939, was kept by George Mosser, an American miner and rancher. Many of the stations have incomplete data for some years, and the period best recorded, 1956-1957, was unusually dry. These conditions were taken into account in arriving at the annual precipitation values shown in figure 6.

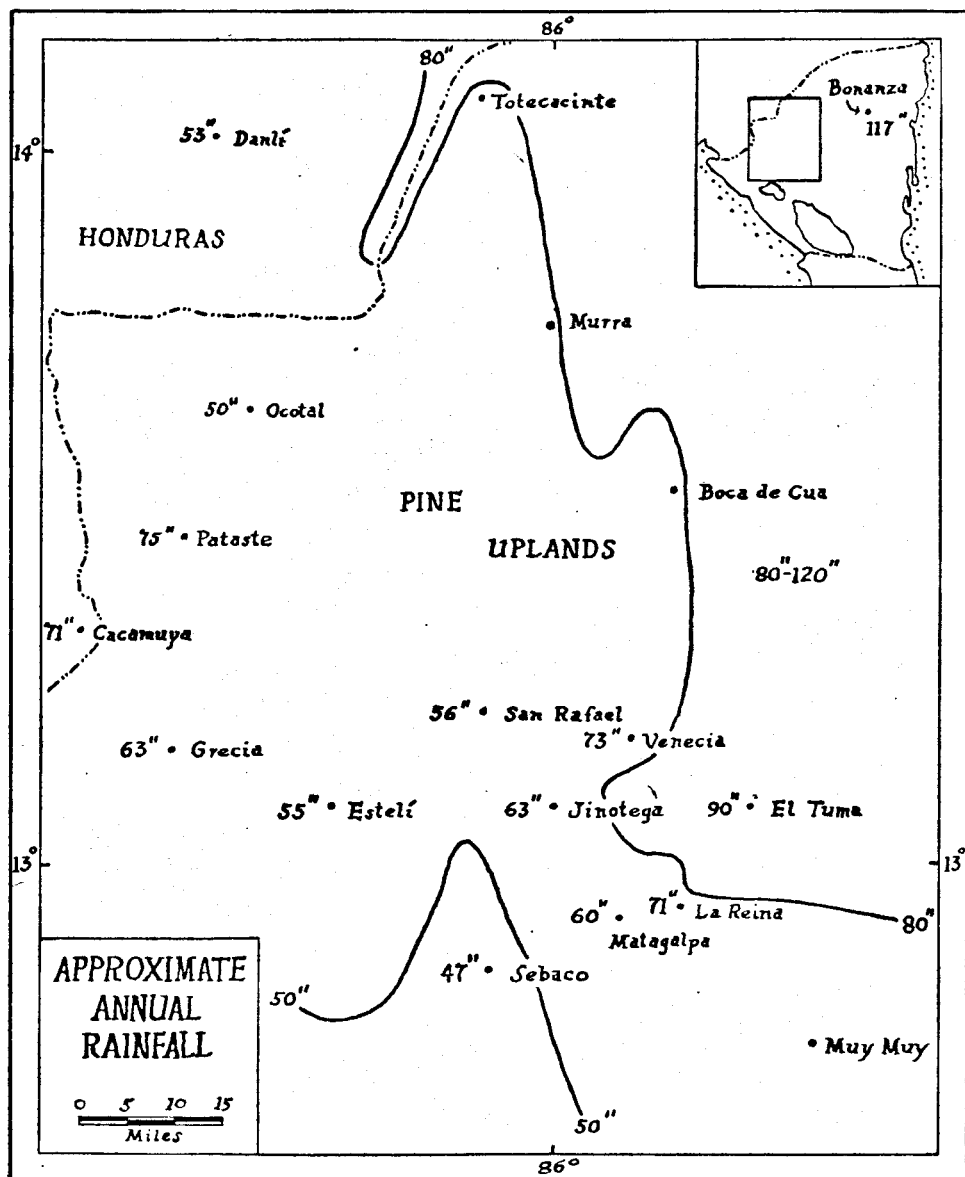


Fig. 6. Approximate annual rainfall in inches.

of northern Nicaragua, precipitation increases with elevation; e.g., La Reina at 4,500 feet elevation receives 71 inches; but the valleys, especially those trending north-south, lie within a rain shadow and are much drier than the surrounding slopes: e.g., Sebaco at 1,549 feet elevation receives only 47 inches. Slopes facing the Caribbean lowlands receive high rainfall at all elevations, as do low valleys open to unblocked northeast winds like that of the Río Tuma, as is indicated by the 90 inches of precipitation recorded at El Tuma. There are no precipitation figures from the valley of the Río Grande east of Matagalpa, but the annual rainfall seems to remain below 80 inches eastward, at least to Matiguás; Matagalpa has 61 inches. This relative dryness seems to be due to the upper Río Grande's leeward position south of the east-west-trending Cordillera de Darién, which partly blocks off the northeast trade winds.

Western Nicaragua has two marked seasons: a wet season (*invierno*) with two periods of maximum precipitation,⁹ and a dry season (*verano*). In general, the longer the dry season the lower the annual rainfall. Köppen defines a dry month as one with less than 2.4 inches (60 mm) of precipitation. For vegetation, however, a dry period may be considered to be one in which the potential evapotranspiration exceeds precipitation, and a month with as much as 4 inches (100 mm) of rain might still be regarded as "dry" in some tropical situations (see Charter, 1940:3, on British Honduras, and Beard, 1944:137, on parts of the West Indies). For the tropics, Mohr and Van Baren (1954:60-66) consider a month with 60 to 100 mm of rain as moist, rather than wet or dry. The length of the dry season is generally more significant to vegetation than is the total amount of rainfall.

West of a line drawn roughly from Matagalpa to Ocotal, the dry season lasts about 6½ months (November to mid-May). During both wet and dry months the mountains receive more rain than the valleys, a contrast clearly shown in the records for Sebaco and Patate. East of Matagalpa the dry period becomes shorter, about 4 months at El Tuma and 2 to 3 months in the coastal foothills at Bonanza and at Puerto Cabezas on the Atlantic Coast; the dry months become less dry; and total rainfall increases.¹⁰ At Sebaco, however, the months of the dry season are completely rainless in most years.

During the dry season the Pacific side of Central America is dominated by the trade-wind inversion. Moist maritime tropical air in the lower layers is overlain by dry air that has been warmed adiabatically while subsiding in the subtropical anticyclonic air flow. The air below the inversion is convectively unstable, but actual instability is not realized because the inversion restricts convection. The inversion is broken up, however, in the wet season, when the equatorial trough (doldrum belt) moves northward over the area: winds become weak and variable, air becomes unstable, clouds build up, and precipitation is induced by convective heating or orographic uplift associated with occasional southerly winds. Violent squalls may accompany the shifting of the intertropical zone of convergence, which

⁹ Over most of western Nicaragua, the heaviest rains occur in June and in September and October. The lessening of rainfall for about four weeks (the *canicula*), from mid-July to mid-August, is associated with a temporary strengthening of the northeasterly trade winds.

¹⁰ Most of eastern Nicaragua has an *Amic* climate with more than 100 inches of rainfall annually; the maximum rainfall occurs along the southeast coast, where there is an average of close to 250 inches at San Juan del Norte (Greytown). Southeastern Nicaragua is the only part of the country that has a true *Af* climate.

TABLE 2
AVERAGE MONTHLY AND ANNUAL RAINFALL AT SELECTED STATIONS IN NORTHERN NICARAGUA

Station and years recorded	Elevation (in feet)	Rainfall (in inches)												
		Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Year
Solaco (1952-1956)	1,519	0.08	0.09	0.00	0.01	7.03	8.78	3.73	3.65	10.58	11.62	1.07	0.18	46.82
Matagalpa (1953-1956)	1,910	0.65	0.70	0.56	0.51	5.36	10.67	9.73	5.94	13.30	10.67	1.50	1.21	60.80
Patate (1915-1939)	4,400	2.08	1.23	0.98	1.28	8.69	13.32	7.83	7.66	12.10	13.44	3.58	2.60	74.79
El Tuma (1952-1957)	1,200	2.77	2.14	2.02	2.22	5.35	15.14	15.37	9.23	10.92	10.40	6.18	7.79	89.53
Bonanza (1939-1952)	760	5.76	3.69	2.27	2.55	11.03	19.86	16.57	13.27	12.78	11.69	8.62	9.04	117.13

TABLE 3
MEAN MONTHLY TEMPERATURE AT SOMOTO, 1951-1954
(Elevation 2,293 feet)

Month	Temperature in degrees Fahrenheit		
	Approx Maximum (2:30 P.M.)	Approx Minimum (6:30 A.M.)	Average
January	85.1	57.2	71.2
February	89.1	57.6	73.4
March	91.8	63.5	77.7
April	92.3	67.5	79.9
May	90.5	70.2	80.4
June	89.1	69.3	79.2
July	87.3	68.0	77.7
August	86.9	67.5	77.2
September	84.2	68.9	76.6
October	83.3	66.2	74.8
November	82.8	60.3	71.6
December	84.2	58.5	71.4
Year	87.2	64.6	76.0

is a band of adverse weather within the doldrum belt. The doldrums remain over Nicaragua until about the end of October, at which time the northeast trade winds again become dominant.

In the later part of the wet season, *temporales* may occur in the mountains of Nicaragua; these are light but steady, long-lasting, widespread rains caused by persistent southwesterly winds. From December through February, northern Nicaragua infrequently experiences heavy mid-latitude storms referred to as *nortes*. Except for these rains, precipitation in the mountains is rather localized, and adjacent areas may receive very divergent amounts of rain in a given period. The mountains above 4,000 feet, however, are shrouded in humid clouds most of the time all year; many high ridges are visible, with greater regularity in the dry season, only for a few hours in the early afternoon.

By February the land in the Segovias becomes fairly dry, roads become passable, and the people turn to clearing brush and forest for their milpa farms. Temperatures are high and skies are usually cloudless during March, April, and early May, but on many days, the sky everywhere is filled with smoke as cleared land is burned over. Milpas are usually burned in May just before the first showers of the rainy season, but dead pasture grasses may be burned earlier. Plant materials are combustible soon after the start of the year, and some fires are haphazardly set in January and February. Lightning storms are uncommon during the dry season; I met no one who had definitely seen a lightning-set fire.

The Segovian highlands are higher and cooler than the rest of western Nicaragua: living is much more comfortable and healthy for man than in the humid coastal lowlands; temperate-elevation crops, including coffee, potatoes, wheat, and various vegetables, can be grown; and the rates of soil weathering and humus destruction are slower than in the adjacent hot lowlands. These are some of the reasons that, even though most of the population of Nicaragua has been and still is concentrated on the much more fertile soils of the west coast, the Segovias have long been an area of human settlement and associated forest destruction. The colder highlands tend to be especially receptive to pine species that thrive best where plant competition is least, but the influence of low temperatures on pine is likely to be much greater in the lofty mountains of northern Central America and Mexico than it is in Nicaragua, where only a very small area rises more than 5,000 feet above sea level.

The only town in the entire central mountain region for which temperature records are obtainable is Somoto, at an elevation of 2,293 feet in the Department of Madriz, for the period 1951-1954 (recorded by Mr. George Mosser). There the average of the approximate daily maximum and minimum temperatures during the period was 76°F. This figure represents roughly a normal decrease of temperature with elevation (3.3°F per 1000 ft), for Managua at an elevation of 165 feet has a daily average of 82°F.

The lowest temperatures usually occur in January; at Somoto absolute minimums near 45°F are recorded. Average temperatures at Pataste (elev 4,400 ft) should be 7 to 8° lower than at Somoto. It would be useful to know if freezing temperatures ever occur in the Segovian mountains; however, frost is probably un-

likely except on the few peaks over 6,000 feet where, although the vegetation is largely unknown, it seems improbable that pines or other conifers exist.

Climate has a major influence on the distribution of pines. Temperature, precipitation, humidity, and the length of drought are all important limiting factors for individual pine species (see fig. 2 and chap. iii).

SOILS

The soils of the Segovias can be divided into 4 main groups: black tropical soils, young alluvial soils, deep residual upland forest soils (brown and reddish-brown latosols) (fig. 5), and shallow upland soils. In general, all of these soils are of low to moderate fertility and offer only a limited opportunity for an expansion of permanent agricultural settlement. They are usually low in phosphorus content but moderately high in potassium, and their nitrogen content depends largely on the history of land use and of vegetation cover. Probably 90 per cent of the upland pines are found growing on shallow soils that are very low in plant nutrients.

Black tropical soils¹¹ occur on most of the Tertiary volcanic areas of flat to rolling relief where annual precipitation is less than 65 or 70 inches and the dry season lasts 4 or more months. These are the common soils on the seasonally flooded llanos of Sebaco, Estelí, and Jinotega; and a similar but residual soil is found on the lava plateaus. Both alluvial and residual black soils are characterized by a top layer of black clay, called *sonsequite* by the Nicaraguans, which varies from a few inches to several feet in depth and overlies a heavy, grey clay subsoil. The surface clays are sticky when wet and tend to crack when dry. The black residual soils on lava are shallow and low to medium in fertility, but the alluvial soils of the llanos are deeper and more productive, although often too heavy for the crude modes of cultivation commonly practised. On the sloping margins of the llanos, however, the top soil may be a clay loam or loam rather than a clay; such soils constitute some of the most intensively cultivated land in the Segovias. The plains, probably originally forested, are now in pasture, savanna, or thorn scrub where not cultivated. Pines seldom occur on the black soils or on dense clay topsoils anywhere. One exception is a stand of *P. oocarpa* growing on the thin black clay soil of a dissected lava plateau northeast of Estelí.

Young alluvial deposits in river valleys and flood plains form the most fertile soils in the Segovias and support most of the permanent field agriculture (maize, tobacco, cotton, vegetables). Patches of alluvial soils are found along all of the large rivers, and are largest near the towns of Limay, Estelí, Sebaco, and in an area just north of Jinotega. These soils differ from the black alluvial soils mainly in being brown in color, well drained, and too young for any profile development. The deposits are up to 30 feet deep, and consist of layers of loam, clay, silt, sand, and sometimes bands of gravel or boulders. No pines occur on young alluvium, but a few stands grow on limited areas of old, possibly Tertiary, unconsolidated lake and river sediments such as the continuous line of gravel beds between Ocotal and Jalapa in Nueva Segovia and smaller areas in the Llanos de Totecacinte north of Jalapa, around Venecia east of Jinotega, and just south of San Rafael del Norte.

¹¹ The black soils of Nicaragua seem to show similarities to black soils elsewhere in the tropics, such as the black cotton and regur soils of India, the black turf soils of South Africa, and the margalitic soils of Indonesia. For a good discussion of these soils, see Mohr and Van Baren (1954:411-435).

Deep residual forest soils occupy the rainy (over 70 inches), sparsely populated highlands east of Matagalpa, Jinotega, and Totecacinte. Most common are brown latosols, which have a top layer of friable brown clay or clay loam about 18 inches deep overlying a heavier clay subsoil. These soils seem to be of high fertility when undisturbed, but soil minerals are leached out when the forest cover is cleared for shifting agriculture. In the humid tropics, the nitrogen content of soil generally drops rapidly if the steady renewal of organic matter which occurs under heavy forest is terminated by forest clearing. The rate of loss of fertility after clearing is slower in cool upland areas than in warm lowlands; however, erosion is more of a problem on mountain slopes. The brown forest soils in the Segovias are well adapted to the growing of shaded coffee trees, and in the Matagalpa and Jinotega areas much coffee has been planted on such soils during the last 50 years. Where the rainfall is over 80 to 90 inches, the soil may be a reddish-brown latosol. This is an old, highly weathered soil generally derived from such iron-rich basic volcanic rocks as basalt, from which iron oxide is set free by weathering. Reddish-brown latosols are less fertile than brown latosols, but are used for milpas and pasture and sometimes for coffee where rainfall is not excessive and temperature not too high.

In the Segovias, only the areas of heavy rainfall and deep soil still have a large amount of mature broadleaf forest. Actually, once a site is cleared in such areas, regrowth is so rapid that burning alone will not maintain pasture and ranchers are often forced to weed by hand. Pines rarely occur on the deep soils of the eastern Segovias, and the stands that do exist are usually on sandy material: many of the pines in the Cordillera de Darién east of Matagalpa are found on coarse soils derived from andesite porphyry.

Shallow upland soils lacking well-defined horizons and low in organic matter occupy most of the moderate to steep slopes of the western Segovias. West of the towns of Jinotega and Matagalpa shallow soils overlie slightly decomposed bedrock of Tertiary volcanic materials; in Nueva Segovia shallow soils occur on rapidly decomposing granites and schists. These soils are usually black where rainfall is over 60 inches and brown or gray-brown and sometimes yellow (on granite) where rainfall is less. On volcanic rocks the topsoil is generally a clay 3 or 4 inches deep overlying 1 to 2 feet of brown or reddish-brown gravelly clay, which merges with the parent material. When extremely thin or eroded, and especially when the parent material has a high silica content, the surface soil may be very gravelly. On granite and schist the topsoil is a dark sandy loam or loam overlying lighter-colored gravelly loam. On the steeper exposed slopes the topsoil is either very thin or nonexistent, but on the gentler slopes and flats the topsoil may be a foot or more deep. Where mature broadleaf forest exists, as on some of the higher peaks, the topsoil is deeper and supports shifting agriculture and even some shaded coffee. Otherwise the shallow upland soils of the western Segovias, under present management methods, have little agricultural value except as pasture.

The shallowness of the soils of most of the pine uplands is partly a natural result of steep slopes, but the condition has been intensified by erosion that has followed deforestation and frequent fires over a period of centuries. Where rainfall is low, protective vegetation is especially slow to reestablish itself after fire. Pines, which generally grow in open stands, are not nearly so effective in preventing erosion as are dense stands of mixed hardwood forest. Today in the pine uplands erosion is

widespread in areas of less than 65 inches of rainfall, and is so severe in areas of less than 55 inches of rainfall that almost no topsoil remains on many slopes, and the surface of lower slopes is buried under debris from above. Most of the erosion has been the less noticeable sheet erosion, but gully erosion is very common throughout the granitic and schistose mountains of Nueva Segovia (pl. 21, b). Accelerated runoff from barren slopes causes streams to dry up quickly, ground water levels to drop, and soil moisture to be rapidly reduced. As a result, vegetation communities are encouraged that are more drought-resistant than vegetation in an undisturbed, moisture-conserving mixed forest. *P. oocarpa* is favored under such conditions.

In the pine uplands of Nicaragua, pines are found growing on a wide variety of soils and parent materials;¹² nevertheless, field observations indicate that pines establish themselves most readily on certain soils. *P. oocarpa*, the most common uplands species, generally occurs on thin, rocky, eroded, and acid¹³ soils derived from rocks with a high silica content; this indicates a tolerance for impoverished conditions in general, and for low levels of phosphate and calcium in particular. Moreover, *P. oocarpa* seems to prefer the good drainage that is characteristic of sandy soils. The Nicaraguan pines will grow on fertile soils, but usually the sites with deep and rich soils are very rapidly occupied by broadleaf vegetation. Pines also grow at times on basic parent materials, usually where the rock is not deeply weathered and the soil is thin, notably in the Department of Estelí. It can probably be said that as climatic conditions become increasingly tropical (warmer and wetter), competition by broadleaf plants becomes more severe, and pines become more restricted to eroded, infertile, and rocky sites, which, other factors being equal, seem more likely to occur where parent materials are acidic and coarse-grained rather than basic and fine-grained.

The shallow and acid soils of the pine uplands can also support tall broadleaf mixed forest, although its growth is not so vigorous as on better soils. I found various successional stages of broadleaf forest on all the major types of soil and parent material in the pine uplands. Pine stands protected from fire for several years all had broadleaf species in their understory. B. W. Taylor has made similar observations, and in a land-use survey of the Nicaraguan highlands (1959b:208) he notes:

Further, although pines cover almost all of the area of soils derived from granite which are undoubtedly the poorest and most acid soils, other communities also occur. There are several extensive areas of broadleaf rainforest and occasional broadleaf species are present in the pine forest growing on poor soils derived from granite. On all other soil types, including acid soils derived from schists and extrusive volcanics, and the more basic soils derived from basic volcanics, broadleaf communities are usually equally as common as pine.

Thus, while the pines of the Segovias do appear to grow on certain soils, this growth is also dependent to a large degree upon nonedaphic factors that eliminate

¹² B. W. Taylor (1959b:208) makes the following observation on the relation of pine growth to soils in the Segovias: "Undoubtedly, the pine communities grow well on poor acidic soils and are much more common there, but they are certainly not restricted to such soils; in fact, pine communities are found on all major soil types above 2,000 feet elevation."

¹³ For 12 soils under pines sampled in the pine uplands, the pH reaction ranges from 5.5 to 6.5 with an average of 5.9. In most of western Nicaragua the range is between 6.0 and 7.0, while soils in areas of heavy rainfall in the east are even more acidic, owing to strong leaching of bases.

broadleaf vegetation with which the pines cannot ordinarily compete. There is strong evidence that chief among these factors are wide-spread man-made fires.

Of significance to the apparent relation of pines to poor soils and burning is the fact that it is very difficult for pine seeds to germinate in a humic soil, possibly because of the toxic effects of carbon dioxide and the presence of a surface litter or growth that prevents seed from reaching mineral soil. Disturbed soil sites often display profuse pine seeding. Moreover, pine seeds carry their own supply of nutrients, and thus are able to germinate on relatively sterile soils and survive long enough for roots and foliage to develop.

VEGETATION

The flora of Nicaragua is very poorly known; only two detailed studies have been made,¹⁴ and little has yet been published on the botanical collections that do exist.¹⁵ In general, the plant cover of Nicaragua is similar in composition to that of neighboring countries; the most notable exception is the absence of the genus *Pinus* south of Nicaragua.

The natural vegetation of Nicaragua, other than pine, can be considered most simply under two categories: deciduous forest and broadleaf evergreen forest. Remnants of a predominantly deciduous forest occur in the western part of the country, where the annual dry season lasts 5 or 6 months; a predominantly evergreen hardwood rain forest covers the central and eastern parts, where rainfall exceeds 70 inches and the dry season is short. The transition between the two types of forest is gradual, and is difficult to represent on a map. Eastward, the percentage of evergreen hardwood species increases, and the deciduous species lose their foliage for a shorter period. In the pine uplands, pines, although covering only about 10 per cent of the total area, occur throughout the gradation, usually in pure stands.

Almost no virgin forest is left in western Nicaragua, and the present vegetation, mainly savanna¹⁶ and scrub woodland, differs markedly from the original forest cover, chiefly because of a long history of human activities.¹⁷ Dense indigenous populations undoubtedly destroyed great stretches of forest long before the Spanish conquest. Destruction spread from the deciduous woodlands of the Pacific lowlands, where population has long been concentrated, into the Segovian mountains and pushed back the margins of the eastern rain forest. This forest has periodically

¹⁴ Miguel Ramírez Goyena published a *Flora Nicaragüense* in 1909, but it is mainly a taxonomic listing and is far from complete. In 1956 Eddie A. Salter published *De la flora Nicaragüense*; although limited in scope and containing numerous errors in identification, it has good discussions of the economic uses of the species mentioned.

¹⁵ B. W. Taylor, plant ecologist with the FAO Mission in Nicaragua, began doing extensive collecting throughout the country in 1957. He has made many of the plant identifications that appear in this study; a more detailed list of Segovian plants can be found in Taylor's land-use survey (1959b).

¹⁶ A number of observers have suggested that the savannas of Central America are largely fire-induced formations that have replaced mixed forest, but few comprehensive studies of these savannas have been made. Recently, Carl Johannessen (1959) has shown that the land-use practices associated with ranching have resulted in the invasion of trees onto Honduran grasslands and savannas. Conditions are comparable in much of western Nicaragua.

¹⁷ The ability of simple hunting and gathering people and practitioners of shifting agriculture to effect great changes in natural vegetation, principally by clearing and burning, is discussed for the world in general by Carl O. Sauer (1950) and Omar C. Stewart (1956), for the tropics by H. H. Bartlett (1956), and for Central America by O. F. Cook (1909).

retreated before recurring waves of settlement, but the new frontiers have tended to be unstable; where they were abandoned the forest has regenerated itself.

In a disturbed area such as the pine uplands, vegetation can be classified under the following categories: (1) a relatively natural climax community, either climatic or edaphic; (2) a successional community, either primary or secondary,¹⁸ in some stage of growth toward a natural climax which it may never reach because of irregularly recurring disturbances; or (3) a deflected succession or climax,¹⁹ a relatively stable successional stage that is sustained through human activities such as regular clearing, burning, and grazing. Most of the grasslands and scrub savannas, which cover a large part of the area of the pine upland, together with the pine forests themselves, can probably be classed as deflected successions. Most of the other vegetation consists of secondary successional communities.

Broadleaf communities.—The vegetation of the dry llanos within the pine uplands consists of low scrub varying in density from a cover of individual trees that just touch to open park savannas and grasslands. Most of the trees are from 15 to 20 feet high: many are thorny species, and most species are resistant to both drought and fire. The character, density, and distribution of the vegetation may be strongly influenced by grazing (Johannessen, 1959). The association is dominated by jiñocuabo (*Bursera simaruba*) and escobillo (*Phyllostylon brasiliensis*); and cornizuelo (*Acacia costaricensis*), madroño (*Calycophyllum candidissimum*), carbón (*Acacia pennatula*), and jícaro sabanero (*Crescentia alata*) are also common. In addition to these deciduous species, the surrounding mountains have, below an elevation of about 3,500 feet, a high proportion of guácimo de ternero (*Guazuma ulmifolia*) and laurel (*Cordia alliodora*), or they may support an oak-pine (*Quercus* spp.—*P. oocarpa*) association. The taller gallery forests along the streams are probably more like the original forest than either the scrub or the oak-pine formations. These gallery forests contain a number of evergreen species including guanacaste (*Enterolobium cyclocarpum*), genízaro (*Pithecolobium saman*), carao (*Cassia grandis*), ceiba (*Ceiba pentandra*), and ronrón (*Astronium graveolens*). Cedro real (*Cedrela odorata*), guayacán (*Guaiacum officinale*), and pochote (*Bombacopsis quinatum*) were once more common, but because of selective logging are now rare.

Where precipitation exceeds 60 or 70 inches, the natural vegetation is best described as seasonal evergreen forest, a subformation of the tropical rain forest formation (Richards, 1957:319–320). Seasonal evergreen forest differs from true rain forest in having 3 stories instead of 4. Standing about 100 feet high, well above lower evergreen layers, the top story is made up of scattered large trees, some of which are deciduous or facultatively deciduous (the extent of leaf fall varies with the intensity of the dry season). Almost everywhere the western margin of the original seasonal evergreen forest has been pushed back approximately to the 80-inch isohyet, and this forest replaced by evergreen shrub, pasture, or a low semi-evergreen secondary forest.

¹⁸ A primary succession is one initiated on material not previously occupied by plants; a secondary succession is one that begins where previously existing vegetation has been destroyed or damaged by felling, burning, flooding, etc.

¹⁹ The term "deflected climax" is used by J. S. Beard (1944:155). Some ecologists use the term "disclimax" in the same sense.

The more common broadleaf species in the wetter forests of the pine uplands below 4,000 feet include guáximo de ternero, madroño, ronrón, ceiba, caoba (*Swietenia macrophylla*), cedro (*Cedrela mexicana*), matapalo (*Ficus glabrata*), tempisque (*Mastichodendron capiri*), maria (*Calophyllum brasiliense*), aguacate montero (*Nectandra* spp., *Persea* spp.), ojoche colorado (*Brosimum utile*), nogal (*Juglans olanchanum*), nispero de montaña (*Achras calcicola*), guavo (*Inga* spp.), and roble encino (*Quercus aaata*, *Quercus brencsii*). The part of northeastern Nueva Segovia that receives 60 to 80 inches of rainfall, however, has pure stands of *Pinus oocarpa* and a few stands of *P. caribaea*. Scattered stands of *P. oocarpa* also occur in the high-rainfall areas east of Matagalpa and northeast of Jinotega.

Little is known of the flora of the higher formations: at elevations above 4,000 feet, a submontane formation occurs, and true cloud forest is probably found on the mountains over 5,000 feet in the eastern cordilleras; *Quercus* spp., Lauraceae, and Leguminosae seem to be common. In Nueva Segovia and parts of Jinotega, stands of *P. oocarpa* and more often of *P. pseudostrobus* do sometimes extend to elevations above 4,000 feet. Although pines often grow on the highest ridges in Honduras and Guatemala, they seldom if ever grow above an elevation of 5,000 feet in Nicaragua, and the highest peaks in the pine belts are almost always crowned with a submontane formation of mixed hardwoods.

Often associated with the higher pine stands is liquidambar (*Liquidambar styraciflua*), a species also common in the southeastern United States. At several sites in Nueva Segovia liquidambar is the transitional species between pine and broadleaf forest (pl. 32). Liquidambar readily invades old fields, but seems to prefer richer soils than those usually characteristic of pine lands. Although the species generally grows in groves, scattered individual liquidambar trees—sometimes as much as 6 feet in diameter—can be found deep within the high broadleaf forests.

The pine-oak-grass association.—The plants associated with the upland pines of Nicaragua are primarily pyrophytic species of oak, grasses, and ferns. The pine stands are usually fairly open (pl. 21, a), but not so open as park savannas: dense stands occur only where there have been no fires for many years. Below 3,000 feet the ground cover beneath pines is mainly pasture grasses, particularly jaragua (*Hyparrhenia rufa*), a tall (4 to 6 ft), aggressive African species of recent introduction. At higher and moister elevations native grasses, including *Andropogon* spp. and *Paspalum* spp., and the introduced species Guinea grass (*Panicum maximum*) and pará grass (*Panicum purpurascens*) predominate along with a variety of low ferns, while the pine branches themselves are draped with epiphytes (especially *Tillandsia* spp.) and mistletoe. Most of the native grasses are short and have been crowded out by the introduced grasses, especially at low elevations. However, there is at least one known tall native grass (6 to 10 ft), sacatan (*Paspalum paniculatum*), which grows in roughly the 65- to 75-inch rainfall area of the uplands.

Ferns show a strong tendency to invade immediately after fire, and shrubs and hardwood seedlings and sprouts rise above the grasses and ferns after only a year or two without burning. Especially common are Compositae, Leguminosae, and *Quercus* spp. The initial invaders may include many pine seedlings; but once a thick understory is established, the young pines are killed by shade, and hardwood

trees dominate. Later stages of succession usually include considerable *Q. aaata* and *Q. brenesii*, and guayabón (*Terminalia chiriguensis*).

Growing with pines at all elevations are species of deciduous and evergreen oaks, the most common of which, *Q. peduncularis* (roble negro), *Q. aaata*, and *Q. brenesii*, are usually in separate stands on the lower slopes below pines, perhaps because of deeper soil on the lower slopes or a shallower water table, or because the pines have been logged off the easily accessible lower slopes. Pure stands of *Q. peduncularis* often seem to be an early successional stage induced by fire, as are the pines, and on some burned-over sites more seedlings of this species have survived than pine seedlings. Pines and oaks often appear to prefer similar sites, but oaks occur on a wider range of soils. As the Segovian pine forests are destroyed by logging, and regeneration is hindered by lack of seed trees and by the excessive burning now prevalent, the pines are often replaced by *Q. peduncularis*. This replacement of pine stands by *Q. peduncularis*, by a low scrub dominated by carbón, or by grass alone (pl. 30, *b*) has happened often enough in recent years to be recognized by local farmers. However, *Q. peduncularis*, carbón, and grasses usually are replaced by communities dominated by *Q. aaata*, *Q. brenesii*, and other oaks if burning is stopped (Taylor, personal communication, 1961).

CHAPTER III

THE PINE SPECIES OF NICARAGUA

THE THREE PINES of Nicaragua, *Pinus oocarpa*, *P. pseudostrobus*, and *P. caribaea*, are widely distributed throughout northern Central America. These somewhat similar species are most easily distinguished from one another by small differences in their cones and needles.

Pinus oocarpa (Schiede).—*P. oocarpa* or ocote pine, which makes up about 90 per cent of the upland pine forests of Nicaragua, is found as far north as central Mexico in the subtropical altitudinal zone; it cannot withstand freezing temperatures. Ocote grows at elevations from approximately 2,000 to 5,000 feet in Nicaragua but grows higher farther north, reaching a maximum known elevation of about 6,500 feet in Guatemala. The species is adapted to less rainfall and a longer dry season than is any other Central American pine (table 1); in parts of Guatemala it grows where there is as little as 30 inches of rain annually. In Nicaragua *P. oocarpa* occurs in areas where the total rainfall is between 50 and 80 inches and there is a marked dry season—for example, near La Reina east of Matagalpa, where there is a 5-month dry period and 71 inches of rain. In Nicaragua *P. oocarpa* usually grows on moderate to steep slopes where drainage is good and topsoil generally thin.

The ocote pine is a medium-sized tree, 50 to 70 feet in height and 16 to 24 inches in diameter at maturity. The needles are from 6 to 12 inches long and usually grow in clusters of 5, but often of 3 or 4. The cones are small, 2 to 4 inches long, and somewhat heart-shaped, with the peduncle persistent to the cone (pl. 24, a). *P. oocarpa* is a serotinous and closed-cone species; that is, the cone releases seeds either very gradually or holds them until it rots apart, is broken up by animals or birds, or more commonly, is heated by fire. After a fire, seeding is generally quite profuse. The seeds are winged, as are those of *P. caribaea* and *P. pseudostrobus*, and may be carried a fair distance by the wind.

P. oocarpa in Mexico is too crooked to make good lumber, but the same species in Nicaragua has been logged commercially; Nicaraguan lumbermen report that the wood has many of the good qualities of *P. caribaea*, and that it is often difficult to distinguish between the sawed lumber of the two species (C. Farr, Dipilto, personal communication, 1957). In the past, however, the main economic value of *P. oocarpa* in Nicaragua was derived from its high content of resin, long tapped for a variety of purposes; the same use has been made of *P. pseudostrobus*.

Pinus pseudostrobus (Lindley).—The long-needled *P. pseudostrobus* or pinabete also ranges from Nicaragua to central Mexico, but at elevations up to 10,000 feet, preferring a colder and more humid climate than is normal for *P. oocarpa*. In Guatemala pinabete grows where precipitation ranges from 48 to 124 inches; in Nicaragua it is unknown where there is less than 60 inches. The species should be suited to the climate of the high eastern cordilleras, but has not been found east of the mapped pine upland area.

There seem to be no previous reports of *P. pseudostrobus* in Nicaragua. I have found it, however, on a few sites in the pine uplands, usually between 3,500 and 5,000 feet, and growing above or with *P. oocarpa*. The species is most abundant just

below the ridges of the Montes de Dipilto and Jalapa on the Honduran border. The southernmost stand I have observed is near San Rafael del Norte north of Jinotega.

P. pseudostrobus is larger than *P. oocarpa*, often growing to a height of 120 feet with a diameter of up to 4 feet. Its distinctive needles are 10 to 15 inches long, thin, and flexible, with 5 to a bunch; the 3- to 6-inch cones are oblong, slightly curved, and longer than those of *P. oocarpa*.

Pinus caribaea (Morelet).—*P. caribaea*, the short-needled Caribbean slash pine,¹ grows in open savannas near sea level on the Caribbean coastal lowlands of Central America from Bluefields in Nicaragua north through Honduras, Guatemala, and Br. Honduras to the border of Quintana Roo. It occurs also in eastern Cuba, the Isle of Pines, Guanaja in the Bay Islands, and on some of the Bahamas (New Providence, Abaco, Andros, Grand Bahama, North Caicos, and Pine Cay). All these are areas of high temperatures, and the mainland coastal sites have a short dry season and as much as 120 inches of rainfall. I have even observed one healthy, mature specimen of *P. caribaea* growing where the annual rainfall is almost 250 inches, on sandy soil in the town of San Juan del Norte (Greytown) at the mouth of the Río San Juan near the Costa Rican border. Although this individual was probably planted, its tolerance for heavy rainfall is interesting. In contrast, *P. caribaea* also grows in central Honduras, Cuba, and other areas with less than 50 inches of rain. Being restricted to elevations below 3,000 feet, *P. caribaea* is the only completely tropical pine in Middle America. Like *P. oocarpa*, it cannot withstand freezing temperatures.

Inland from the Caribbean coastal pine savannas of Central America, *P. caribaea* grows on the highland foothills at elevations up to 2,500 and possibly 3,000 feet, mostly in Honduras and British Honduras. In northern Nicaragua, and to a lesser extent in southern Honduras, there is a gap of up to 150 miles between *P. caribaea* in the savannas and foothills and the interior pine uplands, where *P. oocarpa* is the main pine species. Although there are stands of *P. caribaea* in the pine uplands, the trees show such close resemblance to *P. oocarpa* that some crossing between the two species in the interior of Honduras and Nicaragua seems likely. Until the taxonomic status of these pines is established, N. T. Mirov (personal communication, 1958), who has observed them in Honduras, suggests that they be referred to as an "inland form" of *P. caribaea*. In the pine uplands of Nicaragua this form occurs at elevations of 1,800 to 2,500 feet on gentle relief in the rainier eastern parts of Nueva Segovia including the Llanos de Totecacinte (pl. 22, a), the Río Poteca area, just south of Quilalí, and undoubtedly elsewhere.

The timber of *P. caribaea* is excellent for construction, and has been logged on the Miskito Coast of Honduras and Nicaragua for many years. The tree grows from 50 to 100 feet in height and 20 to 40 inches in diameter with a long, straight, clear lower bole. The short, 7- to 9-inch needles grow 3 and sometimes 5 to a fascicle, and the small, 2- to 3-inch, slightly oblong cones of the "inland form" are quite similar to those of *P. oocarpa*, except that the conelets of *P. caribaea* are often armed with sharp rounded prickles.

P. caribaea grows on flat to rolling slopes, usually on very porous topsoils, both

¹*P. caribaea* has only recently been distinguished from the slash pine of southern Florida, which is now known as *P. elliottii* var. *densa*. See Little and Dorman (1954), who include a complete description of *P. caribaea*.

in the pine uplands and on the Miskito Coast savannas. The relation of *P. caribaea* to soil moisture is uncertain, however. Poorly drained clays on the Miskito Coast and water-permeated limestone flats in the Bahama Islands both contain stands; consequently, it cannot be said that *P. caribaea* tolerates high precipitation only where there is good drainage. Nor does *P. caribaea* seem to be eliminated by a long and severe dry season, for the "inland form" is known in drier parts of Honduras such as the Choluteca Valley near Zamorano. The possibility that the "inland form" is a cross with the drought-tolerant *P. oocarpa* could well be relevant here. *P. caribaea* is certainly suited to the climate of the wet lower eastern uplands of Nicaragua, but it is curiously absent, with a few exceptions such as the site previously mentioned near Bonanza. Yet the species is present in the very wet hilly interiors of Honduras, British Honduras (Mountain Pine Ridge), and Guatemala (Pop-tún), as well as in the Segovias.

The upland pine forests of Nicaragua consist almost entirely of *P. oocarpa*, with only scattered stands of *P. caribaea* and *P. pseudostrobus*. These forests are found mainly between the 50- and 80-inch isohyets at elevations ranging from 1,800 to 5,000 feet, even though elsewhere in Central America the same species have much greater climatic ranges (fig. 2). Extensive pine stands are found in the Department of Nueva Segovia on parent materials of granite and schist; south of the Río Coco, scattered stands, chiefly on old acidic volcanic rocks, extend southward in two groups flanking the Llanos de Estelí and Sebaco to terminate west of Sebaco and southwest of Matagalpa (fig. 3). The entire pine area is and has been subjected to frequent burning and severe erosion. East of the pine uplands, in a very wet, unsettled mountain area where the climate is suitable for *P. pseudostrobus* at high elevations and *P. caribaea* at low elevations and where, seemingly suitable parent materials occur at least locally, there is little burning, there has been no serious erosion, and there is no pine forest.

CHAPTER IV

FIRE AND PINES

"THESE HILLS were covered with long-leaved pines, and the large proportion they bear to the hard wood is said to have been increased by the Indian practice of burning the grass; the bark of the oak and other kinds of hard wood being more combustible, and more easily injured by fire, than that of the fir tribe." This little-known statement, made by Sir Charles Lyell in 1849 (II:69), concerned an area near Tuscaloosa, Georgia, but is equally applicable to many of the pine forests in the tropics.

THE ROLE OF FIRE IN THE ECOLOGY OF TROPICAL PINE FORESTS

O. F. Cook (1909) was probably the first to suggest that many of the Central American pine forests had succeeded mixed broadleaf forest on impoverished soils following shifting slash-and-burn agriculture. He argued that the pines were able to survive because of periodic, mainly man-made fires, which kept out competing hardwoods. A number of reliable observers have since reached similar conclusions about various pine lands in tropical and subtropical regions of the Americas: for Central America, Paul Allen (1955:254), Gerardo Budowski (1959b:275-276), Carl Johannessen (1959:35-37), James Parsons (1955b:45-47), B. W. Taylor (1959a:78-80; 1959b:207-209), and Frederick Vogel (1952:4-6); for the Caribbean islands, J. S. Beard (1953:167), R. Ciferri (1936; see Bartlett, 1957:291-295), W. D. Durland (1922:217), and L. R. Holdridge (1947:64-68); for the southeastern United States, Frank Egler (1952:232) and many others.¹

H. H. Bartlett (1957), in reviewing and summarizing the studies of Ciferri (1936) and C. E. Chardón (1941)² on the pine forests of the Dominican Republic, commented:

It is hard to formulate an acceptable hypothesis for the persistence of pure pineland at low altitudes without involving fire as a factor. Fire, if it occurred frequently enough, would protect established pine forests against replacement by deciduous [species] providing the climatic and edaphic conditions were such as to maintain the pine-forest floor in a seasonally combustible state. (293.) . . . primitive man may well have greatly aided pine reproduction and extended pine forest by burning over land in hunting . . . [but] preparation of habitats for pine may conceivably result not only through the agency of man, but from natural causes such as wind-falls and fires caused by lightning. (284.)

The last qualification by Bartlett, the natural preparation of habitats, is frequently suggested, and although such preparation has been only rarely documented, natural phenomena, including landslides, blowdowns, floods, lightning

¹Comprehensive studies, including observations made over a period of years by W. Wahlenburg (1933, 1946) and others, indicate that the southern longleaf pine (*P. palustris*) is not only unusually fire tolerant, but is largely dependent on periodic fires. H. H. Chapman (1932:230) expressed the opinion that lightning fires can occur frequently enough to account for longleaf pine forests. It has been suggested that pines elsewhere in the United States are dependent on periodic fires; see, for example, Harold Weaver's article "Fire as an Ecologic Factor in the Southwestern Ponderosa Pine Forests" (1951).

²Chardón (1941) argued that the pines of the Dominican Republic were unrelated to human activities because they were geologically ancient and occupied high uninhabited mountains, and because the abandoned *conuco* clearings he had observed had been invaded by *Cecropia* and other plants rather than pines. Bartlett (1957:284) acknowledged the geologic relation, but added: "That the lower-altitude *pinars* may not have been extended by human agency, just as prairies have, by clearing and fire, does not seem as yet to have been sufficiently investigated."

fires, sterile soils, and rocky surfaces, have certainly provided favorable sites for the establishment of pines in tropical areas. It is my contention, however, that man's modifications of vegetation and soils by forest clearing and burning have made possible a considerable expansion of the tropical pine forests.

It is important to note that in Nicaragua *P. oocarpa* and *P. caribaea* are intolerant of shade: they are unable to regenerate beneath other trees, tall grass, or even in their own shade. The shade tolerance of the least common Nicaraguan pine, *P. pseudostrobus*, is unknown. During six months in the pine uplands, I did not once observe regeneration of any pine beneath heavy shade. This intolerance, substantiated by B. W. Taylor (1959b:208) for *P. oocarpa* and (1959a:79) for *P. caribaea*, is characteristic of many pine species. In the humid tropics, periodic fires are by far the most widespread means by which open stands of woody vegetation with little shade are maintained.

In the pine uplands of Nicaragua, light burning by the inhabitants takes place every year. In some areas it has probably been practised since long before the Spanish Conquest. The importance of burning to the survival of pine forests in Nicaragua is partly shown by the existence of mixed hardwood stands, which do not burn, near pines and on comparable sites but with no young pines among them. Where mature pines do grow with a hardwood stand, the pines are apparently older; presumably they grew on an open site, and the hardwoods, no fires occurring on the site, came in later. This situation has been observed, for example, where intersecting trails block off fires.

The initial reaction to protection from fire in an open pine stand is a vigorous growth of young pine, but these shade out further pine regeneration. On some sites in the pine uplands which are protected from fire there are very dense stands of pines, but with hardwoods exclusively—no pine seedlings—in the understory (pl. 24, b). If protection from fire continues and the trees are not thinned, the hardwoods will probably take over such sites as the mature pines die. There have been several reports, from Nicaragua and elsewhere in Central America, of pine logs and buried pine roots amidst tall mixed broadleaf forest. O. F. Cook (1909:20) noted that in Guatemala, in supposedly virgin forests east of Cobán in the bottom lands of the Polochic valley near Panzós and in the coffee district north of Senahu at 3,000 feet elevation and above, dead pine roots were dug up by the Indians, who used them for torches. Cook was of the opinion that pines were once much more abundant when native populations were larger and there was more clearing of the forest. In Chiapas, F. Miranda (1953:289-290) reports buried pine logs south of Monte Libano in mature rain forest at an elevation of 900 meters and at a distance of 15 to 20 kilometers from the nearest pine ridges. He considers pines to be quite alien to the site, and explains the logs as being the remains of either an extinct mesophytic pine species or an existing species which grew when the climate was drier than at present; neither suggestion seems tenable. Buried pine roots have also been observed in Honduras north of the junction of the Río Patuca and Río Guampu in a rain forest that contains tall cedar and mahogany, and buried pine stumps and logs occur in broadleaf forest in the pine uplands of Nicaragua just east of the Río Cua and also between Yalí and the Río Coco. It is surprising that fallen dead pines can resist decomposition under humid tropical conditions for an indefinite length of time. Where buried pine stumps

occur north of Yalí, the present broadleaf forest is said to be at least 30 years old and possibly much older. The heavy bark or the resin content of pines may aid in their preservation.

Although burning can encourage pines at the expense of other plant groups, fire can also limit regeneration of pine if it is so frequent that pine seedlings do not have time to develop a fire-resistant bark and to grow high enough that their needles are above the flames of ground fires (pls. 22, b; 23). (*P. oocarpa* can survive partial but not complete defoliation by fire.) Even if burnings are infrequent, a fire in accumulated debris and dead grass can be severe enough to destroy saplings and older pines. In the pine uplands, a young pine requires from 3 to 7 years to become fire-resistant, depending of course on the severity of the fires. Early in the dry season, fires are less severe than they are at the end of the dry season when there is more and drier fuel. If fires are very frequent, only grass survives, and if they are very infrequent, hardwoods begin to take over a pine stand. Thus both the survival and the density of the pine forests is related to the frequency, severity, time, and extent of burning.

Several Central American foresters have commented on the effects of different frequencies of burning in pine forests. L. R. Holdridge (1953:43), writing of Middle America in general, notes:

Pines also can be extended, as a result of burning, to occupy areas previously covered for the most part by broadleaf forest. With fires spaced at intervals of 5 to 20 years, the pines maintain themselves as dominants; with fires almost every year, the pines change in time to savannas; without fire, the larger part of the pine areas become covered with associations of broadleaf trees. [my translation from Spanish]

After approximately ten years without fire, however, not only do many deciduous species grow large enough to resist infrequent fires, but an evergreen hardwood formation can become so verdant that fire cannot penetrate it.

Frederick H. Vogel (1952:4-6) stresses the harmful effects of too-frequently recurring fire on the pine forests of Honduras:

During the half year from January to June, the pine forests in Honduras suffer annually from hot forest fires that rage unchecked over almost every square mile of the Central Region. . . . Honduran pines seed well, and the climate is favorable to reproduction. The only factor which prevents an excellent stand of young pine for future generations is *frequently recurring fire*. We say 'frequently recurring' because it is quite probable that pine would be succeeded on large areas by various other forest species in a century or two if the forests remained without any fire at all for that period. As a rule, pine does not reproduce well in a heavy ground cover of grass and brush. Only when the ground cover is opened by fire, water, or by mechanical means does the seed germinate and take hold.

But, once germinated and rooted, the seedlings must be protected from fire for the next five to seven years, or they will be lost as surely as if they had never germinated. That is what has happened to pine seedlings everywhere that reproduction is absent today; it has started but has been killed by fire.

It is surprising, considering the amount of burning, that extensive pine forests still exist in Honduras and Nicaragua; apparently rough mountain relief breaks up fires sufficiently so that a few seedlings escape burning long enough to become fire-resistant and thus perpetuate an open pine stand. On the other hand, in the pine savannas on the gentle terrain of the Miskito Coast, though seedling is profuse.

few seedlings survive the sweeping and unimpeded fires except where a close network of trails break the fires. Wind-blown upslope fires in the mountains are, of course, more severe than the slow-moving fires on the flats, but the former burn out rapidly and their coverage is spotty.

All these observations on the relations of fire to the establishment and survival of pine apply to *P. oocarpa* in the northern mountains of Nicaragua, where pines grow up to an elevation of about 5,000 feet, but they do not necessarily apply to all the pines in Middle America. At high elevations, especially where frost occurs (above approximately 6,000 feet), pines may maintain themselves without much aid from fire, although disturbances of sites may still be necessary for initial germination. Most of the Middle American pine forests actually do occur at fairly high elevations. As elevation increases, low temperature reduces the variety of plant species and rate of plant growth, i.e., the competition with which pines must contend. Yet except at very high elevations, there is much dense hardwood forest vegetation above the frost line in the humid tropics; consequently, generalizations about the relation of low temperature to occurrence of pine are not easy to make. Probably the combination of temperature and edaphic factors provides more natural habitats for pines at higher elevations than at lower elevations. But slash-and-burn agriculture in the high mountains would undoubtedly have increased the potential area there for the establishment of pine that was previously dependent upon natural disturbances and unusual localized conditions. Clearing and burning would also make it possible for pines to invade the warm lower mountains and coastal plains and survive. Conclusions similar to these have been reached by a number of observers, including J. S. Beard (1953:167), R. Ciferri (1936:259), W. D. Durland (1922:217), and L. R. Holdridge (1947:66), all with reference to Hispaniola, and O. F. Cook (1909:19) for Guatemala. Holdridge, in his study of the pine forests of the Morne la Salle Mountains of southern Haiti (1947:65-66), comments:

Since a great number of tropical and subtropical tree species are not able to survive under the colder conditions at higher altitudes, the pine would not have been subjected to severe competition and would have been able to exist in pure stands or in mixture with some hardwood trees. Where soils are poor at high elevations, there is little reason to doubt that the pines occurred in pure stands in pre-Columbian days in a very similar state to that found at present.

At lower altitudes below the frost line, the history of the pine distribution may have been quite different. By observations of the rapid invasion of hardwood species on richer soils where fires have been excluded for several years, one becomes conscious of the tremendous population pressure which a pine forest would have to exert to hold its own. Apparently, the pine stands below the frost line were less extensive in pre-Columbian time and occurred as patches or scattered trees mixed with hardwoods in the frost hollows, on areas of poor soil and along the crests of the ridges. As soon as man entered the area, occasional fires began the process of pushing back the hardwoods from sections which the pines were able to invade because local sources of seed were available and to hold because the pines are quite fire hardy except when young.

THE CAUSES AND EFFECTS OF FIRES IN THE SEGOVIAS

The upland pines of Nicaragua are all found at relatively low elevations in a subtropical environment where their establishment and survival seem particularly favored by fire. The question remains whether natural fires occurred frequently

enough before the coming of man to account for large and pure stands of pine.

There is very little documented evidence of lightning fires in Nicaragua or elsewhere in Central America (Budowski, 1959b:265). One lightning fire, which burned through 5 square miles of pine forest, was reported in British Honduras in 1954 (British Honduras, Forest Department, 1955). In Nicaragua most electrical storms take place during the rainy season when the cover of vegetation is verdant and hardly combustible. A few storms do occur during the dry season, when fires could be ignited by lightning if it were not accompanied by heavy, steady rainfall. The frequent occurrence of lightning fires in the Florida Everglades, where the climate is comparable to the tropical *Aw* climate of Central America, has been documented by W. B. Robertson (1955). Lookouts observed 12 lightning fires in 1951 and 11 in the first half of 1952. These were grass fires, however, and it is doubtful that there was much grass in the Nicaraguan mountains before primitive man appeared and began clearing the forest and burning. Areas now being converted to grassland are first manually cleared of forest and undergrowth and then burned; it is unlikely that even the drier mature deciduous forest would be very combustible. Present savanna fires generally do not invade the forests of Nicaragua unless the forests are open, and have a grassy ground cover. However, during an unusually dry season the margins of a mature closed forest might be destroyed by fire, thereby extending savanna. Gallery forests in eastern Nicaragua were invaded by fire during the severe dry season of 1958 according to B. W. Taylor (personal communication, 1961).

What is known about the causes, nature, and ecological effects of fire in the American tropics has been well summed up by Gerardo Budowski (1959b:270-272). He notes that crown fires are not known in primary tropical forests but may occur in very dry secondary forests, and that recurring savanna fires may gradually penetrate the understory of a dry forest and encourage grasses and fire-resistant trees. The ecologist Pierre Dansereau (1957:275) writes about the burning of tropical vegetation: "Although it is too much to say that climax vegetation is immune to fire, . . . humid plant cover (from tropical rain forest to summer-green deciduous forest) hardly ever burns if it has not been previously disturbed. In such areas it is the jungle, the second-growth forest, and the scrub or grassland that burn."

Thus, although both the Florida fires and the fire in British Honduras show that lightning does start fires in the tropics, the frequency and long-term effects of such fires in tropical forests seem minor. However, secondary vegetation, usually a product of man's activities, is often very susceptible to either natural or man-made fires. The dominant role of clearing and burning by man in extending the pine area in the Nicaraguan highlands is suggested by several additional circumstances: man's activities have been the known cause of regular fires in the pine uplands since long before the germination of the oldest pine tree standing today, and existing pine forests are limited to parts of the highlands long settled and long burned-over by man. Possibly there have been pines in Nicaragua only within human times. A recent entry of pines into Nicaragua from northern Central America is certainly suggested by the presence in Nicaragua of only three pine species, none of which are endemic; by the small area of the country covered by

pine in contrast to the large areas of pines in Honduras and Guatemala; and by the fact that the southern limit of the genus *Pinus* in the Western Hemisphere is in Nicaragua, even though there is no major climatic barrier to further advance.

The natives of tropical America, past and present, have always used fire to clear and prepare land for crops. The Indians of Nicaragua must have also set fires intentionally to drive game in hunting (a common practice all over the world), by accident, and for amusement. Where the same site was often fired, grass and fire-tolerant trees would be encouraged. Many grass fires undoubtedly burned over former milpa sites on the forest boundary, preventing regrowth of mixed forest and adding new clearings to the general area of regular burning.

The extent of slash-and-burn agriculture and the frequency of hunting fires would be expected to depend on the density of native populations; and because the upland pine forests in Nicaragua were in existence when the Spanish arrived,³ the size of the Indian population at that time should be meaningful. Within a few years after the entry of the Spaniards into Nicaragua (1522), the expeditions they sent into the northern highlands in search of gold and to secure pine pitch for use in ship construction found an ample supply of settled Indians, probably mainly of the Matagalpa group, that could be put to work. The number of inhabitants in the pine uplands in the early sixteenth century is not known, but there is evidence⁴ that the population of the entire country was possibly half of the 1,300,000 estimated in 1956. Most of the present 37 towns and pueblos of the pine uplands were Indian villages at the time of the Spanish Conquest, and many other villages have since vanished. (Cuadra Cea, 1957, identified at least 28 villages as existing in 1524.) That numerous settlements existed in the pine uplands long before the Conquest is indicated by the uncovering of artifacts, including, pottery, tools, and stone statues, that antedate the sixteenth-century cultures of Nicaragua. If the present 350,000 population of all the Segovian departments (Nicaragua, 1954:22-26) is, like that of the country as a whole, slightly more than twice that at the time of Conquest, the population density at that time would have been about 20 per square mile.

There is reason to doubt, however, that even a fairly dense population is needed to bring about great modifications in vegetation through clearing and burning, especially in regions with a marked dry season, where grass fires, once started, could easily maintain themselves. For example, the Miskito pine savannas of eastern Nicaragua are currently almost completely burned over every year by a population having a density of between 1 and 2 per square kilometer, with most of the people concentrated in a few coastal towns. As far as is known, the main population centers in Nicaragua have always been on the rich volcanic soils of the

³ Pedrarias Dávila, first governor of Nicaragua, in a letter to the Emperor of Spain in 1525, mentions pine forests north of León, where pitch was collected (Dávila, 1954:130). Oviedo, writing in 1547, mentions pines in the "sierras" of Nicaragua (Oviedo y Valdes, 1944, II:57, 270).

⁴ Bartolomé de las Casas (1822:68-69) wrote in 1542 that from 1523 to 1537 the Spanish shipped over 500,000 Indian slaves from Nicaragua to Panama and Peru and killed another 500,000 to 600,000, leaving only 4,000 to 5,000 in the country. These figures are undoubtedly excessive, but are indicative of a rapid demise of a large native population in Nicaragua. Lic. Diego de Herrera, in a letter to the Emperor in 1545, reported 600,000 Indians in Nicaragua at the time of the Conquest, of which, as result of slave exports, disease, and killing, only 30,000 remained in 1545 (Herrera, 1875:398-399).

Pacific coast, the population thinning out eastward through the mountains. Theoretically a small but fairly well-distributed population could have cut into the original broadleaf forest of the highlands, section by section, from the west. Each abandoned plot behind the agricultural frontier might subsequently have been burned over every year or every few years, thus favoring such pyrophytic plant associations as grasslands, scrub savanna, and pine or oak forests. In contrast to tropical forest destruction from shifting agriculture along an expanding frontier is the situation in many of the tropical forests of the world, where either land pressure is so great that the natives dot their shifting farms throughout their territory as part of a planned rotation or forest fallow system, or slash-and-burn farms are dispersed simply because the population is small and very dispersed as is true of the present-day Sumo Indians in the rain forests of eastern Nicaragua.

Where a population is expanding from a nucleus into an unlimited area of new land, little attention need be given to the land abandoned behind the frontier, although it may be burned over freely in hunting or to improve pasture for livestock. Such abandoned land would burn much more readily than the forest ahead of it. Grasslands and savannas have probably been produced in various parts of the tropics as often by this means as from the extensive cultivation by a population too dense to allow abandoned plots to return to forest fallow.

In 1874, Thomas Belt reported section-by-section cutting into the eastern forest in the southern highlands of Nicaragua in the Department of Chontales. Belt showed an early awareness of how the actions of man determined the boundary between the eastern rain forest and the grassy upland savannas. He observed a sharp break between the two without a significant corresponding change in soil, bedrock, or climate. He attributed this break to the practices of the Indians in cutting and burning the forest for planting maize and beans. These farm plots were then abandoned, he wrote, not because the soil was worn out, but because cutting a new clearing was easier than weeding out the invading grasses and shrubs:

Should the brushwood ultimately prevail and cover the ground, the Indian or Mestizo comes again after a few years, cuts it down, and replants it with maize. But as most of his old clearings get covered with grass, he is continually encroaching on the edge of the forest, beating it back gradually, but surely, towards the north-east. As the process has probably been going on for many thousands of years, I believe that the edge of the forest is several miles nearer the Atlantic than it was originally. (p. 187.)

The process of cutting back the forest from the west is still going on today in the eastern parts of Nueva Segovia, Jinotega, and Matagalpa, where pine forest, savannas, and pasture lands end abruptly before a wall of broadleaf forest, which forms the boundary line of regular burning. Aerial photographs reveal that beyond this boundary there is a checkerboard pattern of clearings and forest, the clearings becoming fewer and fewer eastward (pls. 25, 26).

Indian fires on any given site would probably have the irregularity that does not completely destroy pine regeneration. Furthermore, many of the Indian fires must have been light fires occurring at the beginning of the dry season when grasses can be burned but are not so tall, dry, and combustible as at the end of the dry season,

when hot fires would be most destructive of pine seedlings.⁶ Since the establishment of a large number of cattle herds in Nicaragua,⁷ the people have burned their lands every year to encourage and improve annual growth of pasture grasses and to destroy ticks and other harmful insects. Almost all this burning is done in the last few weeks of the dry season just before the first rains bring up new grasses. Jaragua (*Hyparrhenia rufa*), which often grows 6 feet high, is the main pasture grass in the pine uplands. By the end of the rainy season it is usually too coarse to be palatable for cattle, and within a few more weeks it is completely dried out and without food value. Consequently the pasture grasses are not grazed low, even with overstocking, and hot ground fires that are very destructive to pine seedlings and young pines up to 6 or 7 years old are possible. The native grasses, on the other hand, are almost all short and burn less vigorously, even when allowed to accumulate for several years. In either short or tall grass, the fires in the pine uplands are relatively slow-moving ground fires, which seldom race through the tree tops or damage property (pl. 27, a). Most observers agree, however, that present burning practices effectively limit the regeneration of pine in the pine uplands. Still, rugged relief in many sections tends to break up fires, and enough seedlings escape fire long enough to become fairly fire-resistant and so maintain an open stand of pines. In addition, a single logging operation may leave behind a system of fire-breaking trails that helps protect new pine regeneration. Pines are disappearing completely only where regular burning is accompanied by persistent logging.

⁶ Frank Egler (1952:225-228) discusses the time of occurrence and the effects of Indian fires in comparison with subsequent types of burning in the pine areas of southern Florida.

⁷ The size of the cattle herds of colonial Nicaragua is unknown, but Sofonias Salvatierra (1939, II:209-210) commented, without documentation, that during the seventeenth and eighteenth centuries Nicaragua was the leading cattle producer of Central America and regularly provided beef and hides for the other provinces. He wrote that at the start of the eighteenth century, 52,000 head of Nicaraguan cattle were sent each year to the fair at Chalchuapa (El Salvador). Pablo Lévy (1873:477) reported that there were 1,200,010 cattle in Nicaragua in 1872. In 1952, a total of 1,182,000 head of cattle were reported by the Ministerio de Economía (Nicaragua, 1956:35).

CHAPTER V

HUMAN SETTLEMENT AND THE DISTRIBUTION OF PINES IN THE SEGOVIAS

THE EASTERN LIMIT OF UPLAND PINES AND THE SETTLEMENT FRONTIER

THE EASTERN LIMIT of the upland pine forest in Nicaragua lies near the eastern boundary of permanent settlement. This boundary has not changed significantly since pre-Conquest times (fig. 7). From Totecacinte in Nueva Segovia to San Carlos at the southeastern corner of Lake Nicaragua, a frontier line can be traced beyond which there are no settlements, other than a few scattered river villages, in a vast expanse of tropical rain forest that stretches over 100 miles to the savannas of the Caribbean lowland. The upland pine forests are all west of this line, which marks no sudden change in the physical environment, but does roughly mark the eastern limit of regular burning. There is no sharp transition in parent materials or climate, and lateritic soils commence at variable distances east of the pines. The granitic, schistose, and acidic volcanic rocks on which most of the pine stands are found all extend east of the upland pine area (fig. 5). It is true that annual rainfall is high east of the pine zone, usually exceeding the 80 inches that is about the maximum known for *P. oocarpa*; nevertheless, *P. caribaea* is adapted to the rainy lower eastern mountains of Nicaragua, and *P. pseudostrobus* to the cool and humid high eastern mountains of Isabella and Darién.

Soils change from tropical brown soils to reddish-brown latosols as rainfall increases east of the pine uplands, but this change in itself does not seem to prevent growth of pine. The pines grow on soils that are thin with little organic topsoil remaining, while mature broadleaf forest grows on a fairly fertile topsoil, although one rapidly leached of nutrients upon exposure to heavy rains. Today the thin, eroded soils on pine-covered slopes are unsuited for crops, but the same slopes may once have been covered with heavy broadleaf forest on more fertile soils that would have made possible the shifting slash-and-burn agriculture that theoretically prepared the way for colonization by pines. That milpa farming was possible is evidenced by the fact that the poor soils derived from granite and schist in Nueva Segovia—soils that are very infertile under pines—are deep and rich enough where broadleaf forest does exist to support some coffee and food crops.

The pine uplands are an area of thin soil and regular burning. Both of these are conducive to establishment and survival of pine, and neither are characteristic to the east of the settlement frontier. The fact, then, that fires, soil degradation, and extensive replacement of broadleaf forest by secondary and deflected climaxes, including pine forest, are all limited primarily to the area of long permanent settlement, suggests that man's activities have been a major reason for the present distribution of upland pines in Nicaragua.

No corresponding frontier exists in adjacent Honduras except south of the Río Patuca. High mountains bordering the Atlantic coast have produced local rain shadows in central and eastern Honduras, and relatively low rainfall, along with fertile valleys, have made much of interior Honduras more suitable for permanent

settlement than are the dense and humid rain forests of central Nicaragua. As a result, clusters of settlement are dispersed throughout Honduras. Extensive pine forests are also found throughout the country (fig. 1), generally in areas of thin, stony soils, acidic parent materials (schist, granite, sandstone, andesite), and regular burning. Somewhat analogous associations exist in Guatemala and Mexico; there are few areas of pine anywhere in the tropics or subtropics that are not subject to periodic burning.

The easternmost pine stands in highland Nicaragua are usually found with other deflected or secondary plant associations, but often there is a sharp transition from pine to tall evergreen broadleaf forest. I have seen areas where the tension zone between pine and broadleaf forest shows no relation to climate, topography, or parent materials, although the contrasting plant communities suggest two completely different environments. On the 4,500-foot range east of Murra in Nueva Segovia, for example, *P. oocarpa* and *P. pseudostrabus* cover the western slope and the uppermost eastern slope, while all visible vegetation eastward is submontane rain forest. At another site on the Río Tapalehi, a small tributary of the Río Poteca in eastern Nueva Segovia, an open forest of *P. caribaea* ends abruptly at the bottom of a small valley. Here, in May, 1957, I observed the burning of dry grasses beneath the pines (pl. 28, *a*), but the adjacent broadleaf forest undergrowth was too verdant to ignite (pl. 28, *b*). The local inhabitants claimed, however, that if new patches were cut out of the margin of the montaña and abandoned to grass and brush, then the edge of the fire line would tend to advance. A number of settlers had huts among the pines, but in order to clear land for milpas all went into the broadleaf forest where there was a dark organic loam topsoil instead of the reddish subsoil exposed by erosion beneath the pines. The parent material throughout the region is schist containing numerous quartz veins.

In other sites farther south, such as the regions around Ciudad Vieja (Nueva Segovia), northeast of Yalí (Jinotega), and near the Río Cua (Jinotega), patches of pine are interspersed with pasture and tall secondary semi-evergreen forest. Some of these areas, all in the frontier zone, were completely abandoned by both native and Spanish inhabitants during the colonial period because of attacking Indians and English pirates from the east. During the past hundred years, revolutions and bandit uprisings have led to further abandonment. East of the Río Cua and between Yalí and the Río Coco, buried pine stumps and logs are found in the midst of tall secondary broadleaf forest. These seem to be explained only by the fact that burning ceased when settlers were gone. The extent of such replacement cannot even be guessed at. Replacement of pine is also indicated by occasional individual mature pines unaccompanied by seedlings in mixed broadleaf forests on Finca La Trampa east of Venceia in Jinotega and in the mountains south of the town of Matagalpa. In both instances the pines are several miles from the nearest pure stand of pines.

A review of the settlement history of the Segovias shows that the frontier line has not been stable, but until recently has failed to advance significantly without subsequent retreat. The eastern limit of upland pine forest may likewise have fluctuated, but pines have failed to maintain themselves where man has not maintained strong pressure on the broadleaf vegetation by clearing and burning.

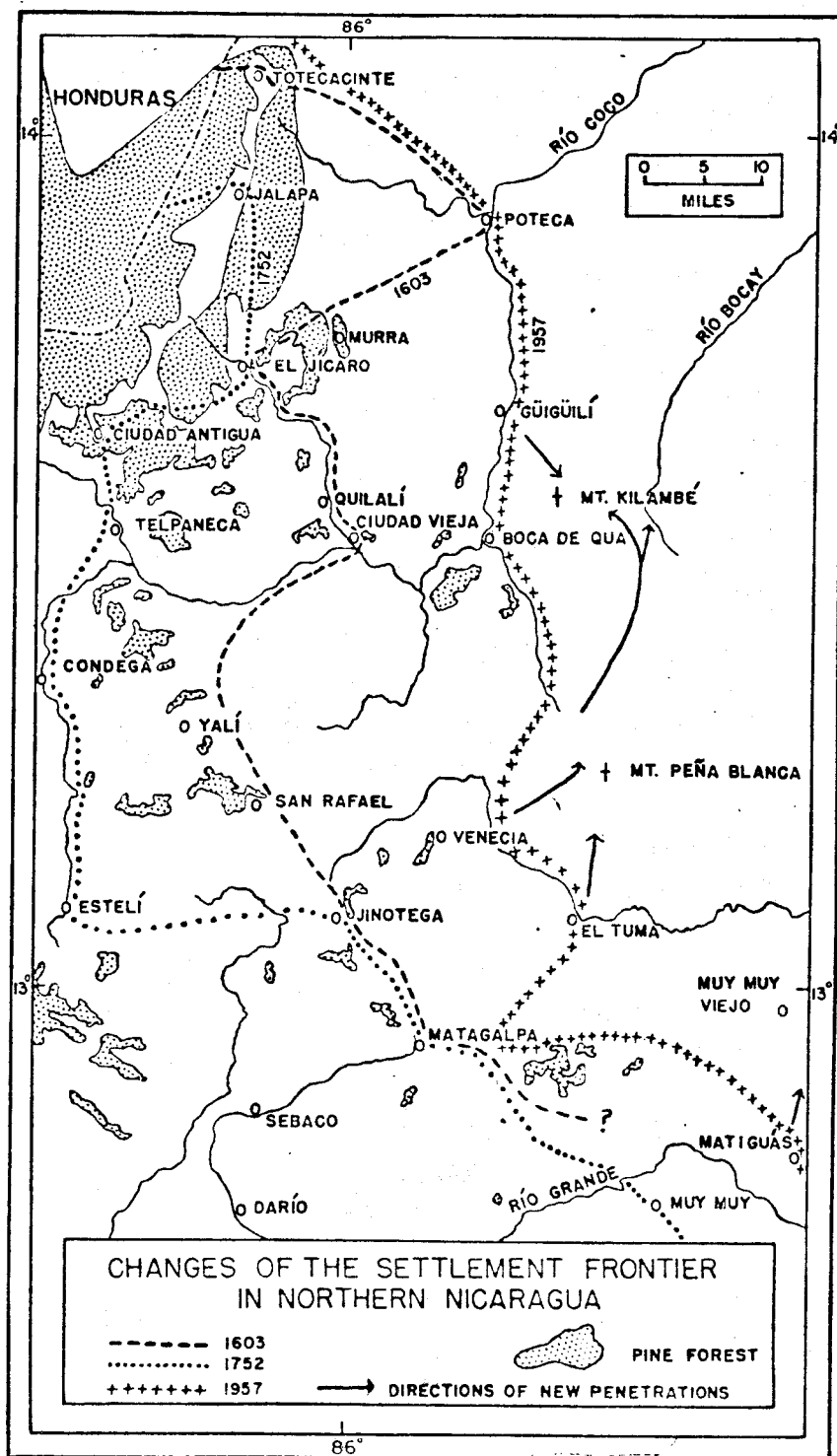


Fig. 7. Changes of the settlement frontier in northern Nicaragua.

THE HISTORY OF SETTLEMENT

The present settlement frontier in northern Nicaragua, as represented by the easternmost highland towns, does not differ greatly from that established by Spanish gold seekers in the sixteenth century (fig. 7), which, with the exception of the town of Nueva Segovia,¹ was based on already well-established Indian villages. These villages include the original sites of Totecacinte, Poteea, Jalapa, El Jícaro, Telpancea, Jinotega, and Matagalpa (Cuadra Cea, 1957). The early Spanish accounts mention no large permanent Indian villages east of these, all of which are located near the present eastern margin of the pine forests. There were, however, numerous roving river and forest tribes (Sumo and Miskito) farther east.

Very little is known about the nature and background of the Indians who occupied the pine uplands at the time of the Spanish Conquest. The Matagalpas were the main tribe; however, they had been overrun by one of the several waves of Nahuatl peoples from Mexico who swept into western Nicaragua between the twelfth and sixteenth centuries, introducing their language but otherwise adopting much of the existing culture. Many of the place names in the pine uplands, including all those on the frontier listed above, are of Nahuatl origin, while most of the others are Matagalpan (e.g., Estelí, Güigüilí, Dipilto, and Yalagüina).

At the time of the Conquest the Matagalpas were a sedentary people with a subsistence economy based on maize farming, as were most of the tribes of western Nicaragua. The Matagalpas lived in large villages in the river valleys or on river terraces where they apparently cultivated alluvial soils but also relied strongly on slash-and-burn milpa farms on the surrounding mountain slopes. The same pattern is still followed by the modern Lencas Indians of Honduras, the Lencas having originally occupied much of the pine lands of central Honduras. Doris Stone (1948:205), in describing the Lencas, writes: "The male members of a family generally spend 5 to 6 days a week in a straw hut built near the field. They return bringing food to the village at the end of a week." Such a system made permanent settlement possible, but the surrounding forests, once cleared, were given little opportunity to reestablish themselves because of burning and frequent reclearing.

The Spanish apparently experienced little difficulty in establishing control over the area occupied by the Matagalpa Indians. The hostility later encountered came from the eastern forest tribes, which are of the Sumo-Miskito language stock. Almost all of the place names east of the Spanish frontier are Sumo-Miskito.² These people were migratory hunters, gatherers, and fishermen; and although they did grow such crops as manioc and plantains, cultivation was (and still is) a less impor-

¹ The original site of the town of Nueva Segovia, which is now the ruins of Ciudad Vieja, was the first permanent Spanish settlement in the Nicaraguan highlands. It is believed to have been founded in 1536 by Rodrigo de Contreras, the third governor of Nicaragua (Guillén de Herrera, 1945:36-38). As the major non-Indian Spanish settlement in the Segovias, the town of Nueva Segovia remained the center of Spanish gold mining activities throughout the colonial period and was long the third city of Nicaragua after León and Granada. Pablo Lévy (1873:164) wrote: "La Segovia fué, durante mucho tiempo, la parte mas rica, populosa y lujosa del país."

² The numerous Sumo-Miskito place names that are found near the margins of the original Spanish frontier include Bocay, Matiguás, Pantasma, and Murra. East of the Spanish frontier line there are only a few Matagalpan names, including Munán and Güina (a tributary of the Río Bocay). See Alfonso Valle (1944) for translations and origins of the Indian place names of Nicaragua.

tant part of their subsistence economy than it was among the tribes of western Nicaragua. The Indians of eastern Nicaragua seem to have always confined their activities, including farming, to the low valleys, and consequently must have had little effect on the vegetation of the high eastern cordilleras. Archaeological investigations, of course, may some day reveal a pre-Columbian people who inhabited the mountains of Isabella and Darién.

Thus the Spanish occupied that part of the Nicaraguan highlands controlled by permanently settled farming Indians. This was the general pattern of the Spanish Conquest throughout Latin America; rain forest areas with wandering tribes received little lasting attention. The Spanish made almost no concentrated effort to penetrate farther into the interior of Nicaragua, partly because no gold was known east of the pine uplands.³ They were also discouraged by the lack of rich soils such as are found on the Pacific coast of Nicaragua and in the highlands of Costa Rica; by the denseness of the tropical rain forest, which makes movement much harder than in the pine forests; and by the extreme hostility of the independent eastern Indian tribes.

Soon after occupying the Segovias the Spanish found this native opposition so intense that time after time the frontier settlers and their conquered Indian slaves were forced to flee. In several instances entire villages were abandoned or transferred westward to more secure sites. The main early encounters seem to have been with Honduran tribes, the Lenca, Jicaque, and Paya, who frequently attacked the Spanish outposts in Poteca, Totecacinte, Jalapa, and the large town of Nueva Segovia. In 1611 Nueva Segovia, the regional capital city, had to be moved from its original site at the junction of the Río Jicaro and Río Coco (Ciudad Vieja) to what is now Ciudad Antigua, and in 1617 Poteca was abandoned when its inhabitants fled to the Llanos de Totecacinte (Guillén de Herrera, 1945:113-115).

Possibly even more feared than the Indians were the Dutch, French, and English pirates who frequently raided the cities and fleets of Spanish Middle America during the seventeenth and eighteenth centuries. Hearing of the wealth of Nueva Segovia, buccaneers sought out the town from both the Atlantic and Pacific coasts. Nueva Segovia and Matagalpa were both sacked in 1654, and in 1688 Nueva Segovia was completely destroyed (Guillén de Herrera, 1945:170-174). In the eighteenth century the raids on the Segovias took on a new character as the British government sought to undermine Spanish control of Nicaragua. Miskito Indians and Zambos (mixed Miskito and Negro), allied with the British and often led by British officers, repeatedly moved up the Río Coco and Río Grande de Matagalpa to harass the highland Spanish settlements. The towns of Nueva Segovia, Telpaneca, Matagalpa, Jinotega, Sebaco, and Muy Muy were attacked many times between 1704 and 1781. The gold camp of Muy Muy (the present site of Muy Muy Viejo) east of Matagalpa was forced to retreat to its modern site in the valley of the Río Grande following a Miskito attack in 1749. In 1789 the town of Nueva Segovia was again moved, this time from what is now the site of Ciudad Antigua

³ The very productive Bonanza and La Luz gold-mining districts of eastern Nicaragua, discovered by rubber gatherers in the 1880's, were apparently not known by either the Indians or the Spaniards (Parsons, 1955a:51). Spanish gold mining in Nicaragua was largely confined to river placers in Nueva Segovia, and it was mainly after Independence (1821) that a large number of hard-rock mines were opened up in the Segovias and in Choptales.

to the present site of Ocotal (Guillén de Herrera, 1945:175-183). Miskito raids ceased in the nineteenth century, but then the Matagalpa Indians turned against their masters. There were major outbreaks in Matagalpa and Jinotega in 1824, 1827, 1844, and 1881 (Gutiérrez Castro, 1954:10).

The colonial period, then, was one in which the settlement frontier did not advance, but retreated, as is best evidenced by the two westward transfers of the city of Nueva Segovia. Bishop Morel de Santa Cruz, who visited and described the Segovias in 1752, found that Totecacinte had also been abandoned by that time, leaving Jalapa, El Jícaro, Nueva Segovia (then at Ciudad Antigua), Telpaneca, Yalagüina, Palacagüina, Condega, Estelí, Jinotega, Matagalpa, San Ramón, and Muy Muy as the outposts of Spanish settlement. He mentions that despite armed garrisons in most of these towns, the people lived in constant fear of the frequently attacking Miskito Indians.⁴

The approximate retreat of the Spanish frontier in the Segovias from 1603 to 1752 is shown on figure 7. It can be assumed that most of the Christianized Indians retreated with the Spaniards; moreover, it is certain that all of the native population of the Segovias was greatly diminished under Spanish rule, as it was elsewhere in Nicaragua. The effects that this retreat of settlement and native depopulation had on vegetation can only be surmised. Much of the originally well-populated land east of Jalapa and El Jícaro, some of which is now in pine, could well have returned to tall broadleaf forest. Behind the frontier, slash-and-burn agriculture undoubtedly decreased appreciably, but vegetation continued to be under attack because of the establishment of large herds of livestock. The Nicaraguan historian Salvatierra (1939, II:209) writes that Nicaragua was the leading cattle-raising country of Central America during the seventeenth and eighteenth centuries, thanks to suitable "condiciones naturales" including "grandes pampas en Chontales y Segovia." The grasslands necessary for stock raising must have been in existence when the Spanish arrived, but they could well have been created by the slash-and-burn agriculture of pre-Conquest natives. Nevertheless, the Spanish ranchers maintained and improved pasture by intentional burning, much as the country people do today. With large herds of cattle it is possible that burning became more regular than it had been among the Indians, even though the human population had greatly declined. The pine uplands having become range land subject to burning, there is no reason to believe that pines would have been replaced by broadleaf forest during the colonial period within the area of Spanish settlement. Burning by the Spanish may either have promoted the extension of the upland pines or have seriously retarded the reproduction of pine, as regular burning often does today. Only speculation is possible, because almost no descriptions of the Segovias under Spanish rule are available.

Since independence was gained from Spain in 1821, general national disorganization and an almost continuous series of revolutions have hindered new settlement in the interior of Nicaragua. The eastern tribes remained troublesome, and the Nicaraguan armies were too occupied elsewhere to attempt to pacify them. How-

⁴According to Morel de Santa Cruz, as summarized by Ayón (1956, II:389-398), the other important settlements in the Segovias in 1752 were Sebaco, Somoto, Totogalpa, and Mazante. Morel found only a few settlements in the southern highlands of Nicaragua. He noted that at least 6 former towns in Chontales had been abandoned by the time of his visit.

ever, the discovery and exploitation of gold and silver veins in the Segovias, mainly by North Americans, led to the founding or reestablishment of several towns, including Macuelizo (1801), Dipilto (1840), Santa Maria (1849), Quilalí (1880), and Murra (1900), all in the Department of Nueva Segovia. Then, toward the end of the nineteenth century, political and economic events sent thousands of Nicaraguans into the central highlands and eastern rain forests. The first economic incentive was the demand for rubber, and the *Castilla elastica* tree of eastern Nicaragua soon became the leading source of rubber north of the Amazon basin.

More recently, coffee has been the main cause of the expansion of frontier settlement in the Segovian highlands. In the 1890's North American, German, and English colonists planted millions of coffee trees in the mountains just east of Matagalpa and Jinotega. Penetration any farther into the interior from these towns was long hindered by the almost complete lack of transport facilities and roads, but motivated by high coffee prices and the successes of the European- and American-owned *fincas*, hundreds of small farmers pushed eastward from the long-established frontier settlements. This pioneer thrust, the first of significance since the Spanish Conquest, was mainly confined to the period of peaceful and progressive rule by the dictator José Santos Zelaya between 1893 and 1911. Several new towns were founded, including Güigüilí, Yalí, San Fernando, and Matiguás, while Telpaneca, Muy Muy, and San Ramón were revived by the coffee boom. After Zelaya was ousted, however, Nicaragua found itself in a revolutionary turmoil that lasted until 1934 and at times involved the United States Marines. Most of the peasants in the country were conscripted into the armies, with the result that small farms were abandoned and the coffee crops of the large *fincas* went unpicked. The Segovias suffered especially from its own infamous rebel leader, Sandino, who turned against all Segovians who did not come to his aid. He killed hundreds of people and destroyed dozens of farms and small villages. The frontier coffee lands were almost totally evacuated as the settlers fled to Ocotal, Jinotega, Matagalpa, and even to Managua. In a few years' time thousands of coffee trees and extensive pasture lands were swallowed up by tropical forest.

Once stability had been returned to Nicaragua under the regime of Anastasio Somoza (1933-1956), people began filtering back to the frontier area. The lack of a program of road construction, together with World War II, hampered new settlement, however, and only in the late 1940's did a major modern pioneer push get under way. The stimulus again was rising coffee prices, but drought and shortage of land in the heavily populated valleys of Estelí and Sebaco also helped encourage thousands of new settlers to move into the Cordillera de Darién east of Matiguás, the Cordillera Isabella northeast of Jinotega, and into the Mt. Kilambé area (fig. 7). New settlements are as yet only beginning to form, but previous outposts such as Quilalí, Güigüilí (pl. 29, b), Yalí, and Matiguás are now boom towns where, during the harvest seasons, long mule trains loaded with sacks of coffee meet convoys of supply trucks. Since about 1950 the settlement frontier has been pushed eastward more persistently than at any other time during the past 400 years.

The eastern limits of the permanently settled part of northwestern Nicaragua, then, have changed little since the Spanish conquest. Between 1603 and 1752, the frontier actually retreated, and only in the last 70 years, and particularly in the

last 10, has it advanced beyond that initially established by the Spanish and by the Matagalpa Indians before them. The eastern limit of pines corresponds fairly closely with the eastern limit of relatively dense settlement up to the present century. Pine forest is found today only where human activities have brought about a fairly continuous disturbance of the vegetation. It is possible that the eastern limits of upland pines have fluctuated with the frontier. The pine trunks, stumps, and roots in the tall tropical forest of the Río Cua and Yalí areas prove that former pine lands have been invaded and the pines replaced by broadleaf species on at least a few sites. Such areas may have been abandoned by settlers and occupied by tropical forest during the recent revolutionary period or possibly earlier.

CHAPTER VI

THE SOUTHERN LIMIT OF UPLAND PINES

THE FAILURE of the genus *Pinus* to extend its range south of Nicaragua has generally been attributed to the marine breaks between Panama and Nicaragua and in southern Nicaragua (the San Juan Depression); the former apparently existed until the Late Cretaceous and the latter from the late Eocene to the late Miocene, both acting as barriers to the spread of South American plants northward and North American plants southward. Both marine breaks, however, were bridged by many plants, largely by means of temporary land connections and by permanent connection since the early Pliocene (Schuchert, 1935: pls. 1-16).

The barrier to the further southward spread of the southernmost North American conifers seems to be largely climatic, based on the absence of high mountains with low temperatures. Between central Honduras and northern Costa Rica there is a distance of approximately 300 miles with no elevations above the 6,560-foot Mt. Saslaya in the Cordillera Isabella in Nicaragua. The frost line in Central America being between 6,000 and 7,000 feet, a large area for the most part below the frost line could well retard further migration of many northern cold-climate species,¹ including most but not all pines. Several North American conifers have their southern limit in the high mountains (up to 9,300 feet elevation) around Lake Yojoa in west-central Honduras; this is apparently the limit of *Abies guatemalensis*, *Cupressus lindleyi*, *Taxus globosa*, *Pinus ayachuite*, and *Pinus montezumae* (see Allen, 1955). Certain pines have been able to migrate farther south than other conifers partly because of their adaptation to the high temperatures of low elevations.

If edaphic conditions and natural fires alone were sufficient to open the way for the migration of pines into tropical and subtropical habitats of Central America, then there seems to have been enough time since the last sea barrier was closed during the Pliocene for pines to spread into southern Nicaragua, Costa Rica, and even farther south. On the other hand, if clearing of broadleaf forest by man and man-made fires are responsible for the extensive spread of pines into Nicaragua from the high mountains of northern Central America, then the period that man has been on the scene, possibly 30,000 or 40,000 years, might be short enough to explain at least partly why pines migrated no farther south than they have.

The actual southern termination of upland pines in central Nicaragua can be attributed to a number of factors, none of which, however, seem adequate to form a permanent barrier to expansion. Parent materials and soils are very important. The parent materials in the southern mountains of Nicaragua are mainly basalts, with a minimum of the acidic rocks that form the soils occupied by most of the Nicaraguan pines.² The larger areas of acidic parent materials in the southern highlands, which would be most receptive to invasion by pine and could there-

¹ The absence of high mountains in Nicaragua and southern Honduras seems also to have been a barrier to the northward spread of tropical American mountain plants, many of which have their northern limit in the Costa Rican highlands (Lauer, 1959:344).

² In Mexico and northern Central America, pines generally occur on parent materials (granite, schist, and rhyolite) similar to those in the pine uplands of Nicaragua. Pines also grow on sandstone, serpentine, and possibly on basalt in the Sierra Occidental of Mexico. *P. caribaea* occurs on limestone in some areas, especially on the Caribbean islands.

after serve as centers for further dispersal, as do the granitic rocks of Nueva Segovia, seem to be mainly at elevations lower than the observed range of *P. oocarpa*.

Climate is a factor. The valley of the Río Grande de Matagalpa probably forms an altitudinal or temperature obstacle to *P. oocarpa*. South of the pine uplands this valley is 10 to 15 miles wide, with an elevation of 1,000 to 1,700 feet; temperatures are probably too high for *P. oocarpa* and *P. pseudostrobus*, while the tropical *P. caribaea* is not found anywhere in the southern region of the upland pines. A leap over the valley to the mountains of Chontales by *P. oocarpa*, whose seeds can be carried by the wind, might be possible, however, if there were suitable soils on the other side.

New invasions by pine, even when competing species are suppressed and climate and soils are suitable, have been further prevented in recent times, or at least hindered, by excessive burning by cattlemen, as well as by heavy grazing and the wide distribution of tall introduced grasses. These are all hazards to the survival of young pine seedlings.

Climate and parent materials do not establish a permanent southern limit for pine in Central America, but together they may have been able at least temporarily to stop the southward march of the upland pines. This barrier is strengthened by present human activities, which make it very difficult for pines to advance farther south, even on a small scale, by natural seeding. It is interesting to note, however, that pines have been planted successfully on the volcanic plateau of Masaya in southern Nicaragua, in Costa Rica, and in various parts of South America.

The southernmost stands of pines in the upland pine area of Nicaragua are widely scattered, but form two southward-pointed prongs separated by the low plains of Sebaco (elev 1,700 ft); one ends west of Sebaco and the other southeast of Matagalpa. Plate 27, b shows two solitary pines overlooking the valley of the Río Grande de Matagalpa. These trees are surrounded by grasslands on which there are no young pine trees or seedlings, apparently because of the severity of recurrent fires. I saw no young pine trees anywhere along the margins of the southern stands, and the local people say that these stands have existed with little areal change for as long as they can remember. The pine forests east and southeast of Matagalpa descend to about 2,500 feet elevation on moderate slopes with thin soils derived mainly from andesitic parent materials. On Cerro Padre, a steep pinnacle rock south of Matagalpa and a few miles northeast of the village of San Dionisio, there is a patch of mature pines that constitutes the southernmost stand of pines known in the highland area of Nicaragua ($12^{\circ}45' \text{ N.}$).

The southernmost stands of *P. oocarpa* do not occur in the pine uplands, however, but slightly farther south, some 30 miles west of Cerro Padre, on the upper slopes of the adjacent volcanoes San Cristóbal (or El Viejo) (elev 5,545 ft) and Casita (elev 5,085 ft) (fig. 4); Casita is the farther south ($12^{\circ}44' \text{ N.}$, $86^{\circ}59' \text{ W.}$). These pines were observed by B. W. Taylor (personal letter, 1958), who commented:

I have climbed Volcán Casita which is immediately south of San Cristóbal to see the pines. These stands are very small but are somewhat bigger than those on San Cristóbal. They are

formed on the typical soils of the volcano, i.e., shallow but fertile silty loam. I suspect that they entered since the last eruption and that the successions were never permitted to mature but were burnt regularly for grazing thus permitting the pines to persist. . . . The trees concerned are young, mostly less than 60 feet [in height] and 10 inches in diameter, and the stands only cover a few hectares each; elevation is from 2,000 to 4,000 feet but could be higher on San Cristóbal.

Pines do not grow on any of the other high volcanoes of western Nicaragua, although they do grow on volcanoes in Guatemala (e.g., Volcán Fuego). On San Cristóbal and Casita the pines may have been planted; and if not, then they indicate how pine seeds can be carried long distances by the wind or by biotic carriers to seed new areas where conditions are suitable for pines. The prevailing winds are from the northeast and therefore from the pine uplands. In general, however, wind direction probably has had little bearing on the distribution of pines in the Nicaraguan highlands.

From time to time there have been rumors that there are pines in the Departments of Boaco and Chontales in southern Nicaragua, but such rumors have never been verified. I searched without success for pines in the mountains of Boaco and Chontales, and B. W. Taylor reports (personal communication, 1958) that he could find none during several weeks of plant collecting in the same Departments. A plant called pino (unidentified) is common in the hills on the southeast side of Lake Nicaragua, and "pino" means pine in Spanish, which may explain the rumors of pines in southern Nicaragua. The Nicaraguans commonly use the Nahuatl Indian term "ocote" for the true pine of the Segovias.

The southernmost pines in the Western Hemisphere, which occur not in the Nicaraguan highlands but on lowland savannas in eastern Nicaragua, where stands of *P. caribaea* extend to 12°10' N. near Bluefields, have a distribution and southern termination closely related to the presence of quartz gravel sediments in eastern Nicaragua; these sediments would probably support a low hardwood forest, however, if it were not for annual burning (Taylor, 1959a:80).

CHAPTER VII

ECONOMIC ASPECTS: DESTRUCTION OF THE UPLAND PINE FORESTS

THE AREA OF the upland pine forests of Nicaragua is being reduced as a result of logging and extraction of resin, and because too-frequent fires keep pine reproduction at a minimum. Government officials tend to blame burning alone, and fires certainly are destructive, but even with regular burning the pine forests on rough terrain are capable of perpetuating themselves at least as open stands. Logging, however, can shift this balance decisively; and there will be an actual decrease in numbers of pines if any trees are felled, or otherwise killed. Such a decrease is especially likely where the logging is noncommercial, involving a gradual reduction of a pine forest as the local inhabitants not only log the better trees for timber, but also cut the smaller trees for fuel, and fell patches of pine to increase the area of pasture land.

A certain amount of clearing of pines still takes place for the making of milpas. Although the presence of pines usually indicates shallow infertile soils—a fact well known to Segovian farmers—on gentle slopes in the high mountains, pines at times grow on deep soils, and such sites may be cleared, burned, and cropped by the same methods employed in broadleaf forest. Pines are more commonly destroyed to increase pasture than for the establishment of milpas, although less frequently now that the value of pine timber is being recognized. In some of the pine areas, saws and axes are still rare, and it is possible to see trees killed by ringing or girdling (pl. 30, *a*). The older residents of Nueva Segovia and Estelí agree that much pine forest has been replaced by pasture within their memory, and they point out slopes that once had pine forest where now only a few pines appear on the ridge tops (pl. 30, *b*).

Organized commercial logging, on the other hand, can actually result in the improved growth of a pine stand by thinning through selective cutting of only large trees, by disturbing soil conditions so as to stimulate regeneration, and by building roads and logging trails, which serve for a long time afterward as fire breaks. Vigorous new pine growth occurs, for example, in the area of active logging around Dipilto in Nueva Segovia. Commercial logging of pine in the uplands has been important only during the last ten or twenty years. Today a half dozen small mills in the vicinities of Somoto, Estelí, Jinotega, and Ocotal supply lumber to the larger highland towns and to Managua, and in 1957, one mill managed by a North American firm, the Nicaragua Lumber Products Company in Dipilto, was even exporting small amounts of pine lumber to the United States (pl. 31, *a*). There is no information on the amount of pine logging taking place in the pine uplands, but probably the total cut has never exceeded 3 or 4 million board feet in one year.¹

¹ Pine lumber has been shipped in quantity from the Miskito Coast of eastern Nicaragua since the end of the nineteenth century, and production has reached as much as 40 million board feet annually in recent years. The extensive logging, mainly by the Nicaragua Longleaf Pine Lumber Company of Puerto Cabezas, has reduced the Miskito Coast pines to only a few small stands of still merchantable timber. The Miskito Coast pine industry has been described by Parsons (1955b:54-58). Recently the Nicaraguan government has been considering a forestry program for the area that would involve fire control.

At times in the past, mining has caused large-scale reduction of pine forests. Mr. John Willey of Matagalpa commented (personal communication, 1957), for example, that soon after the turn of the century he supervised the cutting of a large stand of pines just east of San Ramón in the Department of Matagalpa in order to supply fuel for the La Reina gold mine. He had 100 men logging for him for over three years.

During the colonial period some pine may have been logged for use in the Segovian mines and towns, but the main value of pine was its pitch, which was used in ship construction. During the sixteenth century, Nicaragua, the first available pitch source north of Peru, was the leading shipbuilding country on the Pacific coast of the New World (Borah, 1954:7). Vázquez de Espinosa (1942:245), writing in 1628-1629, commented that during the seventeenth century pitch from Nueva Segovia was not only used in the shipyards of Realejo, the main Pacific port of Nicaragua at the time, but was the leading export of the country. Most of it went to Peru. Of the use and value of this pitch, Vázquez de Espinosa (1942:251) wrote:

... the most important export is pitch, because it is so essential for ships and for the Peruvian vineyards. In this the dealers make extravagant profits, for a quintal of pitch brought down (as has been described) from Nueva Segovia is usually priced at the port of Realejo at 20 reals, and it sells at Callao, the port of Lima, for at least 12 pesos and upward, and a quintal usually gets to be worth 30 reals of 8 and more. Of course it is true that there is much expense for freight and duties; nevertheless with the low original cost and the extensive consumption of it in Peru, the trade is very profitable, for it has made many men rich.

Both the Indian and Nicaraguan inhabitants of the pine uplands have always valued pine resin and have tapped it for medicinal and other uses. Resin-soaked splinters of pine are still the main source of illumination in the more remote parts of Nueva Segovia, just as they probably were when the first Spaniards arrived. I myself spent a night on the Llanos de Totecacinte surrounded by blazing pine torches to ward off swarms of stinging black flies.

The Spanish also distilled pine resin to make turpentine (*trementina*), and the ruins of their crude distilleries can still be found near the town of San Fernando in Nueva Segovia. Although Honduras with some 13 distilleries in 1953^{*} has remained an important producer of turpentine, the industry is now of little importance in Nicaragua except in the town of San Rafael del Norte in Jinotega, from which the turpentine is trucked to Managua. The actual wounds inflicted on the pine trees by the resin gatherers are often fatal to the trees; even if not directly fatal, the wound still renders a tree more susceptible to attacking insects and fires (pl. 31, b). In Honduras, where there is a national program to combat harmful methods of extraction, it is estimated that 300,000 pine trees die annually from resin slashes (Sanderman, 1953:6), and undoubtedly the pine forests of Nicaragua have been and still are being reduced in the same manner. In both countries *P. oocarpa* is the main species tapped for resin, although *P. caribaea* and *P. pseudostrobus* also have a fairly high resin content.

If properly handled, the upland pine forests of Nicaragua would be a valuable national resource, although less so than the more extensive pine savannas on the

^{*} For a description of the extraction of pine resin and the turpentine industry in Honduras, see H. W. Sanderman (1953).

Miskito Coast of eastern Nicaragua, where there is little problem of access and transport. Much good pine timber remains in the highlands, but most of it is in the more inaccessible parts of Nueva Segovia such as the region northwest of Macuelizo, the Montes de Jalapa, and the Río Poteca area. The building of a series of penetration and feeder roads would make profitable logging possible in these areas. The real need, however, is for a forestry program with a goal of production by sustained yield throughout the pine upland. Considering the present density of stands, which is not exceptional, B. W. Taylor (1959b:210) estimates an average of 4,000 to 6,000 board feet of commercial timber per acre. This estimate means that, with more than 600 square miles of pine forest in the pine uplands,³ there would be a total reserve of some 2 billion board feet from which an estimated annual yield of at least 100,000,000 board feet could be obtained.

Forestry programs have been attempted in pine forests elsewhere in Central America, but with only limited success because of the difficulty of enforcing fire prevention and the inconsistent support of often short-sighted officials. The Nicaraguan government has advocated planting pines, and at present requires by law that logging concessions replant or pay a fee, but replanting is unnecessary, since natural regeneration is usually abundant; the real problem is the survival of the young pine seedlings. Complete fire protection for a period of 5 to 10 years will usually allow young trees to reach sufficient size to become relatively fire resistant. Proper management with fire regulations and controlled burning is a major undertaking, however, and can be successful only when accompanied by an effective program aimed at educating the people to the value of the pine forests and the destructive effects of fire. Such a change in local ways and attitudes takes time.

Management policy must give consideration to the fact that while elimination of burning may bring about soil protection and water conservation, it will produce neither healthy, well-stocked pine stands nor suitable pasture. Not to be overlooked is the primary relation between fire and pines and between fire and grasslands in the tropics, whereby fire restricts competing broadleaf species and helps improve pasture for ranchers. Certainly a conflict of interest exists between stockmen and lumbermen; however, in view of the low nutrient values of the pasture grasses on the poor pine-forest soils, it would seem advisable to concentrate grazing activities on the more suitable Pacific lowland grazing lands of Nicaragua and maintain the Segovian uplands as a pine-forest reserve. In such a reserve, however, the danger must be avoided of eliminating all burning for such a long period of time that either pine regeneration is discouraged or such a fire hazard develops that an accidental fire could destroy large areas of mature pine forest.

³ Compare this estimate with the estimated 2,300 square miles (1.5 million acres) of pine savanna on the Miskito Coast of eastern Nicaragua (Food and Agricultural Organization, 1950:48); with the estimated 6,000 square miles (1,546,600 hectares) of pine forest in Honduras (Sanderman, 1953:4); and with the estimated 9,000 square miles (14,500 square kilometers) of pine forest in Guatemala (Schwerdtfeger, 1953:3).

CHAPTER VIII

CONCLUSIONS

THE THESIS PRESENTED HERE is that the upland pine forests of Nicaragua are a deflected climax, a man-made formation resulting from clearing of broadleaf forest and repeated burning, and it is unlikely that extensive and pure stands of pines existed before the appearance of man.

The evidence contained in this paper, which is supported by the literature on many of the pine forests elsewhere in the tropics, suggests that, in general, the degree of disturbance of site and frequency of fire necessary to establish and sustain a tropical or subtropical stand of shade-intolerant pine is greatest in areas with rich and deep soils, basic parent materials, and with high average temperatures and high precipitation; and is less in areas with poor soils, acidic parent materials, low rainfall, and especially with increasingly lower temperatures. Because man is the main disturbing element in the environment, the presence of pines on a given site can in part be related to the extent and nature of man's activities on the site.

There is little doubt that the present upland pines of Nicaragua germinated and matured while being subjected to periodic man-made fires. The question remains whether or not similar pine forests could have existed before the coming of man. Restrictive edaphic conditions may well have originally provided habitats for pines which served as centers of dispersal to receptive sites provided by such natural events as blowdowns, landslides, lightning fires, and volcanic eruptions. Natural habitats were probably only local, however, and natural disturbances do not seem to occur frequently enough on any given site in highland Nicaragua to suppress mixed broadleaf forest continuously.

Of significance is the occurrence of the upland pines only in areas of long-continued, permanent settlement. There are no pines in the central mountains of Nicaragua east of the settlement frontier, although parent materials and climate often appear to be suitable. On the other hand, neither are there pines in the settled part of the southern uplands of Nicaragua, where the history of clearing and burning is similar to that of the pine uplands, but where parent materials generally are better suited to the growth of broadleaf forest than pine.

The conclusions for the upland pine forests of Nicaragua seem to be relevant to the problem of the occurrence and distribution of pines elsewhere in the tropics and subtropics. Many, if not most, of the pine forests of Middle America do occur on acidic parent materials and thin impoverished soils and are subjected to at least occasional fires. There is a danger, however, in attempting to apply ecological interpretations in one region to others, especially with reference to pines. Not only may climatic, edaphic, biotic, and human factors differ in other areas, but pine species differ widely in their requirements and tolerances. Individual studies of the various tropical pine species in different environments are needed in order to understand more fully the distribution of the genus *Pinus* in the tropical world and man's relation to that distribution.

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