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STUDIES ON THE SECONDARY SUCCESSION OF TROPICAL LOWLANDS: THE LIFE CYCLE OF SECONDARY SPECIES[1]

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Introduction

We are living in an era that could be known as the "era of secondary vegetation". With a few exceptions there is no country on earth which has a larger land surface cover of primary (primeval) vegetation than of secondary vegetation. In addition, there is reason to believe that part of the so-called primary vegetation is in fact an old secondary one (Richards, 1963). We are spectators of one of the most important changes occurring in the history of life on earth. The native biota is being extinguished or is adapting to this condition at an impressive rate (Gómez-Pompa, 1971; Gómez-Pompa et al., 1973). In the tropical lowlands this trend is not the exception but the rule.

It is clear to us that man is the greatest cause of vegetational disturbance and, therefore, of succession; his activities represent the most important transient events occurring in nature.

Secondary species (species of secondary vegetation) today represent probably the most important biota of the tropical lowland areas because of their abundance, the remarkable versatility of their responses to disturbance, and their possible use for our generation and for those of the future.

There is not a clear cut difference between a secondary species and a primary one as their characteristics may differ from one species to another. This problem has been discussed previously (Farnworth & Golley, 1974) and in this paper we will deal with the typical "nomad" species which are easily recognized, at least in the lowland humid tropics (Van Steenis, 1958), after clearing a selva.

Several studies with different approaches and interests have been carried on in the tropics on the regeneration process. We can identify some trends in them such as, the ecosystem approach (Farnworth & Golley, 1974), the descriptive approach (Kenoyer, 1929; Budowski, 1961), the evolutionary approach (Gómez-Pompa, 1971), the population approach (Sarukhán, 1964; Rico & Gómez-Pompa, 1974), and the autecological approach (Gómez-Pompa & Vázquez-Yanes, 1974). It is difficult, however, to make clear cut distinctions between these approaches. Nevertheless, the most important fact is that there are two levels, one using the species as the basis for its studies and the other using the ecosystem. We believe that there will be no advancement in the understanding of succession without an understanding of the trends of behavior of the species in the recovery systems.

The problem

While studying the successional process in some tropical lowland areas of México, we have tried to discover what the adaptative characteristics are that permit secondary species to be successful in the disturbed environment in contrast with primary species. It is the purpose of this paper to analyze some of the characteristics that we found important and to present examples chosen mainly from our own work.

Important Characteristics of Secondary Species

Natural selection is the general process that models the phenotype by selecting those characters best suited for the changing environment that promotes succession. Selection can occur at all stages of the life cycle of a plant (Fig. 1) and for this reason our analysis will be presented following discussion of the life cycle.

Time of the life cycle

Secondary species have a short life cycle. This may be genetically controlled (as is the case with annuals and biennials) or evironmentally controlled. The group of species that are environmentally controlled are basically heliophytes that are eliminated by taller plants that shade them out. Of course, the stature of a plant is genetically controlled, but if no light competition occurs they may live for longer periods of time. The size and life form of many secondary species is variable and great plasticity is shown by many of them. Timing of life cycles is an important event in the successional working model (Fig. 2). Very little work has been done in this area and the only known data come from studies in the early successional stages (Sarukhán, 1964; Rico & Gómez-Pompa, 1974). The success of a species can be measured by knowing whether it has reached the flowering and seeding stage. The strategy of "nomads" is remarkably successful in this respect, as they exploit their fast growth and early flowering and in this way fill the time niche successfully.

[1] Flora of Veracruz. Contribution no. 17. A joint program of the Instituto de Biología of the Universidad Nacional Autónoma de México and the Department of Botany of the Field Museum of Natural History to prepare an ecological floristic study of the state of Veracruz, México (see Anales Inst. Biol. Univ. Nac. Autón. Méx., 41, Ser. Bot., 1: 1-2).

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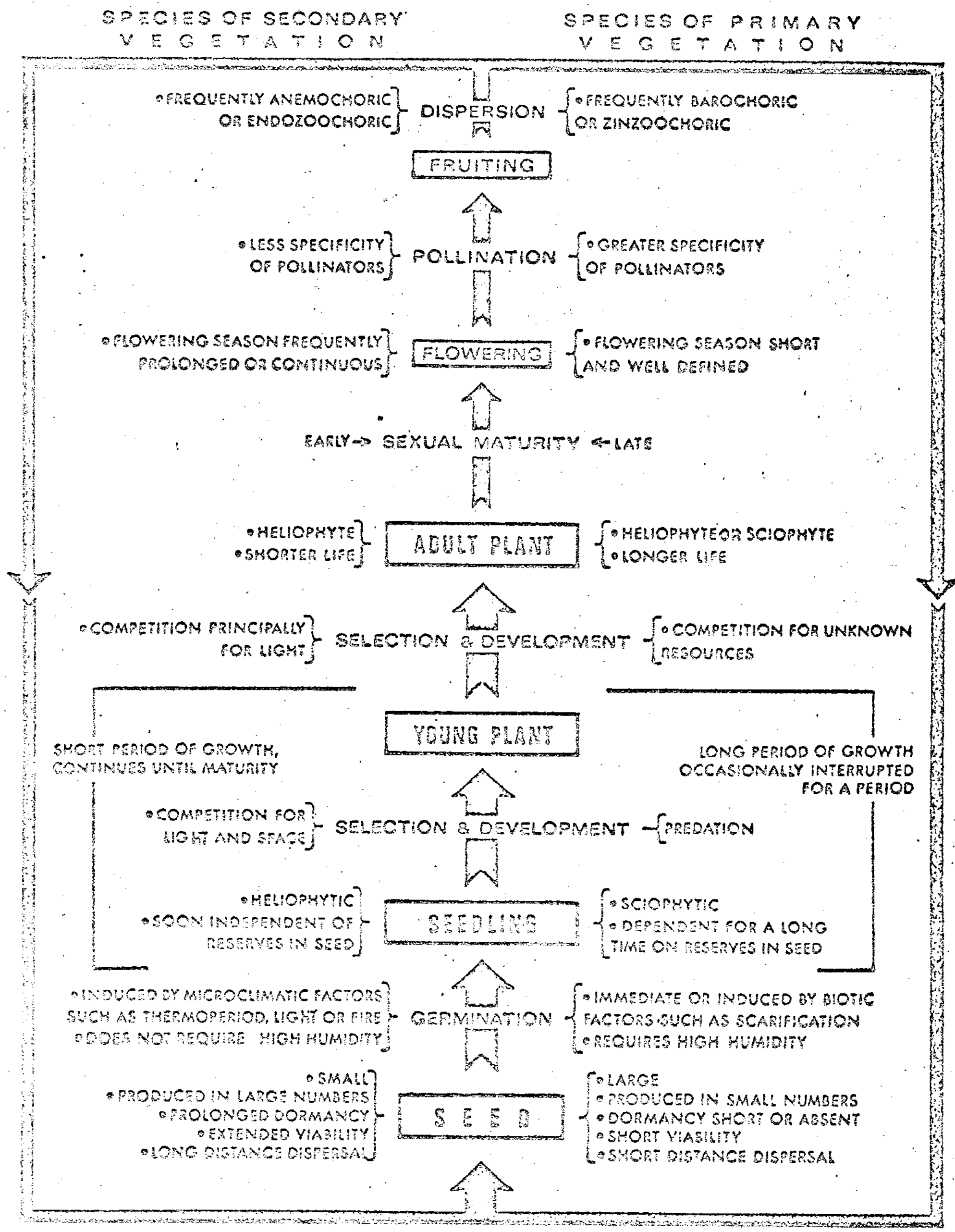

Figure 1. Life cycles of plants. Each step can be isolated and a series of research projects may be planned that will contribute to understanding the whole.

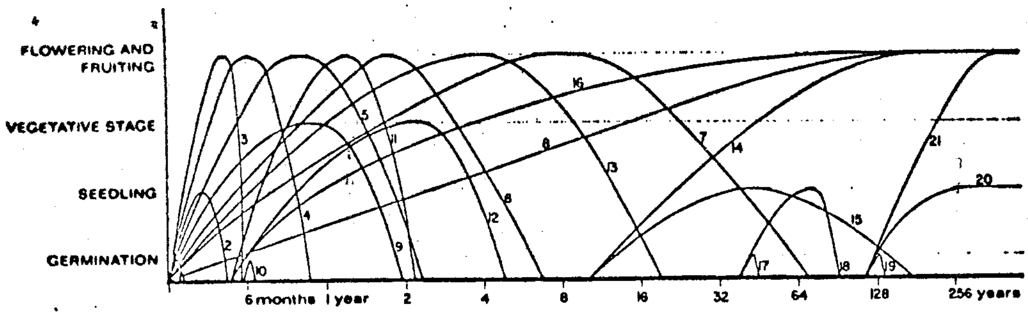

Figure 2. A model of life cycle patterns along a time gradient in the successional process. Each one represents a complete or an incomplete life cycle. 1) Species that germinate and die. 2) Species that germinate, produce a few leaves, and die. 3) Species that complete their life cycle in a few months. 4) Annual species. 5) Biennial species. 6) Species with a life cycle of only a few years (less than 10). 7) Species with a long life span, several decades, but eventually dying (species from old secondary forests). 8) Primary species with life spans of hundreds of years that have lived since the beginning of the succession. 9) Species that never reach the stage of sexual reproduction. 10) Species that germinate a few months after the succession begins and soon die. 11) Annual species that germinate after the succession begins. 12) Species that germinate after the succession begins but do not reach the stage of sexual reproduction. 13) Species with a short life cycle (less than 30 years). 14) Species with a long life cycle that germinate when the succession is well advanced. 15) Species that germinate when the succession is well advanced and remain in the seedling or "young" plant stage for a few years. 16) Species that germinate a few months after succession begins and then have a life cycle hundreds of years long (primary species). 17) Species that germinate and die in old successional stages. 18) Species that germinate and live at the seedling or young plant stage in old successional stages, and then die. 19) Species that germinate and die in the primary forest. 20) Species that germinate and grow to a seedling or "young" plant stage inside the primary forest and remain there waiting for suitable conditions for continuing growth. 21) Species that germinate and grow in the primary rain forest and may reach the reproductive stage after having long life cycles (primary species).

The role of time in plant and animal evolution have been considered in all classical evolutionary studies. Usually it is considered as a factor in evolution on a long term basis, not usually a factor by itself but in relation to environmental changes occurring through time. Even though we can not define time in concrete terms as an objective factor, it seems to us that in the successional process, time is indeed a factor that has acted as a selective mechanism in the evolution of species.

The length of time of the growing period for a secondary species to reach a reproductive stage may vary from a few weeks to months or years, depending on the species and also on changes in the environmental conditions. These changes can be caused by the type and frequency of perturbations, by the preceding species and by nonpredictable changes in the environment. For each set of changes there is a set of species that have a life cycle adapted to the time available. Time viewed in this way becomes a very important selective factor in the successional events.

Time as a selective factor has increased in importance through human activities in nature. In fact, many secondary species have adapted to the time cycles of human use of the land.

Seeds

A great part of the energy budget of secondary species is used for reproduction in comparison to the amount of material used for building the structure of the individual. Reproduction in secondary species is a fascinating phenomenon which is favored by the presence of many characteristics. Among those we wish to mention are, the large number of seeds per plant, the systems for wide seed dispersal, and also the systems for dormancy that permit seeds to persist in soils (Guevara & Gómez-Pompa, 1972) through long periods of time. These characteristics increase the probabilities of successful establishment when a disturbance of the original vegetation occurs (Salisbury, 1949). This is especially true in areas of frequent and continuous disturbance.

The production of seeds through the year tends to be continuous in many groups of secondary species. Examples occur in several species of Piperaceae, Melastomataceae, Malvaceae, and Compositae. One of these species is Piper auritum, a very abundant species in the early successional stages (2-10 years) in the American lowland humid tropics. In this species inflorescences and infructescences can be found simultaneously in almost any month of the year. A similar strategy can be found in species such as Trema micrantha, Urera caracasana, and Cecropia obtusifolia in which several fruiting seasons can be found in a year in different populations and for that reason we find that the production of seeds is also continuous and the only change is in the amount of seed produced through the year.

In some species which are wind dispersed such as several species of Heliocarpus, Ochroma, and many Compositae, the fruiting period is generally in the dry season. They produce a large seed crop and have efficient dispersal mechanisms; in these cases the accumulation of seeds in the soil occurs only in one season of the year.

Seeds of secondary species are mainly small, with low humidity content. Both characters favor long distance dispersal and also may have great value in providing better resistance to predation and attack by microorganisms.

The viability of seeds from secondary species in the soil may be long (Juliano, 1940) as has also been demonstrated in laboratory experiments with seeds from old herbarium specimens (Moreno-Casasola, 1973).

Seeds of secondary species accumulate and remain viable in the soil of primary rain forests (Keay, 1957; Guevara & Gómez-Pompa, 1972) where they form a notable seed bank that remains alive and dormant until the proper conditions appear and trigger germination. Dormancy in these seeds is imposed mainly by light conditions under the forest canopy, caused by the great number of species that have photoblastic seeds (Vásquez-Yanes, 1974b). Other species present tegumentary dormancy that can be broken by the effect of strong thermo-periods, high temperatures, or scarification as is the case with many Leguminosae, Ochroma, and Heliocarpus (Vázquez-Yanes, 1974a).

The microclimatic modifications that induce the germination of seeds of secondary species are produced as a result of the disturbance of the previous vegetation.

Seedlings and Young Plants

Once a seed has germinated, having been triggered by one of the several known mechanisms, the next step of selection occurs at the seedling and young plant stage. This stage is the most critical in determining the success of certain species and individuals over others. There are dramatic changes in numbers in the first months (Fig. 3) and the characteristics that enable the species to compete and succeed are not known. At these early stages light competition is the main environmental factor, shading may become the life or death factor for secondary heliophytes unless some meristematic dormancy occurs. At this time any factor affecting the

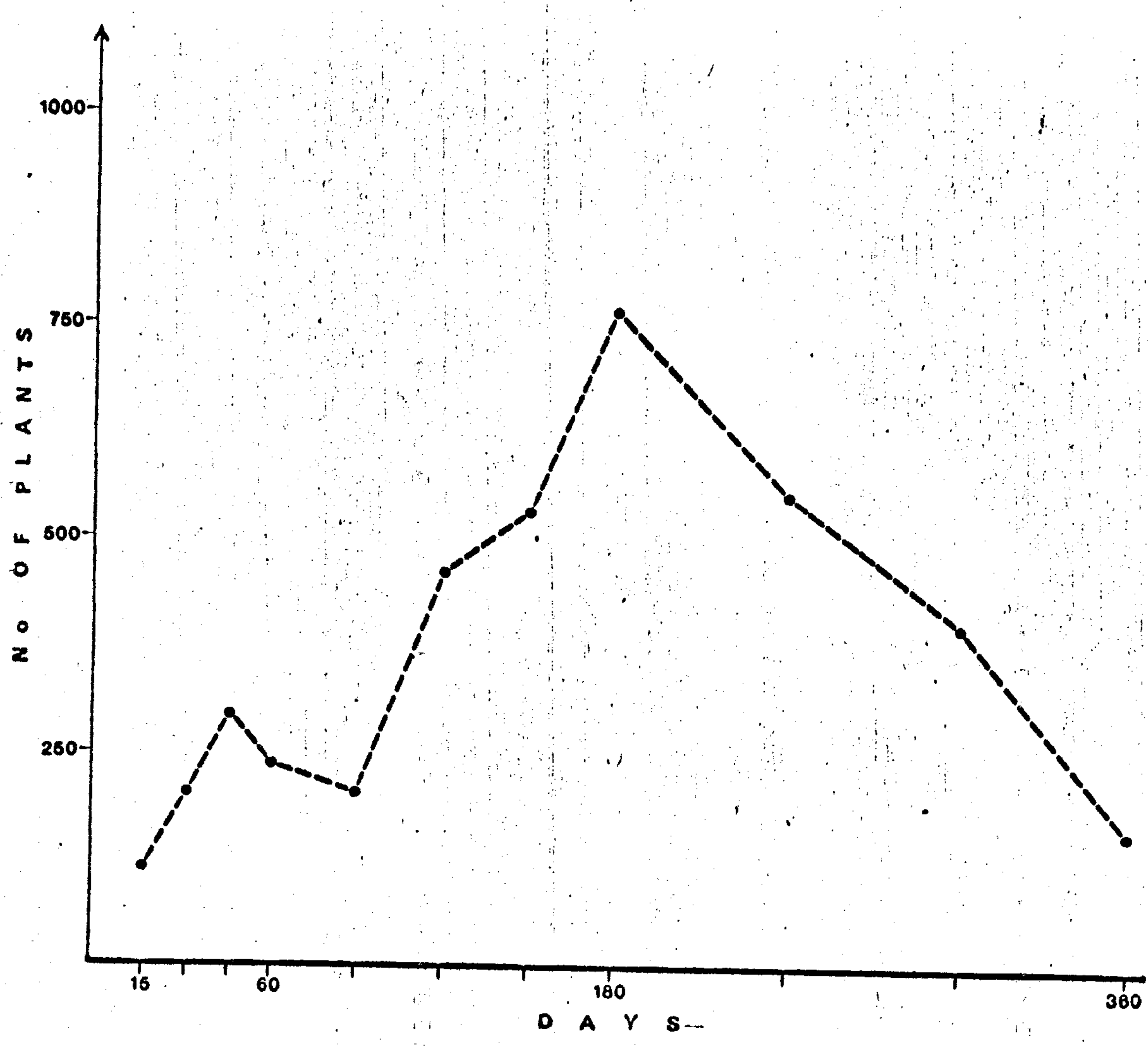

Figure 3. Population changes in the first year period of a cleared area in a lowland humid rain forest region of Veracruz, México.

... the plants may be of paramount importance; chemical competition seems to be a factor of much greater weight that had been suspected (Anaya & Rovalo, 1974).

As the survival of the species depends on success at this stage, several strategies are evident, such as the high number of individuals permitting greater probability of success for a few; fast growth that keeps them at the direct sunlight level. Another character of which we know nothing is the plants' defense against predators; competition for nutrients if it exists at all; and space competition mainly at the root level. Any advantage along these lines will increase the chance of success.

Seeds of small size and limited reserves such as the most common secondary species, originate small seedlings that become readily independent and in the presence of adequate light, start an active and continuous growth (Rico & Gómez-Pompa, 1974). This growth caused by an efficient photosynthesis in these secondary studies produces a fast growing body with a great amount of water, little woody material and with a great amount of cellulose. This growing strategy in full sunlight enables the species to have a large and efficient photosynthetic surface which, in biomass is greater in proportion to the rest of the plant body and is in contrast with what happens in old secondary and mature rain forests. This fact probably results in attaining the reproductive stage rather rapidly.

One important factor to which no one has paid much attention is the nutritional requirement of secondary species. These species have to germinate and grow in poor soils that usually have been abandoned after cultivations, and it is in these conditions where most of the species find their best environmental conditions. This means that most of these species should have very efficient systems for using the low nutrient content of the soil. They have to restore the nutrient pool through restoring the cycling capability of the recovering ecosystem. Great accomplishments should be expected in this area of investigation if a species approach is followed. It is worth mentioning that some experimental work done in Costa Rica (Hartcombe, 1972) applying fertilizers to a Cecropia obtusifolia plantation did not show a resultant increase of productivity when compared with the unfertilized plots. These results may help us to prove the hypothesis that secondary species have low nutrient requirements. According to Kellman (1969) some experiments in fertilization have shown that the requirements for certain cations and phosphorus are very low for secondary plants and an increase in them apparently does not affect the course of succession.

Plants of the primary rain forest may develop a complex system of endotrophic mycorrhiza that close the nutrient cycle. Secondary species in general lack mycorrhiza and have instead a very dense root system that enables them to capture nutrients from the soil. The root system of the secondary species being less specialized than that of primary species, can cope more effectively with the problems of establishment in naked and disturbed soils (Stark, 1969).

Many colonizing species in several well known families of the tropics such as Cyperaceae, Gramineae, Euphorbiaceae, and Amaranthaceae (Black et al., 1969) have a C_4 metabolism of carbon dioxide, which gives them advantages for colonization and competition at the early stages since ir permits efficient photosynthesis at high temperatures, while the night fixation of CO_2 decreases water loss. More studies along this line may also further understanding of the success of colonizing species in the successional process of the humid lowland rain forest areas.

Another important feature of secondary species is the great capability of their resistance to herbivores. This can be accomplished by being unpalatable, as is probably the case for many C_4 plants (Caswell et al., 1973) to the most important herbivores; or by having a rapid recovery after a part of the plant is eaten by an herbivore. In fact, many secondary species are adapted to herbivores, including man, for their dispersal. They are remarkably adapted to withstand trampling and other drastic impacts.

One notable characteristic we have found in several secondary species is that in spite of being heliophytes, they can survive in low light conditions which change some of their structures and functions. In Piper we have observed that individuals in such conditions have limited reproductive capacity (low seed production). The physiological ecology of these selected populations of secondary species living inside the forest is of great importance. Are these populations genetically different from the outside populations, or do they have a plastic genotype ("many purpose genotype") that expresses itself differently in different environments?

The reproductive plant

Many of the characteristics mentioned for young plants can be applied to the reproductive individual. As we have said before, the great trend for secondary species is to reach the age of seed production as soon as possible, insuring the preservation of the species. This is important because the time available for reaching this stage may be limited as the succession advances. Some annuals or biennials may have only one occasion to leave seed progeny available for a new opportunity. For shrubs and small trees there may be only a few years to accomplish this before other taller species take their places. In this sequence we reach the taller size classes of secondary trees that may have many more years to produce their seeds, and finally we reach the stable stage with trees that can produce seeds for hundreds of years. In this sequence we may find different reproductive systems and dispersal strategies.

Almost no information is available concerning the compatibility systems of plants of secondary vegetation. Bawa (1973) reports from Costa Rica several species of secondary trees that are self incompatible, such as, Bauhinia ungulata, Cochlospermum vitifolium, Guazuma tomentosa, Luehea speciosa, Spondias mombin, and several others. It seems from his results that cross pollination is the most common trend in the group of species he studied. Our experience with a few species of Piper of Veracruz also indicates that this is the case.

It would be of extreme interest to study the breeding systems in the early colonizing species, especially those with short life cycles.

To a secondary flora there is a corresponding secondary fauna which interacts with it in several ways, mainly predation, pollination, and dispersion. These are intimately related, even though there is very little information about the relationship of the flora and fauna of secondary vegetation. For those secondary species that are pollinated by animals there is some evidence that very little specificity has been found. In Piper hispidum more than four species of bees have been identified as pollen carriers in one locality of Veracruz; a more drastic example is Ipomoea trichocarpa in which three species of bees and a hummingbird pollinate the species and a beetle and two species of butterflies were seen as possible pollinators also (González-Medrano, Piñol & Toledo, personal communication). Both species of plants are common secondary species in the early successional stages of the lowland tropical regions of Veracruz.

Even though there are very few studies on this subject it seems quite obvious that the trend is rather general as these "nomad" species should find pollinators in many geographical localities and in various ecological conditions. The same trend also should be found in those species dispersed by animals. For Cecropia obtusifolia many different dispersors have been found, local or migratory, insectivorous and frugivorous birds; bats (which have been found to be important agents of dispersal), and probably other mammals, too. The seeds of Cecropia may germinate without passing through the digestive tract of the animal and for that reason dispersal also can be accomplished without the animals (Einsenmann, 1961; Olson & Blum, 1968, and Vázquez-Yanes, 1974).

Productivity

There is almost no information available on the difference in productivity through time for any tropical area. The few studies on productivity of tropical ecosystems have not considered time on the one hand and species differences on the other. The available data show that there is very rapid growth at the beginning of the succession (the first 5 to 10 years) and then a stabilization through time (Kellman, 1969; Jordan, 1971; Farnworth & Golley, 1974). It is clear, even though not proved, that a fast growing species should have a very efficient photosynthetic process which may be responsible for the high productivity of the early stages of succession, and this process should be evaluated at the species level.

Data from Puerto Rico indicate that the annual increase in biomass in a secondary vegetation two years of age is greater than in a mature forest (Jordan, 1971).

Final considerations

It is clear to us that much more research is needed at all levels and degrees of sophistication. It is of great importance to know more about species behavior in known localities through time, and in different environments in the lowland tropics of the world. The evolutionary approach seems to be the basic one for understanding the trends of evolution of these biota and will, at the same time, permit us to draw the guidelines for management of this vegetation type that covers a great portion of the surface of the earth.

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