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(Publication 4527)

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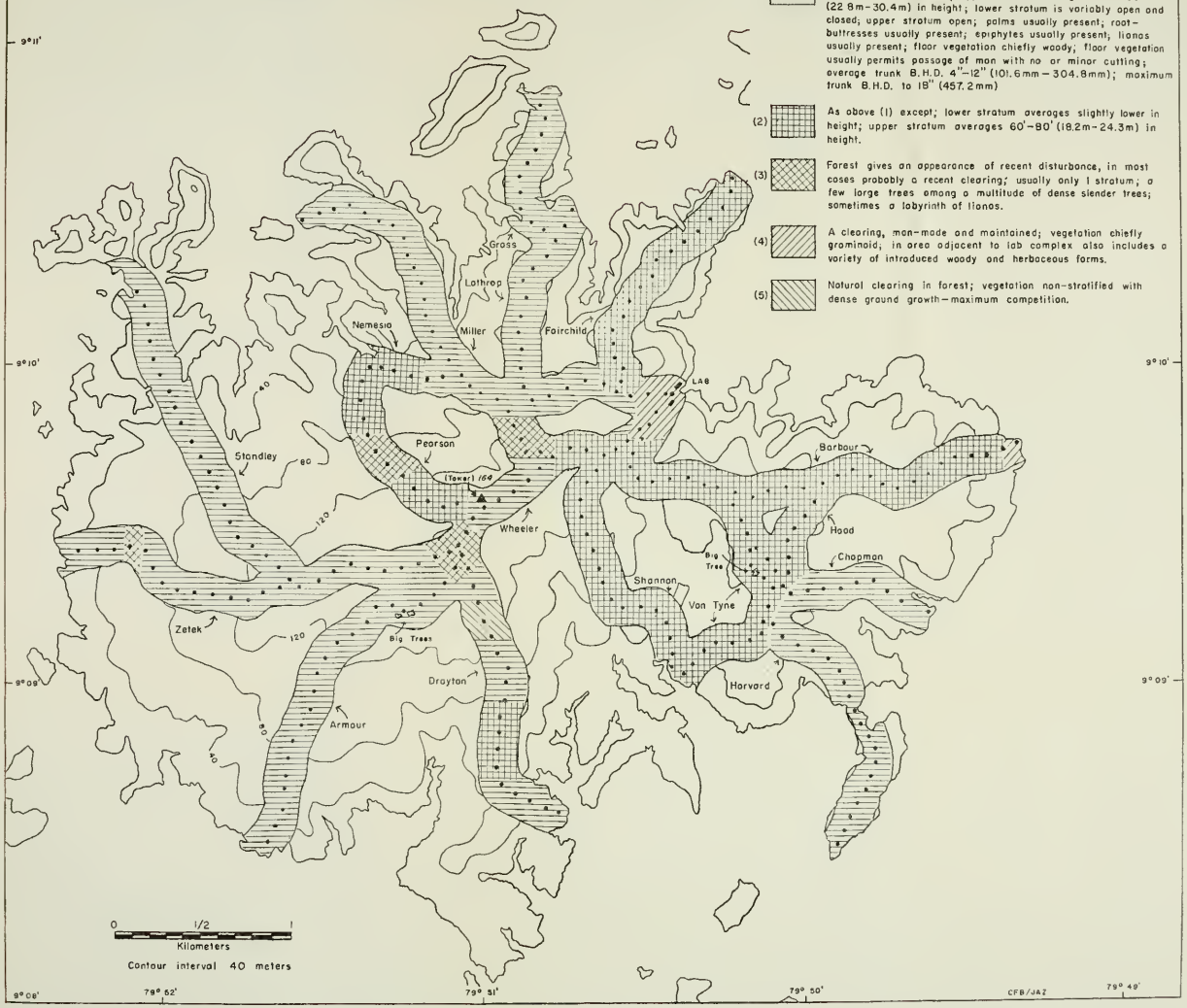
PHYSIOGNOMIC CHARACTERISTICS OF THE VEGETATION OF BARRO COLORADO ISLAND



A PHYTOPHYSIOGNOMIC RECONNAISSANCE OF BARRO COLORADO ISLAND, CANAL ZONE

By Charles F. Bennett, Jr.

Barro Colorado Island (hereafter BCI) has been and continues to be the site of intensive and varied research on problems of tropical biology. Increasingly, during the 40 years of the man-made island's existence, the studies have focused on problems that require detailed analysis of the basic ecological conditions occurring on the island. It is in an effort to make a contribution to the knowledge of one of these basic conditions—the phytophysiognomy—that this paper is written.

With the exception of a sketch map which attempted to show some physical aspects of the forest on BCI (Enders, 1935) no map of the phytophysiognomy of the island has heretofore been made available. This may, in part, account for the numerous allusions to "tropical rainforest," "primeval tropical forest," and "climax forest" that one encounters in many published papers dealing with some aspects of the island's biology.

Possibly it is incorrect to allude to any parcel of arboreal vegetation in the American (or Old World) tropics as being primeval in the sense that it represents an entity quite uninfluenced by the hand of man. Millennia-long human occupance of these lands would seem to preclude such usage. Areas not now settled by man may suggest the primeval but may surprise one when soil samples are taken, as was recently the case in Dutch Guiana where charcoal was discovered (Shulz, 1960). BCI scarcely is sited in an isolated position in the American tropics. It was once a low hill among many similar to it on the isthmus, and it seems fatuous to suggest that shifting cultivators (Cuna-Cueva) who occupied the general area at the time of Spanish entry spared this particular hill from fire and crops. In the four centuries since the Conquest the hill was adjacent to the major routes of transisthmian crossing. The hill's transformation into an island was perhaps only among the most recent of a long series of ecological manipulations by man, for the manipulations did not cease at once—holdings of several small farmers had to be purchased before the island could be turned into a preserve (Anon., 1925).

Previous writers have mentioned the human ecological role on BCI (e.g., Kenoyer 1929; Zetek, n.d.; Standley, 1933; Chapman, 1938), but the import of their statements was sometimes lost through hopeful allusions to the supposed presence of primeval or climax forest on the island. In this writer's opinion, biologists would do well to consider such forest areas as extremely rare entities anywhere in the tropics and to dismiss the idea completely in reference to BCI.

Perhaps even more persistent are the published allusions to the existence of a tropical rainforest cover on BCI. There is some justification for this misconception because of the plethora of vague and inexact ways in which certain specialists have employed the term tropical rainforest. This inexactness has performed no service to biologists and particularly to those seeking to demonstrate similarities and/or differences between spatially separated tropical regions.

In climatology, tropical rainforest has been defined quantitatively and is referred to as tropical rainforest climate. The term refers to precipitation and temperature, *viz,* the average temperature of the coldest month is no lower than 18°C. (64.4°F.), and the average precipitation of the dryest month is not less than 60 mm. (2.2 inches). This is a part of the Köppen Climatic Classification, and the quantitative values given above are coded as follows: the temperature value receives *A* (signifying an always warm tropical climate); the precipitation value receives an *f* (indicating abundant precipitation distributed throughout the year). Together, *Af* signifies tropical rainforest climate, or, to put it another way, only under these climatic conditions can tropical rainforest be expected to occur. Although there are *Af* stations within the Republic of Panama, BCI is not such a station because *f* conditions of precipitation do not occur there. The months of January, February, and March have average precipitation of less than 60 mm. On the other hand, the remaining eight months are usually very wet and much of the annual average precipitation, which exceeds 2,500 mm. (100 inches), falls during this period. The designation for this precipitation pattern in the Köppen system is *m.* Thus BCI has an *Am* or Tropical Monsoon Climate.[1]

The Köppen system represents an attempt to correlate the known data on precipitation and temperature with the distribution of major vegetational regions (based principally on De Candole's system of dividing the world's plant cover into five groups supposedly correlated

[1] The author is in the process of completing for publication the first of a series of climatological studies of BCI. Therefore, more detailed analysis is not here presented.

with their temperature requirements, *viz,* macrotherms, mesotherms, microtherms, hekistotherms, xerophytes). This obviously results in broadly generalized climatic-vegetation regions. One must, therefore, turn to other sources when the plant physiognomy of smaller regions is to be examined. For this purpose the work of J. S. Beard has been considered as most important and applicable (Beard, 1944, 1955).

Although Beard employs the climax concept in his approach to tropical vegetation, which this writer holds to be of doubtful value, it is nonetheless true that the tropical forest formations recognized by Beard, climax or no, have the decided significance of being entities that in fact exist and can be recognized rather easily by investigators employing the classification in the field.

Because the reader is above referred to Beard's work, which is readily available in libraries, only the briefest remarks regarding it will be made here. He recognizes rainforest as constituting a major formation, and in addition to this optimal formation he recognizes six seasonal formations (as well as other special formations) ranked according to their divergence from the optimal rainforest situation. The first two in the ranking concern us here, *viz,* Evergreen Seasonal Forest and Semi-Evergreen Seasonal Forest. On BCI the oldest appearing forest seems to be more or less intermediate with the two just named formations. If one were required to assign a broader term to the older forest cover on the island the term Tropical Monsoon Forest would apply.

To return to my earlier comments, recent vegetation disturbances by man on BCI makes rigorous application of Beard's or any other system to the entire island quite impossible. There are in fact a number of rather distinct phytophysiognomic microregions on the island which are of obvious importance to the distribution and numbers of animal species present. Further, these conditions are not to be considered as static, and as they change so too will the structure of the island's fauna change. In order to contribute in a small measure to the understanding of the phytophysiognomy of the island, I conducted a mapping-reconnaissance during two weeks in August 1960. A discussion of the results of that reconnaissance follows.

As is known to those familiar with the area, BCI is crossed by a network of trails which more or less intercept most of the larger biotopes occurring on the island. It is probable that a large percentage of the field observations on the island are made on or within a few yards of the trails. Therefore, the reconnaissance was confined to the trails,

as the accompanying map (fig. 1) will clearly indicate.[2] Time limitations prevented proper surveys between the trails, and it is believed that map reliability has been increased through refraining from extrapolating trail data to fill the large map interstices between the trails.

Special note should be taken of the fact that the mapping was accomplished during the wet season. This tends to bias the observations to some extent as the forest on BCI is facultatively deciduous, and while sometimes appearing extraordinarily lush and green in the rainy period it will also present a very xeric appearance during an exceedingly well-developed dry season as, e.g., 1958. Also, during those years in which the dry season is not very dry, as e.g., 1963, leaf fall will be found to be very much less than in normal years. This point is stressed because we are often misled by authors whose work in the tropics has almost always been in one season (coinciding no doubt with the academic year summer recess), and many of us have at times almost lost sight of the fact that while the lowland tropics may be the place where winter never comes, it is very definitely a place where ecologically significant seasonal changes of temperature and precipitation occur.

There is not yet a standardized system for mapping the physiognomic characteristics of tropical vegetation. Therefore, I devised my own list of phytophysiognomic characters which seemed to be of importance. The specific details mapped were as follows:

1. Number of tree strata present.
2. Average estimated height of each tree stratum.
3. Canopy characteristics of each tree stratum.
4. Presence of palms.
5. Average breast-height-diameter of trees.
6. Occurrence of the following special features:

    a. root buttresses.
    b. stilt roots.
    c. lianas.
    d. epiphytes.
    e. density of floor vegetation.
    f. nature of floor vegetation.
    g. leaf litter on forest floor.

It is obvious that this list is too detailed to permit all the items being conveniently shown on a map of the scale employed in this paper. Therefore, the details were generalized into five categories which are discussed below.

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[2] The base map employed appeared in Woodring, 1958.

The trails on the island are marked at 100-meter intervals, and it was therefore possible to maintain good mapping control. The distribution of the various categories appearing on the map are correct as read *along* the trail. The width of the distribution of the vegetation type along any given trail has been standardized to approximately 100 meters as a cartographic convenience and does not represent actual field limits to the transects. On the other hand, the width is realistic in that the conditions as mapped usually extend at least 50 meters on each side of the trails.

The five map categories are as follows:

(1) Forest with essentially 2 tree strata; the lower stratum averages 25′ to 40′ (7.6 m. to 12.2 m.) in height; the upper stratum averages 75′ to 100′ (22.8 m. to 30.4 m.) in height: the lower stratum is variably open and closed; the upper stratum is open; palms are usually present; root buttresses usually present; epiphytes are usually present; lianas usually present; floor vegetation density is only moderate and usually permits the passage of a man with little or no cutting; floor vegetation is chiefly woody; average breast-height-diameter of trees is 4″ to 12″ (102 mm. to 305 mm.); maximum breast-height-diameters seldom exceed 18″ (457 mm.).

This unit (1) has a discontinuous distribution on the island. Although rather limited in area in the center of the island, it becomes rather extensive in the extreme west, extreme southeast, and in the north and northwest parts. On a trail-length basis this unit accounts for approximately 11 km. This appears to be the oldest of the various forest units present on the island. I would, however, refrain from calling it either mature or climax for reasons given above.

(2) More or less as (1) above except that the bottom stratum averages slightly lower in height and the upper stratum averages 60′ to 80′ (18.2 m. to 24.3 m.) in height.

As indicated, there is rather little other than height difference to distinguish the second category from the first. This is probably slightly younger forest than (1). It is concentrated in the east, northeast, and central parts of the island. Its linear extent along trails is approximately 7.5 km.

(3) A forest which presents an appearance of recent disturbance, in most cases probably a clearing in the past 40 years. There is usually a single-tree stratum with an occasional larger tree spaced at broad intervals among a multitude of closely spaced very slender trees; sometimes dense labyrinths of lianas occur.

Most, if not all, of the areas mapped as (3) represent sites that not very long ago were devoted to farming. One occasionally encounters rather forceful testimony to this in the form of an isolated mango (*Mangifera indica*) or coconut tree (*Cocos nucifera*), which probably mark old house sites. Those who frequently postulate the rapid recovery of tropical forest on a site after it has been deserted by man would find these situations (3) quite instructive. Total trail length slightly exceeds 0.5 km.

(4) A clearing, man-made and man-maintained; vegetation is chiefly graminoid but in clearing adjacent to laboratory complex there is also a wide variety of exotic woody and herbaceous forms.

Although very limited on the map, areas of (4) occur elsewhere on the island away from trails and adjacent to canal marking devices. The latter are usually in grass or grass, herbaceous forms and young palms. Heavier growth is kept down through regular maintainence by Canal officials. Areas of (4) are among the most interesting from a faunal standpoint of all five units shown on the map. Total trail length is approximately 0.5 km.

(5) Natural clearing in the forest; vegetation is not stratified and ground cover is dense in the earlier seral stages; an abundance of herbaceous species during early seral stages giving way later to an increasing density of woody forms.

This (5) is the most transient phytophysiognomic unit mapped on BCI. These clearings usually result from tree blowdowns during high winds. The map includes only the largest one encountered.

Some further discussion of the phytophysiognomic details recognized in the reconnaissance is desirable, not only to add further to the map detail but also to augment understanding of the physical character of the vegetation of BCI. Since a number of these details have been discussed above in connection with the major categories employed on the map, only the "special features" are discussed below.

a. *Root buttresses.* No areas of marked concentration of this interesting feature were noted. Root buttresses occur as a generally distributed feature with the lowest incidence occurring in areas designated as (3) on the map. Of course this feature does not as a rule occur in clearings.

b. *Stilt roots.* This feature appears to have a random distribution. Sometimes one finds small colonies of the palm *Iriartea* spp. which possess this character.

c. *Lianas.* Although lianas are generally distributed over the island, they are not abundant except at clearing edges, and in area (3).

d. *Epiphytes.* At no place on the island were epiphytes encountered in abundance, although this feature is definitely ubiquitous. Most trees have a complement which becomes abundantly apparent when limbs fall to the forest floor during high winds or as the result of insect tunneling and general decay. But one does not encounter the incredibly festooned limbs of, for instance, the cloud forest of other parts of the tropics.

e. *Density of floor vegetation.* Although the forest floors of BCI never suggest the "vaulted aisles" of some writers, the ground cover under the older forest tends to be moderate and usually allows passage with very little work with the machete. This is somewhat surprising because the sunlight reaches the ground quite abundantly in the normal dry season, and this would seem to facilitate growth. But this is also the period of drought, and the fact remains that for at least 8 months of the year the amount of light reaching the ground is so slight as to probably restrict growth. Other inhibiting factors are also undoubtedly present. In clearings, however, the dense tangles of vegetation prevent all but the most determined person from passing.

f. *Nature of floor vegetation.* Woody floor vegetation is the rule in the older forested areas. But even in these situations considerable quantities of herbaceous vegetation is sometimes encountered although this is usually most abundant in clearings. One special feature deserving mention is the occurrence of dense thickets of a terrestrial bromeliad with the local name piñuela (probably *Ananas* spp.). One of the most extensive of such areas occurs not far from the end of Zetek trail in the western end of the island. These thickets are almost impenetrable to man but provide shelter and food to a considerable array of animal species.

g. *Leaf litter.* I am not aware that this is usually included as a phytophysiognomic feature, but it is so included here because it is of considerable ecologic significance. This is an extremely variable feature varying from season to season, from year to year, and from place to place at any given time. Contrary to numerous published remarks which indicate that leaf litter is virtually nonexistent on the floor of tropical forests except for limited periods during the year, leaves persist in quantity on the forest floor of BCI throughout the year. Although fungal and bacterial action is rapid and more or less continuous, there is a more or less continuous increment of shed leaves to the floor during all periods of the year. The greatest deposition usually occurs during the height of the dry season. It is rare to encounter any sizable area of forest floor completely devoid of leaf litter at any time

of the year. Seasonal conditions, as well as local conditions of slope, and wind exposure are important modifying factors.

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