

ECOLOGICAL STUDIES UPON A PHYSIOGNOMIC BASIS

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RESUMEN

Estudios ecológicos basados en la fisonomía. — El autor hace consideraciones sobre los tipos de vegetación, especialmente de la América tropical, y agrega un apéndice sobre estructura y composición de las "formaciones" y otro con clave analítica para el reconocimiento de las formaciones en el campo.

ABSTRACT

Published descriptions of vegetation-types in the American tropics have not so far been very numerous. We know less scientifically about the tropical regions. Studies of this kind are gradually increasing, however, and it will eventually be possible to piece together a complete picture of the vegetation, framing a classification into which all the types will fit, and which will clarify their ecological relationships. This epoch will be brought nearer if we ensure that ecological studies give us all the information we require, presented in the right manner, and do not omit to deal with important questions.

If descriptions of vegetation are to be of more than local interest, they must embody data which will enable us to compare the types recognised with those described elsewhere and to note similarities and differences. Only in this way can a general picture of vegetation over wide areas be built up. Descriptions of vegetation, therefore, must consist of more than a catalogue of component plants, a fact that has often

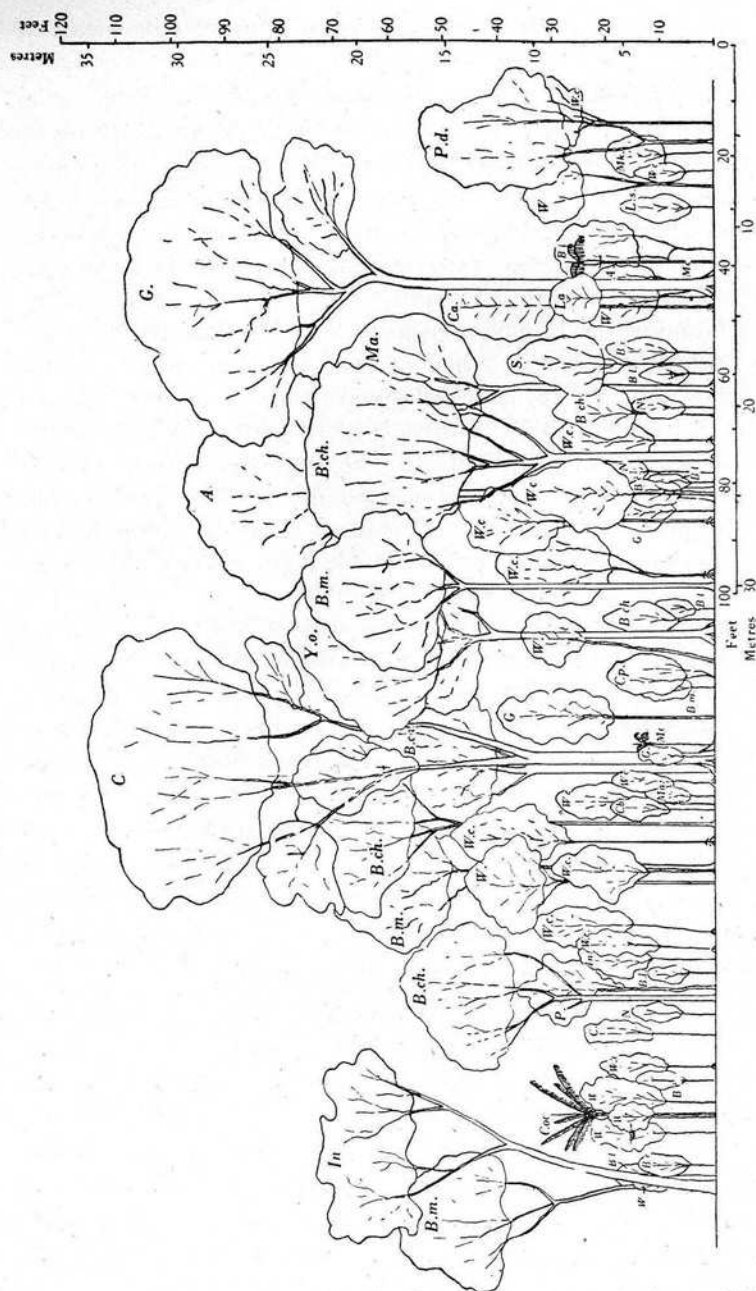
been overlooked in the past, particularly by those students who are systematic botanists by profession. Many important species of the American tropical flora are highly localised in their distribution, especially the members of the more luxuriant communities. The communities of very adverse habitats — swamps, savannas, etc., exhibit a reduced and simplified flora whose components are often of very wide range. Thus, the savanna tree *Curatella americana* occurs from Cuba to South Brasil, a range of some 5,000 Kilometres, and our mangrove trees are common to the Atlantic seaboard of both Africa and America. Such plants are also generally confined closely to their particular unit of vegetation, whose presence is automatically revealed when they are mentioned by name. It is far otherwise with the communities of more favourable habitats, the rain forests and other types of forest which cover the bulk of tropical America. It is safe to state that two examples of tropical rain forest 1,000 Kilometres apart would be unlikely to contain any of the same tree species. Many of the same genera would be represented, but as these genera also provide species for many other forest types, comparisons on a floristic basis are difficult, unreliable and even confusing.

Floristic units of vegetation, defined entirely by their plant components, which we may term *associations*, appear to be very much more localised in the tropics than in the temperate zone. This is due to the rich flora and favourable habitats. Depauperate temperate communities partake of the characters of those tropical communities of adverse habitat alluded to above. In my paper of 1944 (1) it was suggested that a basis for grouping of floristic units lies in their structure and life-form, or physiognomy: by which is meant the height of the plants and their arrangement into strata, the size and type of leaf, the presence or absence of spines, latices, plank buttresses and so on, — any characters distinguishing the plant community as an organic entity. Associations or floristic units which exhibit the same physiognomy may be grouped together in the same *formation*, which becomes a unit of vegetation of higher order defined entirely by physiognomy. If we are given sufficient data on structure and life form in ecological studies, we can readily say to what extent a described community

compares ecologically with one in another locality, even if the flora is quite different.

The English authors Richards, Tansley & Watt in a joint paper in 1939 (5) gave a list of headings under which data on structure and composition of forest types should be collected. This list is reproduced here in an appendix. Perusal of their whole paper is strongly recommended to intending students of South American vegetation. An important adjunct to the study of forest structures is the profile diagram, an invention of the English ecologist Dr. P. W. Richards who has published several of them from different parts of the tropics (6), (7), (8). A number have been prepared by myself for the British West Indies (1), (2), (3), (4), a typical example being appended hereto. The diagram is a scale drawing of an actual strip of forest selected in the field, in which the trees have been accurately measured. English workers have taken strips 200 feet x 25 feet (61 x 7.6 metres). The strip selected must be carefully chosen to show the representative structure of the forest type in question and must not contain irregularities due to fellings or windfalls. The strip is marked out in the forest, undergrowth removed, and the positions of all the trees in the strip mapped. As this is done each tree is allotted a number which is written on a blaze on its trunk. The trees are then cut down and measured on the ground, or measured standing with the use of instruments. For each tree the following should be recorded: name (vernacular and scientific), diameter of trunk, total height, height to lowest branch, height to lowest leaves, and spread of crown. From these data, a drawing can later be prepared.

If we can have more of these diagrams and more accurately compiled information on the structure and life-forms of vegetation, it will soon be possible to put together a general ecological picture for the whole American tropics. An ecologically adequate study of vegetation can be made without mentioning a single plant by name, provided structure and life-form are fully dealt with. A physiognomic key to the provisional list of vegetation-types of tropical America from my paper of 1944 (1) is included here as second appendix.



Perfil de Selva veraniega siempreverde: Isla de Trinidad, Antillas británicas. De BEARD, *The Mora Forest of Trinidad*. — *J. of Ecology* 33: 173-192; 1946.

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APPENDIX I

STRUCTURE AND COMPOSITION

Structure:

- (1) Closed or open canopy: if open the approximate width of gaps or the approximate percentages of shaded and unshaded areas.
- (2) Uniform or irregular spacing of trees: distances apart of the trunks: diameters of trunks of apparently mature trees of different species.
- (3) Description of stratification: how far distinct strata or layers can be recognised: enumerate these.
- (4) Separate description of each well-marked layer, with the height of its foliage above the ground. Where distinct layers are absent, general description of structure in the vertical dimension, with ranges of height of the various components.
- (5) Societies, i. e., local aggregations of individuals of a species observed in any of the layers.

Physiognomy and Life-form:

- (6) Lianes, height to which they ascend: epiphytes, distribution and frequency, particulars of kinds of epiphyte — orchids, bromeliads, ferns, strangling figs, etc.: distribution in height, distance from ground to which they descend.
- (7) Plank buttresses: stilt roots: pneumatophores ('breathing roots') erect or knee-shaped: thorny trunks or branches; cauliflory: peculiarities of bark: succulent leaves or stems.
- (8) Any special life forms present, e. g., palms or cycads, tree ferns, bamboos, rattans, pandanus.
- (9) Trees generally evergreen or deciduous: if mixed, percentages of each form.
- (10) If deciduous the time of foliation and leaf fall.
- (11) Leaves simple or compound: if compound, pinnate or digitate: approximate number of leaflets.
- (12) Leaf size: assignment to one of Raukiaser's 'leaf size classes'.
- (13) Life forms of field and ground layers. General notes on the types present, their frequency and gregariousness, e. g., abundance of tall herbs, ferns, selaginellas, or mosses.
- (14) Periodicity of field layer: seasonal dying down of any subordinate layer or important constituents: annual plants, if any.

Reproduction:

- (15) Seed production of important trees: amount, kind of seed, mode of dispersal (if any). Relation between number of seedling trees and seed-bearing parents. Ability of tree seedling to endure shade.
- (16) Observations on vegetative propagation of trees and shrubs.

Floristic composition:

- (17) List of all species distinguished, whether their proper names are known or not; each layer of the forest should be listed separately. Where there is a number of species present which the observer is unable to separate and identify by name or number the facts should be noted.

APPENDIX II

Clave analítica para el reconocimiento de las formaciones en el campo

1. Crecimiento herbáceo o no leñoso dominante:
2. Principalmente musgos y líquenes. Una comunidad de las montañas altas. *Tundra.*

2. Plantas alpinas, la mayoría de ellas sin tallo y con hojas coriáceas dispuestas en rosetas basales, muchas con flores vistosas. Una comunidad de las montañas altas *Paramo*.
2. Hierbas gigantes tales como *Montrichardia*, *Gynerium* y *Cyperus* spp. gregarias y hasta de 4 metros de altura, en sitios profundamente inundados... *Pantanos herbáceos*. (subformación pantanosa con hierba alta).
2. Gramíneas dominantes o codominantes con pequeñas Ciperáceas:
 3. Las plantas forman un tejido flotante sobre aguas profundas. *Pantanos herbáceos*. (subformación sabana pantanosa).
 3. Plantas no flotantes, hierbas del tipo en manojos. Pueden estar presentes árboles, arbustos o palmetas. *Sabana*.
- 1 Palmas dominantes o presentes en números muy considerables:
 2. Palmas de 20 metros y más de altura, que emergen sobre el crecimiento leñoso o herbáceo:
 3. Palmas de abanico sobre un espesamiento denso de arbustos o arbolillos de 5 a 10 metros de altura. *Palmar de pantano estacional*.
 3. Palmas de abanico o pinnadas sobre un crecimiento inferior irregular, herbáceo o leñoso con arbolillos dispersos. *Palmar de pantano*.
 2. Palmas no emergentes:
 3. Selva baja de cerca de 10 metros de altura compuesta principalmente de palmas y con árboles no muy altos; el suelo con vegetación herbácea muy lozana, musgos y epifitas muy abundantes. Una comunidad montañosa. *Palmar de montaña*.
 3. Una selva con dos estratos de árboles, la superior de árboles dispersos que tienen de 25 a 30 metros, la inferior consiste principalmente de palmas y forman un dosel a los 10-15 metros. Una comunidad de tierras bajas. *Selva de pantano estacional*.
1. Sotos de Bambú *Bamboal*.
1. El crecimiento leñoso es dominante, las palmas y los bambús no se encuentran presentes en números considerables:
 2. Crecimiento arbóreo de más de 10 metros de altura:
 3. Especies deciduas presentes *Selvas veraneras*.
 4. Tres estratos de árboles; cerca de 1/3 de los individuos del estrato superior, deciduos. *Selva veranera siempreverde*.
 4. Dos estratos de árboles, el superior cerrado y con 1/3 a 2/3 de los individuos deciduos. *Selva veranera semidecidua*.

4. Dos estratos de árboles, el superior abierto y con cerca de los 2/3 de los individuos deciduos.

Selva veranera decidua.

3. Selvas completamente siempreverdes (o prácticamente así):

4. Selva alta con grandes árboles que forman un dosel continuo a 20 metros o más sobre el suelo:

5. Tres o cuatro estratos de árboles, los dominantes de 40 metros o más de altura, hojas predominantemente compuestas.

Selva pluvial.

5. Dos estratos de árboles, los dominantes de cerca de 30 metros de altura, hojas predominantemente simples.

Selva pluvial intermedia.

5. Dos estratos de árboles, los dominantes de cerca de 20 metros de altura, hojas simples; los musgos y los helechos arborescentes abundantes.

Selva nublada.

4. Selva más baja sin dosel continuo o con un dosel formado a menos de 20 metros sobre el suelo:

5. Selva de pinos

Pinar de montaña.

5. Árboles de hojas anchas:

6. Dos estratos de árboles, el superior formado por árboles esparcidos, el inferior cerrado formando un dosel a unos 25 metros de altura.

Selva pluvial xerofítica.

6. Únicamente un estrato de árboles, algunas veces de 20 metros de altura, generalmente menos:

7. Raíces zancoas o pneumatóforos erectos presentes. Inundada por las mareas con agua salada.

Manglar.

7. Raíces con sostenes delgados y sinuosos y raíces zancoas y pneumatóforos en forma de rodillas presentes, o ambas cosas. Inundadas por agua dulce.

Selva de pantano.

7. Sin peculiaridades en las raíces, tierra bien drenada.

Bosquete de montaña.

2. Crecimiento de los árboles de menos de 10 metros de altura:

3. Especies predominantes armadas o espinosas:

4. Bosques más o menos cerrados de árboles micrófilos y espinosos de 9-19 metros de altura

Espinar.

4. Vegetación abierta con abundancia de cactus columnares y nopales.

Cardonal.

4. Crecimiento excesivamente esparcido con grandes parches de suelo limpios de vegetación.

Desierto.

3. Especies armadas pocas o ausentes:
4. Vegetación marcadamente doblada por el viento:
 5. Árboles cubiertos con una espesa capa de musgos y epifilas. Epifitas y trepadoras abundantes; una comunidad de las montañas altas. *Bosque enano.*
 5. Los musgos son escasos, no hay epifilas, las epifitas y las trepadoras son muy raras; comunidad costanera. *Bosque de playa.*
4. Vegetación no marcadamente doblada por el viento:
 5. Bosque denso o bosque de arbolillos ramificados. *Bosque de pantano estacional.*

Presentado al II Congreso Sudamericano de Botánica en Tucumán, Sección Geobotánica (Ecología y Geografía de las plantas), en sesión del 15 de octubre de 1948.