Distribution of tropical American rain forest species in the light of successional processes*1

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COMPENDIO

Dentro del bosque húmedo tropical, las especies que integran las diferentes etapas de la sucesión, muestran ciertas características definidas en su distribución.

Las especies pioneras y las secundarias tempranas tienen una distribución amplia. Las especies secundarias tardías son deciduas y pueden alcanzar un tamaño considerable cuando llegan a una edad avanzada. Ellas forman parte del climax en los bosques secos o decidnos. En las comunidades climax se encuentra mucho endemismo, allí, aún cuando la heterogeneidad de especies es la regla, pueden darse casos de dominancia de una o pocas especies debido a la influencia de ciertos factores edáficos. —El autor

Introduction

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, as unjustly received scanty attention.

The present study attemps 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 essencial 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 1, which were taken from a series of plots of which age and past intervention were well known (2, 3).

The generalizations 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,

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Table 1.—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 reaching 50	30-45 some up to 60
Number of woody species	few, 1-5	few, 1-10	30-60	up to 100 or a little more
Floristic composition of dominants	Euphorbiaceae, *Cecropia*, *Ochroma*, *Trema*	*Ochroma*, *Cecropia*, *Trema*, *Heliocarpus* most frequent	mixture, many Meliaceae Bombacaceae, Tiliaceae	mixture, except on edaphic association
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	many variable shapes of crowns
Lower stratum	dense, tangled	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
Life span, dominants	very short, less than 10 years	short, 10-25 years	usually 40-100 years, some more	very long, 100-1000, some probably more
Tolerance to shade, dominants	very intolerant	very intolerant	tolerant in juvenile stage, later intolerant	tolerant, except in adult stage
Regeneration of dominants	very scarce	practically absent	absent or abundant with large mortality in early years	fairly abundant
Dissemination of seeds of dominants	birds, bats, wind	winds, birds, bats	wind principally	gravity, mammals, rodents birds
Wood and stem, dominants	very light, small diameters	very light, diameters below 60 cm	light to medium hard, some very large stems	hard and heavy, includes large stems
Size of seed, or fruits dispersed	small	small	small to medium	large
Viability of seeds	long, latent in soil	long, latent in soil	short to medium	short
Leaves of dominants	evergreen	evergreen	many deciduous	evergreen
Epiphytes	absent	few	many in number, but few species	many species and life forms
Vines	abundant, herbaceous, but few species	abundant, herbaceous but few species	abundant, but few of them large	abundant, includes very large woody species
Shrubs	many, but few species	relatively abundant but few species	few	few in number but many species
Grasses	abundant	abundant or scarce	scarce	scarce

of course, man-made clearings These are the biological nomads as they have been rightly called by van Steenis (5, 6) 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 (1) 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 (5,6), 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 do 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 (4) 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 favor the dominance of one or a few species

Literature cited

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

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

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

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

5 VAN STEENIS C G G J 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 1958

6 ————————Tropical lowland vegetation; the characteristics of its types and their relation to climate *In* Proceedings Ninth Pacific Science Congress, 1957 Bangkok Secretariat Ninth Pacific Science Congress pp 25-37 1958