OUTLINE FOR A CLASSIFICATION OF ANIMAL HABITATS IN HONDURAS

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INTRODUCTION

THIS SYNOPSIS of Honduranian land types has been drawn from four years' field notes, gathered with the view of determining and attempting to define herpetological habitats in the region. Inevitably many of the recognizably different complexes of topography, soil, and vegetation have proved to hold no discernible meaning for reptiles and amphibians, but that the same situations may not be clear-cut habitats for birds or for grasshoppers does not follow. Thus the notes are offered as a framework, not available elsewhere in the literature, on which the specialist may directly begin to build the detailed system required for his particular group of animals. It has been my experience that effective field work in strange and varied territory must await a broad understanding of, and "feel" for, the region which comes only with months of observation. If the present outline helps the visiting naturalist in his preliminary reconnaissance and shortens his orientation period it will have been worth making.

Along with my own field observations I have accumulated from other sources information that has bearing on Honduras as a biotic area; these data are given in the prefatory section below.

ACKNOWLEDGMENTS

Owing to the long duration of the field work on which this paper is based the number of people to whom I have become indebted is large—too large, in fact, to permit mention of them all. As an employee of the Escuela Agrícola Panamericana I had occasion to ask cooperation of a long list of officials of the United Fruit Company, and to all these who furnished help and information I am exceedingly grateful.

Among others who implemented my study of the region, chiefly through stimulating companionship in the field, I must name first Prof. T. H. Hubbell, Museum of Zoology, University of Michigan, who, besides accompanying me on collecting trips that traversed much of Honduras, suggested the organizing and condensing of my field notes to compose the present paper and is thus largely responsible for its existence.

During the early stages of my residence in Honduras I enjoyed the company of Messrs. Hugh Popenoe and George and Peter Hogaboom of El Zamorano and of my old friend Mr. Leonard Giovannoli of Louisville, Kentucky.

The unflagging enthusiasm of my friend Mr. Alphonse Chable of the Research Department of the United Fruit Company, a keen naturalist and unexcelled outdoorsman, contributed beyond measure to the significance of our shared field experience. With Mr. J. C. Dickinson, Department of Biology, University of Florida, I passed pleasantly and profitably a majority of the 60 or more days he spent collecting birds in Honduras.

Nearly all my observations in the tropics have been made in the company of my wife, Marjorie Harris Carr, who by rights should be named as co-author of this paper. Which conclusions are hers and which mine I can in few cases say with certainty.

Mr. Paul Shank, Forester, Escuela Agrícola Panamericana, has placed at my complete disposal his unrivaled store of knowledge of the forests of tropical America, and I count as an extraordinary privilege the many days spent with him in the woods.

For her contribution to the series of photographic illustrations I am grateful to Mrs. Henry Hogaboom, Escuela Agrícola Panamericana. Mr. Sidney Glassman, Department of Plant Sciences, University of Oklahoma, furnished me with considerable information concerning the vegetation of the Tegucigalpa area; and for additional plant identifications I have made repeated demands on the patience of Dr. Paul Standley, Chicago Natural History Museum, and of Dr. Louis O. Williams and Sr. Antonio Molina, Escuela Agrícola Panamericana.

For the remarkable hospitality that made wholly enjoyable my three visits into the little-known Jamastrán Valley and Guayambre River area I am indebted to Mr.

and Mrs. Ocie Sager of Las Lomas, El Paraíso. Señor don Miguel Brooks of Tegucigalpa made possible three collecting trips to the south coast and islands of the Gulf of Fonseca. Señor don Mario Valenzuela of Tegucigalpa generously furnished transportation to the site of his timber operations in the remote Guampú River drainage of the Mosquitia. Through the kindness of Mr. H. K. Matheson, New York and Rosario Mining Company, I was enabled to visit the San Juancito cloud forest under the most favorable of conditions, and for their hospitality and assistance in various ways I am grateful to Messrs. H. V. Hughes and Juan Barreto, Agua Fría Mining Company, El Paraíso.

As regards weather data, besides those furnished by the Research Department of the United Fruit Company, I am grateful for records received from Mr. A. J. Chute, Standard Fruit Company, La Ceiba, and from Mr. Matheson of Rosario, whose help in another respect was acknowledged above. Assistance in taking readings for the 24-hour humidity graphs was given by Mr. and Mrs. Allen Arnold, Escuela Agrícola Panamericana, and by Señores Rodolfo Zamora, Eduardo Jiménez, and Ricardo Cortés, students of the same school.

Help in the above-mentioned project was also contributed by Mr. Charles M. Bogert, Chairman, Department of Amphibians and Reptiles, the American Museum of Natural History, of whose name I reserve mention until last to place special emphasis upon the debt I owe him for his critical appraisal of the problem and the manuscript, for his intelligent and good-natured company in the field, and for invaluable advice and assistance in other, unnumbered ways.

GENERAL DESCRIPTION OF THE REGION

PHYSIOGRAPHY

The three obvious topographic divisions of Honduras are (1) the Caribbean lowlands, (2) the Pacific lowlands, and (3) an interior *serranía* region.

The Caribbean coastal plain is of irregular breadth, its deepest inland extent occurring in the Ulúa-Chamelecón Valley, which includes the wide Sula Plain; in the valley of the Aguán River; and especially in the Mosquitia, where the confluent deltas of the Patuca and Coco rivers have built an alluvial plain that includes more territory than the aggregate of all other Honduranian lowlands and that rises gradually towards the southwest to the higher llanos of Olancho.

From the Ulúa Valley a range of mountains extends obliquely, just behind the coast, to a point opposite the town of Trujillo in Colón and in places constricts the coastal plain to almost nothing. Between the Ulúa-Chamelecón Valley and that of the Motagua River to the west there rise abruptly the mountains of the Espíritu Santo group, the southern extremity of which is lost in the confused *serranía* terrain spreading eastward throughout the interior.

These interior highlands comprise a bewildering system of short, rugged sierras, mostly with east-west trend but often interconnected by cross ranges. The mountains are interspersed with semi-arid plains that lie at elevations between 455 and 1370 meters (1500 and 4500 feet) and are regarded as being in the main of structural origin. The most conspicuous of these valleys is the so-called Honduras Depression, supposedly a Graben produced by north-south faulting. This long trough, continuous with the Comayagua Valley, extends some 40 miles across the country, connecting the Caribbean and Pacific lowlands and interrupting the general structural trend.

Bengtson (1926) recognized two old peneplains in the interior, one lying between 1005 and 1370 meters (3300 and 4500 feet) and the other between 760 and 915 meters (2500 and 3000 feet). A regular accordance of summits in the neighborhood of 1830 meters (6000 feet) is also conspicuous.

The upland streams generally have steep gradients and often flow in canyons. They are subject to drastic annual fluctuation, and many of them that are raging torrents in June and October disappear completely or die out on the dry floors of the high valleys in April. Many of the stream valleys are deeply incised, and the remnants of two former terrace systems are discernible. The lower of these occurs between 90 and 305

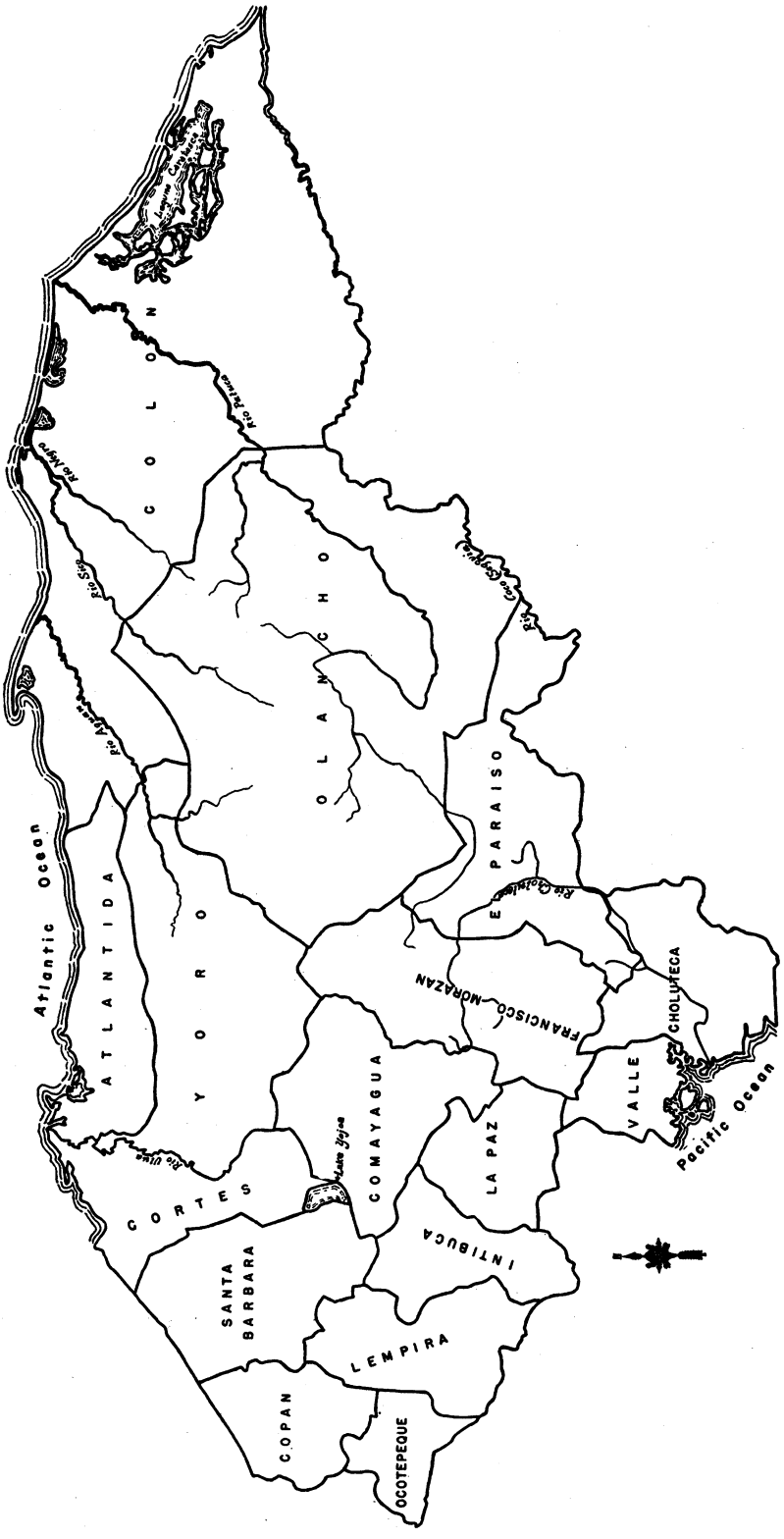


FIG. 1. Map of Honduras, showing departments, principal rivers, and lakes.

meters (300 and 1000 feet), the upper between 610 and 730 meters (2000 and 2400 feet).

The interior highlands give the general impression of a greatly dissected plateau. The greatest relief is found in the Southern Cordillera, which traverses the south-central section of the country from the frontier with El Salvador and Guatemala into Nicaragua and attains its highest elevations in the ranges of the departments of Ocotepeque and Gracias (2440 meters or possibly more) and in the San Juancito Mountains of Morazan (2285 meters). The relatively isolated massif, Cerro de Santa Barbara, rises to 2650 meters (8700 feet) at the west shore of Lake Yojoa (see fig. 1).

The Pacific lowlands form a narrow shelf, shared with Nicaragua and El Salvador. This borders the Gulf of Fonseca, which appears to represent in part the drowned mouths of the Choluteca, Nacaome, and Goascoran rivers. The narrow plain is modified by encroachment of the Colinas de Juacaran, a local volcanic chain that begins in El Salvador in the departments of Sonsonate, La Libertad, and San Salvador and dies out in the Gulf of Fonseca. This is part of a more extensive line of separate volcanic peaks that march down the Pacific lowlands from Guatemala to Costa Rica.

The mountains of Honduras thus fall into three general groups, as follows:

1. The Northern Cordillera, comprising a series of rather disjunct ranges of extensively eroded mountains of ancient crystalline and sedimentary rocks running roughly parallel with the North Coast.

2. The Southern Cordillera, a more southerly, interior system of dissected and faulted mountains overlain in the west by Pliocene ash and lava and with much older metamorphosed sediments exposed in the east.

3. The Pacific Colinas, a short Honduranian segment of a long chain of separate Quaternary and recent volcanoes rising from the coastal plain and from coastal waters.

GEOLOGY

The scattered information on the geologic structure of Honduras has been collated by Schuchert (1935) to extend the basic studies of Sapper (1899, 1905a, 1905b) and has been further summarized by Olson and McGrew (1941).

Honduras is a part of the old Antillean geanticline, forming, together with northern Nicaragua, the oldest part of the Central American nucleus. The southern third of the country, like most of neighboring El Salvador, is overlain by several thousand feet of Pliocene volcanic rocks, mainly tuffs and acid lavas, which dip gently southward to pass beneath the Pacific, and towards the north extend up to a front that in a general way coincides with the crests of the southern mountains. Still farther north they are replaced by older crystalline and sedimentary rocks but recur with some frequency as isolated patches, leading to the assumption that they may have had much more extensive former distribution in central Honduras.

On the surface of the widespread Pliocene volcanics, which appear to have been, at least in part, the product of fissure eruptions, is built the much more recent chain of volcanoes that barely enters the Pacific coastal plain in passing from Guatemala through El Salvador down to Nicaragua. The Pliocene lavas extend to the frontier with El Salvador and at least as far as the department of Intibucá in the west and northwest, while to the east they are replaced by old metamorphosed sediments complexly involved with intrusions of granodiorite, which extend eastward into Nicaragua and at least as far north as central Olancho. These ancient quartzites and schists underlie Cretaceous deposits to the east, and Barreto (MS) believes that they may be contemporaneous with the continental Tegucigalpa formation of upper Triassic age.

Elsewhere in the north, and especially towards the northwest, the most widespread rocks are Cretaceous sediments. Along the precipitous eastern shore of Lake Yojoa hundreds of feet of massive, bluish limestone with distorted invertebrate fossils are exposed, and this and other Cretaceous limestones, with associated shales and sandstones, occur from Guatemala to the Río Coco.

In the ranges parallel to the Caribbean coast in the northern third of the country there occur schists, slates, and phyllites that are the oldest exposures in Honduras, being

generally regarded as of pre-Permian age.

Eocene sediments have been found along the lower Río Coco, and Miocene strata occur in the northwest, where marine Pliocene has also been identified. Fresh-water Pliocene deposits were worked by Olson and McGrew (*loc. cit.*) in the department of Gracias and are also known from the Río Coco Valley. Pleistocene fresh-water sediments appear to be widely, though locally, distributed, and marine Pleistocene is said to occur in the Mosquitia.

The geological events that appear to have been of greatest influence in building the present topography of Honduras are the following:

Pre-Pliocene orogeny—three or four cycles
Pliocene vulcanism
Faulting at various periods, producing Graben valleys
Miocene uplift, initiating the erosion cycle mainly responsible for the present mountains of the *serranías*
Minor subsequent uplifts, leaving at least two recognizable terrace systems

SOIL

Although the soils of the "Banana Coast" of Honduras are relatively well known, those of the interior remain unsurveyed. Moreover, even if extensive data were available, generalization would be difficult because of extreme local variation and of the confusing frequency of azonal and interzonal types. It is well known that the soil of terrain with strong relief tends more to depart from the general scheme imposed by climate than that of a level area; a tropical slope shows even greater azonality; and a tropical slope affected by a strong wet-dry seasonal cycle conforms even less to the zonal norm.

The transported soils of the Caribbean coastal plain range in character from the old leached delta deposits of the Mosquitia to the extremely fertile recent alluvium of the lower river valleys to the westward, the latter including the very valuable silt loams famous in the banana industry.

The residual soils of the uplands include some moderately fertile clay or sandy loams, derived mostly from the crystalline and sedimentary rocks of the lower Caribbean slopes and in the Olancho Plain. For the most part, however, the pine woods of the vast acid lava areas have developed on skeletal (or senile), so-called "*talpetates*," although they vary from nearly unmodified ash (*tierra blanca*, etc.) or crevice debris in bare rock to lateritic sandy or gravelly clays with only the most meager layer of organic litter, which often may be completely lost to the fires and winds of the dry season. The best mountain soils are found on the upper ridges and plateaus, originally covered by mesic vegetation, where the higher and more constant moisture ration (but probably less heavy rainfall) has favored development of brown to reddish loams of some depth and fertility.

The valley soils range from moderately fertile friable loams to sterile deposits of clay mixed with rock debris, similar to that of the surrounding mountain sides, and more rarely highly permeable gravel with standard desert vegetation of cactus and agave. One of the most characteristic and widespread valley soil types is a heavy, granular loam which, even though the clay content may be as little as 5 or 10 per cent, is excessively plastic and sticky when wet. If underlain by pervious layers these soils support a fair growth of xeric or deciduous forest, but where a clay pan occurs the vegetation tends towards short-grass savanna, often with hydrophilous thorn.

The fact that the semi-arid sections of Honduras are mostly regions with plastic soils, sticky when wet and hard baked in *verano*, appears to be of considerable ecological significance. The rigorous dry season favors a strongly secretive fauna. In the *serranías* a large percentage of the reptiles and amphibians, for example, spend much of their time underground, while in the dry valleys the percentage becomes a majority. A glance at the faunal roster for these areas shows numerous forms that (1) dig their own more or less permanent burrows, (2) occupy (modified or unmodified) burrows of other animals, or (3) live under stones. There is, however, an almost complete lack of animals adapted to underground locomotion.

In the upland valleys the pioneer burrowers are tarantulas, *zompopos* (leaf-cutting ants), and armadillos. All three of these are of frequent and common occurrence, and their burrows are plainly of fundamental importance for the survival of a number of

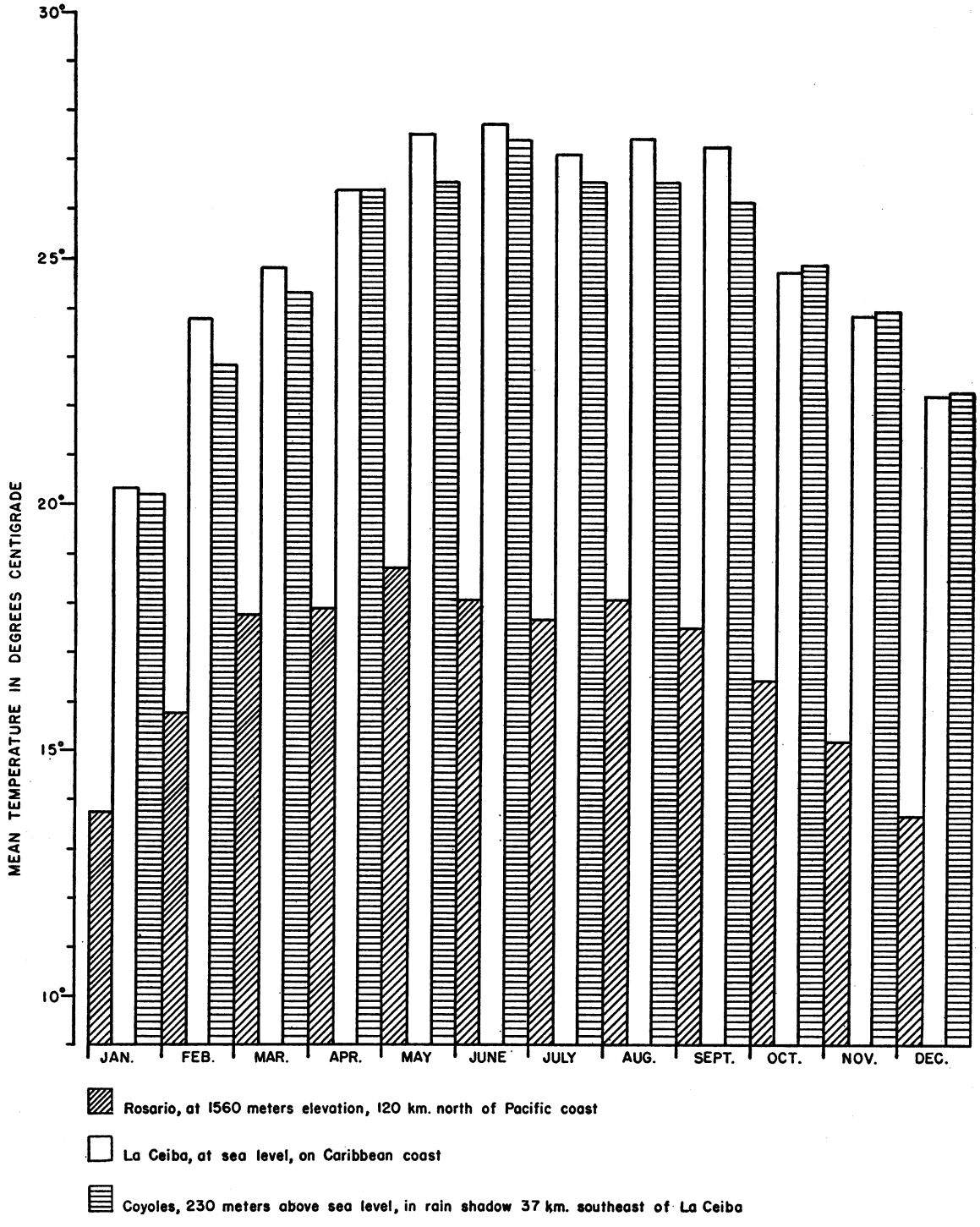


FIG. 2. Histogram comparing mean monthly temperatures, 1944–1947, for three stations in Honduras.

local animals, both vertebrate and invertebrate. As a case in point, the big toad, *Bufo marinus*, locally abundant and apparently incapable of constructing its own burrows in heavy soil, regularly enlarges the small (2-inch diameter or less) holes made by tarantulas to accommodate its much greater girth. On one occasion I flushed three of these toads from a single remodeled spider hole. The gecko, *Coleonyx mitratus*, in many areas where it is fairly abundant, would probably not be able to hold on at all if deprived of old burrows as a refuge from the drought, and a large number of other reptiles use the extensive galleries of the *zompopos* both as habitations and as incubation chambers for their eggs.

It seems probable that the predominantly plastic and seasonally indurate soils of the Honduranian uplands, through restriction of subterranean locomotion in a periodically arid region, may be largely responsible for the extraordinary paucity of individuals encountered, despite the existence of a fair number of species.

CLIMATE

Within limits imposed by a consistent absence of freezing temperatures and, except on a few of the highest peaks, of frost, the climate of Honduras embraces a fairly wide range of local varying conditions (fig. 2). Application of the Köppen system of classification shows two major divisions and several of the subdivisions of that system, and often one type of climate may replace another within a distance of a few miles. The Köppen types more or less clearly recognizable in Honduras are the following:

A. Tropical rainy climates: Af (tropical rainforest climate), Aw (tropical savanna climate), Am (monsoon climate)

BS. A number of facies of the tropical steppe or semi-arid climate, in which evaporation exceeds precipitation and in which no permanent streams originate

Honduras lies in the belt of the northeasterly trade winds, more precisely in the transition area between the two major air masses that mold the weather of the northern tropics. Thus, with the seasonal shifting of the doldrums, the area alternately receives dry, so-called tropical air and the more unstable, moisture-laden equatorial air from the southward. Although the prevailing wind is consistently from the northeast, there is a marked annual cycle of high-sun dry season (*verano*, November through April) and low-sun rainy season (*invierno*, May through October). In the interior a "little dry season," the *canícula*, or *veranillo de San Juan*, occurs with some regularity during the middle of the rainy season and may last for a period of from three to six weeks (see fig. 3).

It seems evident that this monsoon type of rainfall cycle is the most fundamental climatic factor operating in the region, and it may possibly constitute the single most effective agent in determining the biota. The combination of strong wet-dry cycle and high insolation rates with steeply sloping and broken terrain has created steppes and near deserts in areas, the total annual rainfall of which would support mesic vegetation under more propitious conditions. By far the greater part of Honduras shows the influence of the dry season, the only zones where it is inconspicuous being the relatively small areas of primeval forest in the Caribbean plain, certain lowland gallery forests, and the mist-bred cloud forests of the highest mountain summits (see fig. 3).

The dry season is least severe on the lower slopes and in the lowlands of the Caribbean littoral, where convection in the incoming marine air causes it to drop the greater part of its moisture. The rains of the interior are almost wholly confined to the six months of *invierno*, and come mostly as an erratic series of orographic thunder showers, although towards the south fairly regular daily rains may occur at the hour of maximum conflict between the northeasterly wind and the diurnal monsoon from the Pacific. Towards the end of the wet season, especially, an occasional frontal *temporal* may bring short periods of stormy and rainy weather, but for the most part the sky is clear between showers throughout the *invierno*, with only a few gray, drizzly days.

Although the Pacific coast receives the same daily monsoon that elsewhere may produce annual precipitation as high as 200 inches and rainforest growth rivaling that of the Atlantic side, the Fonseca area, perhaps owing to the absence of abruptly rising coastal

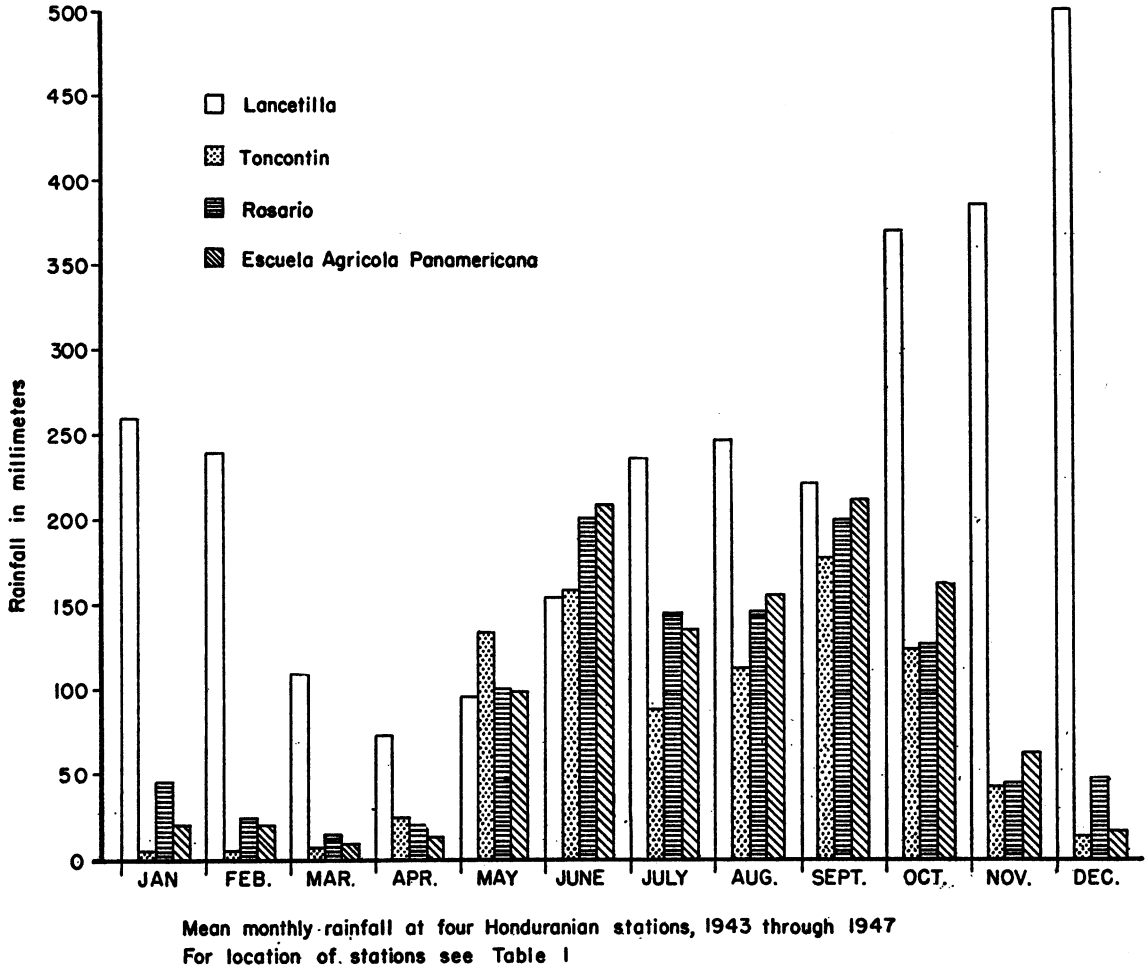


FIG. 3. Mean monthly rainfall at four Honduranian stations, 1943 through 1947. For location of stations, see table 1.

mountains, receives only about 60 inches of rain. This is considerably above the average for the interior but too seasonally distributed to support rainforest.

The monsoon-savanna-steppe series of climates make relatively uninviting habitats, lacking the stability offered by both mesic and true desert environments. The sudden onset of the torrential June rains, after six months of shadeless exposure to the strong sun and the steady, dry wind of *verano*, may remove the last vestiges of plant litter, reduce the moisture-holding capacity of the soil, and augment rather than relieve the austerity of the terrain. The rigors presented by the habitats involved are reflected in the fauna, which, though quite varied, is at the same time very meager.

ORIGIN OF THE FAUNA

Honduras and neighboring areas are part of an ancient elevation which at various times has connected North and South America and the Antillean land mass. Owing to its strategic location and relative geologic stability this area appears to have been of fundamental importance in the history of the faunas of both continents, not merely as a land bridge, but perhaps as a center of evolution as well. This fact has recently received considerable well-warranted emphasis from Simpson (1943) and others.

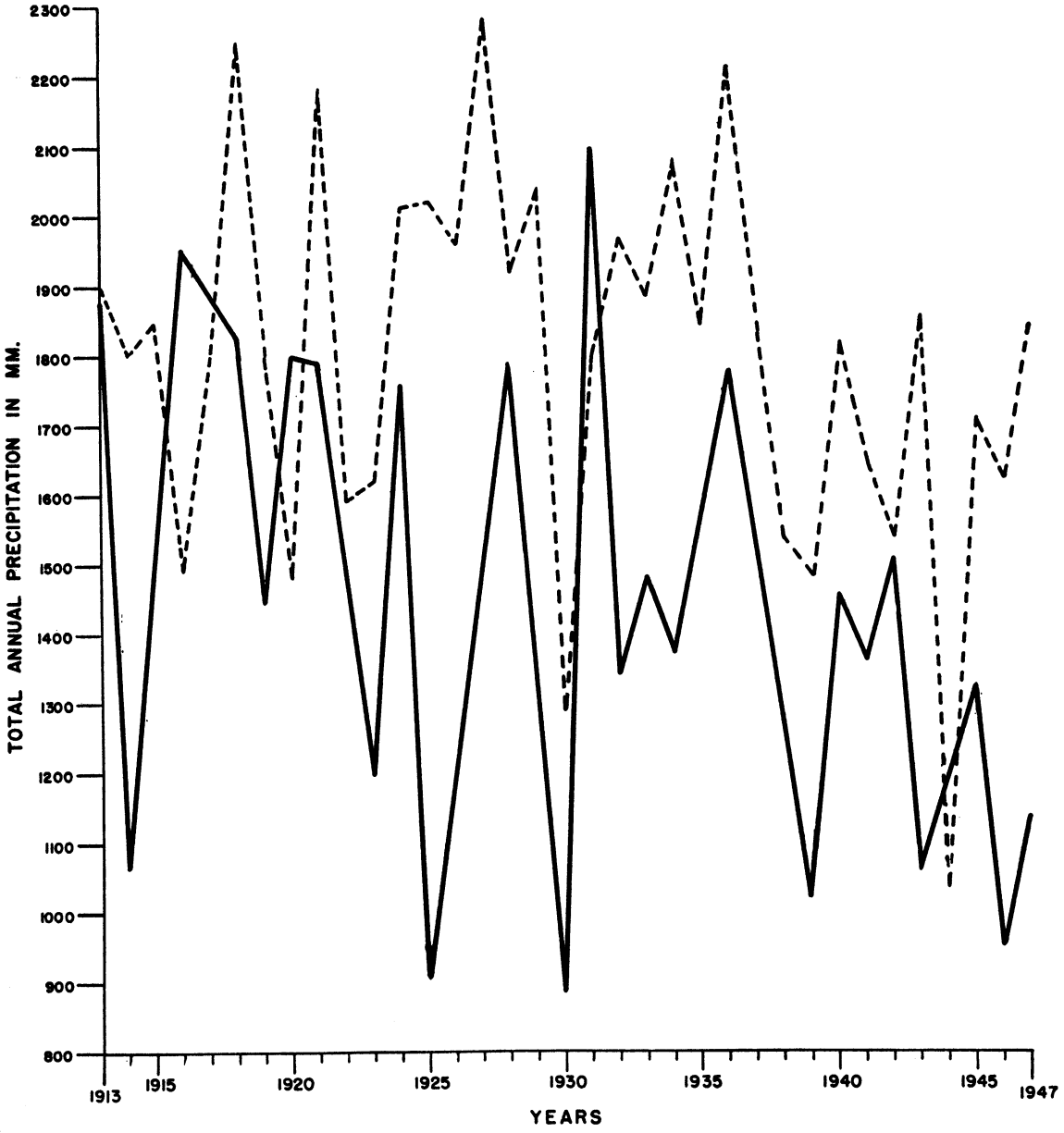


FIG. 4. Graph showing fluctuations in total annual rainfall for two stations, San Salvador, El Salvador, at 682 meters elevation (broken line), and Rosario, Honduras, 230 kilometers north-northeast of San Salvador, at 1143 meters elevation (solid line).

Setting aside pre-Cenozoic events as of little direct influence on the ecological leanings of the modern fauna of Honduras, the more significant events in the Cenozoic history of the area appear to be the following:

1. Existence of a water barrier across southern Nicaragua or Panama or both, leaving Honduras near the tip of a peninsula. Final closure of this portal during late Tertiary, perhaps in late Pliocene.

2. Existence of a varyingly extensive dryland connection with Antillea, final submergence of which occurred during the Pliocene.

3. Occurrence of a mid-Cenozoic water

TABLE 1

TOTAL RAINFALL FOR EIGHT STATIONS IN HONDURAS AND EL SALVADOR, 1946 AND 1947

Station	Department and Location	Exposure	Altitude (in Meters)	Rainfall (in Millimeters) 1946	1947
Escuela Agrícola Panamericana	Morazán; in valley of Río Yeguare, 25 km. southeast of Tegucigalpa	Mostly open towards north	790	942	1129
Toncontín	Upper Choluteca Valley, 7 km. south of Tegucigalpa, Morazán	In rain shadow of Azacualpa Mts.	939	638	862
Rosario	Morazán; 20 miles northeast of Tegucigalpa	Open towards north	1560	957	1143
Cutuco, El Salvador	San Miguel; on Gulf of Fonseca, 5 km. from frontier with Honduras	Open towards Gulf	4	1242	1980
La Union, El Salvador	San Miguel; on Gulf of Fonseca near above	Open to Gulf towards southeast	0	1086	1770
Coyoles	Yoro; 37 km. southeast of La Ceiba	In rain shadow of coastal mountains	230	872	792
La Ceiba	Atlántida; port on Caribbean coast	Open to sea	0	2216	2794
Lancetilla	Atlántida; near Tela; about 35 km. west of La Ceiba	Open towards north	40	2742	2342

barrier across Tehuantepec, which, although perhaps not so important an influence in the development of the fauna as the southern water barrier, must have operated as a strong factor in favoring endemism in the area. Schuchert (1935) believed final closure to have come during middle Pliocene, but Olson and McGrew (1941) give good evidence that it occurred earlier. It appears impossible to determine from available stratigraphic evidence whether or not nuclear Central America had a period of completely insular existence.

4. Widespread and violent vulcanism in late Tertiary.

5. Minor uplifts and submergences throughout the Cenozoic.

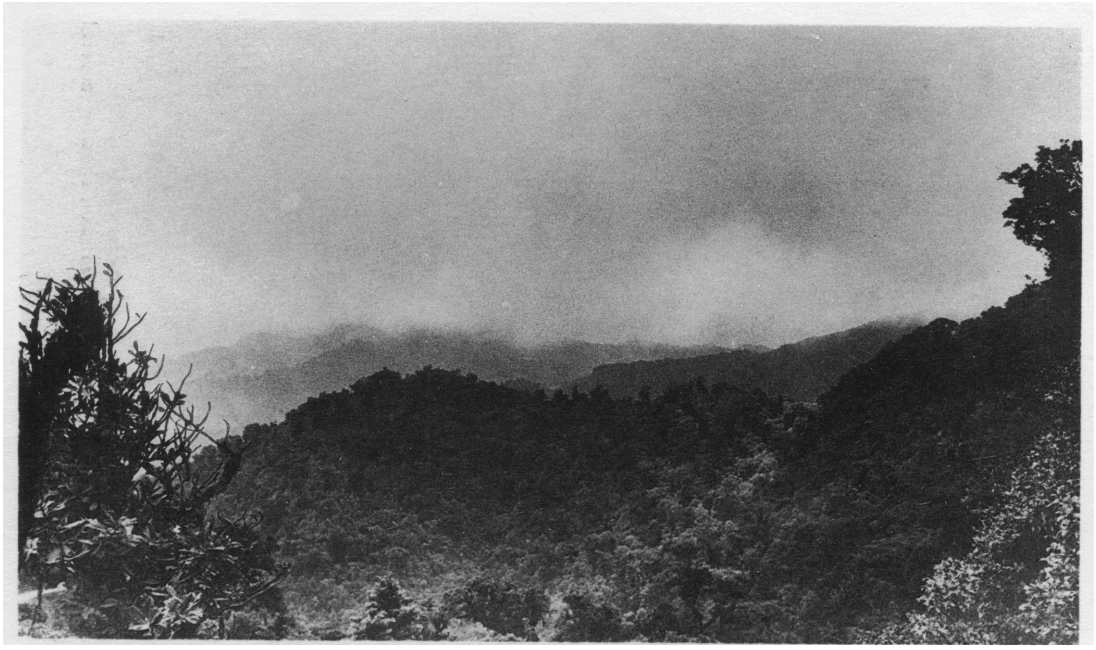
6. Gradual refrigeration during late Tertiary and drastic and repeated climatic changes during the Pleistocene glacial cycles.

The foundation fauna of Honduras is the "Old Northern" (Dunn, 1931), possibly indistinguishable from North American. The area lay near the southern end of the Central American paleopeninsula, which from early times received repeated waves of migration from the north, a fact evident from deep-seated relationships with remote but impressively similar southward extension on other continents (Schmidt, 1946) and from the consistent recurrence of so-called "hanging relict" forms (Schmidt, 1943). This basic northern element has been much modified by the incursion of later migrants from both North and South America, with retention of a few endemic elements.

Fragmentary reflections of the history of the Honduranian fauna appear in its present ecological geography. Roughly, there are four fairly well-marked life areas in the country, as follows:

1. The tropical Atlantic lowland, with a rainforest fauna which is strikingly homogeneous from Mexico into South America.

2. The dry interior valleys, with a very characteristic fauna which, though discontinuously distributed, is essentially homogeneous from Guatemala to Nicaragua, at least. The cloud-forest fauna and that of the interior valleys are the most characteristic of the region. The dry-valley fauna is more tropical in background than that of the *ocotal* and more distinctive than that of the Atlantic lowlands.

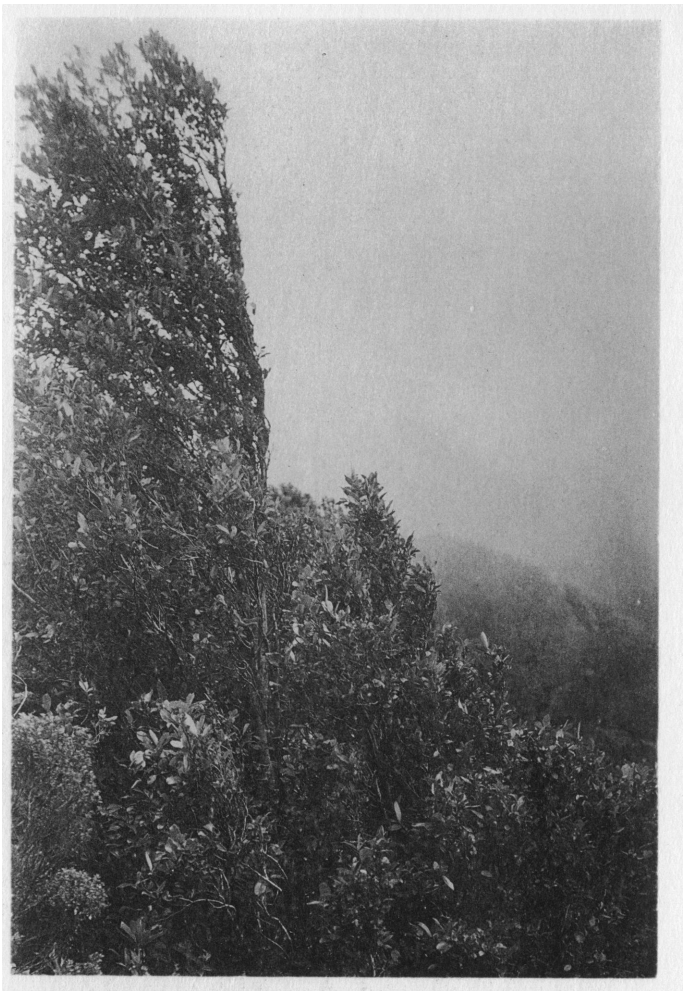


1

2

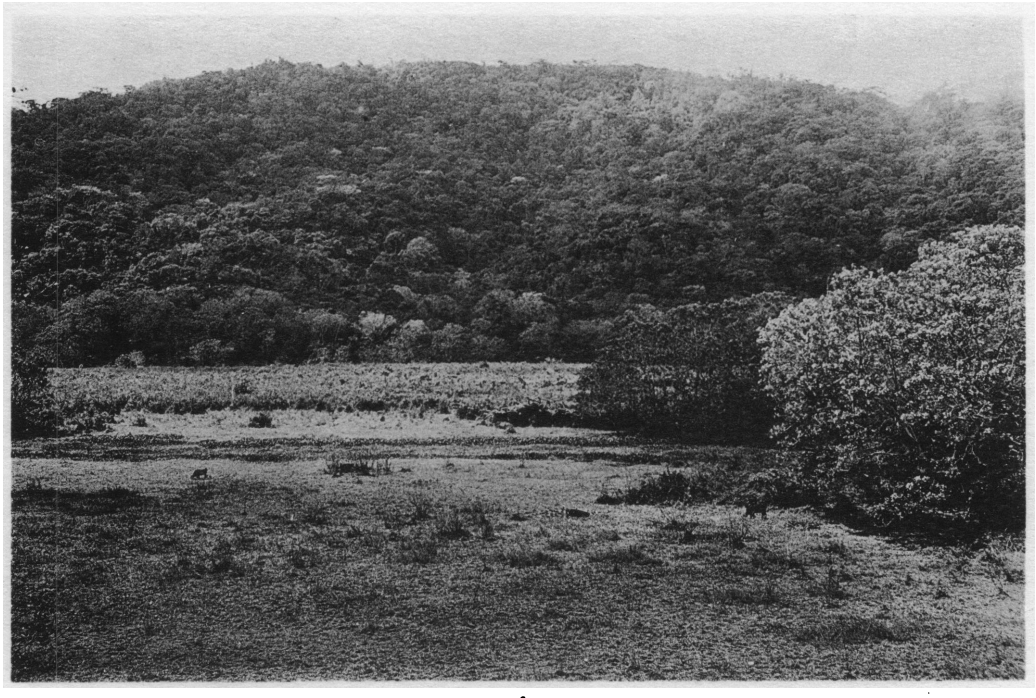
1. The San Juancito cloud forest seen from an elevation of 2135 meters (7000 feet), department of Francisco Morazán. Photograph by Margaret Hogaboom

2. Climax hardwood cloud forest on level ground on Cerro Uyuca, department of Francisco Morazán. Elevation 1860 meters (6100 feet)



2

1. Interior of climax cloud forest, Cerro Uyuca, department of Francisco Morazán. Elevation 1860 meters (6100 feet)
2. *Peña* wind scrub above Rancho Quemado, San Juancito Mountains, department of Francisco Morazán, showing several characteristic species of small-leafed trees and shrubs. Elevation 2135 meters (7000 feet)

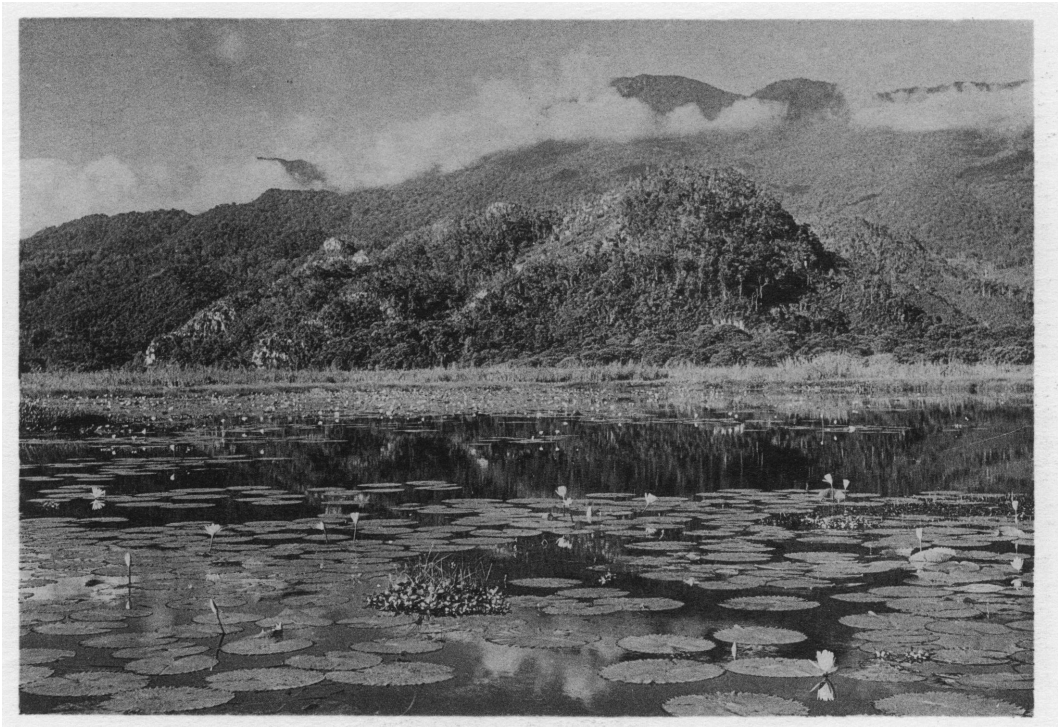


1

2

1. Vegetation zones at the south end of Lake Yojoa, department of Comayagua. The short-grass savanna in the foreground grades into marsh farther back, and this in turn is replaced by marginal tree swamp of *gualiqueme* (*Erthrina glauca*, right foreground and front of the forest in the background). The hill is covered by rainforest. Elevation of foreground 610 meters (2000 feet)

2. *Pinabetes* (*Pinus pseudostrobus*) on the southeast slope of Cerro Uyuca, department of Francisco Morazán. Elevation 1585 meters (5200 feet)



1

2

1. Vegetation zones at the northern end of Lake Yojoa, looking towards Cerro Santa Barbara, department of Santa Barbara. The floating and emergent front-rank vegetation gives way to the usual *gualiqueme* shore swamp (right center); above this the lake margin gallery forest is gradually replaced by luxuriant cloud forest as the mountain is ascended. Elevation at water level 610 meters (2000 feet), of highest *cumbre* approximately 2590 meters (8500 feet). Photograph by Margaret Hogaboom

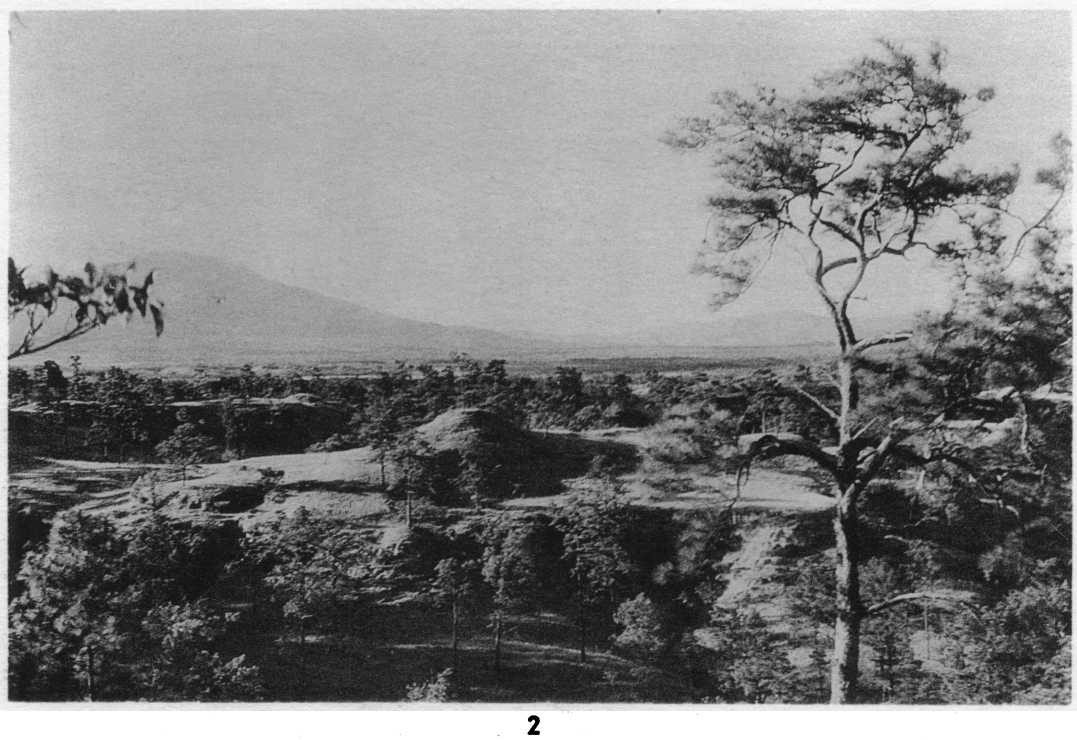
2. *Hondonada* with *palmiche* (*Iriartea durissima*) in woods of *Pinus caribaea*, department of Cortés. Elevation about 625 meters (2050 feet)

1

2

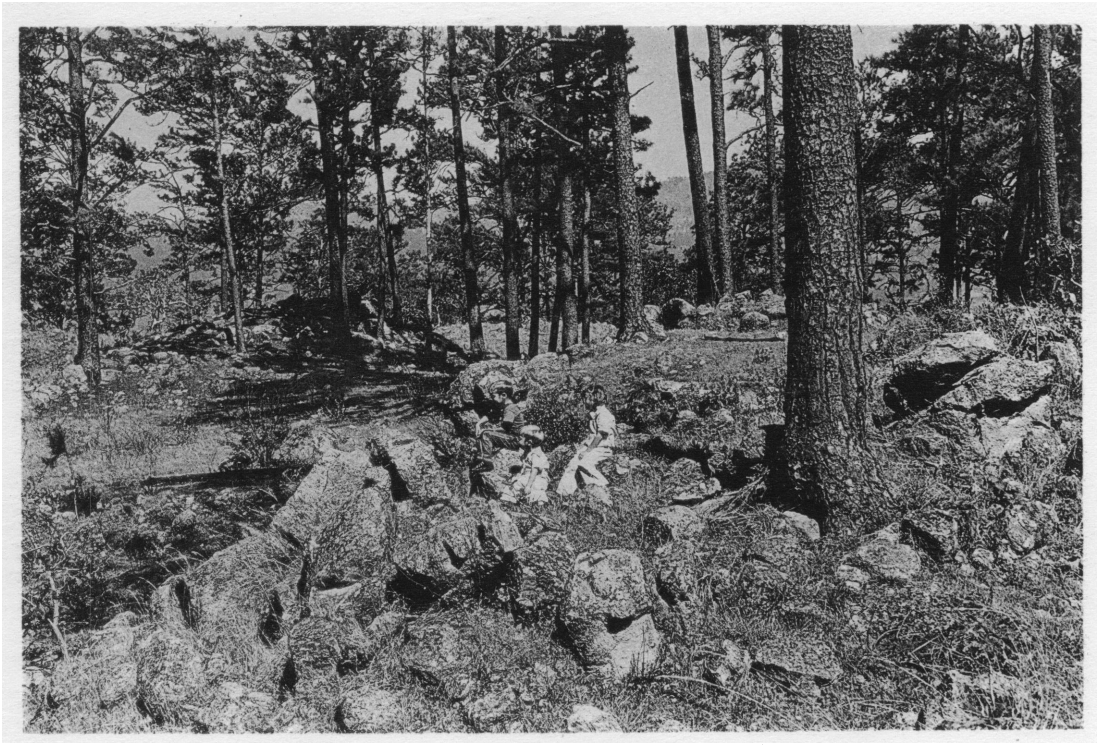
1. Shaded *ocotal*, department of Francisco Morazán. Elevation 1220 meters (4000 feet)
2. *Selva* above Lancetilla Valley, department of Atlántida. The small palms to the left are *lancetillas* (*Astrocaryum cohune*). Elevation about 60 meters (200 feet)

1



2

1. Park *ocotal*, department of El Paraíso. Elevation about 885 meters (2900 feet)
2. *Ocotal* steppe, looking into the Choluteca Valley, department of El Paraíso. Elevation of valley 595 meters (1950 feet). Photograph by Charles M. Bogert



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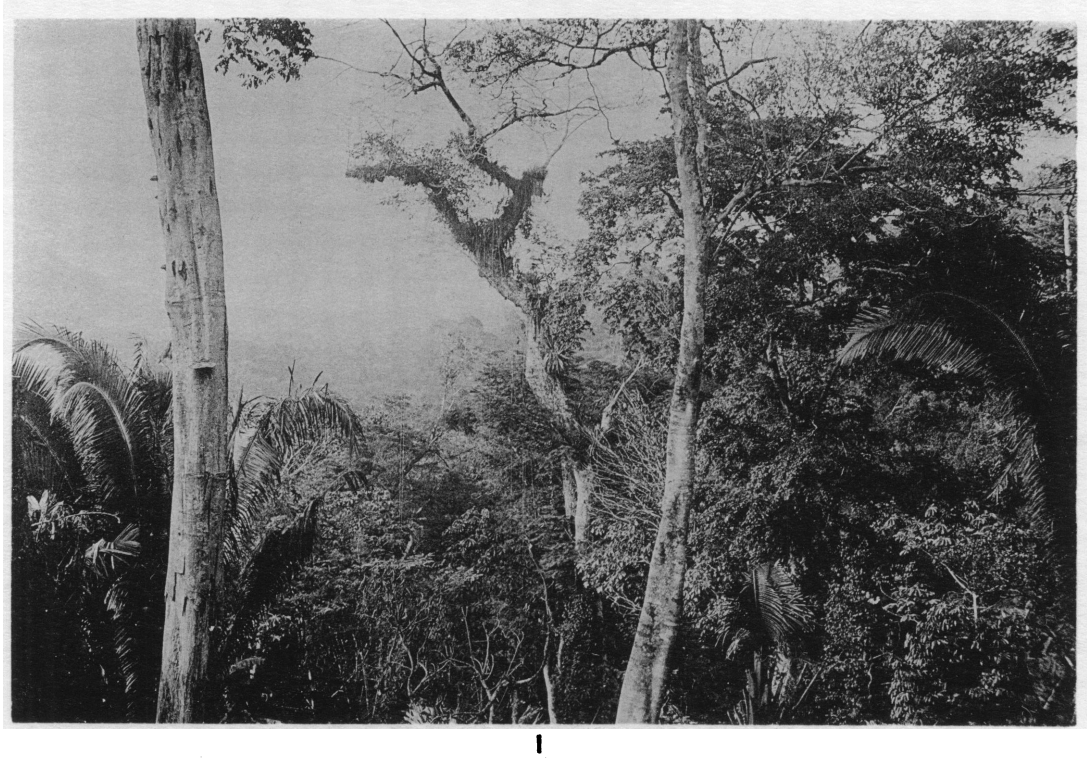
1. *Ocotal-pedregal*, near Las Mesas, department of El Paraíso. Elevation 835 meters (2750 feet)
2. Forest of *diquidumbe* (*Liquidambar*) merging with heavy gallery forest (towards left), department of Santa Barbara. Elevation 945 meters (3100 feet). Photograph by Margaret Hogaboom



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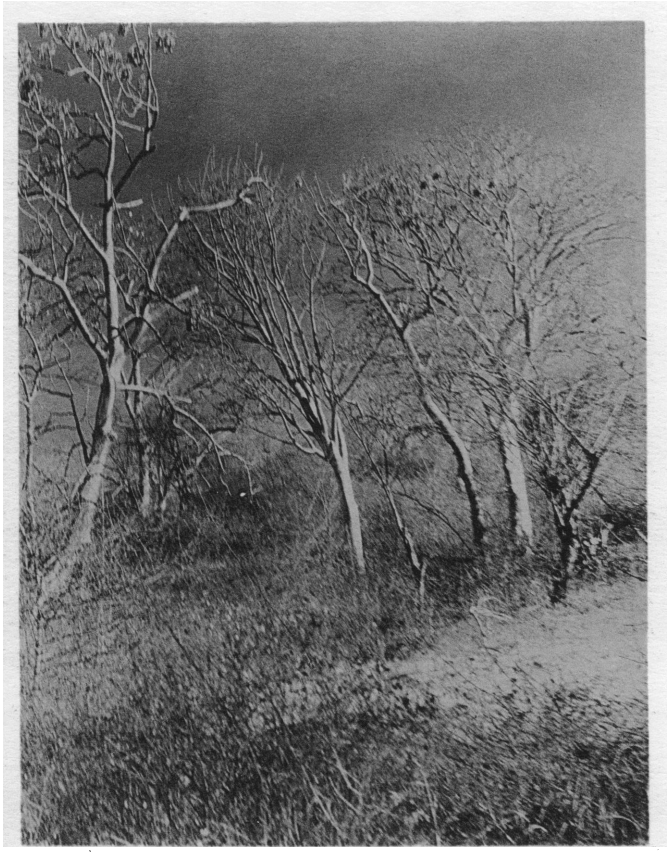
1. View of Lancetilla Valley, looking out to sea from a *selva*-covered hill, department of Atlántida. Elevation of foreground about 150 meters (500 feet)

2. *Selva* above Lancetilla Valley, department of Atlántida. The palms are a mixture of *lancetilla* (*Astrocaryum cohune*) and *manaca* (*Attalea cohune*). Elevation about 60 meters (200 feet)



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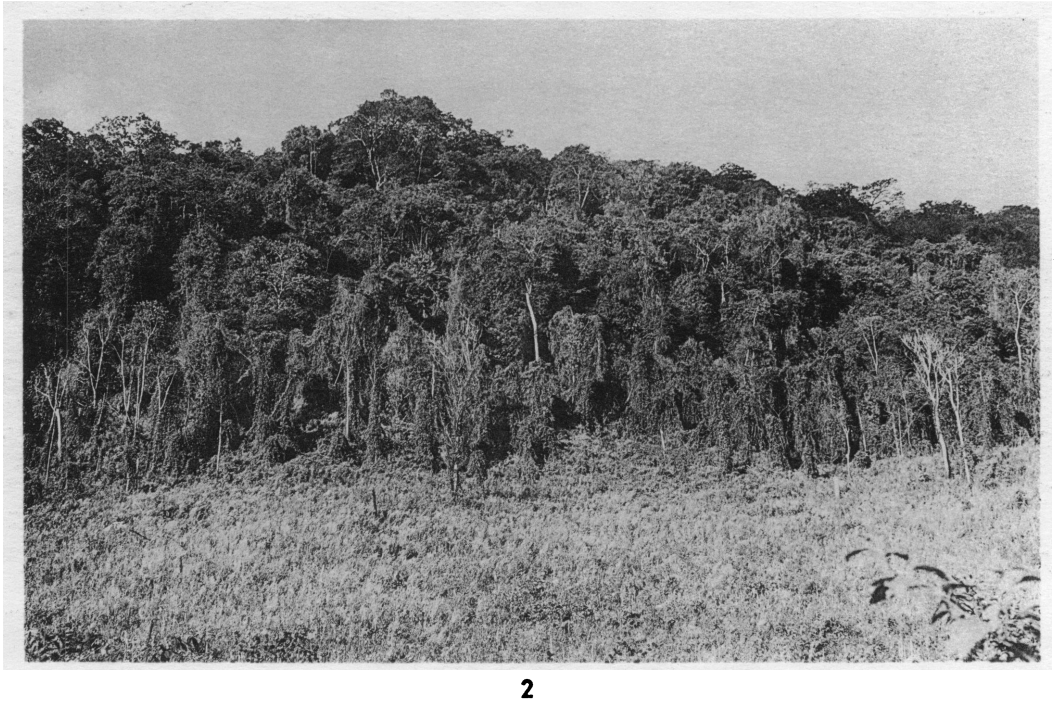

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1. Sea-breeze scrub forest overlooking Gulf of Fonseca, department of Choluteca. Elevation about 30 meters (100 feet). Photograph by Charles M. Bogert

2. *Breña* at edge of clearing in rainforest; south end of Lake Yojoa, department of Comayagua. Elevation 625 meters (2050 feet)

1

2

1. Intergrading of shore forest of black mangrove and buttonwood with mixed scrub. The camera was located in salt marsh, and a part of the tidal flat is seen in the foreground. Bay of Fonseca, department of Choluteca. Photograph by Charles M. Bogert

2. Interior of tree swamp, near south end of Lake Yojoa, department of Comayagua. Elevation 610 meters (2000 feet)

1

2

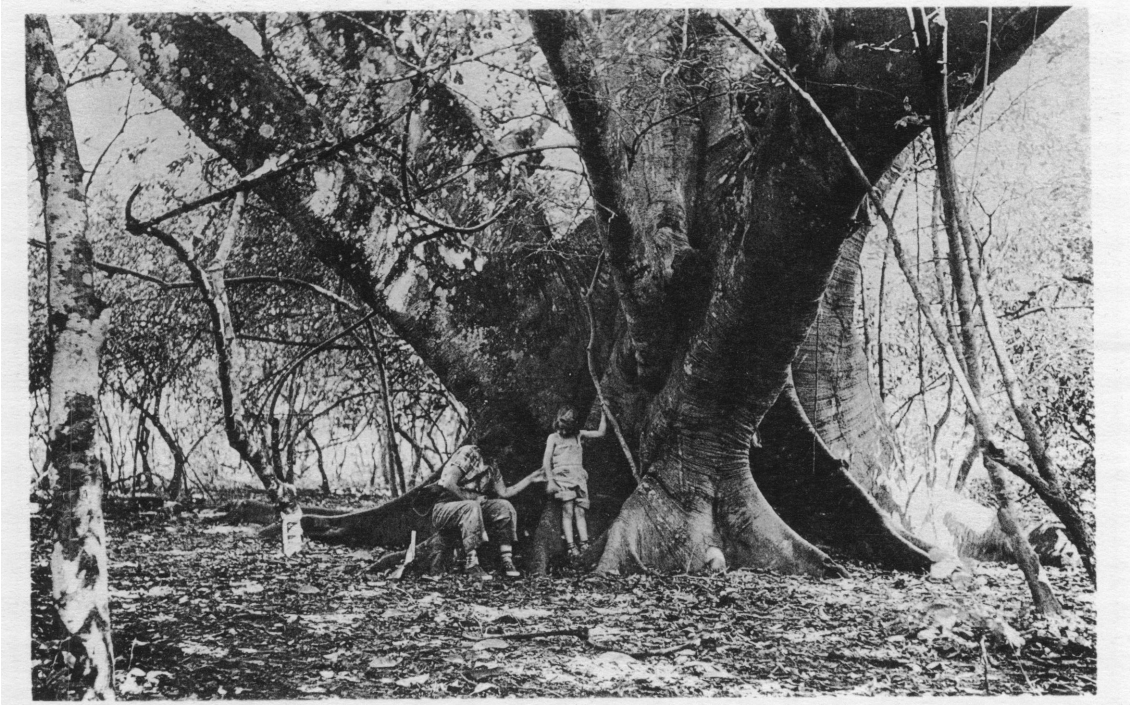
1. Gallery forest tending towards tree swamp, valley of Río Blanco near Amapa, department of Cortés. The small clump palm at the left is *huiscoyol* (*Bactris major*). Elevation 180 meters (600 feet)

2. Clearing in gallery forest on Río Blanco, Amapa, department of Cortés. Elevation about 180 meters (600 feet). Photograph by Margaret Hogaboom

1. Trail through *selva*-like gallery forest at Amapa, Río Blanco drainage, department of Cortés. Elevation 180 meters (600 feet)

2. Heavily wooded ***hondonada*** in rainforest above Lancetilla, department of Atlántida. Elevation about 105 meters (350 feet)

1



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1. Vega forest of Río Yeguare, department of Francisco Morazán. Elevation about 805 meters (2650 feet)

2. Vega forest in flood plain of Río Guayambre, department of El Paraíso. Note the clear understory, kept open by flood scouring. The big tree is a fig. Elevation about 305 meters (1000 feet)

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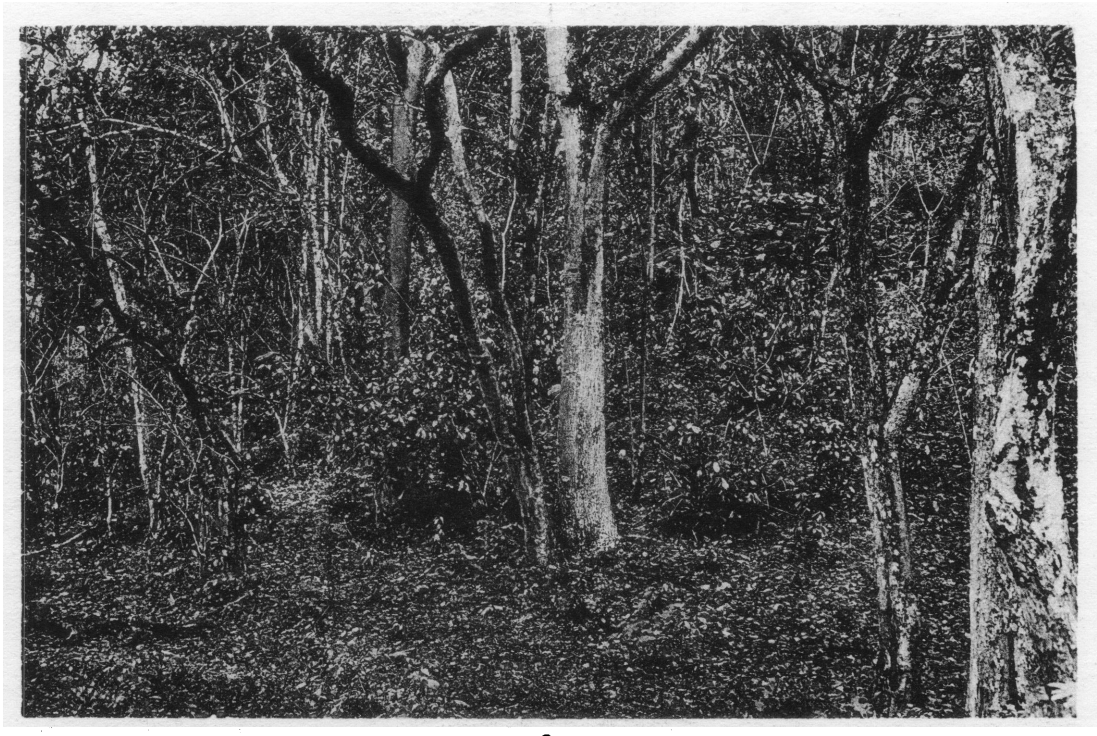
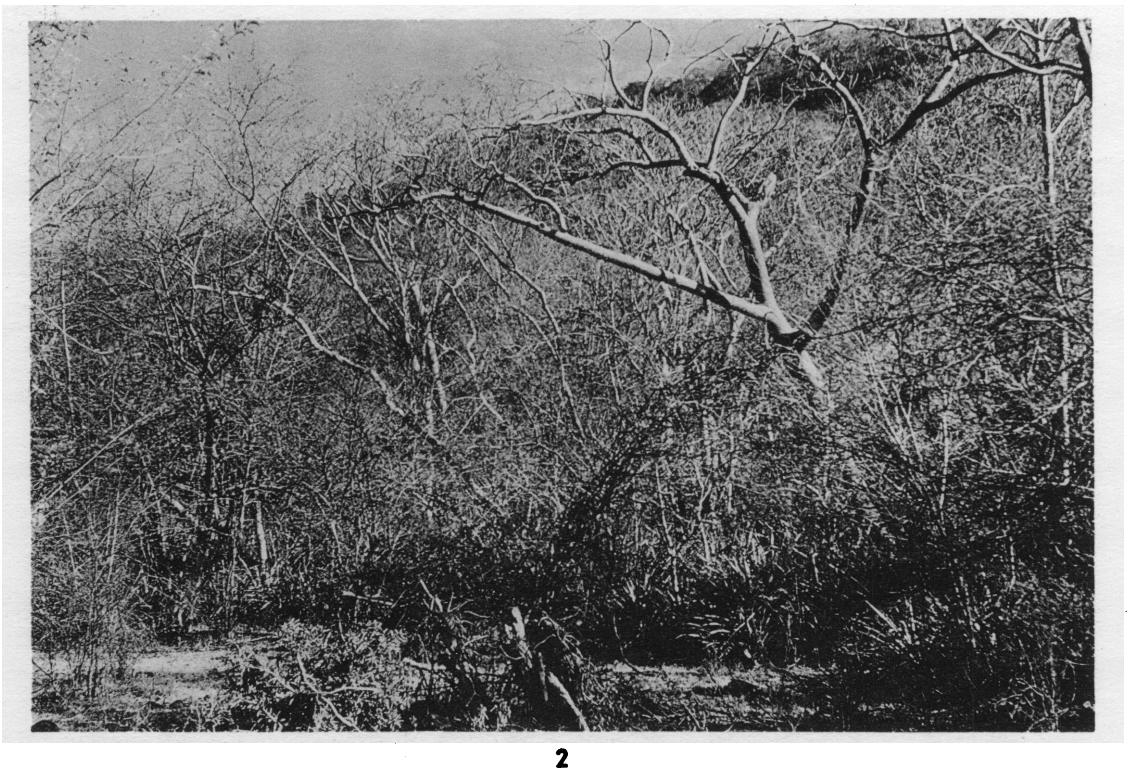


2

1. Road through monsoon forest, Jamastrán Valley, department of El Paraíso. The large tree is a *guanacaste* (*Enterolobium cyclocarpum*). Elevation 555 meters (1825 feet)

2. Monsoon forest (dry season) in valley of Guayambre River near Chichicaste, department of El Paraíso. Elevation 320 meters (1050 feet)

1



2

1. Monsoon forest in the rainy season, showing temporary luxuriance of foliage, nearly all of which will be dropped later; northern rim of Comayagua Valley. Elevation 610 meters (2000 feet)

2. Mixed scrub in the dry season, department of Choluteca. Elevation about 8 meters (25 feet). Photograph by Charles M. Bogert

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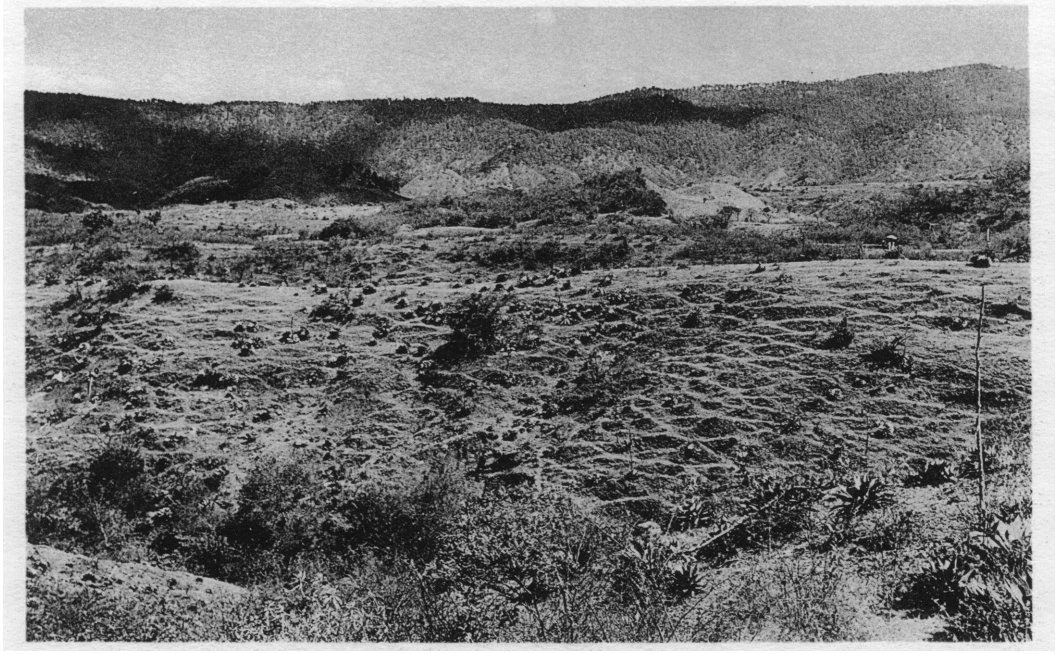
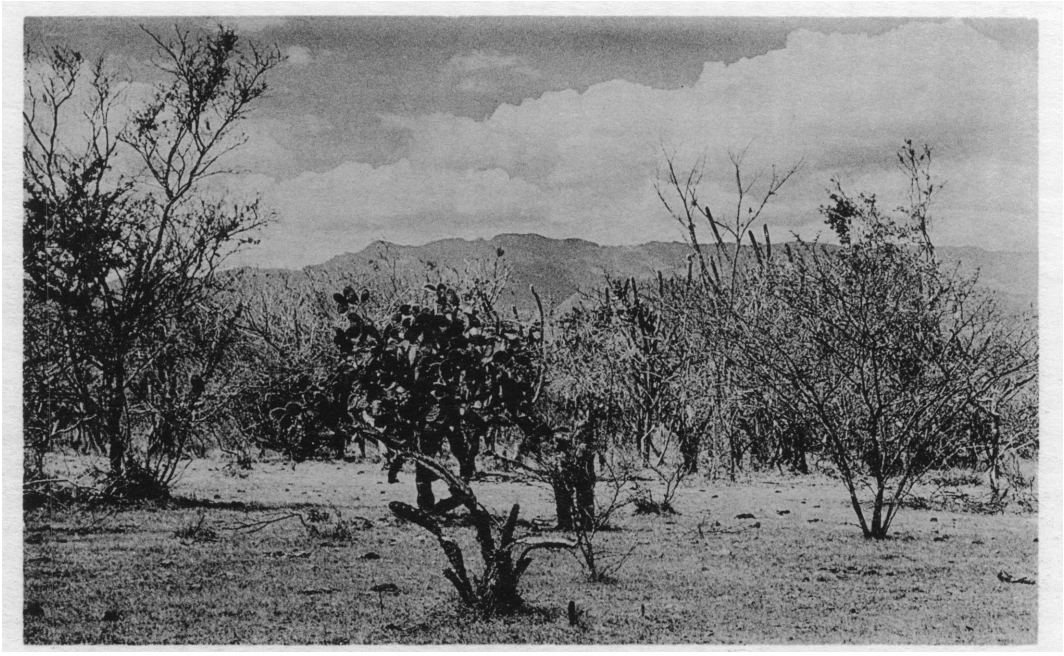


2

1. Thicket of *espino blanco* (*Acacia farnesiana*), Jesús de Otoro, department of Intibucá. Such *espinales* develop on flat ground with a hardpan or with heavy, impermeable soil, and are usually flooded in *invierno*. Elevation 580 meters (1900 feet)

2. Agave steppe above Suyapa, department of Francisco Morazán. Note the characteristic diamond checking of the ground made by grazing animals. The hills in the background are covered by dry *ocotal*. Elevation 790 meters (3600 feet)



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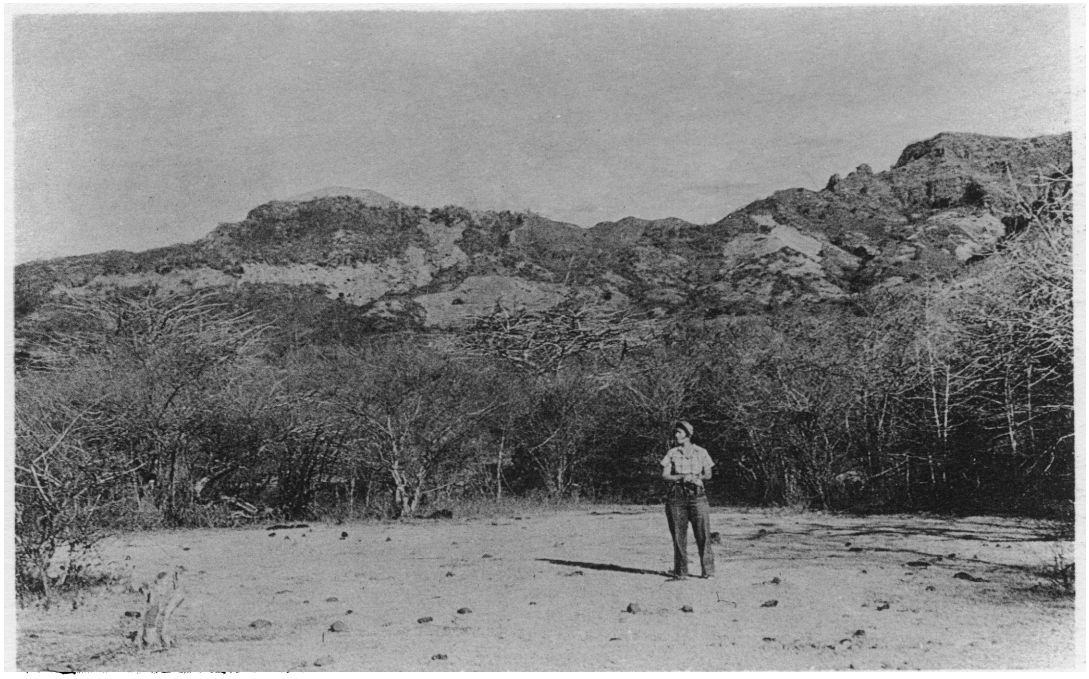
2

1. Dry thorn scrub (dry season) in Comayagua Valley, department of Comayagua. Within a short distance this association grades into almost lifeless steppe. Elevation about 615 meters (2025 feet)

2. Thorn scrub; Comayagua Valley in the dry season. The dark mass in the mimosa tree is a termite nest, and the barely discernible hole in the center of this was probably made by parakeets which use the nests as habitations. Elevation 610 meters (2000 feet)



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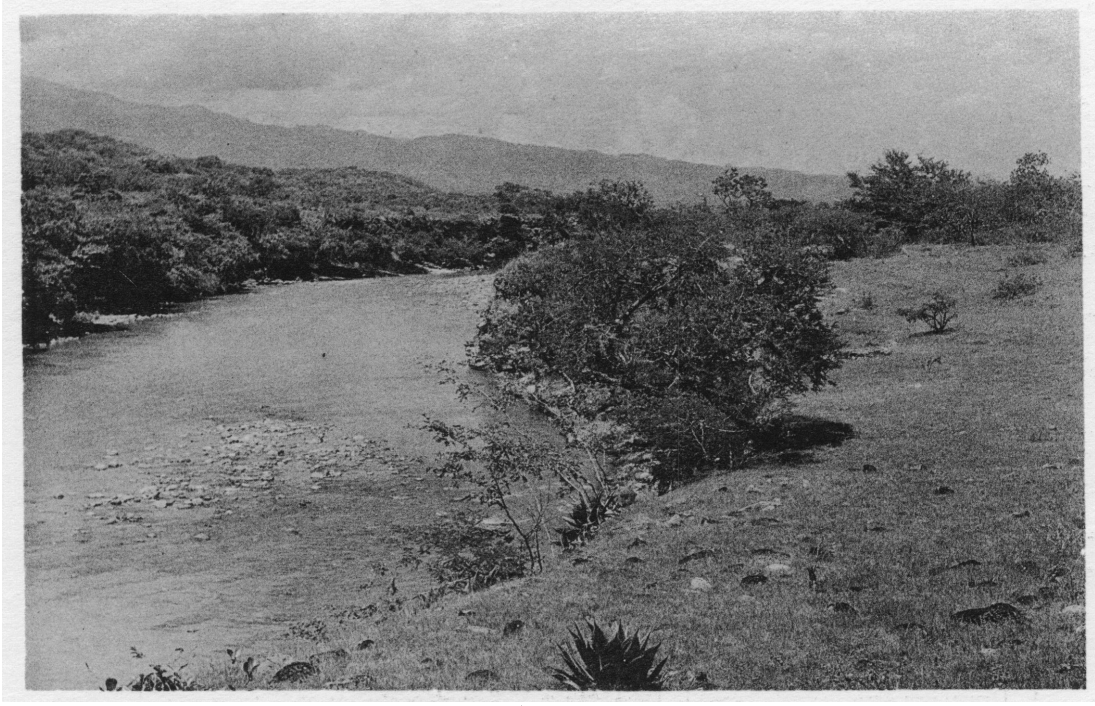


2

1. Steppe, with a patch of thorn forest in the background, department of Comayagua. Elevation 610 meters (2000 feet). Photograph by Charles M. Bogert

2. Steppe terrain along upper Ulúa River near Jesús de Otoro, department of Intibucá. Elevation 580 meters (1900 feet)

1

2

1. Savanna land in Lepaguare Valley, department of Olancho. The grasses are native species, but the association has evidently been strongly modified by grazing. Elevation 610 meters (2000 feet)
2. *Jícaro* savanna near Jícaro Galán, department of Valle. Elevation about 25 meters (75 feet)

1

2

1. Tall-grass savanna, in which the dominant species, guinea grass (*Panicum maximum*), is introduced but not now tended; between Juticalpa and San Francisco de la Paz, department of Olancho. Elevation 365 meters (1250 feet)

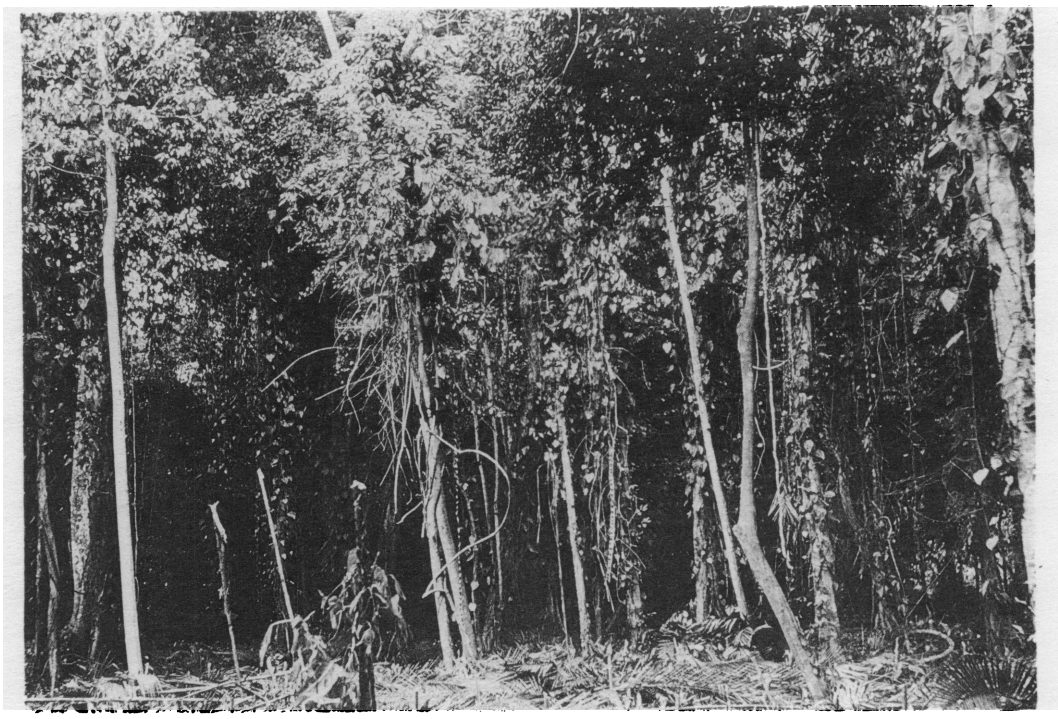
2. Short-grass savanna (llano), Las Mesas, department of El Paraíso. Elevation 915 meters (3000 feet)

1

2

1. Short-grass savanna, Hacienda La Lima, Lepaguare Valley, department of Olancho. The vegetation of this llano is partly cultural, invading *espino blanco* being chopped out annually with machetes. The failure of the pines to encroach upon the flat land is a consistent tendency. Elevation 610 meters (2000 feet)

2. Marsh of *gamalote* grass (*Paspalum fasciculatum*) in depression in Caribbean pine woods, department of Cortés. Elevation about 625 meters (2050 feet)



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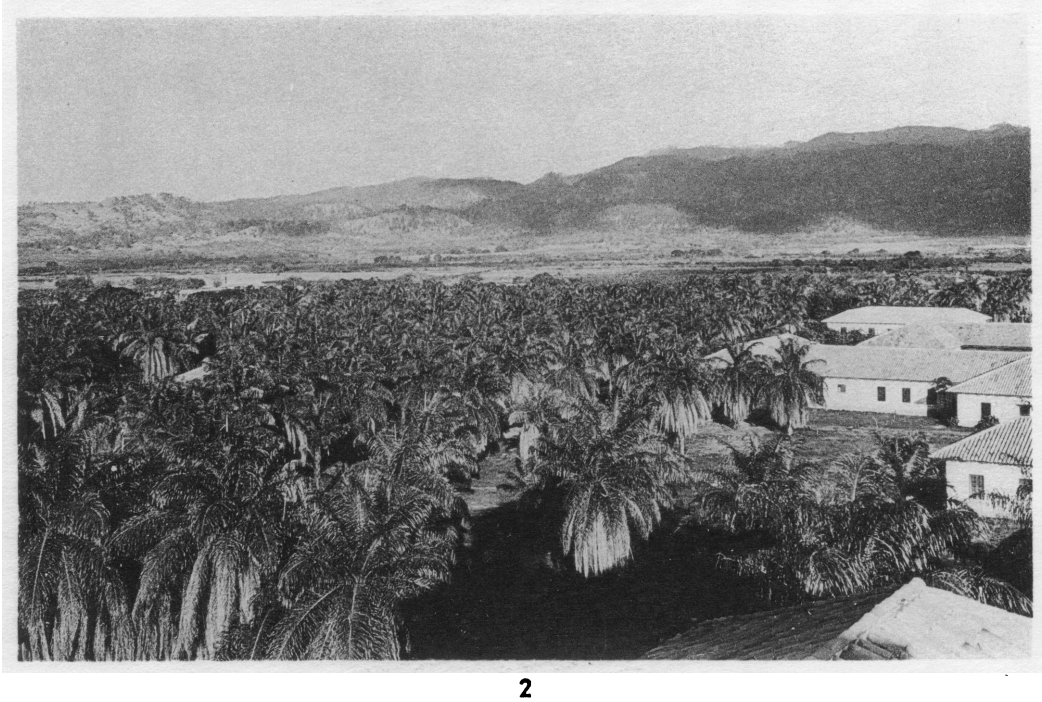

2

1. Edge of a recent clearing in old *guamil* (in this case second-growth gallery forest) near Amapa, department of Cortés. Elevation 180 meters (600 feet). Photograph by Charles M. Bogert

2. *Coyolal* in semi-arid valley of Río Yeguare, at Escuela Agrícola Panamericana, department of Francisco Morazán. The *coyol* palm (*Acrocomia mexicana*) is widespread in Honduras but only occasionally forms dense groves such as this. Elevation 790 meters (2600 feet)

3. The semi-arid slopes of the *serranías*, largely a pine forest area with a biota in part unique but with strong northern affinities.

4. The mountain summits on which lower temperatures and condensation make "temperate" islands of scattered ridges and peaks. The biota of these heights consists of endemics of basically northern blood, with a conspicuous admixture of forms derived from, and in a few cases even shared with, the lowland rainforest.

In my opinion the occurrence of these Humid Lower Tropical elements in the Humid Upper Tropical fauna is the key to the more recent history of the latter fauna. As Griscom (1932) has pointed out, the climatic conditions that presently mold high islands in the Upper Tropical extended far down the slopes during the Pleistocene, very probably to sea level at one time and another. The contact thus established between the upland and lowland biotas left an impression on the modern fauna of the Humid Upper Tropical, which on the whole, and probably for ecological reasons, is greater than the influence of the now contiguous Arid Upper Tropical fauna of the *ocotal*.

The dry *ocotal*, being a more or less unbroken highway from the north, shows marked faunal community with the Mexican region and thus constitutes a wedge of xerophilous Mexican life separating the upper and lower humid communities.

The narrow Pacific coastal plain does not constitute a distinct faunal area, its fauna being a composite of forms shared with the upland valleys and with the Atlantic rainforest.

TABLE 2

SCHEMA SHOWING RELATION BETWEEN MAJOR HABITAT TYPES, LIFE ZONES, AND TOPOGRAPHIC DIVISIONS IN HONDURAS

SERRANÍAS		LOWLANDS	
		ATLANTIC	
		PACIFIC	
UPPER TROPICAL		LOWER TROPICAL	
HUMID	ARID	ARID	HUMID
CLOUD FOREST High *Ocotal* *Pinabetal* *Diquidumbal* Hardwood Climax	STEPPE THORN SCRUB MIXED SCRUB		RAIN FOREST *Selva* Jungle *Breña*
MARSH			
FIELD CROPS AND *GUAMIL*			
GALLERY FOREST			
SAVANNAS			
OCOTAL	TREE SWAMP		
MONSOON FOREST			

THE HABITATS

HABITATS PECULIAR TO THE *SERRANÍAS*

CLIMATIC ASSOCIATIONS

Cloud Forest

THIS OFTEN LOOSELY APPLIED TERM is used in the present case in its broader sense to include any upland woods that owes its character to lower temperatures and cloud condensation, or perhaps more directly to the resulting low evaporation rates (fig. 5), rather than to direct precipitation. The scant data available suggest that a cloud forest may develop on heights that receive about the same amount of actual rainfall as the surrounding semi-arid lowlands (see table 1), and my own observations tend to support the existing records. Obviously certain peaks and ridges do get an extra ration of orographic rainfall, but the discrepancy appears to be of little effect in modifying the major features of the cloud-forest formation. Because of strategic location with respect to the prevailing northeasterly winds, this association develops at lower levels on the Caribbean slopes than in the interior.

In certain sections, notably in the south-central part of the country, isolation of the cloud forests is complete, and they comprise scattered mesophytic islands in the semi-arid *ocotal*. Elsewhere, however, there may be intergradation with other hardwood associations. In the department of Olancho, for example, cloud forest merges with the local deciduous forest types on several fronts. In parts of Paraíso the gallery forests of the upper Patuca drainage occasionally thrust fingers of broad-leafed vegetation up the same ravines that, headward, receive extensions of the cloud-forest periphery. Around the south end of Lake Yojoa there is a magnificent and ostensibly primeval woods (pl. 14, fig. 1) which appears to owe its existence to three distinct factors, as follows: (1) augmented moisture content of the prevailing northerly wind sweeping across the lake, (2) higher rainfall, apparently caused by local convection effects, and (3) widespread limestone outcroppings, since lava flows in the same area are consistently covered with open woods of *Pinus caribaea*.

Where the cloud forest is most typically developed as a disjunct mountain-summit environment, it usually comes in at elevations of between 1050 and 1370 meters (3500 and 4500 feet), perhaps more frequently near the latter height (see fig. 6).

As defined here the cloud forest is comprised of three quite different associations. While certain animals range throughout the formation, only a handful of the larger, more active mammals are common to the dry valleys and the upper, hardwood facies of the cloud forest, although some forms from the semi-arid lowland habitats range well into the *pinabetal*. However, the quetzal and numerous other birds, several mice, two species of shrews of the genus *Cryptotis*, and a long list of other animals, both vertebrate and invertebrate, clearly recognize the lower limits of the hardwood climax and rarely cross them. On the other hand such birds as the black *chachalaca* (*Penelopina*) and the ocellated quail (*Cyrtonix*) appear not to discriminate between hardwoods and high pine, and another group of forms (the toad *Bufo coccifer*, the lizard *Sceloporus malachiticus*, and the snake *Imantodes* sp.) occurs in all three of the associations.

The three major cloud-forest associations are as follows:

HIGH OCOTAL ASSOCIATION

This is essentially a moist woods of *ocote* pine (*Pinus oocarpa*), or of pine and oak, with the limbs of the trees supporting a large epiphyte flora, and with more or less luxuriant undergrowth of small trees and shrubs, often dominated by melostomes. The bromeliads are mostly of narrow- and hard-leafed species. Shade is constant and often dense. Obviously this community is merely a belt of transition from *ocotal* to higher cloud forest, but its zonal breadth, frequence of occurrence, and consistency in composition make necessary its recognition as a distinct habitat.

PINABETAL

Plate 14, figure 2

At elevations varying according to the exposure but with the mean perhaps close to 1370 meters (4500 feet), the preceding type gives way gradually or suddenly to a com-

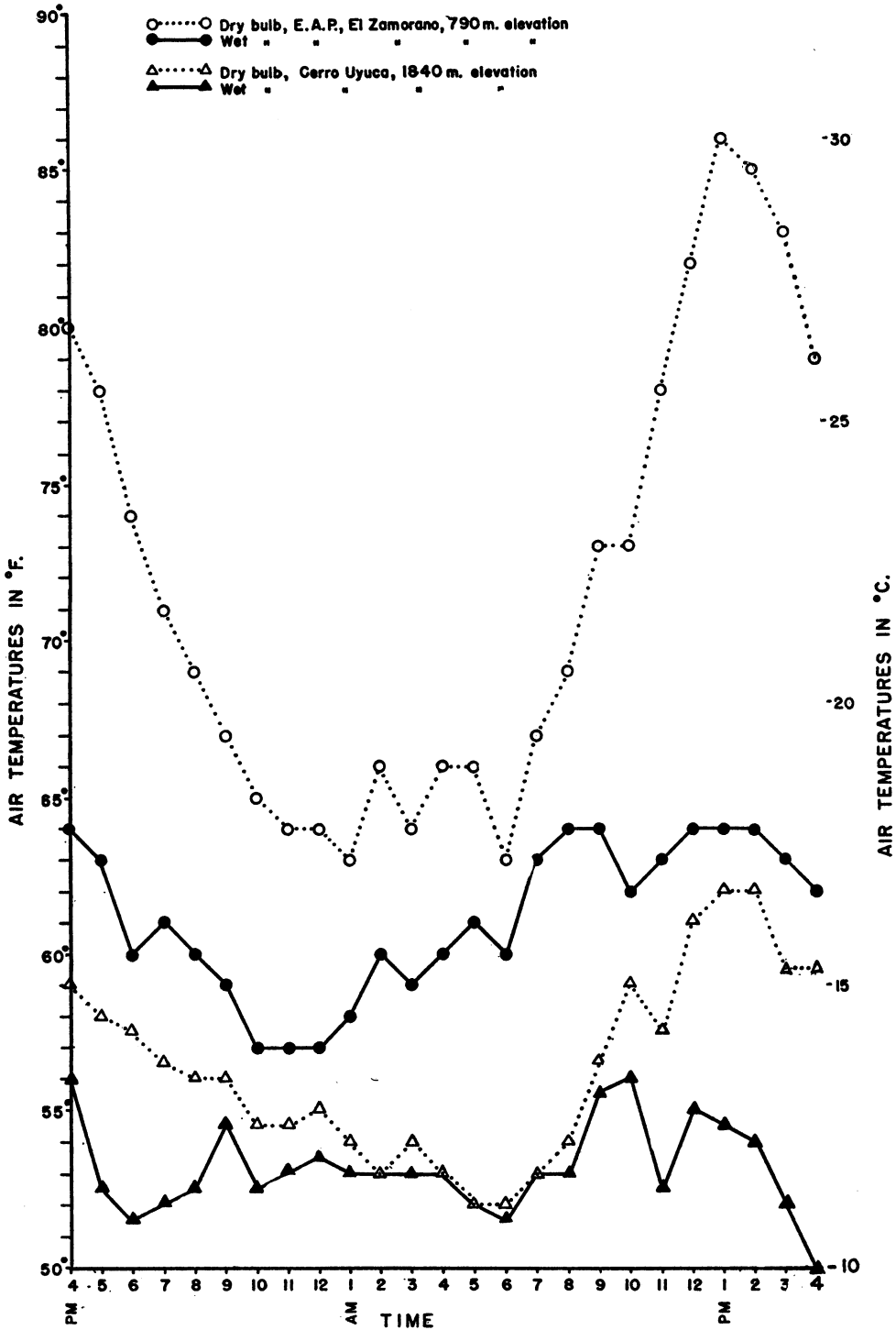

FIG. 5. Graph comparing dry-bulb and wet-bulb temperatures in the semi-arid Yeguare River Valley, Honduras (at Escuela Agrícola Panamericana, elevation 790 meters) and in the broad-leafed cloud forest on Cerro Uyuca at an elevation of 1840 meters. The horizontal distance separating the two stations is approximately 3 miles. Simultaneous readings were made with sling psychrometers at hourly intervals throughout a 24-hour cycle during the dry season (March 3–4, 1949). As mentioned in the text, the cloud forested peaks of the Pacific drainage appear to receive little or no more rainfall than many of the semi-desert valleys, and the heavy, mesophytic vegetation of the former must thus be attributed mainly to lower evaporation rates.

munity dominated by *Pinus pseudostrobus*, usually with epiphyte flora similar to that of the foregoing type and with admixture of smaller trees and shrubs derived from both upper and lower levels. Despite the transitional nature of the subdominant elements, this is a conspicuously distinct community that nearly always separates hardwood cloud forest from *ocotal* on mountains on which the former is present, while on the numerous peaks that rise no higher than 1220 to 1525 meters (4000 to 5000 feet) *pinabetes* usually crown the summits.

HARDWOOD CLOUD FOREST

Plate 12, figures 1, 2; plate 13, figure 1

The truly primeval vapor forest is similar in superficial appearance to the most luxuriant tropical rainforest, but is almost wholly different in details of composition. On the average it is a mesic woods in which various species of oaks and *aguacates* usually predominate and with an epiphytic flora of often bewildering variety, incomparably more varied than that of the lowland *selvas*. The trees are large—often immense—and usually strongly buttressed; a large proportion of them produce fruits palatable to mammals and birds. The annual accretion of organic litter is great and, while soils of these woods include some of the finest in the highlands, under certain circumstances there may be almost no humus production. On some of the steeper slopes the forest may be footed on bedrock under only a few inches of reddish or brown clay.

It is convenient to recognize three zones within the hardwood forest, as follows:

1. The typical oak-Lauraceae association on more or less exposed slopes and summits up to 1980 to 2135 meters (6500–7000 feet), with relatively open understory of melostomes, Piperaceae, treeferns, and other shrubs.

2. The local, edaphic variant of the above in protected glens and ravines, where treefern growth is at a maximum and where the lower levels are shared with slender palms of the genus *Chamaedorea*. Begonias are abundant, and the low evaporation rates that prevail permit growth of liverworts regardless of the presence or absence of surface water. Throughout most of the year big planarians glide about on the wet leaf mold.

3. *Peña* wind scrub (pl. 13, fig. 2), an extraordinary association confined to the highest peaks or ridges with maximum exposure. It is a seemingly incongruous combination of dwarfed and twisted microphyllous and sclerophyllous trees and shrubs, Ericaceae, Myrtiaceae, Myrsinaceae, and the like, implying xeric conditions but with an astounding array of mosses, filmy ferns, selaginellas, and similar delicate hygrophyllous epiphytes. Although at first glance this is an altogether ill-assorted looking flora, the incongruity is only apparent, since each of the two floristic elements is in its own way adapted to withstand drastic reversals in its water economy. On these *peñas* the wind blows almost constantly, often violently, and while it usually brings in abundance of moisture, it imposes a heavy penalty when the supply fails for even a short period. The wind-pruned trees meet the situation by conservation of their moisture, while their cryptogamic guests yield freely to desiccation, lasping into dormancy almost on a moment's notice, and without permanent injury.

Further accentuation of the factors that mold these wind scrubs, coming with altitudes slightly higher than the usual maxima for Honduras, may produce either of two very different and distinctive habitats. These are a dense, humid forest of cypress (*Cupressus* spp.), or of cypress, fir (*Abies religiosa* or related forms), and other conifers, and a series of bleak, alpine scrub communities, which, according to Paul Standley, in Guatemala have a predominantly boreal flora but which in the Talamanca Range of Costa Rica are real paramillos of distinctly Andean cast. In Honduras the cypress forest was thought to be confined to a few peaks along the Guatemalan border, but Alphonse Chable of the Tela Railroad Company, Agua Azul, recently found at 2285 meters (7500 feet) the beginning of a zone of cypress (*Cupressus*) on Cerro Santa Barbara west of Lake Yojoa (pl. 15, fig. 1). The true paramo is not represented in Honduras, its northern outpost being (again according to Standley) the exceedingly interesting example on the crest of the Cerro de la Muerte in Costa Rica, but there is marked similarity in general appearance between this cold and wind-swept muskeg and the highest and most exposed of the Honduranian wind scrubs.

The faunas of these highest levels are virtually unknown but certainly are meager in Honduras. It is perhaps worth noting that in both the wind scrub of Honduras and the Talamancan paramillo a form of tapir is a frequent and common resident or visitor, sometimes climbing the most incredibly steep and slippery moss-draped rock faces in its wanderings.

EDAPHIC ASSOCIATIONS

Ocotal

The pine woods, or *ocotal*, usually formed by *Pinus oocarpa*, but on some of the leeward slopes in the north by *Pinus caribaea*, is easily the most widespread association in the interior of Honduras. It occurs, primitively, on all well-drained slopes, apparently with little regard to the soil type, between elevations of roughly 610 and 1370 meters (2000 and 4500 feet). It includes a host of facies, the extremes of which are so divergent as to have in common only the one constituent species of pine tree and the fact that they always develop on inclined terrain, avoiding even the most restricted patches of flat land. As animal habitats the various types of *ocotal* probably differ more widely from one another than from many other communities with wholly different vegetation. The more obvious subtypes of the *ocotal* are as follows:

SHADED OCOTAL

Plate 16, figure 1

This is a relatively moist pine woods found on the higher or more northerly slopes of the mountains. The better hygric conditions permit fairly close spacing of the pines and moderate to good growth of shrubs, bracken, and tall grass substratum. Fence lizards (*Sceloporus*) are rarely found in this woods, but craneflies and mosquitoes may be seasonally common.

PARK OCOTAL

Plate 17, figure 1

More widespread than the above, this open, park-like pine forest covers the countless dry slopes of the interior where the skeletal soils may be extremely shallow or nearly non-existent. Bunch grass or other herbaceous ground cover may dry out during *verano*, but the ground is never bare over large areas. Fence lizards are relatively common here and craneflies and mosquitoes apparently completely lacking, even during the height of the wet season.

OCOTAL STEPPE

Plate 17, figure 2

In this phase of the *ocotal* the trees are dwarfed by drought and sterility of soil and show wide and desultory spacing. During the dry season the annual herbaceous vegetation dries up and blows away, exposing the raw surface of the undifferentiated beds of clay or of white or red ash. The fauna of this rather widespread habitat is poor to almost non-existent.

OCOTAL-PEDREGAL

Plate 18, figure 1

This is an excessively rocky type of pine woods that has somehow established itself on broken and usually sharply inclined lava flows where soil, and consequently an herbaceous understory, are almost completely lacking. In general the vertebrate faunas of these *pedregales* are fairly well developed, especially in the basaltic flows in which extensive fragmentation affords unlimited refuge from drought in the form of cracks and deep fissures. This is the optimum habitat of the local rock wren (*Salpinctes*).

Diquidumbal

Plate 18, figure 2

A forest of sweet gum (*Liquidambar*), known widely in Honduras by an extraordinary corruption of the generic name of the tree, *diquidumbe*, occurs where the water tables rises or is intercepted, at elevations usually above the *ocotal* and below the cloud climax, thus most often replacing *pinabetes*. The trees, which attain heights of well over 30 meters (100 feet) in favorable locations, may occur in nearly pure stands over considerable areas, forming groves that are far more imposing than any sweet-gum woods I ever saw in the southeastern United States. Around the northwest shore of Lake Yojoa, Alphonse Chable called my attention to a curious overlapping of the tropical gallery forest of the lake shore and the sweet-gum woods of the slopes above. In the drier interior the lower-level edaphic equivalent of the

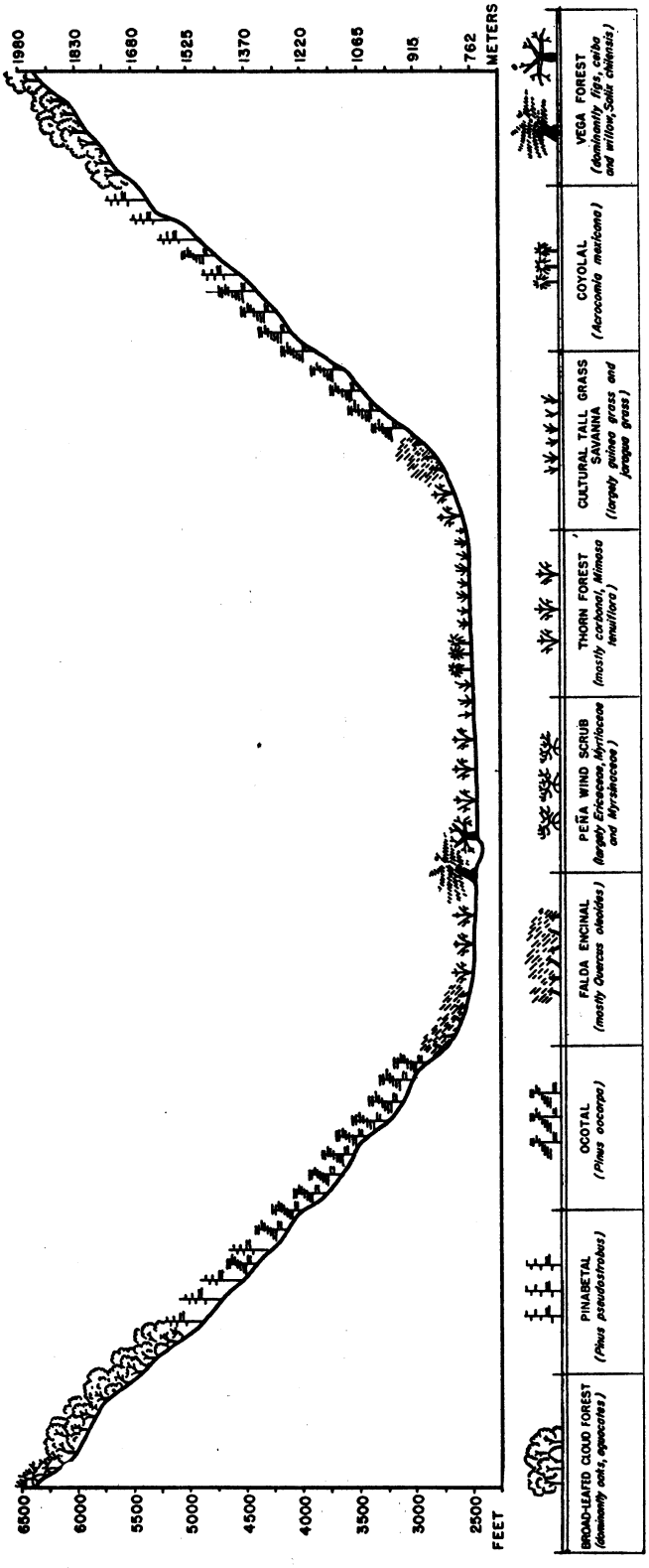

FIG. 6. Sketch transect of the Yeguare River Valley, south-central Honduras, from the peak of Cerro Uyuca (right) to El Volcán, showing vertical distribution of major vegetation types. The bearing of Uyuca from El Volcán is 292°; the horizontal distance between the two peaks is approximately 12 miles.

diquidumbal appears to be the groves of *roble* (broad-leafed) oaks, and the two frequently occur in mixed stands.

Falda Encinal-Robledal

Wherever ground water rises in the pine woods oaks tend to come in. Since interception of the water table occurs regularly where the mountain inclines level off to the valley floors, oak forest is characteristically found in this *falda* zone. The oaks are of two general groups, a large-leafed series (one or more species), known locally as *roble*, and a small-leafed group, the most common of which is *Quercus oleoides* and which goes by the name *encino*. *Roble* and *encino* may grow in either mutually exclusive or mixed stands, and the woods that they form vary from dense, impenetrable, second-growth scrub to open, shaded forest. It should be mentioned that both *roble* and *encino* occur in several other associations, but that one or the other is nearly always a conspicuous feature of the vegetation of the lower seepage slopes.

HABITATS PECULIAR TO THE LOWLANDS

Savanna

PINUS CARIBAEA SAVANNA

This formation is most extensively developed on the broad plains of the Mosquitia, where drastically leached and highly acid alluvial soils support open stands of Caribbean pine with ground cover of small shrubs or of either tall or short grasses, usually the latter. This appears to be the nearest thing to a true climatic savanna that Honduras affords, although even here the nature of the soil is intimately involved in the character of the community; whether this is cause or effect, however, is not immediately apparent.

Rainforest

The tropical rainforest, with 80 inches or more of annual precipitation coming with minimum seasonal fluctuation, formerly had much greater distribution in the Caribbean lowlands, having been markedly reduced by agriculture and by timber operations in the more accessible areas. Shank (MS) gives 5,000,000 hectares as the total remaining area of virgin rainforest, making this the most extensive forest type in Honduras, but this estimate comprehends all classes of timber lands in which such commercially important trees as mahogany, cedar (*Cedrela*), laurel (*Cordia*), San Juan (*Tabebuia*), and rosewood (*Dalbergia*) occur and thus includes a number of communities, both edaphic and climatic, that are segregated in the present outline.

SELVA

Plate 16, figure 2; plate 19, figures 1, 2

This is the true primeval forest, the term primeval being used in the present paper as the equivalent of "virgin mesophytic climax," implying as well that the vegetation is sustained by atmospheric water and not by some azonal edaphic condition. In the tall *selva* the annual rainfall is relatively steady, and the trees, which occasionally attain heights of more than 60 meters (200 feet), are of the most amazing specific variety, only very rarely composing pure stands of single or few species, and including a minimum of deciduous forms. In the mahogany trade a frequency of one tree per acre is an exceptional and valuable stand, and while some few *selva* species may occur more abundantly, the majority are perhaps just as thinly dispersed or even more so. The upper leaf canopy is continuous, and the trunks are mostly buttressed to sustain the huge burden of foliage. The tree crowns stratify at several levels, but the understory is open, with relatively meager, typically soft-stemmed shrubby or herbaceous undergrowth, including no grasses. Lianas are numerous. Leaf litter is deep, but the humus content of the soil varies from high to surprisingly low.

JUNGLE

Plate 22, figure 2

In its present sense the term jungle is restricted to natural, usually local, and frequently edaphic variants or subclimax stages of the rainforest community. It is necessary to stipulate "natural" inasmuch as some of these jungle associations, although untouched by man, may have much the same appearance as the cut-over *guamiles* described later. In the vast rainforest area of Nicaragua, which includes some of the most impressive

selva in the American tropics, there are large areas of absolutely virgin territory in which, however, the low, close cover is evidently not climax. I had the opportunity of accompanying Mr. Paul Shank on a 100-mile timber cruise through the uninhabited territory behind Pearl Lagoon, on the Caribbean coast, where we spent several weeks wandering about in woods that showed every sign of having grown up from cleared fields within the preceding 30 or 40 years. In this particular case it seems possible that the curiously subclimactic character of the forest may have been due to damage, possibly repeated blowdown, by hurricanes, of which there have been a few severe ones in the past half century. I use the word jungle to include also local rainforest variants with heavy underbrush, or in which for any natural cause one or two species of smaller trees are conspicuously dominant, as in the thickets formed by various palms, notably by the manaca palm (*Attalea coyune*), and in the better-drained bamboo brakes.

Except for its relatively sterile, pure-stand facies, the jungle rainforest, while lacking the imposing, cathedral-like interiors of the tall *selva*, may often offer even richer environments, especially for the larger animals. Such browsers as deer, brocket, and tapir require an abundant and varied understory flora such as the jungle affords, and for some reason tinamous, penelopes, and agoutis also reach their culminating abundance in the more cluttered woods. While the treetop fauna in general favors the *selva*, the toucans and whitefaced monkeys among its members occur more commonly in the smaller trees of the jungle. The small bands of *sajino*, or collared peccary, may be true *selva* animals, but for the great nomadic hordes of white-lipped peccary, which range widely in the climax forest and may reside there when some preferred fruit is falling, the optimum permanent habitat remains the jungle thickets or broken *breña* country where concealment is easier and sloughs and creeks are more frequent.

BREÑA

Plate 20, figure 2

Where the rainforest is dissected by ravines or invaded by meandering streams that undercut and topple the big trees, and wherever else light is admitted to the forest floor, there may develop impenetrable tangles of shrubby and herbaceous growth overgrown and roped together into a solid mass by vines and creepers. Such vegetation is characteristic of the banks of the lower streams and the edges of clearings and occasionally, for no apparent reason, it replaces rainforest over fairly extensive areas. *Breña* is the habitat *par excellence* of wild pigs, tapir, and many species of mice, rats, and snakes. While pavas (*Penelope*) abound, the curassow appears never to enter such situations.

Sea-Breeze Scrub Forest

Plate 20, figure 1

This is a very locally distributed community of small- and medium-sized, partly deciduous trees, found only in restricted patches on seaward slopes of exposed cliffs and volcanoes in and around the Gulf of Fonseca. Its composition appears to be more or less completely duplicated in some of the more widespread wet-season forests of the Pacific slopes, but the location and orientation of the several tracts that I have observed, such as that above the town of Amapala on Tigre Island, would appear to indicate dependence on vapor brought in by the local sea breeze rather than on the seasonal monsoon effect. However, even here there is considerable annual variation in the hygric level, since the diurnal monsoon varies with the height of the sun, and the rain-bearing (or rain-generating) northerlies tend to fall off during *verano*.

Swamps

MANGROVE SWAMP

Plate 21, figure 1

As on most low, tropical shores the dominant littoral vegetation on both coasts of Honduras is the saline tidal swamp of red mangrove, although this alternates in places with patches of grass marsh. Behind the *mangledal*, on somewhat drier ground, the red mangroves are gradually replaced by black mangrove (*Avicennia*), white mangrove (*Laguncularia*), buttonwood (*Conocarpus*), manchineel (*Hippomane*), and similar halophilous trees. Inland, the saline communities either grade into fresh-water marsh or are replaced by pine savanna or rainforest.

FRESH TREE SWAMP

There is considerable hydrophytic forest on the North Coast and a small amount in the Pacific coastal plain. Of this major habitat the following intergrading subtypes should be mentioned:

FRESH TIDAL SWAMP: This specialized environment is particularly common towards the western end of the north coast. It is a transition zone between mangrove and fresh swamp and obviously offers peculiar conditions as a habitat. As Standley (1931) pointed out, a conspicuous feature of these tidal swamps is the consistent presence of the tree *sangre* (*Pterocarpus belizensis*), which may dominate the association throughout considerable change in salinity, being found from fresh into quite brackish water.

SWAMP FOREST (PL. 14, FIG. 1; PL. 21, FIG. 2): These swamps vary widely in respect to degree and duration of flooding and accordingly comprise a number of different communities. On the Pacific coast the only important swamp associations undergo severe drought in *verano* and are inhabited only by plants and animals content to live on drought-hardened clay or cracked and fissured mud during several months of the year. Various species of *Ficus* thrive under these conditions and in many such swamps may constitute perhaps 80 per cent or more of the tree association. Elsewhere on the south coast the wet-season swamp community may be a somewhat varied association of such trees as *tempisque* (*Sideroxylon*), *ojushte* (*Trophis*), *tambor* (*Schizolobium*), *hule* (*Castilia*), and others, intermixed or not with the big figs. It is only in the Caribbean lowlands that there are large areas of swamp offering year-around hygric conditions. Here the forests that develop on low vegas, behind natural levees, and on lake shores or in old lake basins may approach (but never quite attain) the luxuriance of the mesophytic rainforest. Even in the heaviest swamp timber the size of the trees is relatively small. While in some swamps the lower stories are inhibited by intermittent flooding, there may be rank growth of tender herbaceous plants, especially of climbing species of aroids, begonias, and the like. Creepers and lianas with aerial roots are conspicuous. Standley (*loc. cit.*) describes a swamp forest of the Tela area as made up largely of *Pithecolobium longifolium*, *Cynometra* spp., *Dalbergia monetaria*, and *Inga* spp., and the same writer points out the occurrence there of the *gualiqueme* or *pito* swamp, a wet-ground consocies of *Erythrina* spp., found also to a limited extent on the Pacific coast. Cecropia, balsa, willow (*Salix chilensis*), and *tambor* (*Schizolobium*) are ubiquitous in the river swamps, and heliconias may be abundant.

CAÑA BRAVA BRAKES: Rank stands of *caña brava* (*Gynerium*) may replace tree swamp in poor flood-plain soils.

BAMBOO THICKETS: Of fairly frequent occurrence, again usually on stream banks, but on better soil than the above, are groves of big-stemmed bamboos that may be so densely spaced as to be nearly impenetrable.

HUISCOYOL SWAMP (PL. 22, FIG. 1): This exclusive community of *Bactris* spp., a slender clump palm with ghastly, glass-hard stem spines, is widespread in the Caribbean plain and of occasional occurrence on the south coast. Even more than the two preceding situations the *huiscoyol* swamp is a dreary and forbidding environment, for the human intruder at least. I rate as one of the more harrowing misadventures of my field experience three hours spent lost in a maze of tunnel-like tapir trails in knee-deep water in a *huiscoyol* swamp. These swamps are relatively well populated by mammals and larger birds, owing probably to the large crops of fairly palatable fruits that they produce.

HABITATS COMMON TO *SERRANÍAS* AND LOWLANDS

GALLERY FOREST

VEGA AND RIVER-BOTTOM FORESTS

Plate 22, figures 1, 2; plate 23, figure 1; plate 24, figure 1

These are corridors of varying breadth confined to the flood plains and valleys of streams. Usually dominated by fig and ceiba, or by *guanacaste* and other monsoon forest species at the higher levels, there is progressive admixture of rainforest trees as the lowlands are approached, until finally the gallery forests of the lowland Caribbean streams may show only minor differences from the sur-

rounding tropical rainforest. The vega forests are obviously of the greatest zoogeographical significance, serving as mesic highways for the rainforest biota. As was mentioned earlier, they may even extend up ravines and establish contact with descending fingers of cloud forest.

DRY GULLIES AND FENCE ROWS

In the upland valleys and drier lowlands the strips of slightly modified soil environment following the beds of dry gullies and draws and the more ancient trails and fence rows produce narrow files of trees which often belong to species that occur widely scattered in the surrounding territory, but which in the hedge rows may afford a fairly continuous leaf canopy, during the wet season at least, and include several species that produce edible fruits in abundance. Some of these trees are heavily infested by mistletoe, the berries of which are a major seasonal item in the diet of a number of birds. Some of the more common trees of this widespread vegetational type are *molinillo* (*Luchea candida*), *tapaculo* (*Guazuma ulmifolia*), *Indio desnudo* (*Bursera simaruba*), *jocote* (*Spondias mombin*), *piñón* (*Jatroplin curcus*), *madrecacao* (*Gliricidia sepium*), *calgalera* (*Celtis iguanaea*), and *macuelizo* (*Tabebuia pentaphyla*).

HONDONADAS

Plate 15, figure 2; plate 23, figure 2

Although sharing many features with the two preceding habitats, the ravine forests, known locally as *hondonadas*, show certain characteristic aspects that probably warrant their recognition as separate biotic communities. Here again, however, it should be emphasized that the *hondonadas* may undergo more divergence in details of vegetation from lowland to upland than may be seen when their extremes of variation are compared with some vega forest or fence row types. Typically, however, *hondonadas* are relatively deep, narrow troughs with probably higher and more even humidity than the preceding communities and certainly with more constant temperature and conspicuously less illumination. They are not subject to annual flood scouring of their lower levels as are the vega forests, and mostly the dry season produces little change in the upper leaf canopy. Faunistically they are virtually unexplored, and when data become available this major habitat will almost certainly require extensive subdivision. Since the *hondonadas* furnish relatively cool, damp, and shady corridors for crossing dry savanna, steppe, and *ocotal* and merge with the floodplain forests to afford often continuous connection between lower tropical rainforest and upper tropical cloud forest, they must be regarded as a factor of prime importance in the ecology of the region.

MONSOON FOREST

Plate 25, figures 1, 2; plate 26, figure 1

Inland from the marine-climate rainforest and away from the vega forest of the larger streams, the lengthening dry season gradually suppresses many of the trees of the primeval *selva* and favors deciduous species. Thus, there develops a modified rainforest, called variously "dry forest," "deciduous forest," "wet-season forest," or "monsoon forest," which is of vast extent in Honduras, in places climbing the windward slopes to elevations of 610 meters (2000 feet) or even 915 meters (3000 feet), to be lost in the *ocotal* or in cloud forest. Typically it is by no means a benign environment, a fact that repeatedly is reflected in the poverty of its faunas. While in the rainy season the association gives the superficial impression of a primeval forest, a closer scrutiny reveals strong differences. The trees are smaller, more widely spaced, and markedly less varied as to species. Since the burden of their foliage is lighter they are rarely buttressed. The ground is not necessarily completely shaded, even in *invierno*, and the greater illumination often permits growth of grasses, while arums, peperonias, begonias, and similar tender herbs do not thrive. Many of the trees (sometimes a majority, sometimes not) lose their leaves at the end of the wet season, bringing a drastic change in the appearance and ecology of the habitat. Sunlight penetrates freely, and wind sweeps through the woods, drying out and hardening the soil, tumbling the leaf litter about, and retarding development of humus. Only the larger animals or those capable of going into aestivation, or the fauna of the bromeliads (which are sometimes abundant, sometimes absent), can survive in the higher, more xeric extensions and outlying patches of monsoon forest. There are ob-

viously a large number of local variations of this major habitat and all sorts of intergrading between it and most of the other land types.

Mixed Scrub

Plate 26, figure 2

This is a generic term, but one with evident validity as a broad type that apparently recurs with frequency throughout the world under similar conditions of climate and perhaps to some extent of soil. In general climatological terms the requirements for the type have been given as a 40- to 60-inch rainfall with markedly seasonal distribution. While in Honduras the association does not turn up invariably within these precipitation limits, it nevertheless appears to be largely a climatic phenomenon and one that is favored by hygric conditions intermediate between those of monsoon forest and those of thorn forest, with both of which it shares its flora. While often found on cut-over land as a successional stage, it appears to be the climax association for some areas. To what extent it is affected by edaphic factors is not known, although in the Comayagua Valley abrupt transition from mixed scrub to thorn forest and to steppe vegetation may be observed, with little or no concomitant variation in climate or elevation, and it is believed that these changes are due principally to differences in the character of the subsoil.

The intermediate position of the mixed scrub is illustrated by its relationships with locally contiguous types. Besides the relationship mentioned above I have seen many examples of transition from scrub to *espinal* (wet meadow of *espino blanco*, *Acacia farnesiana*, pl. 27, fig. 1) or to short grass and sedge meadow, where a hardpan is present. Where ground water lies deep but fertility is moderate it may grade or break into *carbonal* (*Mimosa tenuiflora* in pure stand), and on permeable sterile gravel and eroded soils it often gives way to cactus-agave steppe (pl. 27, fig. 2). On the drier slopes with poor, shallow soils it is replaced by *ocotal*. As the bases of the steeper cliffs are approached and seepage ameliorates the effects of *verano*, the scrub loses thorn components, acquires mesophytic elements, and either becomes a mesic woods closely similar to wet monsoon or gallery forest or grades into *robledal*.

Thorn Scrub

Plate 28, figures 1, 2

In Honduras thorn forests or thickets of various types are widespread in dry country on well-drained to poorly drained soils of fair to good fertility. Perhaps the most ubiquitous thorn forest in Honduras is the *carbonal*, a more or less pure stand of carbon (*Mimosa tenuiflora*); frequently mixing with this, especially in cut-over and burned areas, is the pink-flowered *Mimosa albida*, which on occasion forms its own exclusive thickets both in the valleys and in *ocotal* draws. Elsewhere, and most notably in the extremely interesting thorn forests of certain sections of the Honduras Depression, the association may be made up of a wide variety of thorn trees, both leguminous and otherwise. The pure-stand *carbonales* and *espinales* for the most part support poor permanent faunas, although they are used extensively as refuge cover by the more vagile animals such as the larger mammals and ground birds. In the big mixed-thorn woods, however, the variety and relatively large size of the trees make for more stable ecology, offering especially a more constant and varied food supply. In some of these forests deer and peccary may be common and such forest animals as the *pava*, the *tepescuinte* (paca), and *pisotes* (coatí) evidently find year-around sustenance. As was mentioned previously, only a very slight disparity in moisture economy supports the divergence of thorn scrub and mixed scrub. Although the former is in general the more xeric environment of the two, it usually has a richer vertebrate fauna, owing presumably to a higher percentage of trees bearing edible fruits.

Steppe

Plate 27, figure 2; plate 29, figures 1, 2

With or without the sanction of the climatologists it is necessary to recognize the occurrence of steppe communities in Honduras. I use the term to embrace all semi-desert terrain in which whatever tree or shrub growth may occur is very widely, and often erratically, spaced and in which most or all of the herbaceous vegetation disappears during the dry season. Such steppes may be either natural or artificial. It is hard for the observer to distinguish between the two types, and I

doubt if the fauna ever does. Such wastes occur regularly in rain shadows, on either valley or mountainside, where the rainfall is minimum and the *verano* is trenchant and uncompromising. What I take to be wholly natural steppe associations occur on the terraces of sterile quartzite gravel along the Choluteca River, in the southern part of the Comayagua Valley, in the lee of the mountains of the Caribbean coast, and on numerous undifferentiated ash beds and lava flows throughout the country, especially on the Pacific slope. In the *ocotal* regions what appear to be artificial steppes are encountered with depressing frequency. While gullying and such more evident forms of soil loss are astonishingly inconspicuous in Honduras, the insidious processes of sheet erosion are nearly everywhere evident in the inhabited uplands. Through burning, clearing, overgrazing, and the other classic forms of land abuse the organic content of the soil is constantly reduced and its capacity to retain water lost. Runoff of the occasional torrential rains of *invierno* sweeps down the slopes and eventually bears away everything portable, leaving only bare rock, coarse rock debris, or raw ash. These processes are not confined to ruderal lands but go on all the time in the lower and more open *ocotal* where ground vegetation is sparse. There seems to me to be little ecological justification for a distinction between these erosion steppes and the indigenous climatic variety, since living conditions are equally rigorous in the two. The harshness and parsimony of the relatively huge areas in which steppe conditions occur in Honduras are in my mind sufficient explanation for the faunal poverty which, despite a strategic zoogeographic location and large species list, is a salient faunistic feature of the interior of Honduras, and one that is remarked upon by nearly all visiting zoologists.

Savannas

Although the so-called savanna climate prevails over a large part of Honduras, there is no certainty that any of the several types of savannas found in the region are primarily of climatic origin. Instead, except possibly for those of the outer Mosquitia, the savannas of Honduras appear to owe their existence to a number of topographic, edaphic, and cultural factors. Certain more obvious conditions favoring savanna formation are flat terrain, presence of hardpan, seasonally or sporadically high water table, overgrazing of potentially more hygric associations, repeated burning of potentially more hygric associations, and agricultural operations permitting invasion of cleared land by exotic or native grasses as a successional stage.

The mere fact that nearly all the savannas of inland Honduras occur on flat land suggests strongly that they are caused primarily by other than climatic factors. For example, throughout the highlands *ocote* pines cover most of the slopes. Wherever the land levels off, however, whether in a quarter-acre swale or in a 10,000-acre valley floor the *ocotal* is replaced either by savanna or by some type of hardwood or thorn forest. While the relationship between savanna and the various forest types may sometimes be a question of local climatic effect, the influences that segregate these associations from *ocotal* are almost certainly most frequently edaphic.

It appears likely that the superficially similar savanna environments may often have developed through the operation of distinct sets of factors. It is usually difficult to see any difference between a natural short-grass subclimax and a purely cultural *potrero* in which the same grasses are favored and natural succession is held in check by the direct grubbing out of invading bushes and trees. Some of the grazed llanos are clearly of composite origin (pl. 30, fig. 1). One often sees large tracts of llano on rolling land where the flat, short-grass areas between the hills are essentially natural (pl. 31, fig. 2; pl. 32, fig. 1) but where the same clean grassland sweeps up the hillsides to meet and even enter the pine woods, this inclined portion being maintained only by machete work. A close comparison of the flat and sloping sections of these llanos usually reveals marked differences in the component grass and sedge species, even though the appearance of the two zones is very similar. If such terrain as this is untended and not grazed, the inclined edges often revert to thicket or *ocotal* while the flat areas remain meadow or savanna.

Of the great variety of savannas that occur in Honduras the following three groups suggest themselves:

TREE SAVANNA

This is essentially a flat or gently rolling grassland set with more or less widely spaced trees which usually are of one or two species in a given tract of savanna. A type that is widely distributed on the Pacific slope from near sea level up to at least 1220 meters (4000 feet) in elevation is the distinctive *jícaro* savanna (pl. 30, fig. 2) in which an orchard-like stand of *jícaro* or *guacal* (*Crescentia alata*) is associated with a grass-sedge understory and varying concentration of meadowland bushes. The characteristically hollow trunk and limbs of the *jícaro* trees are usually occupied by various insects, frogs, and reptiles, and it is perhaps for this reason that the *jícaro* orchards are among the more populous savanna habitats. The association occurs on soils that are often boggy in *invierno* and hard-baked in *verano*. Where a definite hardpan retains the wet-season water to the extent of forming marshes or shallow ponds, the main arborescent type is *espino blanco* (pl. 27, fig. 1), sometimes intermixed and rarely even replaced by guava and *roble*. In eastern Morazán and Olancho I have seen the latter two species in pure stands in marshy meadows.

TALL-GRASS SAVANNA

Plate 31, figure 1

This term serves as a catch-all for a variety of habitats in which some species of tall grass is the dominant plant but in which the vegetation is not determined by a permanently high water table, as in the various kinds of grass marshes. In sections of the Mosquitia, associations of tall coarse grasses cover great areas of what may be true climatic savanna, but these merge with similar types that in central Olancho are certainly partly cultural. Such introduced pasture grasses as Jaragua, Guinea, Para, some of which are said to have reached Honduras as many as a hundred years ago, have taken over huge tracts of suitable terrain, and while in some sections they may be replaced by thorn, elsewhere they appear to be in equilibrium with local conditions.

SHORT-GRASS SAVANNA

Plate 30, figure 1; plate 31, figure 2; plate 32, figure 1

This is essentially a meadow-soil environment with short grasses (here called indiscriminately *grama*), usually including carpet grass, and a number of diminutive sedges. It is evidently consistently edaphic in nature and ranges in extent from small mountain meadows and blanket-sized microsavannas in the highland *ocotal* to the great *grama* plains of Olancho. Here again it is frequently impossible to identify the effects of natural as opposed to cultural factors, but here also the distinction is probably academic from the standpoint of the fauna.

FRESH MARSH

Plate 15, figure 1; plate 32, figure 2

While marshland is represented by relatively small total area in Honduras, it includes a rather wide variety of hygric situations. These may be locally disjunct, azonal *chaguïtes* or may grade gradually into other communities such as tree swamp and meadow-soil savanna types. As used here the term marsh indicates any association of hydrophitic grasses or herbs on soil that remains inundated or boggy even during the height of the normal dry season. The communities range from such single-form consocies as the peat swamps of *gamalote* grass (*Paspalum fasciculatum*) of the lowlands and the micromarshes of *Juncus* 6000 feet (1830 meters) or more up at the cloud forest margins to the lush and teeming wet "prairies" and lake- and lagoon-shore marshes of the coasts and of the Lake Yojoa area. The latter semi-aquatic habitats are insistently similar in their varied biota to equivalent situations in the southeastern United States. The flora is usually dominated by such familiar floating and emergent plants as *Nymphaea*, *Castalia*, *Jussiaea*, *Pistia*, *Eicornia*, *Thalia*, *Typha*, *Pontedaria*, *Persicaria*, and *Hibiscus*. The "Sabalian" atmosphere is heightened by the bird fauna, both by its composition and by its extraordinary luxuriance. When one poles a boat through a marsh in which purple and Florida gallinules tread the pads, wood ibises and whole series of familiar heron species stand in the shallows, redwing blackbirds sing in the reeds, and teal and pintails puddle in the open holes, one is loath to accept the fact that the marsh lies at an elevation of 2000 feet (610 meters) in the mountainous interior of Honduras. The patches of white-shelled snail eggs cemented to the emergent plant stems by

the same snail, *Ampularia*, that feeds the Florida limpkin in no way help the observer in orienting himself. It is only when he realizes that the dark, log-like form gliding before his boat is a crocodile and not an alligator, or when he flushes a flock of black-and-white muscovies or whistling tree ducks, or notices the spur-wings feeding with the rails and gallinules that the site settles down for him in its proper place on the map.

I have mentioned earlier the extraordinarily dilute character of the fauna of inland Honduras. Compared, for example, with such an area as northern Florida, much of the interior of Honduras must be regarded as a faunal desert as regards the majority of the forms included in its relatively long species list. It is only in the marsh community that the two regions meet on common ground. It seems to me a most noteworthy fact that the same habitat, which in the rich Florida region supports vertebrate life in maximum luxuriance, should show equal and perhaps even greater fecundity in Honduras where generally animal life is varied but not abundant. It may be worth mentioning that if I were asked to recall the most prolifically populated animal habitats of my limited experience, I should name without hesitation Bivan's Arm of Paynes Prairie in Alachua County, Florida, the Choluteca Lagoons in the Pacific coastal plain of Honduras, and the shore-line marshes at the northern and southern ends of Lake Yojoa.

CULTURAL SITUATIONS

GUAMIL

Plate 33, figure 1

Throughout Honduras the term *guamil* is applied to abandoned farm lands that have grown up in thickets of brush, vines, and saplings. Enormous tracts of former banana lands are at present *guamil*, as are considerable areas in the more fertile valleys not currently under cultivation. In the higher mountains where terrain covered primitively by cloud forest has been under cultivation for centuries, the *guamil* stage is a regular part of the endemic tillage cycle. When the primeval forest has been felled and burned and several crops made among the stumps, the parcel is allowed to lie fallow through a grass-herb-vine stage and a brush stage. When good-sized saplings have become established in stands dense enough to shade out the grass and weeds, the area is cleared and burned once more and a new crop is planted.

Despite their cultural origin, the *guamil* habitats are important ones with often varied faunas which, though in large part made up of the materials available in contiguous areas, usually include as well a number of extraneous forms, and nearly always show the increased abundance in individuals that is a well-known feature of forest margin communities generally. Moreover, when the *guamiles* occur, as they often do, in such critical sites as the zone between the upper limits of the *pinabetal* and the lower margins of the cloud forest, where two very different biotas have met in them for periods of hundreds and possibly thousands of years, these habitats would seem peculiarly propitious for speciation through the type of "introgressive hybridization" discussed by Anderson (1948).

FIELD CROPS

Although the ratio of crop-producing land to unused terrain is low in Honduras, there are a few field crops, such as rice, corn, coconuts, cane, and bananas, plantings of which hold an important place in the list of animal habitats. While a field or orchard located in a rich natural area may support only a relatively impoverished fauna because it effects a reduction of the natural ecological diversity, other cultural sites may offer asylum from unfavorable factors of the environs and may thus be relatively well populated. Thus, a *milpa* or a bean patch offers what may be an attractively abundant food supply if it occupies flood-silted vega land; an irrigated *bananal* located in a rain shadow may afford the zoologist the only good collecting in an entire region; for geckos, certain snakes, and rats, a coconut plantation may be a far more favorable environment than any natural one at hand; and if the zoologist wants lizards of the genus *Cnemidophorus* he may count himself blessed if a pineapple field is at hand.

SELECTED BIBLIOGRAPHY

ANDERSON, EDGAR

1948 Hybridization of the habitat. Evolution, vol. 2, pp. 1–9, fig. 1.

BARRETO, JUAN

[MS.] La geología del distrito de Agua Fria.

BENGTSON, N. A.

1926. Notes on the physiography of Honduras. Geogr. Rev., vol. 16, pp. 403–413, figs. 1–8.

BEVAN, ARTHUR

1945. Forestry in Latin America and its future. *In* Verdoorn, Frans, Plants and plant science in Latin America. Waltham, Massachusetts, Chronica Botanica Co., pp. 174–176, 1 table, 2 maps.

BOURNE, W. CLINTON, ET ALIA

1946. Preliminary survey of conservation possibilities in El Salvador. Serv. Coop. Interam. de Salud Publica, xiii+167 pp., 72 figs., 12 tables.

CARR, ARCHIE F., JR.

1949. La Montaña Llorona. Sci. Monthly, vol. 68, pp. 225–234, pls.

CLARAMOUNT, ANTONIO, ET ALIA

1947. An. del Observatorio Nac. Meteorologico de San Salvador, Pub. Minis. Cult. Pop., 1947, pp. 1–46.

DICKEY, DONALD R., AND ADRIAAN JOSEPH VAN ROSSEM

1938. The birds of El Salvador. Field Mus. Nat. Hist., zool. ser., vol. 23, no. 406, pp. 1–609, figs. 1–29, pls. 1–24.

DUNN, EMMETT REID

1931. The herpetological fauna of the Americas. Copeia, pp. 106–119, figs. 1–6.

1932. Reptiles and amphibians from Honduras. Proc. Acad. Nat. Sci. Philadelphia, vol. 84, pp. 21–32.

FOYE, WILBUR G.

1918. Notes on a collection of rocks from Honduras, Central America. Jour. Geol., vol. 26, pp. 524–531, fig. 1.

GOLDMAN, EDWARD ALPHONSO

1920. Mammals of Panama. Smithsonian Misc. Coll., vol. 69, pp. 1–309, pls. 1–39.

GOODWIN, GEORGE GILBERT

1942. Mammals of Honduras. Bull. Amer. Mus Nat. Hist., vol. 79, pp. 107–195.

GRISCOM, LUDLOW

1932. The distribution of bird life in Guatemala. Bull. Amer. Mus. Nat. Hist., vol. 64, pp. i–ix, 1–439, figs. 1–11, maps 1–2.

KOVAR, P. ANTON

1945. Vegetación de El Salvador. *In* Verdoorn, Frans, Plants and plant science in Latin America. Waltham, Massachusetts, Chronica Botanica Co., pp. 56–57.

OLSON, EVERETT CLAIRE, AND PAUL ORMAN MCGREW

1941. Mammalian fauna from the Pliocene of Honduras. Bull. Geogr. Soc. Amer., vol. 52, pp. 1219–1244, figs. 1–5, pls. 1–4.

PENDLETON, ROBERT LARIMORE

1945. Some important soils of Central America. *In* Verdoorn, Frans, Plants and plant science in Latin America. Waltham, Massachusetts, Chronica Botanica Co., pp. 163–165.

PETERS, JAMES LEE

1929. An ornithological survey in the Caribbean lowland of Honduras. Bull. Mus. Comp. Zool., vol. 69, pp. 397–478.

POPENOE, WILSON

1945. Plant resources of Honduras. *In* Verdoorn, Frans, Plants and plant science in Latin America. Waltham, Massachusetts, Chronica Botanica Co., pp. 273–275.

REDFIELD, ARTHUR H.

1923. The petroleum possibilities of Honduras. Econ. Geol., vol. 18, pp. 474–493, fig. 67.

REHN, JAMES ABRAM GARFIELD

1932. A naturalist in Honduras. Bull. Pan Amer. Union, vol. 66, pp. 390–400, 7 pls.

SAPPER, KARL

1899. Ueber Gebirgsbau und Boden des Nordlichen Mittelamerika. Petermanns Mitt., suppl. vol. 27, no. 127, pp. 1–119, 3 maps, 25 profiles.

1905a. Grundzuge des Gebirgsbau von Mittelamerika. Rept. 8th Internatl. Geogr. Congr., Washington, pp. 231–238, 1 map.

1905b. Ueber Gebirgsbau und Boden des sudlichen Mittelamerika. Petermanns Mitt., suppl., vol. 32, no. 151, pp. 1–82, 2 maps, 2 profiles.

1932. Klimakunde von Mittelamerika. Handb. Klimatol., vol. 2, pt. H, pp. 1–74.

SCHMIDT, KARL PATTERSON

1926. Honduras. *In* Shelford, Victor E., Naturalist's guide to the Americas. Baltimore, Williams and Wilkins Co., pp. 601–602.

1942. A cloud forest camp in Honduras. Chicago Nat., vol. 5, pp. 23–30, figs. 1–3.

1943. Corollary and commentary for "Climate and evolution." Amer. Midland Nat., vol. 30, pp. 241–253, 1 table.

1946. On the zoogeography of the Holarctic region. Copeia, pp. 144–152, 1 map.

SCHMIDT, KARL PATTERSON, AND LAURENCE COOPER STUART
1941. The herpetological fauna of the Salamá Basin, Baja Verapaz, Guatemala. Field Mus. Nat. Hist., zool. ser., vol. 24, pp. 233–247, figs. 21–22.

SCHUCHERT, CHARLES
1935. Historical geology of the Antillean-Caribbean region. New York, John Wiley and Sons, Inc., ch. 22–28, pp. 314–390, figs. 51–61.

SHANK, PAUL J.
[MS.] Forest resources of Honduras. Paper read at Internatl. Congr. Conservation, Denver, Colorado, August 1, 1948.

SIMPSON, GEORGE GAYLORD
1943. Turtles and the origin of the fauna of Latin America. Amer. Jour. Sci., vol. 241, pp. 413–429.

SMITH, ALBERT CHARLES, AND IVAN MURRAY JOHNSON
1945. Phytogeographic sketch of Latin America. *In* Verdoorn, Frans, Plants and plant science in Latin America. Waltham, Massachusetts, Chronica Botanica Co., pp. 11–18, pls. 5–20b, 1 map.

SQUIER, EPHRAIM GEORGE
1858. The states of Central America. New York, Harper and Bros., xvi+774 pp., 57 figs., 8 pls., 5 maps.

STANDLEY, PAUL CARPENTER
1931. Flora of the Lancetilla Valley of Honduras. Field Mus. Nat. Hist., bot. ser., vol. 10, pp. 1–418, pls. 1–68.

STANDLEY, PAUL CARPENTER, AND JULIAN ALFRED STEYERMARK
1945. The vegetation of Guatemala. *In* Verdoorn, Frans, Plants and plant science in Latin America. Waltham, Massachusetts, Chronica Botanica Co., pp. 275–278, 1 map.
1946. Flora of Guatemala. Fieldiana: Botany, vol. 24, pt. 5, pp. 1–502.

STONE, ROBERT GRANVILLE
1945. Climatology and meteorology [of Latin America]. *In* Verdoorn, Frans, Plants and plant science in Latin America. Waltham, Massachusetts, Chronica Botanica Co., pp. 156–163, figs. 1–6.

STONE, WITMER
1932. The birds of Honduras, with special reference to a collection made in 1930 by John T. Emlen, Jr. and C. Brooke Worth. Proc. Acad. Nat. Sci. Philadelphia, vol. 84, pp. 291–342.

STUART, LAURENCE COOPER
1948. Amphibians and reptiles of Alta Verapaz, Guatemala. Misc. Publ. Univ. Michigan Mus. Zool., vol. 69, pp. 1–109, figs. 1–10, tables 1–35, 1 map.

TREWARTHA, GLEN THOMAS
1943. An introduction to weather and climate. New York, McGraw-Hill Book Co., xi+545 pp., 198 figs., 5 pls.

VERDOORN, FRANS (EDITOR)
1945. Plants and plant science in Latin America. Waltham, Massachusetts, Chronica Botanica Co., xxxvii+381 pp., 45 text figs., 38 pls.

WELLS, WILLIAM V.
1857. Explorations and adventures in Honduras. New York, Harper Bros., xxiv +588 pp., 63 text figs.

YUNCKER, TRUMAN GEORGE
1938. A contribution to the flora of Honduras. Field Mus. Nat. Hist., bot. ser., vol. 17, pp. 287–407, pls. 1–18.
1940. Flora of the Aguán Valley and the coastal regions near La Ceiba, Honduras. *Ibid.*, bot. ser., vol. 19, pp. 245–346, figs. 1–8.
1945. The vegetation of Honduras, a brief review. *In* Verdoorn, Frans, Plants and plant science in Latin America. Waltham, Massachusetts, Chronica Botanica Co., pp. 55–56.