

In Golley FB (ed). Tropical rain forest ecosystems.
Structure and function. Ecosystems of the world. 14A
Elsevier 1983. pp. 217-223

Chapter 13

SUCCESSION

JOHN EWEL

AGENTS OF DISTURBANCE

Although the impact of people on tropical forests has never been greater than it is today, disturbance is not a new phenomenon to these ecosystems. Tropical forests have always been exposed to small-scale perturbations from tree falls (Hartshorn, 1978; Whitmore, 1978), herbivore outbreaks, and the movements and feeding activities of large mammals. Some coastal tropical forests at 10° to 20° latitude are regularly buffeted by cyclones (Webb, 1958; Wadsworth and Englerth, 1959; Whitmore, 1974; Lugo, 1978). Flooding, vulcanism, and earthquakes (Garwood et al., 1979) all exert their toll, assuring that tropical forests are continually disrupted. Because of the rapidity of weathering, and the preponderance of illites over the more stable kaolinites that would succeed them if weathering were to proceed further, landslides are extremely common in wet tropical mountains (Tricart, 1972).

Except for areas where tropical forests are regularly subjected to widespread devastation by hurricanes, earthquakes, and floods, successional communities probably occupied relatively little area during the course of recent evolution. Disturbed ecosystems were patches in a background matrix of mature forests. Today, however, the situation is fast becoming reversed. Rampant tropical deforestation, often followed by land abandonment and shifting land use patterns, is producing a situation in which mature tropical forests are predominantly islands against a background matrix of successional vegetation.

Some land use and colonization schemes turn out to have been inappropriate for the climate and soils where they are located. Many of these areas will not support permanent agriculture, so are allowed to

revert to natural regrowth, as is occurring with some pastures in the neotropical lowlands. The net effect is a dramatic increase in fast-growing tropical second-growth vegetation.

Although the scale of devastation has changed, human-induced deforestation differs very little from that due to natural causes. Thus, the repair mechanisms already exist. The demise of mature forests, together with many of their specialized mature-phase species, has been accompanied by a dramatic increase in the successional vegetation. The ranges of many weedy generalists have expanded greatly, and today these species dominate the landscape throughout much of the tropics.

Shifting agriculture, especially as it is practised by land-hungry colonists seeking permanent farmlands, has long been recognized as a major cause of tropical deforestation. Logging is another major cause of disruption. Most humid tropical forests recover quickly from selective removal of high-grade timber, but logging roads often provide the accessibility that colonists are waiting for, so the logged forest never gets a chance to recover. Perhaps the most important cause of widespread tropical deforestation today is the establishment of huge monocultures such as rice, oil palm, pasture grasses, bananas, cacao, and rubber.

STRUCTURAL CHANGES

There are several general descriptions of tropical succession in the literature, but few have added much to the quarter-century-old concise overview of Richards (1955) or the exhaustive review by Budowski (1961). More recent contributions — and there have been many (e.g., see the Supplement on

Tropical Succession, *Biotropica*, 1980) — have emphasized specific findings on forest dynamics, plant reproduction, and nutrient cycling, plus succession in tropical environments other than the humid lowlands. Regional patterns are described in UNESCO (1978, chapter 9).

Succession in the wet tropical lowlands usually starts with rapid soil coverage by a mixture of weedy herbaceous plants and fast-growing vines. The distribution of these earliest colonizers seems to be due to chance distribution of seeds, both those in the soil and those dispersed onto the site immediately following disturbance. The importance of the pre-disturbance seed storage in the soil should not be underestimated, especially in areas where successional vegetation abounds. For example, we germinated 67 species from only 0.11 m² of soil (nearly 8000 individuals per m²) from an eight year old forest in Costa Rica (Ewel et al., 1981).

The pattern in the earliest stage of colonization is one of small patches, 2 to 30 m², dominated by single species. The distribution and size of the patches probably reflects seed dispersal rather than site differences, as most of these earliest colonizers seem to be able to occupy a broad range of sites. Diversity of this early, herbaceous stage is often very high. I have enumerated an average of more than 38 species on each of eight 18 m² plots in vegetation that was only three months old on Costa Rica's Osa Peninsula.

The initial herbaceous phase does not last long, except in the seasonally dry tropics where the process is arrested by the dry season and, in some cases, on a long-term basis by fires. Grasses are prominent successional components in the seasonally dry tropics.

In the humid lowlands the herbaceous plants usually die within a year. Vines that do not die grow up with the canopy, and woody pioneer species soon begin to dominate. These pioneer trees become established very early in the successional process; they can usually be found in the understorey of the herbaceous layer during the first few months following clearing. They grow up through the herb layer, and are first noticed as scattered emergents poking out of the top of the dense tangle of greenery beneath them. Some are covered by vines as they grow upward; others seem to escape the vines either by chance or by rapid growth, shed-

ding leaves and even branches as they grow; and still others (e.g. some *Cecropia* and *Musanga* spp.) support ant colonies that attack competitors. Vine control has long been recognized by tropical foresters as one of the most costly impediments to plantation establishment. Perhaps we could follow nature's example, and seek useful species that come equipped with their own biological control tools.

Within a few years, these fast-growing pioneer trees form a nearly closed canopy, often dominated by a single species. The vegetation changes from a mosaic of small, monospecific patches to a more uniform stand dominated by species tolerant of a broad range of site conditions. The lifespan of these pioneers is usually less than 25 years, and they survive by seed dispersal — usually wind or animal mediated — onto other, newly disturbed sites.

What happens after the demise of the pioneers is not quite so clear. Tree diversity increases, and the frequency and distribution of the species reflect a complex interaction of seed abundance, seed predation, competition, herbivory, and microsite differences. Budowski (1963, 1965, 1970) has enumerated twenty characteristics of early and late successional forests, and the tree species found therein; he has also compared them with mature forest. Some changes that occur have important economic implications. For example, growth rates of trees are highest in successional ecosystems, but wood densities are lower. The structurally "cheap", short-lived building blocks of successional ecosystems are later replaced by heftier materials — denser woods, tougher leaves — that are produced more slowly, but last longer.

The high net primary productivity of successional ecosystems supports large animal populations, although not the same species, usually, as the mature forests. Because of their high secondary productivity, patches of second growth are often favored hunting grounds of indigenous peoples (Linares, 1976). Most of the kinds of animals that thrive in successional habitats are "weedy" generalists, but that is not always the case. For example, in the subtropical Everglades of extreme southern Florida (U.S.A.), white-tailed deer are extremely abundant in succession on former farmlands. These deer, in turn, support numerous Florida panthers, one of the most endangered mammals in North America.

One difficulty is that tropical forest succession

has often been described as a process terminating in some well-defined end point: a mature forest composed of a diverse mixture of large-seeded, shade-tolerant plants (e.g., Richards, 1973, pp. 64-65). In spite of the pedagogic value of this heuristic model of the steady-state tropical forest, we must remind ourselves that it does not exist in nature: certainly not at the scale of a square kilometer, and probably not at the scale of a hectare.

Although there are great taxonomic differences among the successional floras of distinct biogeographic regions, the physiognomy of successional vegetation is remarkably homogeneous throughout the tropics. Furthermore, pantropical generalists such as *Trema*, *Ceiba*, and *Ficus* provide more floristic similarity among successional vegetations than among mature communities.

Plants typical of stressful tropical environments such as mangrove swamps, alpine communities, and semideserts often exhibit a high degree of ecological convergence. The same is true of successional species. One conspicuous example is the huge, palmately lobed leaves and low degree of branching characteristic of certain species of *Cecropia* (Americas), *Musanga* (Africa), and *Macaranga* (Asia). Such pioneers often form an even-aged canopy that dominates successional forests for up to twenty years, but, because they cannot reproduce in the understorey, they are dependent upon further forest disturbance for their survival.

STABILITY

It is convenient to consider ecosystem stability to have two components: resistance and resilience. Resistance, or the degree to which an ecosystem maintains itself in the face of forces that would change it, is not meaningful unless one specifies the type of outside changing force involved. For example, a lowland, moist tropical forest might be very resistant to physical changes such as high winds, but might be very susceptible to disturbance from a very modest decrease in temperature — much more so than would a boreal forest, for example.

Resilience may be an easier concept to deal with quantitatively. It can be measured as the rate at which an ecosystem returns to its initial, or pre-disturbance, condition. There are two ways to

interpret succession as a measure of ecosystem resilience. The first is simply to measure the rate of change of a successional ecosystem. Thus, successional ecosystems that grow faster would be considered to be more resilient than those which grow more slowly. Another possibility is to measure the amount of structure accumulated in a successional ecosystem after a given time, and express that structure as a fraction of the amount of structure in the predisturbance, steady-state ecosystem.

The difference between these two interpretations of resilience might best be illustrated with an example. Suppose we have two steady-state ecosystems: a tropical dry forest in which the dominants average 20 m tall, and a lowland, wet forest in which the dominants average 60 m tall. Suppose that these two forests are felled and that the rate of regrowth is monitored. Further, suppose that, after five years, the dominant successional plants on the dry forest site are 10 m tall, while those on the wet forest site are 20 m tall. In one sense one might regard the wet forest ecosystem as more resilient because its successional vegetation is twice as tall as that on the dry forest site. On the other hand, one might regard the dry forest ecosystem as being more resilient because after only five years of regrowth its height is 50% of that of the original steady-state forest, whereas the height of the successional vegetation on the wet forest site is only 33% of its original steady-state value.

There is some evidence that, in the short term, tropical ecosystem resilience does indeed follow such patterns in wet and dry environments (Ewel, 1977). However, succession in dry tropical areas suffers repeated setbacks because of rainfall variability, so resilience in dry areas tends, in the longer term, to be lower by either measure: absolute rate of recovery, or relative rate of recovery. The least resilient tropical ecosystems of all may be those of high elevations. Tropical montane forests regrow extremely slowly, both on absolute and on relative scales (Ewel, 1980).

Fig. 13.1 is a model of ecosystem resilience. The x-axis is time; the y-axis is some measure of environmental quality, ranging from harsh to benevolent (e.g. dry to wet, cold to warm, infertile to fertile, etc.); and the z-axis is structure or maturity. Structure increases with maturity in the sense that Margalef (1968) uses maturity to describe both

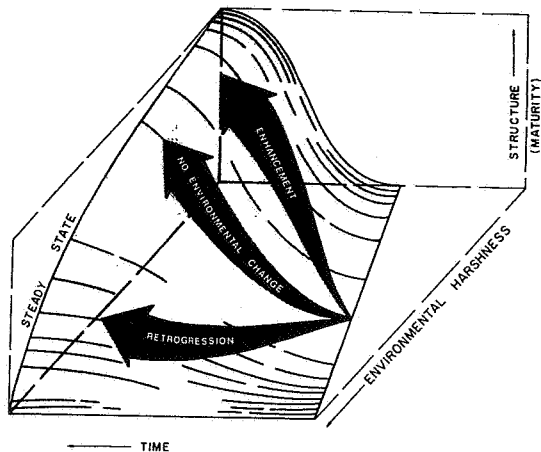


Fig. 13.1. Ecosystem resilience as a function of environmental quality and changes resulting from disturbance. See text.

short-term successional changes and evolutionary changes associated with environmental gradients.

The left-most plane of the figure represents the amount of structure in any ecosystem at maturity. In keeping with current ideas regarding the response of a steady-state ecosystem to increments of a potentially limiting factor, the curve of structure (=maturity) at steady state increases hyperbolically as environmental quality increases. Thus, it takes a greater increment of environmental quality to produce a given amount of increase in structure at steady state in a benevolent environment than it does in a harsh environment. At the harsh end of the spectrum, however, a small increase in environmental quality (or in some limiting factor) produces a substantial increase in the structure of the steady-state community.

Recovery of structure, or return to maturity, is shown in the figure as a sigmoid growth function. Other formulations might be better representations of certain responses, but the sigmoid curve is common to many kinds of growth measures, including biomass and leaf area development. Note that the time axis is compressed at the far end, i.e. in non-limiting environments. Almost all models that incorporate a measure of environmental resistance to regrowth produce responses indicating that recovery is slower — both relatively and absolutely — in harsh environments than in benevolent environments.

A steady-state ecosystem that is disrupted slides

from left to right along the curved surface illustrated in Fig. 13.1. As the system recovers, it can traverse three kinds of paths. First, it might recover by moving along the surface described as “no environmental change” in the figure. If it does, it will be more resilient than equally displaced systems located in harsher environments and less resilient than ecosystems in more benevolent environments.

Another possibility — and a common one in nature — is that the disruptive force, either natural or human-induced, reduces environmental quality. Landslides or volcanism that remove or cover nutrient-rich, mycorrhizae-laden surface soils are examples of natural events of this type. Some farming practices lead not only to vegetation destruction, but also to environmental degradation. Succession proceeds along the path labelled “retrogression”. It is slower than the succession that might have occurred if the ecosystem had been subjected only to vegetation destruction, without concomitant degradation of the site. Furthermore, the new steady-state system may be less structured than the one that originally occupied the site. Return to the original condition must await amelioration of site conditions, a process that may occur extremely slowly.

Retrogression does not arise only from physical degradation of the site as a part of ecosystem disruption. Sometimes retrogression occurs as succession proceeds. One example is allelopathy, whereby one plant species releases substances into its surroundings that inhibit the growth, survival, or vigor of potential competitors. There has been relatively little work done on allelopathy in tropical succession (e.g., Gliessman, 1976, 1978), but there is no reason to think that allelopathy is less common in the tropics than in the temperate zone. Because many allelopathic substances are water-soluble, allelopathy may exert more control over succession in the dry tropics than in the wet tropics, where vast amounts might have to be excreted just to replace the amount leached away.

Another naturally mediated retrogression syndrome consists of colonization by successional species that are prone to fire. Repeated fires can lead to depletion of nitrogen and sulfur supplies, thus site degradation. A classic example from the tropics is *Imperata cylindrica*, the fire-adapted grass that often captures deforested sites in Malesia

(sensu Whitmore, 1975), preventing their recolonization by tree species for decades, if not permanently (e.g. see Eussen and Wirjahardja, 1973).

Succession can proceed along a third, although less common route. This is the process of enhancement (see Fig. 13.1), whereby either the disruptive agent or the successional community improves environmental quality, such that the post-succession community is more structured than the predisturbance community. This can result from the deposition of nutrient-rich volcanic ash on top of an infertile soil; erosion of a highly weathered surface soil, exposing a more fertile subsoil; or farming practises that improve soil physical characteristics or fertility (Fig. 13.2). Enhancement is often biologically mediated, as when exotic plants are introduced onto species-depauperate islands. The resulting successional vegetation is often more

complex than the original system, although this is not always regarded as a desirable trait by ecologists. Ecosystem enhancement may be a more common phenomenon than we realize. This may partly reflect our conditioned response to regard natural disasters and human-induced change as environmental evils. Although degradation is the general rule, there are undoubtedly exceptions in which disruption of steady-state systems leads to environmental improvement and increased structural complexity.

Does the immense diversity and structural complexity of wet, tropical lowland forests automatically lead to fragility? Not necessarily. Although tropical forests are being destroyed at an alarming rate (Farnworth and Golley, 1974; Goodland and Irwin, 1975; Myers, 1979, 1980), the fragility of these ecosystems is a measure of the magnitude of

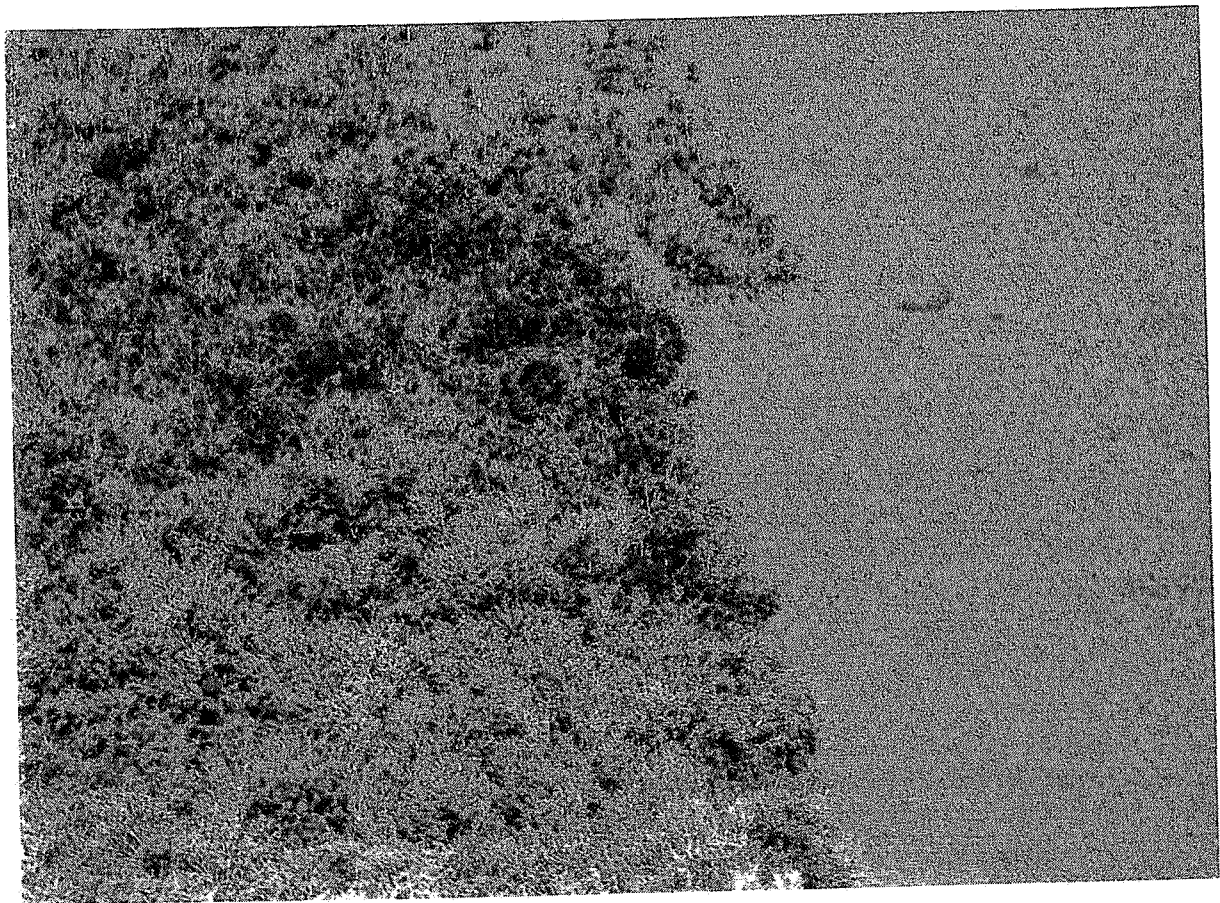


Fig. 13.2. An example of ecosystem structural enhancement after disturbance. The original, mature ecosystem (right) is a glade dominated by herbaceous plants. The successional community (left) follows farming that improves site quality, permitting invasion of the exotic tree *Schinus terebinthifolius*. Everglades National Park, Florida, U.S.A.

the destructive forces working against them, rather than an inherent property of the ecosystems themselves. When forests of the lowland humid tropics are subjected to large-scale disruption, recovery can be painfully slow. This is especially true if essential mycorrhizal fungus populations are destroyed (Janos, 1980) or if the seed sources needed for recolonization of mature-system species are removed from large areas (Gómez-Pompa et al., 1972). On the other hand, when disturbance is small scale, and comparable in frequency and magnitude to the kinds of disturbance that these tropical ecosystems evolved with, recovery is extremely rapid. Regrowth proceeds quickly, partly because of favorable conditions for plant growth, and partly because seeds of successional species are present in the soil (Keay, 1960; Guevara and Gómez-Pompa 1972; Liew, 1973; Kellman, 1974; Cheke et al., 1979) and are readily dispersed (Opler et al., 1980).

How does the resilience of wet, lowland tropical forests compare with that of other forests? If, in the simple model presented in Fig. 13.1, "maturity" is expressed as physical structure, such as biomass, then tropical ecosystems are probably as resilient as most others. If, however, the "maturity" axis incorporates not just any kind of high diversity, but diversity consisting of the same array of species that occupied the site prior to disturbance, then tropical lowland forests may be among the world's most fragile ecosystems. Although a denuded site may revegetate quickly, it will only return to the pre-disturbance floristic composition if nearby seed sources are left intact. When disruption is widespread the ability of the site to undergo succession is not necessarily impeded, but complete resilience — or return to the predisturbance floristic composition — may be lost completely. In that sense, tropical, lowland wet forests are indeed fragile — perhaps more so than their less diverse, and less "mature" temperate-zone counterparts.

In general, ecosystems in benevolent tropical environments, epitomized by the humid lowlands, are more resilient than ecosystems in cooler or drier environments. If, however, ecosystem retrogression or ecosystem enhancement occur, either as part of the disruptive process or as part of the recovery sequence, resilience is affected accordingly.

One useful guideline for tropical ecosystem manipulation might be to avoid any kind of disruption

that would preclude eventual self-replacement of the original community. This guideline is admittedly a very conservative one, but until we know more about tropical forest ecosystems and their regeneration, and the long-term viability of the systems we are replacing them with, a cautious approach to change would seem to be in order.

REFERENCES

- Budowski, G., 1961. *Studies on Forest Succession in Costa Rica and Panama*. Dissertation, School of Forestry, Yale University, New Haven, Conn., 189 pp.
- Budowski, G., 1963. Forest succession in tropical lowlands. *Turrialba*, 13: 42-44.
- Budowski, G., 1965. Distribution of tropical American rain forest species in the light of successional processes. *Turrialba*, 15: 40-42.
- Budowski, G., 1970. The distinction between old secondary and climax species in tropical Central American lowland forests. *Trop. Ecol.*, 11: 44-48.
- Cheke, A.S., Nanakorn, W. and Yankoses, C., 1979. Dormancy and dispersal of seeds of secondary forest species under the canopy of a primary tropical rain forest in northern Thailand. *Biotropica*, 11: 88-95.
- Eussen, J.H. and Wirjahardja, S., 1973. Studies on an ilang-ilang (*Imperata cylindrica* (L.) Beauv.) vegetation. *Biotrop. Bull.*, 6: 1-24.
- Ewel, J., 1977. Differences between wet and dry successional tropical ecosystems. *Geo-Eco-Trop.* 1: 103-117.
- Ewel, J., 1980. Tropical succession: manifold routes to maturity. *Biotropica*, 12: 2-7.
- Ewel, J., Berish, C., Brown, B., Price, N. and Raich, J., 1981. Slash and burn impacts on a Costa Rican wet forest site. *Ecology*, 62: 816-829.
- Farnworth, E.G. and Golley, F.B. (Editors), 1974. *Fragile Ecosystems*. Springer-Verlag, Berlin, 258 pp.
- Garwood, N., Janos, D.P. and Brokaw, N., 1979. Earthquake-caused landslides: a major disturbance to tropical forests. *Science*, 205: 997-999.
- Gliessman, S.R., 1976. Allelopathy in a broad spectrum of environments as illustrated by bracken. *Bot. J. Linn. Soc.*, 73: 96-105.
- Gliessman, S.R., 1978. Allelopathy as a potential mechanism of dominance in the humid tropics. *Trop. Ecol.*, 19: 200-208.
- Gómez-Pompa, A., Vázquez-Yanes, C. and Guevara, S., 1972. The tropical rain forest: a nonrenewable resource. *Science*, 177: 762-765.
- Goodland, R.J.A. and Irwin, H.S., 1975. *Amazon Jungle: Green Hell to Red Desert?* Elsevier, Amsterdam, 156 pp.
- Guevara, S. and Gómez-Pompa, A., 1972. Seeds from surface soils in a tropical region of Veracruz, Mexico. *J. Arnold Arbor.*, 53: 312-335.
- Hartshorn, G.S., 1978. Tree falls and tropical forest dynamics. In: P.B. Tomlinson and M.H. Zimmermann (Editors), *Tropical Trees as Living Systems*. Cambridge University Press, Cambridge, pp. 617-638.

SUCCESSION

- Janos, D.P., 1980. Mycorrhizae influence tropical succession. *Biotropica*, 12: 56-64.
- Keay, R.W.J., 1960. Seeds in forest soils. *Nig. For. Info. Bull.*, N.S., 4: 1-4.
- Kellman, M.C., 1974. The viable weed seed content of some tropical agricultural soils. *J. Appl. Ecol.*, 11: 669-678.
- Liew, T.C., 1973. Occurrence of seeds in virgin forest top soil with particular reference to secondary species in Sabah. *Malay. For.*, 36: 185-193.
- Linares, O.F., 1976. "Garden hunting" in the American tropics. *Human Ecol.*, 4: 331-349.
- Lugo, A.E., 1978. Stress and ecosystems. In: J.H. Thorp and J.W. Gibbons (Editors), *Energy and Environmental Stress in Aquatic Ecosystems*. USDOE Symp. Ser. (CONF - 771114). NTIS, Springfield, Va., pp. 62-101.
- Margalef, R., 1968. *Perspectives in Ecological Theory*. University of Chicago Press, Chicago, Ill., 111 pp.
- Myers, N., 1979. *The Sinking Ark*. Pergamon Press, New York, N.Y., 307 pp.
- Myers, N., 1980. *Conversion of Tropical Moist Forests*. National Academy of Science, Washington, D.C., 205 pp.
- Opler, P.A., Baker, H.G. and Frankie, G.W., 1980. Plant reproductive characteristics during secondary succession in neotropical lowland forest ecosystems. *Biotropica*, 12: 40-46.
- Richards, P.W., 1955. The secondary succession in the tropical rain forest. *Sci. Progr.*, 43: 45-57.
- Richards, P.W., 1973. The tropical rain forest. *Sci. Am.*, 229: 58-67.
- Tricart, J., 1972. *The Landforms of the Humid Tropics, Forests and Savannas*. (Transl. by C.J. Kiewiet de Jonge.) St. Martin's Press, New York, N.Y., 306 pp.
- UNESCO, 1978. *Tropical Forest Ecosystems, A State of Knowledge Report*. *Nat. Resour. Res.*, 14: 683 pp.
- Wadsworth, F.H. and Englerth, G.H., 1959. Effects of the 1959 hurricane on forests in Puerto Rico. *Caribb. For.*, 20: 38-51.
- Webb, L.J., 1958. Cyclones as an ecological factor in tropical lowland rain forests, north Queensland. *Aust. J. Bot.*, 6: 220-228.
- Whitmore, T.C., 1974. *Change with Time and the Role of Cyclones in Tropical Rain Forest on Kolombangara, Solomon Islands*. Institute Paper No. 46, Commonwealth Forestry Institute, University of Oxford, 78 pp.
- Whitmore, T.C., 1975. *Tropical Rain Forests of the Far East*. Clarendon Press, Oxford, 281 pp.
- Whitmore, T.C., 1978. Gaps in the forest canopy. In: P.B. Tomlinson and M.H. Zimmermann (Editors), *Tropical Trees as Living Systems*. Cambridge University Press, Cambridge, pp. 639-655.

