ECOLOGY

VOL. 25 APRIL, 1944 No. 2

CLIMAX VEGETATION IN TROPICAL AMERICA

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INTRODUCTION

Since 1940 the writer has been able to devote a considerable portion of his time to the study of problems of vegetation and land usage in the islands of Trinidad and Tobago in the West Indies. The aim was to acquire sufficient knowledge for the preparation of a comprehensive account of the vegetation types and of accurate and detailed vegetation and land utilization maps on a scale of 1 : 50,000. Early it became clear that to get the fullest value from that part of the work which dealt with vegetation types, its horizon must be extended beyond the limits of Trinidad and Tobago, and that an attempt should be made to relate the vegetation types to those of other parts of the world. Suitable names for communities had to be chosen. It was further desirable to obtain a system of classification into which local vegetation would fit and by which the successional and other mutual relations of the communities would be clarified. None of the objects proved easy of attainment. It will be some time before an integrated ecological world-picture can be assembled, particularly one which includes the tropics, and in the meantime nomenclature and classification of tropical vegetation are unfortunately in great confusion. The numerous workers in this field during the last thirty years mostly found that accepted systems of nomenclature and classification were unsuitable for use under their local conditions, having been evolved to suit other—generally temperate—circumstances, and each had to build his own system. It is still doubtful whether anything better than this can be expected. Burtt-Davy's very courageous attempt ('38) to correlate the nomenclature and harmonize the classification of tropical woody vegetation types has not met with complete success and has not been generally accepted. The great obstacle in attempts of this kind is the difficulty of securing adequate comparative data. Undoubtedly a great advance has taken place with Richards' elaboration of technique for physiognomic description, including his profile diagram (Davis and Richards, '33; Richards, '36; Richards, Tansley and Watt, '39).

After study of the literature it was decided that it would not be possible in the present state of knowledge to correlate the vegetation of Trinidad accurately and in detail with types of the Old World. For this reason Burtt-Davy's system could not be unreservedly adopted since it is based upon African and Asiatic descriptions. It was decided to restrict the general horizon to tropical America alone, though the project was still faced with considerable difficulties. The vegetation of the American tropics has received even less study than tropical Africa and Asia so that accurate and detailed accounts are few, and there is even less approximation to general agreement upon basic principles. This relative lack of attention from the ecological standpoint which tropical America has received is unfortunate in view of the exceptional opportunities which it presents for the study of mature, relatively undisturbed communities. The American tropics have not for millions of years carried the dense animal populations so notable in Africa, and even today human settlement has but scratched the fringes of a vast wilderness. In consequence many ecological problems are easier to elucidate since biotic factors are less important. The writer believes that the key to the understanding of many African types, particularly those where fire and grazing are present factors, may lie in the study of communities in the Americas.

An attempt has recently been made by Barbour ('42) to regularize the nomenclature of forest types in tropical America by a method very similar to that of Burtt-Davy. His divisions are only "primary forest types"; that is, they constitute the most obvious and easily recognized groups and hence the system is easy to apply in the field. The principal objection in Trinidad was that work has progressed so far that more than primary forest types can be recognized. It was decided that the vegetation of Trinidad and Tobago would be best served by inclusion within a more detailed system of classification embracing all of tropical America and based upon floristic, physiognomy and habitat, with the chief emphasis upon physiognomy. Biotic communities, in Phillips' sense ('31), could not be dealt with at the present stage. There is no desire to decry the soundness of Phillips' concepts, but as that author has himself pointed out, in early stages of study nomenclature and classification must of necessity be based upon the plants.

No attempts to classify tropical vegetation can afford to neglect the works of Schimper ('03), Warming ('09), Chipp (in Tansley and Chipp, '26) and Champion ('36). The nomenclature of the two last-named authors should not be applied without great care to tropical America at present, but Schimper and Warming attempted a world-wide picture and it would be desirable to follow them wherever the facts warrant. These four works were reviewed in some detail by Burtt-Davy ('38) as the basis of his paper. The writer has built upon the same basis and as far as possible has followed the method and nomenclature of Burtt-Davy, to whom grateful acnowledgment is due.

Classification begins with climax floristic groups or associations, which are arranged into formations on the ground of physiognomy and the formations are later placed together in series according to habitat.

Only climax communities are here considered by the writer. A discussion of the theoretical questions relating to succession and the nature of the climax is beyond the scope of the present paper. Briefly, the writer has classed as "climax" any community which is apparently stable, mature and integrated, and has relegated to the status of "seral" any community which is patently in a state of change, development or transition. In the words of Tansley and Chipp ('26, p. 7) "a climax type is relatively permanent under the given conditions." Admittedly it is difficult to give a satisfactory definition of climax but in practice there exists little confusion between communities which are permanent in terms of human time and those which have appeared on bare areas and are in relatively rapid evolution. This view of the climax would include the "deflected climax" (Godwin, '29) but the writer has excluded communities of this order and will deal only with "natural" climax types.

Floristic Groups

If we consider a hypothetical case of a field worker commencing a vegetation survey of an unstudied area in the tropics, his first step will be to identify the more important members of the flora and to collect data on the relative abundance of species by enumerating sample plots or strip traverses. From these data he will be able to define a certain number of distinct floristic groups. From the enumeration records or field observation it will in practice be found that stocking (floristic composition) varies from point to point but in any one locality may remain relatively constant over a certain area, large or small, and that when a change takes place it may often do so fairly abruptly. The actual definition of a floristic group must rest with the field worker. The group will be any community whose composition remains fairly constant over a given area, but the size of the area chosen as a unit must depend upon local circumstances. A certain number of transitional types (ecotones) will be recorded wherever changes of habitat are gradual. The next step is the selection of a diagnostic species, which will usually be among the principal dominants. As an ecological term, "dominant" refers to those members of the community which exert a controlling influence over the other components and differs from the silvicultural usage which is commonly taken to refer to trees whose crowns are more than half exposed to full illumination. The two usages do not necessarily coincide. The ecological dominants of a community are the members of the highest *closed* stratum—the grass layer in savanna, the lower, middle or upper story in forest according to structure. The most abundant dominants are usually selected as the diagnostic species from which the assemblage is named but there is no absolute rule and any common species whose presence is felt to be diagnostic may be selected.

Having delineated floristic groups and named them, it is necessary to decide their place in classification. It will be clear, probably, that not all the groups are of equivalent rank. Some will be extremely small and localized and may appear to be sub-types of groups covering wider areas. For climax communities it seems desirable to adopt the Clementsian system ('36), using the terms *association*, *consociation*, *faciation*, *lociation*, *society* and *clan*, though in applying these terms to tropical usage some slight modification may be necessary. The writer is applying them to climax communities in his own and not in Clements' sense. The term *association* is the best known and most widely used. It is commonly employed by ecologists in the tropics to name any floristic group with which they happen to be dealing, regardless as to whether the group in question is genuinely an association or not. In this class belong the present writer's "associations" of the Trinidad mountains ('42) and Stevenson's Orbignya-Dialium-Virola "association" of British Honduras ('42). While not knowing the wider range of the group and allied groups under review, it is impossible to decide whether they should rank as associations or not and the word serves as a temporary label. It would, however, probably be preferable to speak at present of the *Licania ternatensis-Byrsonima spicata* "assemblage" and the Orbignya-Dialium-Virola "assemblage." Correctly, the term "association" should be applied to the largest possible group which has consistent dominants, either of the same or closely allied species. For example, throughout the Lesser Antilles there is a certain zone in the mountain forests dominated generally by *Dacryodes excelsa* Vahl. and sundry species of Sloanea, and a zone in dry areas near the coastline dominated by *Bursera simaruba* (L.) Sarg. and sundry species of Lonchocarpus. All such assemblages belong to the Dacryodes-Sloanea or Bursera-Lonchocarpus association. The composition varies locally in the different islands, even to the extent of ousting the association dominants (as dominants, though they will still be present as associates). The local type in each island should be regarded as a *faciation* and named from some species which comes locally into prominence; thus in Grenada one may speak of the *Licania ternatensis* faciation of the Dacryodes-Sloanea association, and in St. Vincent of the *Ormosia monosperma* faciation. It is difficult in the tropics to use the term *consociation* in Clements' sense as a sub-group of the association characterized by a single dominant and it is preferable to adopt the British usage of the term which is applied to a group of equivalent rank to the association where there is only one clear dominant. The *Pterocarpus officinalis* consociation is well known in the Caribbean, a swamp forest composed almost exclusively of this species, and there are Clusia consociations in the cloud forest zones of Trinidad and some of the Lesser Antilles.

The *location* is a division of the faciation and is found on relatively restricted areas within the latter where, due to some slight alteration of the habitat factors, floristic composition is locally varied. It is a localized phase of the local assemblage which itself is a phase of the major group. *Societies* are yet smaller groups of plants and the term is most commonly applied to *stratum-societies* (e.g. Davis and Richards, '33), plant assemblages characteristic of certain levels in the complex stratification of tropical forest. Thus we have societies of sun-epiphytes and shade-epiphytes, made up of bromeliads, orchids, aroids and so on, and field- and ground-layer societies containing small woody plants and herbs, grasses, ferns, filmy ferns and mosses. A *clan* is the smallest group of all and consists of a group of a few square yards extent dominated by individuals of one species. Clans are usually confined to the ground layer and include the patches of Heliconia or ferns found in "moist" forest or the aggregations of terrestrial species of Bromelia in "dry" types. Descriptions of societies and clans are only to be found in the most detailed ecological works and little is as yet known of these groupings in tropical America. They are, however, of more than academic interest, for the study of bromeliad societies is now coming into prominence in anti-malarial work.

Hitherto there has been little attempt to define floristic communities as other than "associations," irrespective of their true rank. It is hoped that the present attempt to clarify the position may result in greater attention to this point in the future. In general, an association proper will be found to have a fairly considerable range and probably overstep the boundaries of any one island or republic. The assemblage studied in any one locality is probably at highest a faciation. The mangrove association *Rhizophora mangle-Avicennia nitida-Laguncularia racemosa* ranges throughout the tropical Atlantic seacoasts of Africa and America. The pine barrens of Florida are probably one association with those of Cuba, the Isle of Pines, Honduras and Yucatan, and it may well prove that the rain forests (in the strict sense defined below) of the whole Guiana region should be considered as one association, probably to be named Eschweilera-Licania, with the almost pure stands of greenheart and wallaba as Ocotea and Eperua faciations.

Clements restricts the use of the above terms to climax communities only and it is recommended that his appropriate terms be applied also to seral communities in the tropics.

Physiognomic Groups

The total flora of the floristic unit, the association, and the relative abundance of component species are an expression of the action of a certain complex of environmental factors (concisely, a local habitat) upon the total available flora of the region. It is clear that the local habitat will remain essentially constant throughout the range of a given association, for any changes of a degree greater than is required to bring about variations in sub-types of the latter will lead to the appearance of an entirely different association. The flora of a climax association consists of such species of plants inhabiting the geographical region as can grow *in competition* under the conditions of the local habitat, and their relative abundance is decided by their relative degree of suitability under competition to those conditions. An association will exhibit also characteristic structure and life-form, features which like the flora are expressions of environment. It will frequently be found throughout the tropics that certain associations of different floristic composition exhibit the same structure and life-form, due to the action of essentially similar habitat conditions upon a different regional flora, or in the same region to slight alterations in local habitat, which have affected floristic composition, but not physiognomy. According to modern practice and especially to that recommended for the tropics by Richards, Tansley and Watt ('39) such associations may be grouped together into a larger unit, the formation, which thus is a physiognomic unit with a characteristic essential habitat, just as the association is a floristic unit with a characteristic local habitat. This conception appears to correspond with the early use of the term by Grisebach (1838) and is probably also in essence what was intended by Warming's definition ('09). Not all of the "formations" of this order which the writer describes below would be recognized by Clements as climax formations. Certain groups of them would be regarded as sub-climax. English workers would regard some of the writer's formations as climatic and some as edaphic climaxes. Since all of the associations of which the formation is composed are climax in the writer's sense (apparently mature, stable and integrated), the formation is likewise a climax unit. Another system of classification and nomenclature would have to be evolved (if necessary or desirable) for physiognomic groups containing associes, or seral floristic groups.

The physiognomic basis of classification meets all the essential requirements for the treatment of tropical formations. First, structure and life-form are capable of exact measurement and record in the field, and secondly, on the basis of actual types so recorded, structure and life-form of any desired formation can be mathematically defined. The first step is the field description of communities: structure can be demonstrated by means of diagrams prepared from actual measurement, life-form expressed mathematically in the form of percentages in various ways, such as by stating that 56 per cent of trees forming the topmost story of the forest have compound leaves. Having decided on the relative position in classification of a set of communities so described, it is possible to define precisely a formation to be called, say "Lower Montane Rain Forest" by a diagram to show typical structure and by tabulating the data showing the percentage abundance of certain life-forms. Once this has been done, a worker in some other part of the tropics can determine typical structure and life-form of any community in his area and can readily tell to what degree it corresponds with the formation so defined. An essential feature of the study is the profile diagram. It is a representation of a strip of forest, usually 200 feet long and 25 feet wide, drawn exactly to scale from measurements in the field. The strip is carefully selected to show mature structure considered typical of the formation.

A system of nomenclature has to be set up in conjunction with the system of classification, since types recognized must be given names. The writer dislikes the practice advocated by many authors of inventing pseudo-Latin or Greek names for plant communities. The aim is praiseworthy—to set up names internationally comprehensible. Unlike taxonomy, however, plant ecology has not yet been presented with a suitable system of Latin names which if sufficiently expressive were not of cumbersome length or if sufficiently concise were also comprehensible. In ecology there is not the same need for Latin names since precise vernacular names for communities seldom exist and local usage can be led to adopt a scientifically suitable name in the language of the country. For the vegetation of tropical America a parallel system of simple descriptive names in English, Spanish and Portuguese should be adequate and the writer proposes to suggest his nomenclature in parallel in these languages.

In naming formations, an important consideration is that it is desirable if possible to perpetuate names already popularly accepted. Many Schimperian terms such as rain forest and monsoon forest are already associated in general usage with certain definite types and there is no reason why this should not continue whatever system is employed for classification of those types. The writer sees no urgent reason for fresh nomenclature based consistently upon physiognomy in order to follow a classification so based. In selecting names for the formations the writer has endeavored primarily to apply terms in common use. Some of them relate to habitat, some to physiognomy, some to both. Terms belonging to Old World types have only been adopted where it was felt with reasonable certainty that they were applicable. Otherwise alternative or parallel terms are suggested. As far as possible an endeavor has been made to harmonize the nomenclature and make it consistent, but it is nowhere purely physiognomic. The classification, however, is physiognomic as the construction of the analytical key in table V will make clear. Habitat characters have only been introduced into this key in a few places for the sake of clarity and are incidental.

On theoretical grounds, it is true, the formation, as a physiognomic unit, should bear a name descriptive of the physiognomy, just as the floristic association bears a floristic name. It is not desirable to apply floristic names to the formation as Clements has done in North America. Primary definition should deal with general life-form type—forest, scrub, grassland. Secondary definition will be necessary in addition in most cases and the most obvious secondary feature of the physiognomy should be employed for the purpose, giving terms such as "deciduous forest" and "thorn woodland." It is legitimate to use such terms as palm and cactus in this connection as descriptions of life-form. Names should be as concise as possible and consist of the minimum number of terms. Useful simplification can be secured in the case of the Spanish and Portuguese forms by adopting convenient terms from common usage, such as *espinar*, *caatinga* and *paramo*. The principal difficulty in this nomenclature is encountered with the many different kinds of evergreen forest. It would be possible to differentiate them physiognomically into "high three-storied evergreen forest," "high two-storied evergreen forest," but the result is cumbersome. Conciseness and greater clarity are secured by adopting in such cases a term from popular usage whether it relates to habitat or physiognomy, so that we have "lower montane rain forest," "swamp forest," etc.

Habitat Groups

The writer found that a clearer picture of the status and successional relations of his formations was obtained by further grouping them together into higher units which for want of a better term will be called "formation-series." This grouping was done on the basis of habitat. The formations appeared to fall together naturally into certain groups of closely related type of habitat, some of the groups containing "climatic" formations and others "edaphic" types.

Since floristic and physiognomy have been employed as the bases for naming and delimiting associations and formations respectively, the system of classification is completed and rounded off by the introduction of habitat at a third level. The picture becomes complete with the collation and sifting of essential information under the three headings—floristic, physiognomy and habitat—by means of which, according to a dictum of Clements ('28: p. 127), development in succession of the formation may be traced and analyzed. Exact data about habitat are, it is true, frequently hard to collect in the tropics at present. This is one important reason why systems employing habitat at an early stage in classification have been unsuccessful. At this final stage, however, the arrangement of formations into series, we are only concerned with broad questions of habitat which are relatively easily decided. All that may be necessary for purposes of classification is a determination of preponderating influences in the environment, which in most cases can readily be made in the field, though it is more than a question of determining whether climatic or edaphic factors are predominant. Modern work in soil science in the tropics tends more and more to show that the mutual effects of all the environmental factors and the vegetation are inextricably interrelated: form, in fact, one *ecosystem*, as Tansley ('35) has defined it. It would be of considerable advantage, at any rate in tropical studies, if the idea of analyzing habitat into its factors could be discarded in favor of viewing the local habitat of any given community as a complex, in the form of broadly considered moisture relations.

Hardy ('35: p. 6) in reviewing the relations between soil and vegetation-types in British Honduras concluded that the main factor deciding forest distribution in British Honduras is the water factor, whose magnitude depends, not only on total rainfall and its distribution between the wet and dry seasons, but also on the effects of topography and soil type on the available water-supply of the soil. As a result of more recent work in the same country, Charter ('41: p. 5) expressed a like viewpoint, and Hardy reiterated it in his studies in Trinidad ('36: p. 27). Warming, in his classical work ('09: p. 132) emphasized the importance of the moisture factor in very similar terms.

Moisture relations, in this connection, must be broadly viewed and must include consideration of the evaporating ability of the air in addition to soil moisture. In temperate latitudes the cold of the winter may greatly reduce the availability of soil moisture for plant growth. If the soil is frozen, moisture is totally unavailable. This winter condition is known as physiological drought and the characteristic trees of such latitudes are either deciduous or sclerophyllous, indicating a mechanism for prevention of the depletion of temporarily irreplaceable moisture. Tropical vegetation tends to be specialized in a similar manner in response to comparable conditions. The most luxuriant vegetation will be found only where soil moisture is constant and readily available and where violent winds or extremely dry air are not effective factors. Reduction and specialization begin to be noticeable in the vegetation in cases where in wind-sheltered country available soil moisture falls below the requirements for optimum growth (as on some deep, loose, sandy soils) or where available soil moisture is copious but violent winds are capable of causing excessive evaporation (as in many mountain situations). A still more marked effect may be observed where there is both violence of wind and lack of soil moisture. Where for any cause the availability of soil moisture is inadequate to meet the demands of transpiration, it may be said that there is drought, actual or physiological. It is the writer's view that all observed physiognomic (as distinct from floristic) variations in vegetation may be explained in terms of this conception of moisture relations.

For purposes of classification, therefore, consideration of the habitat of formations resolves itself into questions of available moisture. We may begin by envisaging a mesic or optimum habitat where availability of moisture—and thus every condition for plant growth—is as ideally favorable as it can be in the tropics. To achieve this state of affairs the land must usually be well-drained, the soil deep and permeable, moisture must be available in sufficient quantity throughout the year and the situation sheltered from violent winds. There must be neither inundation nor seasonal drought, evaporation must be moderate and frost unknown. Such conditions naturally favor the tallest, most luxuriant and most complex type of vegetation in the American tropics, the vegetal optimum, rain forest. Rain forest is by no means so common in the tropics as is popularly supposed, for these ideal growth conditions are rare. Almost everywhere there is a scarcity of moisture in some manner to some extent at some period of the year, which inhibits development to the highest type of community.

Turning therefore from the optimum to habitats where conditions are adverse, it appears that these may be classified into five categories, viz.:

1. Well-drained lands with seasonal lack of available moisture, due to ill-distributed rainfall.

2. Well-drained lands with constant lack of available moisture, evaporation exceeding moisture supply all the year round.

3. Relatively elevated lands, exposed and cold: evaporation exceeding available moisture due to violent winds, and/or available moisture inadequate to replace evaporation owing to low temperature.

4. Ill-drained lands subject to flooding.

5. Ill-drained lands subject alternately to inundation and desiccation.

This classification is closely comparable to Warming's ('09). It is erected upon the same basis—the water-supplying ability of the soil—but the writer believes that his six categories (including the optimum rain forest as one category) each contain types of related habitat with greater consistency than Warming's six groups of ecological classes and present a more convenient picture. The writer's last category (ill-drained lands subject alternately to inundation and desiccation) is one not specifically recognized by Warming.

Since alkali soils are not found in the American tropics, no heading is required to include them. While transitional conditions embodying characters of two or more of the above divisions are from time to time encountered, in a surprisingly large number of cases a habitat can readily be allotted to its proper category. In each series conditions at the extreme become so adverse that terrestrial plant growth ceases altogether: one comes out upon a barren desert, mountain snowfield, the open sea or the open water of a river, lake or lagoon. For each category a distinct physiognomy characterizes the ultimate point of adversity of the habitat at which plant growth ceases and for each there is a distinct series of structures transitional between the optimum and the adverse extreme. One is, therefore, able to arrange formations into five "Formation Series" within each of which are structures and life-forms expressing every degree of transition from optimum to extreme adversity for a single major type of habitat (table I). The following names are suggested for the five Formation-Series.

1. Seasonal Formations
2. Dry Evergreen Formations
3. Montane Formations
4. Swamp Formations

TABLE I. *Summary of formations*

Formations and formation-series	Linguistic equivalents * Spanish	Portugese
1. Rain Forest.	Selva pluvial.	Mata pluvial.
2. Seasonal Formations.	Formaciones estacionales.	Formações estacionais
Evergreen seasonal forest.	Selva veranera siempreverde.	Mata de verão sempreverde.
Semi-evergreen seasonal forest.	Selva veranera semidecidua.	Mata de verão meio decidua.
Deciduous seasonal forest.	Selva veranera decidua.	Mata da verão decidue.
Thorn woodland.	Espinar.	Espinhal.
Cactus scrub.	Cardonal.	Caatinga.
Desert.	Desierto.	Deserta.
3. Dry Evergreen Formations.	Formaciones siempreverdes secas.	Formações sempreverdes seccas.
Xerophytic rain forest.	Selva pluvial xerofítica.	Mata pluvial xerofitica.
Littoral woodland.	Bosque de playa.	Bosque de praia.
4. Montane Formations.	Formaciones de montaña.	Formações de montanha.
Lower montane rain forest.	Selva pluvial intermedia.	Mata pluvial intermedia.
Montane rain forest.	Selva nublada.	Mata nublada.
Palm brake.	Matorral de palmeras, Manacal.	Mato de palmeiras.
Elfin woodland.	Bosque enano.	Bosque anão.
Frost woodland.	Bosque de helada.	Bosque de geada.
Mountain pine forest.	Pinar de montaña.	Pinhal de montanha.
Bamboo brake	Bamboal.	Bambual.
Paramo.	Páramo.	Paramo.
Tundra.	Tundra.	Tundra.
5. Swamp Formations.	Formaciones de pantano.	Formações de pantano.
Swamp forest.	Selva de pantano.	Mata de pantano.
Palm swamp.	Pantano de palmeras.	Pantano de palmeiras.
Herbaceous swamp.	Pantano herbáceo.	Pantano herbaceo: campo de várzea.
Mangrove woodland.	Manglar.	Mangueiral.
6. Marsh or Seasonal Swamp Formations.	Formaciones de lodazal o de pantano estacional.	Formações de lagoa o de pantano estacional.
Marsh forest.	Selva de lodazal.	Mata de lagoa.
Marsh woodland.	Bosque de lodazal.	Bosque de lagoa.
Palm marsh.	Lodazal con palmeras, Morichal.	Lagoa de palmeiras.
Savanna.	Sabana.	Campo, campo firme.

* The writer is indebted to Sr. O. del Arco and Mr. G. Rodriguez for assistance in preparing respectively the Spanish and Portugese equivalents.

5. Marsh or Seasonal-Swamp Formations

These series are additional to the single optimum formation, rain forest. Each series consists of stages between the optimum and the extremely adverse and thus the head of each series approaches closely to the optimum. Rain forest could be included within each series with consistency and in some treatments of vegetation it may be desirable to do this. The series may be regarded as radiating outwards from the optimum like the spokes of a wheel or, better, three-dimensionally like radii from the centre of a sphere. It is, however, difficult to picture this idea geometrically. Since different factors may sometimes be compensatory or exert similar effects on vegetative growth it may be expected that the various formation series will show on occasion approximations in physiognomy. In other words, the formation series may not radiate out from (or converge on) the optimum in straight lines but may flex sometimes further, sometimes very near: in fact, since all must end in absence of vegetation, one might conceive them as ultimately reconverging to a "pessimum."

Descriptions of the Formations

The Optimum Formation (Rain Forest)

We have a very fine detailed physiognomic study of rain forest in British Guiana by Davis and Richards ('34), who described five associations of this formation. The forest is arranged in four tree strata: first, a layer of occasional, scattered, huge "outstanding trees" attaining 40–60 meters of height (90–120 feet) which forms the canopy in four of the associations but is not a closed layer in "mixed forest," an association which seems to tend somewhat to evergreen seasonal forest. Lower strata occur at about 24 meters (75 feet) and 14 meters (45 feet). The structure is demonstrated diagrammatically in figure 1 (photograph, fig. 2). The "outstanding trees" are not invariably present and are not an essential feature of rain forest, being absent from the rain forest of French Guiana described by Benoist ('24) as featuring a layer of trees 30–40 meters high, an *étage dominé* 10–25 meters and *arbustes* below 10 meters. True rain forest always gives the impression of the vault of cathedral aisles. The dominant trees have long, clean boles, usually from 20 to 30 meters before the first branch, and relatively restricted crowns: they appear crowded and drawn up. Lianes are of little importance and epiphytes do not grow near the ground. Buttressing is not diagnostic and may be well or poorly developed. Peculiarities of growth such as stilt roots, pneumatophores, thorns and spines are only rarely present, if at all, and have no significance. Palms may or may not be abundantly present: commonly they are occasional only and present as immature, stemless plants. The forest may contain a few deciduous or partially deciduous species but is to all intents and purposes evergreen. (The addition of the term "evergreen" to rain forest preferred by some writers is therefore redundant as there is no semi-evergreen or deciduous rain forest.) Compound leaves predominate in the upper stories but simple leaves are usual in the lower story. The predominant leaf size is "mesophyll" using Raunkiaer's leaf-size classes ('16).

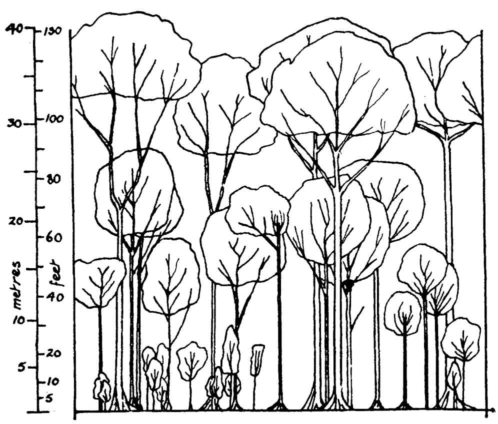

Fig. 1. Profile diagram of rain forest, from measurements at Mayaro, Trinidad. Note the great height of the dominants and their long, clean trunks, and arrangement into three tree strata.

It is understood that the above descriptive definition of rain forest (and the similar descriptions of other formations which follow) apply to the American tropics but do not necessarily hold true for the physiognomy of rain and other forests elsewhere which belong to the same "formation-types"—in the sense of Richards *et al.* ('39).

Rain forest is rather less widespread than generally supposed, for there are many other types of evergreen forest which are likely to be labelled rain forest in popular parlance. It is perhaps most fully developed in the Guianas, from the Orinoco to the Amazon, in a strip 150–200 miles inland from the coast. It is contained in the Amazon basin, though most of the forests of Amazonia are not rain forest. Parts of lowland Central America, Colombia and Ecuador carry rain forest and it occupies a restricted zone in some of the Lesser Antilles.

Seasonal Formations

The predominant character of the habitat is the seasonal drought, i.e. a period of the year during which evaporation exceeds available moisture. It is further an essential feature that the ground must not become inundated or waterlogged (except for very short periods) during the wet season, but must be well drained. Seasonal formations occur generally on lowlands but may be found in certain mountainous regions. The term seasonal is adopted in preference to Schimper's term monsoon since the latter is of Asiatic origin and applicable to forests which belong to the same formation-type as the neotropical seasonal forests but are not homologous, being higher and denser and of better bole form. The more xerophytic seasonal types also differ significantly from the Asiatic and African equivalents in their lack of grass cover. "Deciduous formations" could not be adopted as a term since the most xerophytic are evergreen. These formations are typically the expression of a seasonal —as against a well-distributed—rainfall, causing seasonal desiccation of the soil and lowered atmospheric humidity. Total annual precipitation is a meaningless figure in this connection: during rainy months much excess moisture falls and drains away and is not utilized by the plants—once precipitation is exceeding evaporation, 6 inches or 30 inches may fall in a month without affecting the vegetation, except perhaps over long periods, by erosion, leaching and so on. The critical question deals with the number of months in the year in which excess of evaporation over precipitation leads to drought. According to Charter ('41: p. 3) this point is reached in British Honduras with a monthly fall of under 4 inches (100 mm.). This agrees with the writer's observations in the West Indies, at any rate for soils of normal porosity. Soils with excessive internal drainage show drought at a higher monthly figure. The duration of seasonal drought determines the degree of divergence of physiognomy in the formation from rain forest. Types with very short seasonal drought show many of the characteristics of rain forest. Longer and longer drought brings increasing poverty of flora and of stature and greater specialization of life-forms. There must in nature be an infinite number of gradations in plant communities from rain forest to the extreme seasonal type. For convenient classification the series may be divided arbitrarily into six grades, so that between certain limits a community may be said to belong to a certain formation. It is proposed to name the six seasonal formations thus delimited:

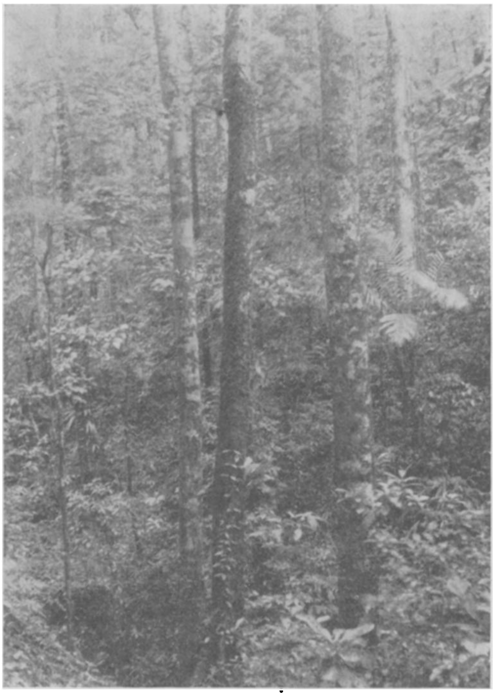

FIG. 2. Rain forest in the Rain Reserve, Grenada, B.W.I.

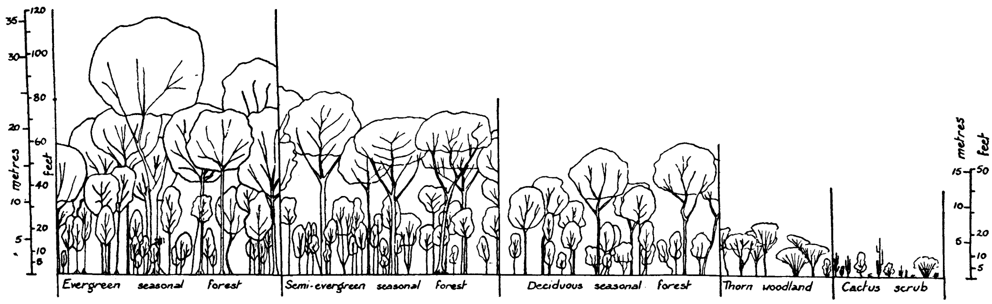

FIG. 3. Profile diagrams of seasonal formations. Evergreen seasonal forest measured at Arena, Trinidad; semi-evergreen at Marac, Trinidad; deciduous at Chaguaramas, Trinidad. Thorn woodland and cactus scrub from descriptions and photographs, Venezuela.

1. Evergreen Seasonal Forest
2. Semi-Evergreen Seasonal Forest
3. Deciduous Seasonal Forest
4. Thorn Woodland
5. Cactus Scrub
6. Desert

Their structures are shown in figure 3. Probably very few seasonal communities belong exactly to one of these types, but each must correspond to one more or less closely.

1. *Evergreen Seasonal Forest:* (fig. 4). This is a forest with three tree strata. Uppermost is a highly discontinuous layer of occasional emergent trees reaching 35 meters (100 feet) and upwards. The middle stratum is almost continuous, though irregular in height, ranging from 14 to 30 meters (45–90 feet) and forms the canopy. There is a lower story between 3 and 10 meters (10–30 feet). The canopy is closed but is lower than in rain forest so that light penetrates deeper among the trees. Individual trees may attain very large sizes, of 3 meters or more in diameter, but these are very occasional. The general impression is of an occasional huge tree in the midst of smaller growth and the closely ranked columnar effect of rain forest is lacking. The large trees branch relatively low down and clean boles of over 20 meters are rare. The crowns of the dominant trees are large, spreading and rounded. Lianes are fairly abundant and epiphytes are rather well developed, growing as low as 6 meters from the ground. Buttressing may be a prominent feature of the large emergents. Peculiarities of growth are not present to any degree. Palms are frequently prominent in the lower story, with either pinnate or fan leaves. The forest is predominantly evergreen, though a number of species (about 25 per cent), many of which may be abundant, among the large emergent trees are deciduous. Species not rising above the middle story are all evergreen. Compound leaves predominate in the emergent and middle strata, but simple leaves in the lower stratum. Leaf size is overwhelmingly mesophyllous. Mature leaves of most species are thin and papery, dark green and shiny above: new leaves are pink to redbrown, limply drooping. Ground vegetation is abundant. The flora is very rich, with 80 or more tree species per association.

2. *Semi-evergreen Seasonal Forest:* A two-storied forest (tree strata) with a more or less closed canopy (in the rainy season) formed by an upper story between 20 and 26 meters (60–80 feet) and a lower story between 6 and 14 meters (20–45 feet). Rare trees reach gigantic thicknesses, but most mature trees average about one-half meter in diameter. They fork or branch low down and crowns are umbrella-shaped. Lianes seem to reach their optimum development here, crowns of the largest

FIG. 4. Evergreen seasonal forest in the Arena Reserve, Trinidad.

trees being completely loaded. Epiphytes are relatively scarce. Buttressing of large trees may or may not be present. A few armed species are present but no growth peculiarities are important. There is a noticeable absence of ferns and mosses, fan-leaf palms are usually a feature in both stories, and Guadua bamboo may be present. Species confined to the lower story are almost all evergreen but those attaining the canopy are mostly deciduous. A few are evergreens with hard leathery leaves, but most are *facultatively* deciduous, i.e. their degree of leaf-fall varies with the intensity of the drought. In a wet year the forest may hardly go out of leaf at all. In a dry year, the crowns begin gradually to thin out and at the close of a long drought the canopy appears practically leafless for miles. Young leaves of evergreens are bright red or pale green. Deciduous species have soft, paler green leaves, seldom shiny above and their new leaves are pale green. Compound leaves predominate in the upper story, simple in the lower. Leaf size is predominantly mesophyllous in the upper story, but there is some tendency to microphylly in the lower. There is a marked shrub layer of hard, woody, mostly myrtaceous bushes, and ground vegetation is scanty. The flora is fairly rich with 50 to 80 tree species per association.

3. *Deciduous Seasonal Forest:* (fig. 5).

FIG. 5. Deciduous seasonal forest in Tobago, B.W.I.

A two-storied forest with canopy formed by the lower stratum between 3 and 10 meters, and an upper layer of scattered trees attaining 20 meters. There are very few stout trees, one-half meter in diameter being about the largest size. Stems fork or branch low down and tend to be bent or crooked; many of the lower story species tend to clumped growth. Lianes and arboreal epiphytes are rare. Trees are not buttressed, stilt roots are absent, but there are a few important armed species. Ferns and mosses are noticeable absentees and palms are not usually represented though small fan-palms (palmettoes) are sometimes abundant. Over two-thirds of the individuals composing the upper story are deciduous though those confined to the lower story are almost all evergreens. Deciduousness is here *obligate*, the trees which drop their leaves doing so with unfailing regularity and completeness during the dry weather. Compound and simple leaves are about equally distributed in the upper story and simple leaves predominate in the lower. The lower story is largely mesophyllous though containing many microphyllous species and these two leaf characters are evenly divided in the upper story. The evergreen leaf type is microphyllous, dark green, shiny and leathery. The deciduous leaf type is mesophyllous, pale green, often pubescent and seldom shiny above, soft and limp. In both cases young leaves are pale green. Ground vegetation is remarkably scarce, the soil being commonly bare, except where societies of terrestrial bromeliads cover the ground often for scores of square yards. The flora is poor, with 30 to 50 tree species per association.

4. *Thorn Woodland:* A scrubby type, varying from fairly open to more or less closed, with hard-leaved, microphyllous, evergreen spiny trees, 3 to 10 meters high (10–30 feet). Leaves often show adaptations additional to the reduction in size for decreasing transpiration. The soil is not grassed, ground vegetation being practically absent, save for rare bromeliads and succulents. Most of the thorn trees belong to the Mimosaceae and Caesalpiniaceae. Tree flora is poor with 30 or less species.

5. *Cactus Scrub:* (fig. 6). Open vegetation dominated by column cacti and prickly-pears, with scattered gnarled bushes, micro- or leptophyllous, often thorny, and terrestrial bromeliads. The main characteristics are extreme reduction and specialization of leaves, spines, low growth and disproportionately strong development of the root system. Many plants develop storage tissue. The ground is not grassed but frequently shows bare soil.

6. *Desert:* The exceedingly impoverished vegetation of very arid regions. Plants are widely spaced but often have disproportionate root systems and con-

sist mainly of little, thorny shrubs, succulents and herbs.

It will be clear from the diagrams and the foregoing descriptions that the series of seasonal formations is one of gradual simplification of structure with reduction of stratification, gradual loss of stature, reduction of leaf-size and specialization of life-forms.

The distribution of seasonal forests in Tropical America cannot be exactly delimited owing to the vagueness of the physiognomic descriptions of most writers. Evergreen seasonal forest has usually been labelled "rain forest" and semi-evergreen and deciduous seasonal forest "monsoon forest," or "dry forest." The lowland forests of British Honduras appear to include both evergreen and semi-evergreen seasonal forest (Charter, '41) and the semi-evergreen and deciduous formations are represented in Cuba (Bennett and Allison, '28). All three seasonal forests are abundantly represented in Amazonia (Ducke, '38), in Venezuela around the fringes of the Cordilleras (Myers, '33; Pittier, '39) and in Trinidad. They occupy restricted zones in the Antilles. In regard to thorn woodland and cactus scrub there is more precise information. These formations are found in all the Greater Antilles and to a very restricted degree in the Lesser; along the north coast of Venezuela and the islands lying off it (Pittier, '39) and the northern edge of the llanos (Myers, '33); and in the Guajira peninsula of Colombia (Dugand, '42). The *caatingas* of Brazil (Noronha, '38) belong largely to these two formations. Desert is found notably on the Pacific coast of Peru.

Dry Evergreen Formations

Dry evergreen formations are somewhat rare, expressing a habitat where the moisture supply shows no relatively effective seasonal fluctuations but is fairly consistently inadequate—having regard to particular climatic conditions—for the most luxuriant growth. The

FIG. 6. Cactus scrub on Patos Island, Venezuela

term is chosen for want of a better to express the idea of sclerophyllous evergreen formations in a form popularly acceptable. A rainfall regime of such a type is rarely met with, though Champion ('36) describes "dry evergreen forests" in the south of India, which express it. The development of dry evergreen forest and woodland is due usually to strong winds and/or excessively freely draining soil, the soil moisture being thus inadequate to meet the evaporating ability of the air. The vegetation of windy sea shores is the best known member of this group and will be described as littoral woodland, using Schimper's term, though it is not correct to relate it, as he does, to telluric moisture.

Littoral Woodland (fig. 15) is developed along the seashore above high water mark and not subject to inundation. It is however subject at all times to strong wind carrying salt spray which is deposited on the leaves of the plants. Typically the formation consists of low gnarled or windswept trees and shrubs presenting their crowns to the wind in the form of dense domes or flat laminae edge-on. Leaves are generally simple, fleshy, very shiny, covered on the upper surface with a thick layer of cuticle which is able to counter the dehydrating effect of a coating of salt and is an effective protection against powerful drying winds. Woodland of this type is universal to the American tropics. Occasionally also groves of tall Roystonea palms are found.

The present writer has only encountered one other community in the Americas belonging definitely to this group, a type in Tobago which was named Xerophytic Rain Forest (Beard, '44). It is probable that the association of *Mammea americana-Calophyllum antillanum* described by Gleason and Cook ('26) in Puerto Rico belongs to this or an allied formation and it may be that the wallaba (Eperua) forests of British Guiana (Davis & Richards, '34) are to be regarded as a type of dry evergreen forest close to the optimum in view of the comparative studies made by Richards ('36) in Sarawak. The Brazilian "campina" (Ducke, '38) may also belong to this series.

Xerophytic Rain Forests: The Tobago formation is characterized by two tree strata and is illustrated in figures 7 and 8. A more or less continuous canopy is formed between 13 and 20 meters (40–60 feet); below this the smaller trees are not arranged in any definable layers, but above the canopy occasional large solitary trees stand out up to 30 meters (90 feet) in height. The emergents occur at the average rate (though of no constant distribution) of 10 per acre and attain up to 1.20 m. in diameter. The remainder are about 135 per acre, not exceeding 30 cms. in diameter, and appear thin and drawn up, like a young timber plantation. The forest is entirely evergreen, predominantly mesophyllous, without thorns or succulents. Over 80 per cent of the individual emergent trees and 50 per cent of the individuals in the lower story possess some specializations of the leaves which appear to serve the purpose of reducing transpiration. Nearly half the trees in the lower story shed their bark in sheets. Compound leaves are virtually absent. There is no shrub layer and ground vegetation is very sparse.

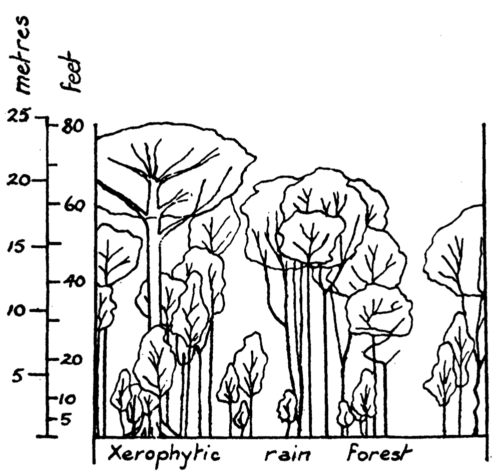

FIG. 7. Profile diagram of xerophytic rain forest, measured in the Rain Reserve, Tobago.

Montane Formations

It is a matter of common observation that different zones of vegetation are encountered on ascending mountains. The vegetation is found to change progressively with higher altitude and to fall into a series of formations which differ from lowland types in the tropics, though they tend to resemble strongly the lowland types of progressively higher latitude. The rain, seasonal and dry evergreen forests of tropical lowlands will be found to ascend into the mountain ranges, often very far and to a considerable altitude. The writer's use of "montane" is not a synonym for "mountain." Montane formations are a group expressing conditions peculiar to mountain chains and associated with mountains in the majority of cases; but in suitable conditions any other formation could conceivably occur in mountainous country. If the mountains are high and extensive enough, however, a point is always reached where the peculiar montane conditions become dominant. The change may be felt at first in the form of increased precipitation, producing a luxuriant forest close to the optimum. Higher, conditions become gradually more adverse. Structure is gradually reduced, more and more specialized life-forms appear and the forest gives way to meadow and this to a tundra of moss and lichen.

The following series of montane formations can be recognized:

1. Lower Montane Rain Forest
2. Montane or Temperate Rain Forest
3. Palm Brake
4. Elfin Woodland
5. Frost Woodland
6. Mountain Pine-Forest
7. Bamboo Brake
8. Paramo
9. Tundra

Not all of these types will be represented on the same mountain nor will they appear at any constant altitude, the latter depending on the genera character of the land-mass, determined by relative exposure. A low mountain on a small island rising abruptly from sea level bears types only found at a much greater altitude in the Andes, and the same formation may appear at a different altitude on different slopes of the same mountain-mass, this depending largely on wind direction.

As a generalization, the series of montane formations is a reflection of succeeding zones of temperature becoming steadily more frigid from tropical to arctic, as Schimper recognized ('03). The following is a rough correlation of formations with his temperature belts:

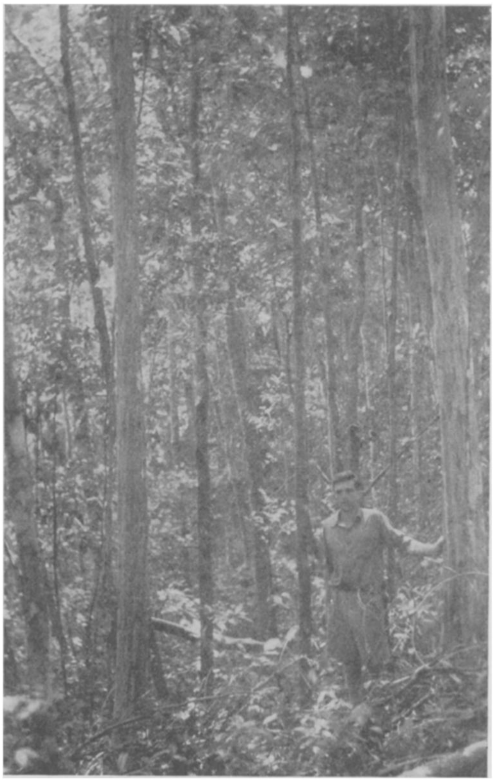

FIG. 8. Xerophytic rain forest in Tobago. Trees mostly small and attenuated. Two with peeling bark in the foreground.

Warm belt. Tropical. Lower montane rain forest.

Temperate belt. Av. temperature 15° –20° C. Montane rain forest, palm brake, elfin woodland.

Cool belt. Temperature sometimes below 0° C. Frost woodland, pine forest.

Cold belt. Temperature usually below 0° C. Paramo, tundra.

Clearly the temperature factor is by no means the only important one. The composition of light is different at high altitudes where there may possibly be an injurious proportion of ultra-violet rays. Humidity is often an adverse factor. In the cloud belt it is often so high that plants scarcely transpire. Exposure to wind is certainly a most important factor to consider. There is the mechanical aspect, soils being generally shallow on high ridges and winds strong so that any trees growing to a certain size may be uprooted and a low type of forest perpetuated. The writer's impression is, however, that the physiological effect of wind is more important than this and is one of the most important factors in the montane habitat. In montane formations the predominant leaf-type is reduced from compound to simple and leaf-size to microphyllous or smaller. Leaf-size is found to vary on the same tree, leaves being often larger low down where they are sheltered than in the upper crown where they are fully exposed to the atmosphere. Many species have leaf specializations which appear to serve the purpose of restraining transpiration. In the mountains of Grenada, British West Indies, it is most noticeable that lower montane and montane rain forest and elfin woodland alternate with one another according to exposure to the prevailing wind. Falling temperature exerts a limiting effect upon vegetation as it becomes harder and harder for plants to draw water from the soil and the transpiration rate is so limited that only plants specialized to guard against excessive evaporation can be successful. It is suggested that wind may produce an essentially similar effect at lower altitudes in that it can be capable on clear days of evaporating water from leaves faster than transpiration can supply it, leading to wilting of the leaves which are not specialized to restrain excessive evaporation. Probably in most cases the temperature and exposure factors are working in conjunction.

The Schimperian nomenclature has been retained for certain of the woody types as there appears to be considerable agreement upon them. To those who would prefer separate titles for the American formations, "lower cloud forest," "cloud forest" and "mossy woodland" are commended as alternatives for the "lower montane rain forest," "montane rain forest" and "elfin woodland" respectively. These alternatives would fall into line with the Spanish nomenclature and also avoid confusion with rain forest proper.

Figure 9 shows typical structures for part of this series of formations, which show gradual reduction in stature, simplification of structure and specialization of life-forms.

1. *Lower Montane Rain Forest:* (fig. 10). Many writers have classed this type as a subformation of rain forest, for which attitude there is some justification. The formation differs from lowland rain forest principally in that tree

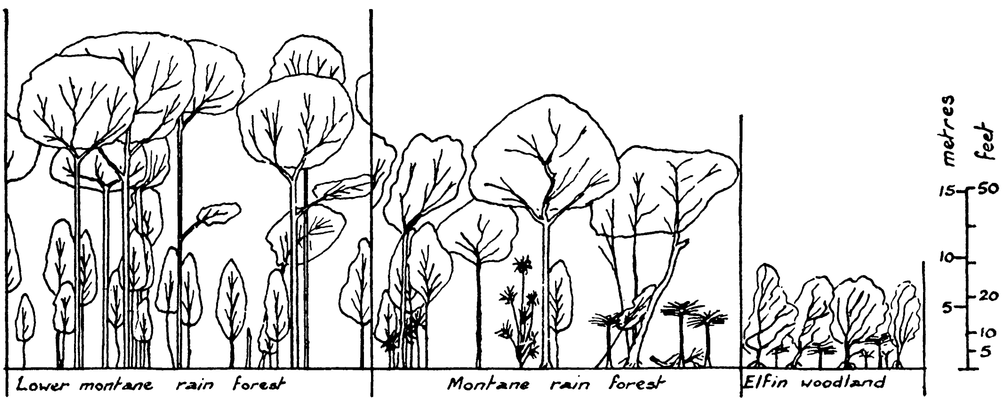

FIG. 9. Profile diagrams of montane formations. Lower montane rain forest measured at 300 meters elevation at Guanapo and montane at 800 meters at Aripo, Trinidad; elfin woodland sketched, Aripo, Trinidad, at 1000 meters.

FIG. 10. Lower montane rain forest in the Rain Reserve, Grenada, B.W.I., about 600 meters.

strata are reduced to two, a canopy layer between 24 and 33 meters (70–100 feet) and a lower story 3 to 16 meters (10–50 feet), and that leaves are predominantly simple.

This is a very widespread formation and occurs throughout the Antilles (Beard, '42; Stehlé, '35, '38, '41; Gleason and Cook, '26) between 260 and 800 meters (800–2,500 feet). It appears to be present in British Honduras above 250 meters (Charter, '41), which probably indicates conditions for Central America as a whole, and in the Andes (Pittier, '39), though descriptions here are not very precise.

2. *Montane Rain Forest:* (fig. 11). There are a number of permissible synonyms for this formation. In a classification dealing with the tropics alone "montane rain forest" is perhaps best, but in a world-wide review the title "temperate rain forest" must be used as the formation occurs in New Zealand, Chile, Formosa and other places outside the tropics. Another title with much to commend it is "cloud forest." The forest is in two closed stories, at 20 and 10 meters (60 and 30 feet) with a shrub layer formed mainly of simple-leaved dwarf palsms and tree ferns. The trees have heavy crowns, branch low, and are loaded with moss and epiphytes. Leaves are simple, mesophyllous, and covered with epiphylls. The association of this type of forest with a mist belt in the mountains has been graphically described by Pittier ('39: p. 20), who delineates its extension throughout the lower levels of *tierra templada* in the Andes of Venezuela from 700 to 2200 meters (2200–6800 feet). In the Lesser Antilles, the range of altitude is 800 to 1000 meters (Beard, '42;

FIG. 11. Montane rain forest, El Tucuche, Trinidad, 800 meters.

FIG. 12. Palm brake of *Euterpe globosa* Gaertn. in St. Vincent, B.W.I., about 800 meters.

Stehlé, '35, '38, '41). The montane rain forest described by Shreve in Jamaica ('14) includes also elfin woodland, the range of both being 1500 to 2500 meters.

3. *Palm Brake:* (fig. 12). In some localities consociations of palms occur above the montane rain forest, and are stated to be of climax order. Thus, there is *Euterpe globosa* in Puerto Rico between 650 and 750 meters (Gleason and Cook, '26), *Areca regia* (?) in Guadeloupe above 1000 meters (Stehlé, '35) and *Ceroxylon klopstockia* in Venezuela about 2000 meters (Pittier, '39). Brake of *Euterpe globosa* in the Lesser Antilles is however a seral community.

4. *Elfin Woodland:* (fig. 13). This formation appears at the upper limit of tree growth in the Antilles and is presumably found in the Andes. An alternative title is "mossy woodland." It is an open woodland about 8 meters high of stunted gnarled trees, often stilt-rooted and with thick fleshy leaves, with long rambling branches pointing away from the wind. There may be an understory of dwarf palms and tree ferns. The whole is loaded with moss, lichens and epiphytes and forms a completely impenetrable thicket. Pure stands of *Clusia* spp. constitute this formation in some of the Lesser Antilles (Beard, '42; Stehlé, '35, '38) between 1000 and 1100 meters, but there is a richer flora in Puerto Rico's "mossy forest" (Gleason and Cook, '26) above 750 to 1100 meters, and in Jamaica (Shreve, '14).

5. *Frost Woodland:* In the very high mountain masses, this formation appears above the montane rain forest and palm brake of the mist belt. Very little is known at present of this formation, except that it occurs above the frost line. Pittier ('38) distinguished it above 1200 meters in the Coastal Cordillera of Venezuela and above 3000 meters in the Merida Andes and it was noted by Standley ('41) in Guatemala. The Araliaceae seems to be an important family

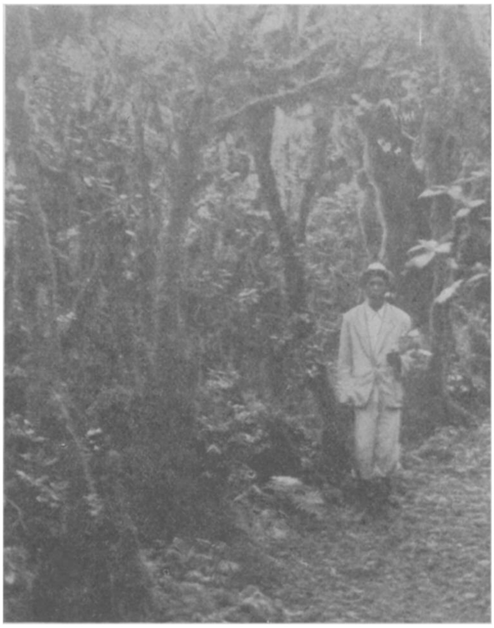

FIG. 13. Elfin woodland in the Rain Reserve, Grenada, B.W.I., about 800 meters. Note the enormous abundance of moss.

in this formation, which includes also many temperate genera such as Alnus and Acer.

6. *Mountain Pine Forest:* In the restricted portion of tropical America where Pinus is present, more or less pure pine forest appears to be the equivalent of various of the broadleaved formations described above, though its exact relations to them are not clear at present. Ref: Standley ('41) for Guatemala, Chardon ('41) for Hispaniola.

7. *Bamboo Brake:* It has been reported to the writer that dense thickets of a bamboo occur in the Merida Andes of Venezuela at about 5000–6000 feet. This evidently corresponds to the Old World bamboo brakes.

8. *Paramo:* (fig. 14). The Spanish name is preferable to "alpine meadow," to distinguish the purely tropical American formation. To those who prefer an English term "Andine meadow" is suggested. Paramo is characterized by Pittier ('39, p. 16) thus: (translation)

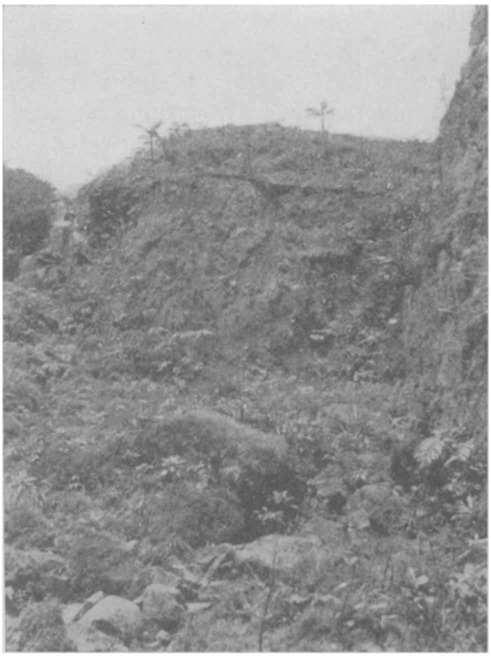

FIG. 14. Paramo on the Soufriere mountain, St. Vincent, B.W.I., 1000 meters.

FIG. 15. Littoral woodland in Tobago, B.W.I., planed off and streamlined by the wind.

"At variable altitudes, but never much below 1800 meters, the upper edge of the forests becomes gradually stunted and then passes into the formation of the *páramos*. In its usual context, *páramo* means a cold desert, swept by violent winds and not seldom beaten by tempests of snow and hail, which may threaten the lives of travellers. In our Andes, while these storms and their attendant risks are not lacking, the expresson is applied to the most elevated parts, almost entirely devoid of woody vegetation and covered mostly with stemless plants having enlarged root-systems and coriaceous leaves, arranged usually in basal rosettes and protected against the rigors of the climate by means of various adaptations. In proportion to their size, many of the plants have large and showy flowers, in such a way that the *páramo* at the flowering season is comparable up to a certain point with any alpine meadow."

Variants in the Antilles (Stehlé, '35, '38) are meadow with giant Lobelia and with the terrestrial bromeliads Pitcairnia and Guzmania, but it is possible that these are seral communities.

9. *Tundra:* Sphagnum bog has been described by Stehlé in the French Antilles at the summits of the highest peaks.

Swamp Formations

It is well known that only specialized plants can long survive if the soil in

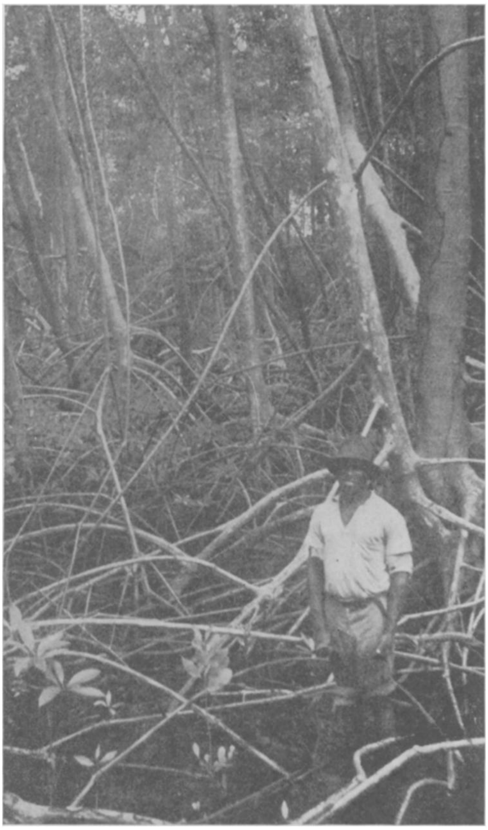

FIG. 16. Mangroves in the Nariva Swamp, Trinidad. *Rhizophord mangle* with stilt roots.

which they grow is flooded with water. An annually or perennially flooded site, therefore, will develop a specialized vegetation. The type of habitat where the soil is waterlogged or inundated perpetually or is so affected for a part of the year but never becomes absolutely dry is here defined as a "swamp." Differentiation from the optimum rain forest begins when flood water covers the soil for a short period annually. Longer periods of inundation lead to a reduced physiognomy, specialization of life-forms and poverty of flora. Forest is reduced to tall, herbaceous growth, this to a grass mat floating on water and finally open water is reached. The following stages in this series may be delimited as formations: (fig. 17)

A. Fresh Water.
1. Swamp forest
2. Palm swamp
3. Herbaceous swamp, including tall herbaceous swamp and swamp savanna

B. Brackish Water.
1. Mangrove woodland

A. Fresh Water.

1. *Swamp forest:* (fig. 18). This is usually a forest of a single tree story, somewhat resembling mangrove in appearance, 20–30 meters high and rather open underneath. The ground is waterlogged or just covered with water for over half the year and the trees show root specializations—sinuous plank buttresses or stilt roots. Under the circumstances there is little or no ground

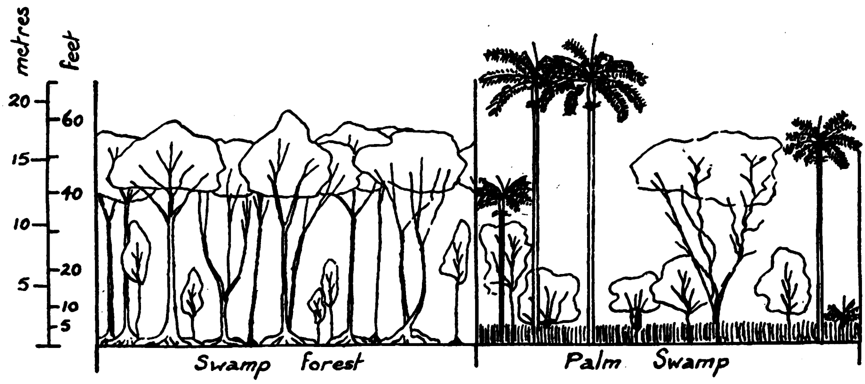

FIG. 17. Profile diagrams of swamp formations. Swamp forest from measurements, Oropouche, Trinidad; palm swamp from a photograph, the Nariva Swamp, Trinidad.

vegetation. Leaves are compound, mesophyllous and not specialized. There is a tendency to purity of stand, Pterocarpus being prominent.

2. *Palm swamp:* Transition from forest to herbaceous vegetation is marked by a zone of scrubby woodland in which palms are dominant (Roystonea, Mauritia, Attalea, Oenocarpus). Associated are scattered trees of the swamp forest and patches of herbaceous swamp.

3. *Herbaceous swamp:* (fig. 19). The soil in herbaceous swamp is waterlogged more or less all the year round and water stands for a part of the year 0.30–1 meter deep. There are two sub-divisions, tall herbaceous swamp and swamp-savanna.

Tall herbaceous swamp is the more shallowly inundated and consists of such giant herbs, growing usually in large

FIG. 18. Swamp forest of Pterocarpus near the Oropouche River, Trinidad

FIG. 19. Tall herbaceous swamp of *Cyperus giganteus* in the Nariva Swamp, Trinidad.

pure patches, as Montrichardia, Gynerium and Cyperus spp. They are rhizotomous. At best growth attains 4 meters high, but is much reduced in deeper water.

Swamp savanna is formed by a herbaceous mat floating on top of water which seasonally may be 2 meters deep. Usually it is made up of grasses but other herbs—Nymphaea, etc.—are found.

B. Brackish Water.

1. *Mangrove woodland* (fig. 16) is too well known to need any new definition. It is characteristic of tidal mudflats covered with brackish water at high tide. The mangroves will not survive either in pure sea water or fresh river water. A striking feature of mangrove trees is their vivipary. Some develop stilt roots, others pneumatophores. Leaves are simple, mesophyllous and thickly cutinized. At its best, mangrove forms a closed forest 25 meters high. Along the Atlantic sea-

board mangrove woodland is of very constant floristic composition and also along the Pacific, but the two coasts differ from one another.

Swamp vegetation is principally developed in the deltas of the great rivers and includes the *esteros* of the Venezuelan llanos (Myers, '33) and *varzeas* of Amazonia (Ducke, '38).

Marsh or Seasonal Swamp Formations

One further series of formations remains to be considered, namely those where the soil is seasonally waterlogged or inundated, seasonally desiccated. It is suggested that this type of habitat should be termed ecologically a "marsh" in distinction to "swamp," which while seasonally inundated is never completely dried out. This distinction between the terms "marsh" and "swamp" does not, admittedly, exist in popular usage: the writer suggests setting up the distinction for use in ecological work. It may be found preferable to adopt "seasonal swamp" in place of the word "marsh" put forward by the writer, but "marsh" is more concise. The marsh habitat implies a severe alternation of moisture conditions between waterlogged and very dry and is almost always associated with impedance of subsoil drainage whether due to the presence of unweathered rock or of ironpan or claypan. Since there is no downward percolation of rain water, the soil waterlogs in the rainy season. In the dry season the shallow upper layer to which roots are confined dries out completely and quickly. Marsh vegetation therefore requires a seasonal rainfall regime but will develop (as at Berbice in British Guiana: Martyn, '31) where the distribution is so slightly seasonal that the vegetation of deep soils is rain forest. Probably no rainfall anywhere in the tropics is entirely devoid of periodicity.

Four marsh formations can be distinguished (fig. 20):

1. Marsh forest
2. Marsh woodland
3. Palm-brake
4. Savanna

1. *Marsh forest:* (fig. 21). A two-storied forest, with the canopy formed between 3 and 10 meters by a lower story, above which stand out scattered large trees reaching about 25 meters. Fifty per cent of all individual trees and seventy five per cent of the lower story are composed of pinnate-leaved palms, Manicaria, Jessenia and Euterpe. Trees do nor reach larger sizes than about $\frac{1}{2}$ meter in diameter. Strangling epiphytes (Ficus and Clusia) may be common on the larger trees; otherwise lianes and epiphytes are poorly represented. Trees do not buttress to any degree but many have stilt roots or

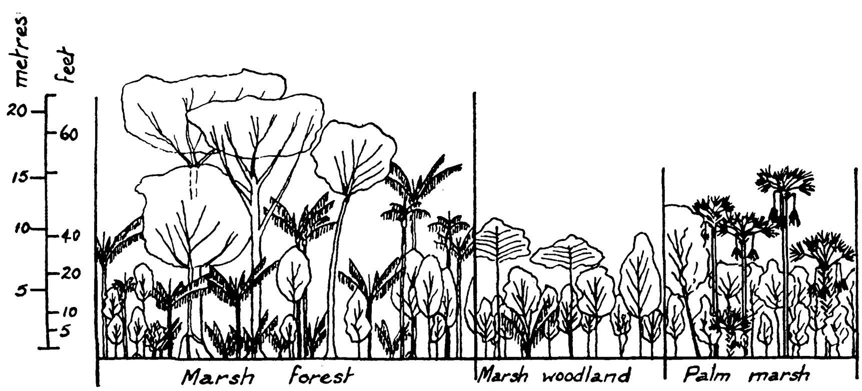

FIG. 20. Profile diagrams of marsh formations. Marsh forest measured at the Long Stretch Trinidad; marsh woodland after Charter ('41); palm marsh from a photograph at the Aripo savanna, Trinidad.

pneumatophores. The forest is entirely evergreen, leaves are simple, mesophyllous and inclined to be leathery or cutinized. Ground vegetation is mostly composed of palm seedlings. Ground surface is "hogwallowed" (definition by Bennett & Allison, '28).

2. *Marsh woodland:* A low dense woodland of small trees only a few centimeters in diameter but often with rather spreading branches. Some palms are still present. The ground carries sedges (Rynchospora) and razor grass (Scleria) and is hogwallowed.

3. *Palm-marsh:* (fig. 22). This type occurs principally as a fringing belt around savannas or as "islands" therein. Fan-palms (Mauritia, Copernicia, Acoelorraphe) stand out above a thicket of bushes, often microphyllous. The ground carries Rynchospora and Scleria.

FIG. 21. Marsh forest at the Long Stretch, Trinidad. Palms are mostly *Jessenia oligocarpa* Gr. and Wendl.

FIG. 22. Palm marsh with *Mauritia setigera* Gr. and Wendl. fringing the Aripo savanna, Trinidad.

4. *Savanna:* (fig. 23). This is a very well-known formation. Primarily a grassland (Andropogon, Cymbopogon, Sporobolus), it may take the form of pure grass (open savanna), grassland with scattered gnarled bushes (orchard savanna), with pine (pine savanna) or with occasional fan-palms (palm savanna). In regions of high rainfall small sedges compete with the grass. Characteristic bushes are *Curatella americana*, *Byrsonima* spp., *Bowdichia virgilioides* and *Anacardium occidentale.* Palms belong to Copernicia, Acoelorraphe, Chrysophila. Pine savanna is confined to the extreme north where Pinus is present and appears to be largely equivalent to orchard savanna.

The degree of reduction and specialization of the vegetation is determined by the severity of the alternations of water-logging and desiccation. In general, level topography and greatest impedance of subsoil drainage with approach of obstruction or pan to the surface coupled with a highly periodic rainfall regime produce greatest severity of conditions. It seems possible to correlate this series of formations with maturity sequences of soil and topography (Bennett and Allison, '28, p. 70–71; Charter, '41, p. 26–30). It should be stressed that the formations of this series are invariably associated with the particular

FIG. 23. Savanna, the Piarco Savanna, Trinidad. The low woody plants in the foreground are *Byrsonima verbascifolia* (L.) Rich., and the larger shrubs are *Byrsonima crassifolia* H.B.K. and *Curatella americana* L.

moisture conditions characterized. The grasslands of tropical America are not, therefore, directly comparable with those of Africa from which they differ in physiognomy no less than in habitat. Acacia savannas of strongly African appearance have developed in the West Indies from the repeated firing of drier seasonal types of vegetation, but they must be regarded as seral or as a deflected climax. Burning occurs on savannas in the Americas but is held by the writer to be an effect rather than a cause. Certain types of African savannas must doubtless represent the same habitat conditions as the American and resemble them somewhat closely. Attention is drawn to the attempted correlation between the writer's formations and the vegetation-types of Africa as described by Shantz ('23) which appears in table III. The exact status of grassland in tropical America is too wide a subject for discussion here.

Much of the low-lying land along the Amazon appears to carry marsh forest (Ducke, '38); to this formation belong also the Haematoxylon "swamps" of Central America and the Calophyllum-palmae association of Trinidad (Marshall, '34); and the "truli" swamp of British Guiana (Davis, '29) is evidently related. Marsh woodland is the "broken ridge" of British Honduras (Charter, '41). Palm-marsh occurs everywhere associated with savannas which are tremendously widespread in tropical America and of strikingly consistent floristic composition throughout their range from the pine barrens of Florida to the campos of south Brazil. To savanna belong the "oak ridge," "pine ridge" and "pimento swamp" of British Honduras and Yucatan (Charter, '41), the savannas of Cuba and the Isle of Pines (Benmett and Allison, '28), the savannas of Trinidad (Marshall, '34; Myers, '33), the great llanos of the Orinoco (Myers, '33), the savannas of the Guiana coastal belt (Martyn, '31; Pulle, '06, '38) and of the Rupununi and Rio Branco and the Pakaraima Mountains (Myers, '36), the "campos firmes" of Brazil (Ducke, '38) and the palmaceous "caatingas" of Maranhão and Piauí in Brazil with *Copernicia cerifera* (Noronha, '38).

Atypical Formations

Classification by physiognomy into habitat groups, as outlined above, meets with two major complications: atypical physiognomy due to purity of stand and indeterminate physiognomy due to intermediate habitat-type.

1. *Associations of Atypical Physiognomy:* Pure forest composed largely of only one species of tree is extremely rare in the tropics as a whole, but by some peculiar circumstance which is by no means understood at present is fairly common in Guiana. The difficulty in classifying by structure and life-form an association of this type is that the physiognomy impressed on the community by the predominant species is unlikely to be the same as that of a mixed forest in which different species belong to life-forms that are different but seem to fit the tree equally well (or nearly so) for success in the particular habitat. Further, in a pure forest all trees will tend to reach the same height on maturity, whereas a mixed forest is formed of trees attaining varying sizes and thus leading to a less regular structure. The pure *Mora excelsa* forests in Trinidad for example show the structure of rain forest though the habitat is that of evergreen seasonal forest and carries this formation wherever the invading Mora has not yet reached. The Dicymbe forests of interior British Guiana (Davis and Richards, '34; Myers, '36) are clearly *sui generis* and cannot be fitted directly into any general physiognomic group based on mixed stands. Such cases have to be decided on their merits from direct examination of the habitat and flora. Later, when more is known of such communities, it may be possible to delimit them as subtypes of definite formations.

2. *Formations of Intermediate Physiognomy:* Just as a plant association generally merges gradually into an adjoining one through a "tension belt" or "ecotone" where species from both associations are encountered, so does the formation also possess its ecotones where structures and life-forms of different formations are intermingled. Examination of a given area for example may disclose physiognomy intermediate between rain forest and evergreen seasonal forest, even though the floristic association of the area is distinct and does not show transitional features. It is probably on the uncommon side for a community belonging to any one formation-series to correspond exactly to one of its defined formations since these are only artificially delimited stages in one long series. Once this fact is recognized, no real difficulty should be experienced in "placing" types. A rather more complicated type of ecotone is that where a community lies intermediate between formations of different formation-series. Such a case happens to be extremely uncommon, but appears now and again due to special conditions. The writer has encountered one such in the mountains of Trinidad, between 300 and 800 meters on limestone outcrops where there is very little soil and water is immediately drained away between the rocks. The rainfall here shows seasonal fluctuations but is so abundant even in relatively dry months that on other than limestone soils the formation is lower montane rain forest. The excessive drainage of the limestones exaggerates the seasonal fluctuations in rainfall to produce a sharp dry season; on the other hand the area lies in the lower mist belt with its high humidity and frequent condensation. In total, the forest type shows affinities both to lower montane rain forest and semi-evergreen seasonal forest and is partly montane, partly

seasonal. Such cases can but be classified separately.

Comparative Data

In order to relate the plant formations described here to world types, the writer has constructed tables in which a tentative correlation is made with the nomenclature of Schimper (table II), Shantz (table III) and Barbour (table IV). Schimper's climatic formations appear generally to correspond with the writer's seasonal series, with rain forest added at the head of the series, except in regard to grassland which Schimper views as climatic and related to seasonal conditions. This view does not appear correct to the writer. Schimper's montane formations correspond with the writer's, as do his littoral and mangrove woodlands. Schimper's fresh-water swamp forest would embrace a variety of marsh and swamp types. Dry evergreen types are unknown to Schimper beyond littoral woodland.

The writer finds it easier to correlate with the African types of Shantz ('23) than with those of Chipp (Tansley and Chipp, '26). Shantz omits mention of littoral, fresh-water swamp and marsh types but there seems to be a ready correlation with all the forest types of his list. Most of the African grassland types are not found in tropical America except in limited areas of intensive human interference. The writer suggests that such African types may perhaps be found to be deflected climaxes due to fire and grazing. Doubtless there are savannas

Table II. *Correlation of formations with those of Schimper ('03)*

Schimper's nomenclature	Correlation	Remarks
Climatic Formations.		
Woodland.		
Tropical rain-forest.	Rain forest.	
Monsoon-forest.	Evergreen and semi-evergreen seasonal forest.	
Savanna-forrest.	?Deciduous seasonal forest.	Grass not prominent in the American formation.
Thorn-forest.	Thorn woodland.	
Grassland.		
Savanna (including true savanna, grass-steppe and meadow).	Savanna (in part).	It is difficult to correlate with Schimper's grassland types owing to his radically different view of the habitat.
Desert.		
Tropical desert.	Cactus scrub, desert.	
Edaphic Woodland Formations.		
Fringing forest.	Various seasonal types.	Regarded as belonging to several formations, generally seasonal forest.
Fresh-water swamp forest.	Swamp forest, palm swamp, marsh forest, palm marsh.	
Littoral woodland.	Littoral woodland.	Falsely related by Schimper to telluric moisture.
Mangrove woodland.	Mangrove woodland.	
Montane Formations.		
Sub-tropical rain forest of the lower montane region in the tropics.	Lower montane rain forest.	
Temperate rain forest.	Montane or temperate rain forest.	
Elfin woodland.	Elfin woodland.	
Alpine steppe.	Paramo.	
Alpine desert.	Tundra.	

TABLE III. *Tentative correlation of neo-tropical formations with those of tropical Africa as described by Shantz ('23)*

Shantz' vegetation type	Correlation	Remarks
Forests.		
Mangrove forest.	Mangrove woodland.	
Tropical rain forest.	Rain forest and evergreen seasonal forest.	These types appear to correspond somewhat closely.
Temperate rain forest.	Montane or temperate rain forest.	
Dry forest.	?Deciduous seasonal forest.	
Thorn forest.	Thorn woodland.	
Grasslands.		
High grass-low tree savanna.		?Deflected climax, formerly "tropical rain forest."
Acacia-tall grass savanna.		?Deflected climax, formerly "dry forest."
Acacia-desert grass savanna.		?Deflected climax, formerly "thorn forest."
Desert grass.		?Deflected climax, formerly scrub and desert.
Mountain grassland.		?Deflected climax, formerly "temperate rain forest."
Alpine meadow.	Paramo.	
Marsh grass.	Herbaceous swamp.	
Deserts.		
Desert shrub.	Desert.	

TABLE IV. *Correlation of nomenclature with that of Barbour ('42)*

Barbour's primary types	Correlation
1. Dry forests.	Thorn woodland, cactus scrub.
2. Deciduous forests.	Semi-evergreen and deciduous seasonal forest.
3. Rain forests.	Rain forest, evergreen seasonal forest, xerophytic and lower montane rain forest.
4. Cloud forests.	Montane rain forest, palm brake, elfin woodland.
5. Special types.	
(1) Mangrove forests.	Mangrove woodland.
(2) Lowland pine type.	Savanna (subformation of).
(3) Non-forested types.	Paramo, tundra, herbaceous swamp, savanna.
(Not listed.)	Swamp forest, palm-swamp, marsh forest and woodland, palm-marsh, littoral woodland.

within the African grasslands, perhaps of low bunch-grass type, which will be found related to moisture conditions like those of America.

The writer's formations, given in correlation with types of Schimper and Shantz, may be physiognomically identical or may only belong to the same formation type. Students of African vegetation are invited to test the validity of these correlations by application of the analytical key in table V.

SUMMARY

During work on the vegetation of Trinidad, a system of classification was worked out to include all the known climax types of vegetation in tropical America.

It is proposed initially to recognize floristic groups, to which the nomenclature of Clements ('36) is applied. These floristic groups or associations are then classified into formations on the basis of structure and life-form according to the recommendations of Richards, Tansley and Watt ('39). The formations are finally grouped into formation-series on the basis of habitat.

Detailed descriptions have been given of twenty-four formations of which a summary appears in table I. Tentative

TABLE V. *Analytical key for recognition of formations in the field*

1. Herbaceous or non-woody growth dominant:
  2. Mainly moss and lichen. A high mountain community . . . . *Tundra.*
  2. Alpine plants, mostly stemless and with coriaceous leaves arranged in basal rosettes, many with showy flowers. A high mountain community . . . . *Paramo.*
  2. Giant herbs such as Montrichardia, Gynerium and Cyperus spp., gregarious and up to 4 meters tall, on deeply inundated site . . . . . *Herbaceous Swamp* (subformation: tall herbaceous swamp).
  2. Gramineae dominant or codominant with small Cyperaceae:
    3. Plants form a mat floating on deep water *Herbaceous Swamp* (subformation: swamp savanna).
    3. Plants not floating, grasses of "bunch" type. Small trees, shrubs or palmettoes may be present . . . . *Savanna.*
1. Palms dominant or present in very considerable numbers:
  2. Tall palms, up to 20 meters and more high, emergent over lower woody or herbaceous growth:
    3. Fan palms over a dense thicket of bushes and small trees 5 to 10 meters high *Palm marsh.*
    3. Fan or pinnate palms over low and irregular herbaceous or woody undergrowth with scattered small trees . . . . *Palm swamp.*
  2. Palms not emergent:
    3. Low forest about 10 meters high composed mainly of palms and with no large trees; very luxuriant herbaceous ground vegetation, abundant moss and epiphytes. A mountain community . . . . *Palm brake.*
    3. A forest with 2 tree strata, the upper of scattered trees up to 25–30 meters, the lower consisting mainly of palms and forming the canopy at 10–15 meters. A lowland community *Marsh forest.*
1. Thicket of bamboo . . . . *Bamboo brake.*
1. Woody growth dominant, palms and bamboos not present in considerable numbers:
  2. Tree growth over 10 meters high:
    3. Deciduous species present . . . . *Seasonal forests.*
      4. Tree strata 3, under $\frac{1}{3}$ of the individuals in the topmost story deciduous *Evergreen seasonal forest.*
      4. Tree strata 2, the upper closed and with from $\frac{1}{3}$ to $\frac{2}{3}$ of individuals deciduous *Semi-evergreen seasonal forest.*
      4. Tree strata 2, the upper open and with over $\frac{2}{3}$ of individuals deciduous *Deciduous seasonal forest.*
    3. Forest entirely evergreen (or practically so):
      4. Tall forest with large trees forming a continuous canopy at 20 meters or more above ground:
        5. Tree strata 3 or 4, dominants 40 meters or more tall, leaves predominantly compound *Rain forest.*
        5. Tree strata 2, dominants about 30 meters tall, leaves predominantly simple *Lower montane rain forest.*
        5. Tree strata 2, dominants about 20 meters tall, leaves simple; abundant moss, tree-ferns present . . . . *Montane rain forest.*
      4. Lower forest without continuous canopy or with a canopy formed below 20 meters from the ground:
        5. Pine forest . . . . *Mountain pine forest.*
        5. Broadleaved trees:
          6. Tree strata 2, the upper formed of scattered trees up to 30 meters, the lower closed and forming the canopy at about 15 meters . . . . *Xerophytic rain forest.*
          6. Tree stratum one only, sometimes 20 meters high, usually less:
            7. Stilt roots or erect pneumatophores present. Inundated tidally with brackish water . . . . *Mangrove woodland.*
            7. Sinuous plank buttresses and/or stilt roots and knee-shaped pneumatophores present. Inundated with fresh water . . . . *Swamp forest.*
  2. Tree growth less than 10 meters high:
    3. Species predominantly spinescent or thorny:
      4. More or less closed woodland of microphyllous, thorny trees 3 to 19 meters high *Thorn woodland.*
      4. Open vegetation with abundant column cacti and prickly pears . . . . *Cactus scrub.*
      4. Exceedingly sparse growth with large bare patches of soil . . . . *Desert.*

TABLE V.—*Continued*

3. Armed species few or absent:
    4. Vegetation markedly windswept:
        5. Trees covered thickly with moss and epiphylls. Abundant epiphytes and climbers; a high mountain community. . . . . *Elfin woodland.*
        5. Moss scarce, no epiphylls, epiphytes and climbers very rare; a seashore community *Littoral woodland.*
    4. Vegetation not markedly windswept:
        5. A fairly open woodland containing some stout trees. Temperate genera present. High mountains. . . . . *Frost woodland.*
        5. A dense woodland or thicket of small, branchy trees. Tropical genera. Lowland *Marsh woodland.*

correlations with the nomenclature of Schimper, Shantz and Barbour are given in tables II, III and IV. An analytical key for the recognition of formations in the field is given in table V.

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