DISTRIBUTION OF TROPICAL AMERICAN RAIN FOREST SPECIES IN THE LIGHT OF SUCCESSIONAL PROCESSES

by Gerardo Budowski *

Distribution patterns of rain forest species are the result of many inter-acting factors among which climate, soils, relief and historic geology have been treated in detail. There are also some studies on the role of wind, animals and water in seed dispersion.

However, there is still another important factor, namely plant succession, which bears important implications on distribution patterns and which, for the tropical rain forest, has unjustly received scanty attention.

The present study attempts to show certain relationships between successional processes and distribution patterns for the tropical American lowland forests. The areas studied cover large extensions in northern tropical America and Central America with a mean annual temperature over 22ºC. (71.6ºF) and a mean annual rainfall over 2,000 mm. (approximately 80 inches).

THE CLASSIFYING OF COMMUNITIES IN THEIR PROPER SUCCESSIONAL STATUS

In order to appreciate the relationship between successional patterns and the distribution of rain forest species, it is essential that successional seral stages be recognized. This can be done by recording carefully a series of critical floristic, physiognomic and structural features which will give enough clues for classifying the different seral stages. These stages can be called -- for convenience -- pioneer, early secondary, old secondary and climax, and comprise the critical characters shown in Table I, which were taken from a series of plots of which age and past intervention were well known (Budowski 1961, 1963).

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TABLE I

CHARACTERISTICS OF ARBOREAL COMPONENTS OF SERAL STAGES IN TROPICAL AMERICAN HUMID FORESTS

	Pioneer	Early secondary	Late secondary	Climax
Age of communities observed years	1-3	5-15	20-50	more than 100
Height, meters	5-8	12-20	20-30, some over 50	30-45, some over 50
Number of woody species	few, 1-5	few, 1-10	30-60	up to 100 or a little more
Floristical composition of dominants	Euphorbiaceae, Cecropia, Ochroma, Trema	Ochroma, Cecropia, Trema, Heliocarpus most frequent	mixture, many Meliaceae Bombacaceae, Tiliaceae	mixture, except on edaphic associations
Natural distribution of dominants	very wide	very wide	wide, includes drier regions	usually restricted, endemics frequent
Number of strata	1, very dense	2, well differentiated	3, increasingly difficult to discern with age.	4-5, difficult to discern
Upper canopy	homogeneous, dense	verticillate branching, thin horizontal crowns	heterogeneous, includes very wide crowns	[illegible] of crowns,
Lower stratum	dense, tangled herbaceous frequent	dense, large herbaceous species frequent	relatively scarce, includes tolerant species	scarce, with tolerant species
Growth	very fast	very fast	dominants fast, others slow	slow or very slow

The generalization shown on the table have been simplified to indicate relative values rather than absolute numerical ones, since the latter would be very difficult to render in detail at this stage. However, experience has shown that the recording of these characters does not offer a serious problem to those who have a fair acquaintance with tropical rain forest vegetation.

When such classification is achieved, a distinct relationship between distribution patterns of some species and their proper successional status can be found.

THE DISTRIBUTION PATTERNS OF PIONEERS AND EARLY SECONDARY SPECIES

These two groups, here lumped together for convenience, are found over areas of very different climatic and edaphic conditions. Under conditions of closed undisturbed forest the presence of species of these successional stages is limited to openings or gaps made by falling trees, landslides or other accidents including, of course, man-made clearings. These are the "biological nomads" as they have been rightly called by van Steenis (1958). However, these species are also found in other niches such as the river banks, the edges of swamps and, in some cases, they are also components of the early stages of succession of the drier formation, i.e., the deciduous forest, although they are not deciduous themselves. The obvious implication is that these species are well adapted to drought, be it lack of rainfall or physiological, through flooding. Very poor soils or rocky outcrops also constitute niches where these species take refuge. Their seed dissemination mechanism is very efficient. The small seeds are not only produced profusely but can remain dormant for a considerable period under the shade of high canopy species until full sunlight triggers their germination.

The distribution of pioneers and early secondary species has, of course, considerably increased over the last 50 years as a result of man's impact on the vegetation.

THE DISTRIBUTION PATTERN OF LATE SECONDARY SPECIES

The most striking characteristic of these species is their deciduousness, even in areas of very heavy rainfall. The most significant factor in connection with distribution is that many of the species are also

found in drier habitats, mainly the deciduous forest or the very dry forest. In some of those formations they actually reproduce well, and hence may be considered as members of the climax. This possibility has been discussed by Troll and Richards (as comments on a paper by Aubert de la Rue, 1958). It is definitely true for many American species, such as Goethalsia meiantha, Bursera simaruba, Luehea seemanii, Cordia alliodora, among others. Possibly Ceiba pentandra, of pantropical distribution, enters into that category too. Some of these older secondary species may actually remain in place for centuries and attain great size. This has also been pointed out by van Steenis (1958), among others. Curiously, then, some of the largest trees of the tropical rain forest may often be old secondary species which have remained in the area for a long period, but not regenerate. This is certainly the case for some of the valuable Meliaceae, such as Swietenia macrophylla, Cedrela mexicana and some Bombacaceae, such as Bombacopsis sepium and Ceiba pentandra. In Panama and Colombia Cavanillesia platanifolia is another outstanding example.

THE DISTRIBUTION OF CLIMAX SPECIES

For convenience of definition, a climax community is the end product of a successional sere when a relatively stable -- although certainly not static -- community has been reached and when changes of floristic composition, structure and physiognomy over the age span of the dominants become insignificant.

The rule in climax communities is a thorough mixture of species whenever drainage is not extreme or impeded. This has been stressed, among others by Richards (1963). As soon as one single or a few species become dominant, some edaphic factor, usually related to excessive water -- at least during part of the year -- can be suspected; but, generally speaking, endemism is frecuent from the floristic standpoint.

In conclusion it is felt that in order to understand distribution patterns of rain forest species much consideration should be given to successional patterns. The classification of communities into their proper successional sequence, a matter which can be achieved by carefully recording indicative floristic, physiognomic and structural characteristics

of the communities, seems to be an essential previous step. A large proportion of pioneers, early secondary, old secondary and climax species appears to display a distribution pattern which is typical of their successional status.

SUMMARY

Within the tropical rain forest the species that integrate different seral stages display characteristic distribution patterns. Pioneers and early secondary species have a wide distribution. Late secondary species are deciduous and may attain considerable size when they grow to old age. They are part of the climax in the drier or deciduous forest. Much endemism is found in climax communities; while a mixture of species is the rule, there may be edaphic factors which will favor the dominance of one or a few species.

LITERATURE CITED

1. AUBERT DE LA RUE, E. 1958. Man's influence on tropical vegetation. In Proceedings, Ninth Pacific Science Congress, 1957. Bangkok, Secretariat, Ninth Pacific Science Congress. pp. 81-94.

2. BUDOWSKI, G. 1961. Studies on forest succession in Costa Rica and Panama. Doctor of Philosophy thesis. New Haven, Yale University, School of Forestry. 189 p.

3. _____. 1963. Forest succession in tropical lowlands. Turrialba 13(1):42-44.

4. RICHARDS, P. W. 1963. What the tropics can contribute to ecology. Journal of Ecology 51(2):231-241.

5. VAN STEENIS, C. G. G. J. 1958. Rejuvenation as a factor for judging the status of vegetation types: the biological nomad theory. In Study of Tropical Vegetation. Proceedings of the Kandy Symposium, Ceylon 19-21 March 1956. pp. 212-215.