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# Tropical Succession: Manifold Routes to Maturity

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## ABSTRACT

Several characteristics of successional species and communities typical of the lowland, humid tropics are compared with those of drier and colder tropical environments. Suggested trends of successional species characteristics along a gradient from benevolent to harsh tropical environments include: fewer but more specialized taxa; more striking ecological equivalence between biogeographic regions; increased vegetative reproduction; less palatable leaves; denser wood; and decreased importance of chlorophyllous stems. Hypothesized trends of the communities along this same gradient include: slower regrowth; increased resilience (drier sites only); fewer seral stages; and patchier distribution of leaf area. As tropical soils are degraded through misuse, there is a tendency for ruderal vegetation from drier (or colder) environments to invade degraded landscapes in wetter (or warmer) areas. Regrowth and resilience of high-elevation tropical forests are so slow that these communities may never reestablish after clearing.

TROPICAL SUCCESSIONAL ECOSYSTEMS conjure up an image of dense tangles of luxurious, impenetrable regrowth: the "jungles" of popular fiction. However, there are many more combinations of rainfall and temperature regimes in the tropics than in temperate zones. Just as this environmental heterogeneity leads to a broad array of mature ecosystems, it also produces a tremendous variety of successional communities.

Tropical succession has been studied most intensively in the humid, lowland tropics. It is important to remember, however, that the humid lowlands account for less than a third of the total land surface in the tropics. Most tropical lands have a distinct dry season, making them seasonally analogous to temperate landscapes. In the dry season, organisms dramatically modify their life styles: many plants drop their leaves and flower, while many animals migrate to wetter habitats or switch foods. In the seasonally dry tropics succession is rapid in the rainy season, but the process is partially set back during the dry season. Graphs of structural changes over time thus consist of ever-increasing sinusoidal blips: each wet season the system gains more structure, but some of the gain is lost during the subsequent dry season. The process continues until the structure eventually oscillates around a steady-state mean value at maturity.

In addition to the differences caused by moisture, there is a substantial amount of variability in tropical succession caused by the temperature changes associated with altitude. Because of the higher mean sea-level temperatures that pertain in the tropics, there are more bands or belts of vegetation on tropical mountain ranges than on temperate-zone mountains. Furthermore, tropical alpine and subalpine

ecosystems are climatically monotonous with respect to temperature, compared with arctic communities or temperate alpine systems. The temperate and arctic systems have a strong seasonal change. Their long, cold winters are broken by short periods of long daylength, high solar radiation, and high daytime temperatures. On tropical mountain peaks, however, there is no months-long growing season when primary productivity exceeds respiration to the extent that large biomass accumulates. Winter arrives every night, and vegetation recovery following disturbance is extremely slow.

In the following sections, several characteristics of tropical successional plants and plant communities are discussed, with emphasis on the variability of these characteristics among different tropical environments.

## PLANT SPECIES CHARACTERISTICS

**REPRODUCTION.**—In the continuously wet tropics, one or more pioneer tree species always seem to be in fruit in every forest. Furthermore, the small, readily dispersed seeds of these colonizers retain viability long after they reach the soil (Guevara and Gómez-Pompa 1972, Moreno 1976, Vásquez-Yanes 1976b). Thus, revegetation following disturbance comes from two sources: seeds that were dispersed and remained viable in the soil prior to the disturbance, and seeds dispersed into the disturbed area following destruction of the original vegetation.

In temperate-zone forests, with small numbers of tree species, trees can be grouped according to their phenology, tolerance to competition, and dispersal characteristics. This information can then be used to predict the floristic changes likely to occur over

succession. This is the approach that has been used (perhaps unconsciously) by temperate-zone foresters for decades, and more formally by Horn (1975) for the northeastern U.S. In the humid tropical lowlands, however, there are a great many species to contend with, and something always seems to have seeds ready to capture a site. Markovian approaches to predicting successional trends are probably just as applicable in the tropics as they are in less diverse ecosystems, but the number of potential outcomes is likely to be so huge as to add little to our ability to predict the course of succession. Any one or more of a number of species might capture a given site, and the outcome is more likely to be determined by timing, location, and dispersal than by site differences.

The successional tree flora of the seasonally dry tropics is also diverse, but less so than that of the wet tropics. In the dry tropics successful regeneration from seed becomes a critical stage in the life cycle of a tree. Timing of dispersal and germination is crucial, and there is a high probability that a given seedling will be left stranded in a drying soil. Partly because of the higher risks and lower probability of successful regeneration from seed, and partly because trunk bases are less subject to rapid decay in the dry tropics, trees in seasonally dry tropics are much more prone to reproduce vegetatively through coppicing than are trees in the wet tropics (Ewel 1977).

The basal area of mature forests in the dry tropics is often nearly as high as that in the wet tropics. In the dry tropics, however, the basal area is made up primarily of scattered, large individuals, whereas forests in the wet tropics tend to have more, but smaller, individuals. This difference in stem density may partly reflect the difficulty involved in successful seedling establishment in the seasonally dry tropics compared with the wet tropics. Similarly, the broad, spreading crowns of canopy trees in tropical deciduous forests may simply be another manifestation of the relatively great distances between individuals.

Vegetative reproduction also seems to be much more prevalent in the high-elevation tropics than in the wet lowlands. It may account, in part at least, for the purported high frequency of polyploidy in tropical alpine and subalpine communities (Knapp 1974). Polyploidy may simply go unpenalized in a system where most regeneration is vegetative. For example, escape from viruses is one of many advantages to reproduction via seeds in most environments, but it may be that these parasites are less debilitating in the continuously cold, high-elevation tropics.

**STRUCTURAL QUALITY.**—Leaves of successional species tend to be more palatable than leaves of mature-forest species. In the wet lowlands, leaves of successional plants are often large, thin, and have a high turnover rate. The monolayered upper canopy of a 10- to 20-year-old second-growth forest dominated by *Heliocarpus*, *Cecropia*, *Dillenia*, *Musanga*, *Macaranga*, or *Cestrum*, for example, is usually pock-marked with holes made by herbivorous insects. The holes commonly account for more than 20 percent of the total area of the leaf. Well-protected leaves (toxic, tough, thick, hairy, waxy) are inevitably present, but they represent the exception rather than the rule.

The difference in palatability between successional and mature-ecosystem species seems to decrease as environmental harshness increases. In the most stressful kinds of tropical environments (salt-water swamps, semideserts, alpine communities) there may be little difference in palatability between leaves of successional and mature-ecosystem species.

The wood of many fast-growing, tropical secondary species, which is composed of thin-walled, large-lumened cells (Rowlee 1921), is just as structurally "cheap" as are their large, flimsy leaves. Most of the world's lightest woods (specific gravities in the range of 0.04 to 0.40) come from the humid tropical lowlands (Kanehira 1933), and most of these are successional pioneers.

The wood density typical of successional trees is much lower than that of mature-forest species, especially in the humid lowlands. In harsher environments the difference seems to be less marked; in drier and colder environments there are likely to be smaller differences in wood density between successional and mature-forest species. Some dry-environment successional legumes, for example, have specific gravities of more than 1.0.

The growth rates of tropical weed trees characteristic of the humid lowlands are quite remarkable. I have measured naturally regenerated *Trema micrantha* in Costa Rica's Osa Peninsula which were 9 m tall at 1 year, and more than 30 m tall at 8 years. It is these fast-growing, low-density trees which will constitute the wood resource of the future as mature tropical forests are felled and regenerate. A utilization technology aimed at the high-density woods which characterize mature tropical forests will have but short-lived usefulness in the humid lowlands, but it may be more appropriate in the long term for harsher environments such as the dry tropics or montane forests, where the successional species tend also to have high-density woods.

**PHOTOSYNTHETIC MACHINERY.**—Leaf area increases

quickly in successional tropical ecosystems: more quickly, probably, than most other structural characteristics. In the wet lowlands the ground is quickly (often < 3 months) covered by a monolayer of greenery. As height growth occurs more layers are added, until the vegetation has a leaf-area index (LAI)  $\geq 3$  by the time it is a year old (Ewel 1971) and an LAI which approaches that of the mature forest by the time it is six years old (Golley *et al.* 1975). The same process takes place in the wet highlands, except that it occurs much more slowly. Here, the vegetation may barely achieve LAI = 1 during the first year, and it may be several years before an LAI of 3 or more is attained.

In the dry tropics, leaf-area development is different. Because regeneration is dominated by vegetatively reproducing clumps, leaf-area development is patchy. Some individual clumps may have exceptionally high leaf areas (I have measured LAI's as high as 16 in vertical-point intercept measurement of one-year-old clumps), but the clumps are interspersed with bare ground. The average LAI may be the same in both wet and dry areas, but the distribution of leaf area is uniform in wet areas and patchy in dry areas (see Ewel 1977 for a quantitative evaluation of this patchiness).

Photosynthesis in leaves is probably substantially augmented by stem photosynthesis. This situation is especially true in successional vegetation in the humid lowlands, which is often dominated by green-stemmed woody plants. Although I have not seen reports in the literature of photosynthesis measurements based directly upon the stems, it is known that they are green because they contain chlorophyll. Even without stomata or lenticels, sufficient gaseous diffusion could occur through thin tissues to provide carbon dioxide for photosynthesis, but such tissue would also be susceptible to water loss. While this water loss may not be very significant in continuously wet areas, it could be detrimental in the dry tropics. It is not surprising, therefore, that green stems are abundant in the humid lowlands, but less so in the seasonally dry areas. This observation seems to hold for wet and dry areas in the upland, as well as in the lowlands.

**BIOGEOGRAPHY.**—Within a given biogeographic region, there is likely to be a large core of successional species which are dispersed throughout the region. The ranges of mature-ecosystem species, on the other hand, are likely to be more restricted in their distribution to only part of a biogeographic region. Tropical successional tree species are notoriously site tolerant, much more so than the mature-forest species

which succeed them. For example, a forest type map of 20-year-old successional vegetation that includes four soil series in the humid tropics would likely consist of a single, relatively homogeneous map unit. A type map of mature forests on the same four soils, however, would probably contain four units: the mature vegetation reflects the soil differences better than does the successional vegetation.

With the exception of a few pantropical weed trees, the woody successional flora of each major tropical region—Africa, Americas, and Asia—is restricted to that region, even though it might be quite widespread within the region. However, the prevalence of ecological equivalents among the successional tree floras captures the attention of even the most casual observer. Just as the floras of harsh tropical environments, such as subalpine and semidesert zones, seem to contain a preponderance of ecological equivalents (*viz.* euphorbiaceous and cactaceous plants in semideserts; *Espeletia*, *Senecio*, and *Lobelia* in subalpine communities), the same seems to be true of the successional tree floras. *Cecropia* (Americas), *Musanga* (Africa), and *Macaranga* (Asia) are successional tree genera that contain species that closely resemble those of other genera from different regions. All have one or more species with huge, simple, palmately lobed, short-lived leaves; low-density wood; and few orders of branching. It may be that, just as there are relatively few ways for natural selection to solve the riddles of adaptation to harsh environments, there are relatively few solutions to designing prolific, fast-growing pioneer trees.

The examples mentioned above (*Cecropia*, etc.) are part of the successional floras of the humid lowlands. The ecological equivalence of successional species in cold or dry tropical environments is likely to be even more striking. Not only must the plant be successionaly successful (well-dispersed, competitive, site tolerant), but it must also be able to tolerate the rigors of a relatively harsh environment. These two sets of constraints impose even greater limitations upon the successional flora than on that of the mature community, and should result in a very high degree of ecological equivalence among biogeographic regions.

## PLANT COMMUNITY CHARACTERISTICS

**RATES OF REGROWTH.**—Regrowth occurs much more rapidly in some tropical environments than in others. For example, table 1 shows four measures of structure for young regrowth on five sites, ranging from the very wet lowlands (nearly 5 m rain per year),

to very dry lowlands (< 1 m rain per year), to very cold uplands (2900 m above sea level). Recovery was most rapid for all variables at the warmest, wettest site, and slowest at the high-elevation site (Montane Rain Forest). The vegetation on the wet, mid-elevation site (Subtropical Wet Forest) was shorter and had less biomass than that of the Tropical Dry Forest site, but it did have substantially greater LAI. The three sites of intermediate harshness each had about 31 plant species per 18 m<sup>2</sup> plot: about 14 percent fewer than the warmest, wettest site, but 35 percent more than the coldest site.

Figure 1 demonstrates the relative rates of vegetation regrowth for these same five sites. The figure

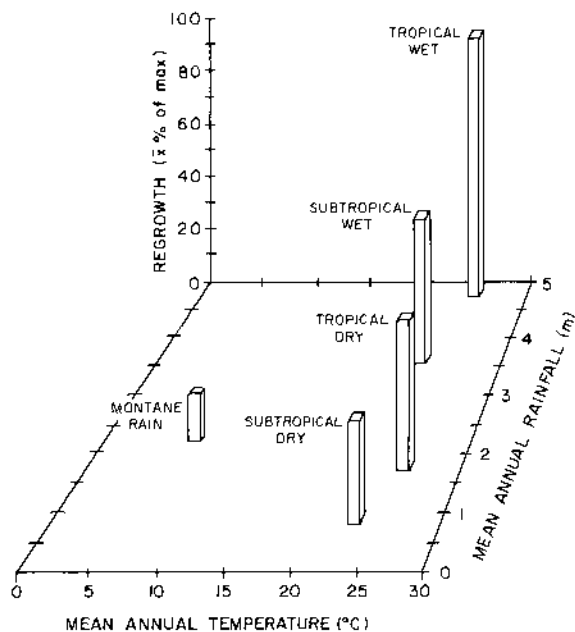


FIGURE 1. Regrowth of 13-month-old vegetation at five sites. Regrowth is a mean of 13 structural measures (enumerated in the text), each expressed as a percentage of the maximum value observed among the five sites. Each value is a mean from eight 3 x 6 m plots at each of the sites listed in table 1.

TABLE 1. Structure of 13-month-old regrowth at five sites. Life zones sensu Holdridge (1967). Each value is a mean from eight 3 x 6 m plots. All Tropical sites were in Costa Rica; Subtropical in Puerto Rico.

Life zone	Location	Biomass (g/m <sup>2</sup> )	Avg. ht. of 3 tallest plants (m)	No. of species per plot	Leaf Area Index (LAI)
Tropical Wet Forest	Osa Peninsula	1159	4.7	36	4.5
Tropical Dry Forest	La Pacifica, Guanacaste	951	2.4	30	2.7
Subtropical Wet Forest	Caribbean National Forest	634	2.0	31	4.5
Subtropical Dry Forest	Guanica Forest	459	1.6	32	2.4
Tropical Montane Rain Forest	Ojo de Agua	135	0.7	23	1.2

synthesizes data for 12 structural measurements, including the four shown in table 1. They include: four measures of foliage density (% cover; LAI; 100-% light transmission; and optical density); stem density; three measures of height (summed height of all individuals; average height of three tallest plants; average height of all individuals); three measures of species richness (species per plot; species per 1000 individuals; and species per plot, excluding plots with n < 1000); and biomass. The 12 structural variables of each site were each expressed as a percentage of the maximum value obtained at any of the five sites studied, and then averaged for each site.

Near sea level, rate of regrowth is about linearly proportional to rainfall. Average recovery at the Subtropical Wet Forest site (3.6 m annual rain), however, was about the same as that of the Tropical Dry Forest site (1.8 m annual rain). Growth slow-downs due to altitudinal differences (180 m compared to 45 m), latitudinal differences (18°25' compared to 10°20'), cloud cover, seasonality, or biogeography seem to be about equal to those resulting from the six-month dry season at the Tropical Dry Forest site.

Recovery at the high-elevation site was remarkably slow. This site, which until recently supported a magnificent oak-dominated (*Quercus* spp.) forest more than 20 m tall, recovered very little in the first year following clearing. Succession on these high-elevation sites, even those that receive abundant rainfall, is a painfully slow process. Human interference here will leave its mark for many decades, and as seed sources are cut over ever-increasing areas it becomes increasingly doubtful that these forests will ever regrow. These are truly the tropics' most fragile ecosystems.

RESILIENCE.—Resilience is not necessarily synonymous with regrowth. Regrowth is an absolute amount of recovery: rate of height growth, for example. Resilience, on the other hand, is a measure of the rate

at which a system returns to its initial (predisturbance) condition.

I have attempted to evaluate the relative resiliences of the five successional stands listed in table 1. To do so, I determined the value of various structural characteristics of the second growth at one year of age. I then expressed the value at age one as a percentage of the mature-ecosystem value. The results obtained using height data (height of three tallest plants on each of eight replicated successional plots expressed as a percent of mature-forest canopy height for that same site) are representative: Tropical Wet Forest, 7.8 percent; Tropical Dry Forest, 8.9 percent; Subtropical Wet Forest, 9.7 percent; Subtropical Dry Forest, 10 percent; and Tropical Montane Rain Forest, 3.2 percent.

At the Tropical Wet Forest site, where the regrowth was rapid and luxurious, the percentage height recovery in one year was substantially less than at all other sites except the one at high elevation. Even though the absolute rate of height regrowth was fastest at the warmest, wettest site, the mature vegetation is substantially taller there than at any of the other sites. Thus, the successional vegetation has further to go than it does in more stressful sites: i.e., it is less resilient. At drier or slightly cooler sites, however, the vegetation may have high resilience, not because it bounces back so quickly, but because the mature ecosystem that it is replacing had relatively little structure to begin with.

The resilience of the vegetation at the Tropical Montane Rain Forest site was lower than at any other site, just as its absolute rate of regrowth was slowest. The slow regrowth coupled with low resilience reinforce the concept of great fragility of high-elevation tropical forests.

**NUMBER OF SERAL STAGES.**—In the humid tropical lowlands, vegetation undergoes numerous changes, both structural and floristic, as succession proceeds. When disturbance covers a sizable area, as after farming, short-lived forbs and vines quickly invade, and cover the ground completely. These are followed by heliophytic shrubs and longer-lived herbaceous plants. The process continues with the increased dominance by fast-growing pioneer trees, and later takeover by tree species that may be somewhat more shade tolerant, but less readily dispersed, than the pioneer weed trees. By the time a second-growth forest in the humid lowlands is 30 to 50 years old it is structurally very similar to the predisturbance forest, but it may differ significantly with respect to species composition.

Unlike the wave-after-wave of species that in-

vade disturbed sites in the wet lowlands, succession in the drier tropics is floristically simpler, and involves fewer seral stages. In part, I think this difference reflects the great difficulty of establishment from seed in the dry tropics. As many species regenerate by coppicing, it is apparent that mature-community species that resprout would have a head start on species that might invade as seeds from the outside.

Tropical swamps, both freshwater and saltwater, may represent the ultimate in tropical successional simplicity. Because of the low oxygen which accompanies inundated substrates, these ecosystems are usually dominated by only a few (sometimes one) non-mycorrhizal species. Because most tropical trees have mycorrhizae, the number of potential colonizers of these flooded sites is very low. Some mangrove sites, for example, are immediately reoccupied by the pre-disturbance species following clearfelling; others go through a single seral stage (e.g. a fern, *Acrostichum* sp., in the neotropics) prior to reestablishment of the original forest species. Similarly, I have seen logged swamp forests in Colombia that had been pure stands of *Campnosperma* sp. later dominated completely by a palm, *Euterpe* sp. Local foresters claim that the palm will soon be replaced by *Campnosperma*.

Most problems of tropical silviculture are really problems of understanding and manipulating successional vegetation. It seems, therefore, that silviculture should be much more straightforward in harsh tropical environments, especially swamp forests, than on well-drained soils in the humid lowlands. Tropical swamp forests have been widely exploited, but seldom managed. They obviate many of the classic problems of tropical forest management (e.g. heterogeneity of species composition), and should be capable of supplying a sustainable, uniform-quality wood resource.

**EXPANSION OF RUDERAL VEGETATION.**—Imagine two contiguous, tropical, lowland sites, each with fertile soil: one has a dry climate and the other a wet. If the mature vegetation on each site is cut, and succession allowed to proceed, each site will be occupied by a characteristic secondary vegetation. If, however, the disturbance is repeated and site quality is degraded through improper land use (erosion, nutrient export, soil compaction, etc.), the character of the successional vegetation will change. The regrowth on the dry site is likely to differ only slightly from that which would have occurred had site quality been maintained. Succession on the wet site, however, is likely to be characterized by second-

growth vegetation more typical of the neighboring dry site.

A similar phenomenon occurs where high-elevation ecosystems grade into low-elevation systems: following site-degrading disturbance, the second-growth typical of the colder site invades the warmer ecosystem.

The following generalization may be useful: site disturbance often leads to expansion of secondary vegetation typical of stressful environments into less stressful environments; ruderal vegetation characteristic of benevolent environments seldom invades harsh environments. Thus, paramos move downhill, and semi-deserts invade the humid tropics. Human activities result in the expansion of ruderal vegetation characteristic of dry and cold ecosystems, at the expense of communities typical of warm, moist ecosystems.

## IMPLICATIONS

It is apparent that there are more constraints, floristic, physiognomic, and physiological, on second-growth vegetation in cold or seasonally dry tropical environments than there are in the humid lowlands. The tradeoff seems to be one of durable structure (inedible leaves, strong stems) in the harsh environments for extremely rapid growth in the wet lowlands. Selection results in high-quality building materials in the harsh environments, but greater quantity in less stressful environments. If so, we might predict potentially higher yields, but concomitantly greater risk of devastating pest outbreaks and storm damage in the humid lowlands than in drier or colder tropical successional ecosystems.

In addition to the lower risk associated with vegetation in harsh environments, successional vegetation there seems to undergo fewer seral stages. The original system is likely to return floristically, if not structurally, more rapidly than would be the case in benevolent environments. Management actions concerned with species composition, therefore, are less complicated in the relatively simple communities of harsh environments than in the floristically complex systems of environments more favorable for plant growth.

Furthermore, although the absolute rates of regrowth following natural- or human-induced disturbance may be very high in the humid lowlands, the

resilience (the rate at which they return to their initial condition) may be slower than that of ecosystems in intermediate-stress environments. In the coldest environments that support tree growth in the tropics (Montane Altitudinal Belt, *sensu* Holdridge 1967), however, regrowth is so slow that the vegetation can be considered to be almost completely non-resilient. Human tampering with these high-elevation forests will lead to their irrevocable loss. Because such systems are the headwaters of many, if not most, major tropical river systems, and because high-quality water (for irrigation, industry, and hydroelectric power) is one of the most valuable and abundant resources of the humid tropics, such forests should be meddled with cautiously, if at all.

Many of the fast-growing glamor trees which have captured the attention of tropical foresters (e.g. *Gmelina*, *Anthocephalus*, some *Eucalyptus* spp.) are successional pioneers. The same characteristics that make them successful within their natural range (rapid growth, prolific seed production, high competitiveness) may enable them to become successful naturalized exotics, especially in areas that have been heavily disturbed. The transfer of aggressive weed trees among biogeographic regions can lead to substantial benefit, but the inherent dangers are obvious. The probability of successful naturalization, possibly leading to a pest-control problem, is much greater for successional than for mature ecosystem species.

Haphazard introduction of successional species from moderately harsh tropical environments may be even more dangerous than introductions from the humid lowlands. Such species are likely to colonize successfully not only those environments similar to the ones where they originated, but also degraded sites in the warm, wet areas. As the impact of humans on the humid tropical lowlands becomes increasingly pronounced, it seems certain that secondary vegetation characteristic of drier, colder climates and poorer soils will continue to expand.

It is evident that it is no longer useful to speak of tropical succession in the singular. Rather, the tropics encompass a broad array of tropical successions. People are not only the main force today which creates tropical successions, but they thrive in them. It behooves us to appreciate and attempt to understand this variability.