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DIFFERENCES BETWEEN WET AND DRY SUCCESSIONAL TROPICAL ECOSYSTEMS

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RÉSUMÉ.

Différences entre les écosystèmes secondaires des régions tropicales humides et sèches.

L'auteur compare le développement structural, la stabilité et la régénération pour des végétations secondaires tropicales correspondant à divers degrés d'humidité. Les mesures ont été effectuées pour des recrûs en sept stations à Costa-Rica et Porto-Rico, dont trois emplacements situés dans la zone forestière sèche. Le développement du couvert pendant la première année, l'index foliaire, la taille et l'irrégularité du couvert, ainsi que la stabilité, la germination, l'installation des plantules et la richesse spécifique sont comparés pour les deux séries progressives.

ABSTRACT.

The author compares structural development, stability and regeneration among successional vegetation in tropical ecosystems of varying degrees of wetness and dryness. Measurements on second growth vegetation were made in seven sites in Costa Rica and Puerto Rico, of wich three are in dry forest zones. Data on canopy development during the first year, leaf area index, height growth and canopy patchniness as well as stability, seed germination, seedling establishment and species richness are compared for both secondary successional ecosystems.

INTRODUCTION

The complex, mature forests of the tropical lowlands have historically attracted considerable ecological attention, but the much-neglected successional forests are certainly of at least equal importance for two reasons. First, the successional ecosystems are, by definition, those with a positive net primary productivity ; they are, therefore, those with some potential for yield of food and fiber for human needs. Second, the successional ecosystems occupy tremendous areas, principally

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because of shifting agriculture, logging operations, and, more recently in the neotropics, the abandonment of unsuccessful attempts to convert humid lowland forests to improved cattle pastures. The studies reported here compare structure, growth, and reproduction among successional vegetation in tropical ecosystems of varying degrees of wetness and dryness.

There is as much difference among secondary successional tropical ecosystems as there is among the mature ecosystems which preceded them. These differences are particularly evident when comparisons are made between wet and dry tropical ecosystems, where the distinct environments require different adaptive strategies on the part of the species which make up these two kinds of vegetation. In the dry tropics survival requires the ability to cope with factors (or their absence) which are of direct physical origin, especially water. In the humid tropics, however, survival requires the ability to surmount problems which are primarily biological, involving the competition among species for light, space, and nutrients. Both strategies require that an individual acquire those physical factors necessary for life : in the dry tropics this involves energetically expensive physiological, morphological, and anatomical adaptations directly concerned with obtaining (or retaining) water, while in the humid tropics the adaptive features required concern rapid colonization and growth, competition for sites, and nutrient retention.

THE STUDY AREAS

Measurements were made on second-growth vegetation in seven sites in Costa Rica and Puerto Rico (Table 1). Four of the sites were part of a larger successional study and those sites have been described in detail elsewhere (EWEL 1971). The regrowth on these four sites was studied over 13 months from the time each was cleared of all vegetation. Measurements were made after approximately 3, 5, and 13 months. The exact time intervals between successive remeasurements are given in Table 2. The remaining three sites contained older vegetation (5 — 12 years) which had grown up following pasture abandonment and were studied at only one time. Three of the sites (Palo Verde, La Pacifica, and Guanica) are in dry forest zones (mean annual potential evaporanspiration (P.E.T.) exceeds mean annual rainfall) ; the other four (Las Cruces, La Selva, Osa, Jimenez) are in wet forest zones (mean annual P.E.T. less than mean annual rainfall). Detailed descriptions of the vegetation at or near the Costa Rican sites can be found in HOLDRIDGE et *al.* (1971) ; EWEL & WHITMORE (1973) described the vegetation typical of the Puerto Rican sites.

METHODS

The data from the young regrowth plots of La Pacifica, Guanica, Jimenez, and Osa were obtained from 3m × 6m plots, with eight plots per site. Leaf area index (LAI) was determined by placing a thin metal rod vertically at 20 locations within each plot and counting the number of leaves intercepted by the rod. Per cent cover was calculated from the leaf area samples : where LAI = 0, cover = 0%;

Table 1. Descriptions of the study sites

Name	Mean Annual Rainfall (mm)	Life Zone (sensu Holdridge 1967)	Location (country; W longitude ; N latitude ; elevation (m))	Age of vegetation studied	Description of mature vegetation
Dry Sites					
La Pacifica	1800	Tropical Dry Forest	Costa Rica ; 85°08' 10°26' ; 45	0 to 13 months	17m tall ; broad crowns ; deciduous
Palo Verde	1700	Tropical Dry Forest	Costa Rica; 85°23' ; 10°22' ; 5	5.5. years	same as above
Guanica	880	Subtropical Dry Forest	Puerto Rico; 65°52'; 17°57' ; 160	0 to 13 months	12m tall ; half deciduous ; succulents common
Wet Sites					
Las Cruces	4000	Tropical Premontane Wet Forest	Costa Rica; 82°57' ; 8°48' ; 1250	12 years	30m tall ; evergreen
Jimenez	3600	Subtropical Wet Forest	Puerto Rico; 65°48'; 18°21' ; 180	0 to 13 months	22m tall, evergreen
La Selva	3700	Tropical Wet Forest	Costa Rica; 84°01; 10°26' ; 110	c. 11 years	40m tall ; evergreen
Osa	4800	Tropical Wet Forest	Costa Rica; 83°30'; 8°42' ; 20	0 to 13 months	45m tall ; evergreen with deciduous emergents

Table 2. Age of vegetation (days) on the young second-growth study plots

	First Remeasurement	Second Remeasurement	Third Remeasurement
Dry Sites			
Guanica	96	170	371
La Pacifica	79	173	401
Wet Sites			
Jimenez	102	183	381
Osa	85	164	397

where LAI $\geq$ 1, cover = 100 %. Each 3m × 6m plot was subdivided into 36 subplots, each measuring 0.5m × 1m. Six of these subplots were randomly selected from each plot for complete tallying of species and heights. The three tallest plants encountered in the total subsample formed the basis for the height data presesented here. Plots containing little vegetation were not subdivided ; all plants were measured in those cases. The species data were derived by completely surveying each plot and recording the species present.

In the older successional stands (La Selva, Las Cruces, Palo Verde) a 10m × 15m transect, subdivided into six 5m × 5m plots, was laid out. The height and species (all morphs distinguished, but not identified) of all wood plants > 0.5m tall were recorded ; where multiple stems obviously originated from a common stump or below-ground stem this fact was noted also.

RESULTS AND DISCUSSION

Canopy Development During the First Year

Succession is generally a slower process in dry tropical environments than in wet areas. Often, however, the end point is structurally the same : it just takes longer to reach it in dry areas. Such is the case with cover (Fig. 1), which increased relatively slowly in dry areas, yet reached a value greater than 90 per cent even on the driest site after 13 months. On the wettest site, by comparison, the 90 per cent cover value was exceeded during the first six months of regrowth. In the wet areas the soil is quickly covered with green regrowth ; this rapid coverage may inhibit the leaching of soil nutrients, although this assumption has recently been questioned by HARCOMBE (1973).

The vegetation canopy in most mature dry forests is less dense than that of wet forests. If the cover is similar in the two forests, then the difference must be due to the horizontal and vertical distribution of leaf tissue within the stand. The horizontal distribution determines the patchiness of the canopy, while the vertical distribution determines the leaf area over a given point. The leaf area data are summarized in Figure 2, which again shows that canopy development was more rapid on the wet sites than the dry sites. The mean leaf area index (c. 5) measured

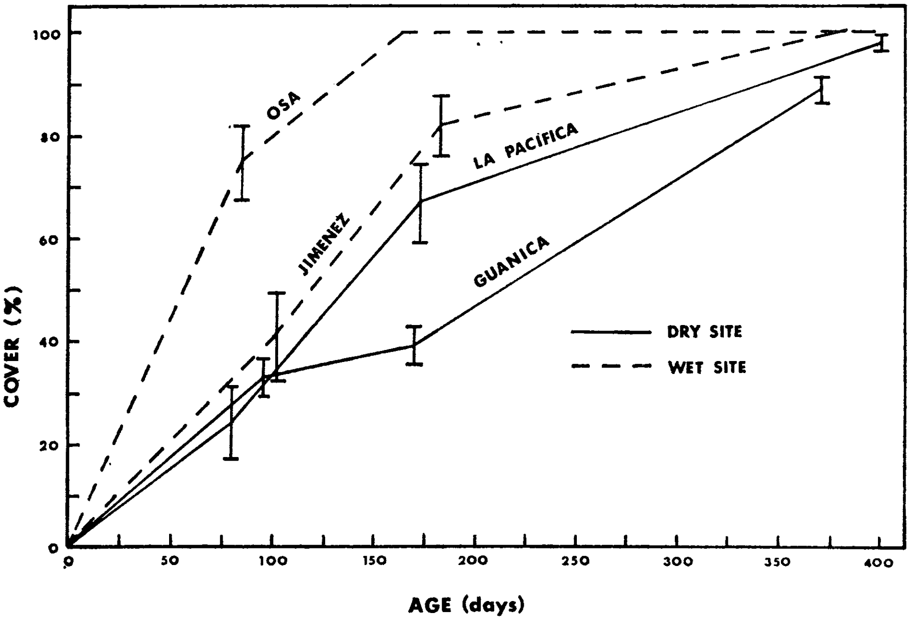

Figure 1. Cover development during early succession on wet and dry sites. Bars are ± S.E.

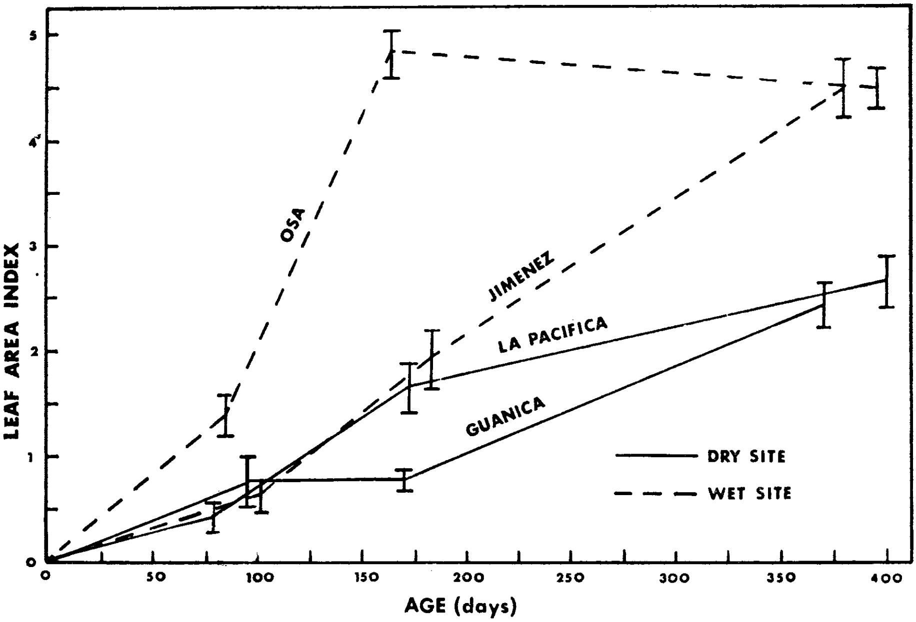

Figure 2. Leaf area index development during early succession on wet and dry sites. Bars are ± S.E.

at the wettest site when the vegetation was only six months old is higher than the value reported for a mature forest in the Ivory Coast (MULLER & NIELSEN 1965) and approaches thatreported for a mature wet forest in Puerto Rico (ODUM 1970). It is about two-thirds as high as other values reported for mature forest in the Ivory Coast (AUBREVILLE 1938) and Nigeria (JONES 1956).

Figures 1 & 2 give the impression that canopy development follows a similar pattern in wet and dry forests, merely being a more rapid procedure in the wet areas. There are, however, important differences between the two. In the wet areas the ground was quickly covered with a homogeneous layer of leaves ; as stem elongation took place more leaves were added. Ghus, the canopy started as a monolayer, then became uniformly thicker as additional layers of leaves were added. In the dry areas, however, the process followed a different path. Here the ground was covered more slowly and leaf area increased in parallel with ground cover. Clumps of leaves appeared (often from stump sprouts) and later increased in size. Thus, coverage increased along with leaf area. In some cases the scattered clumps of regrowth had individual leaf area values which were extremely high (as high as 16 in two instances), but were separated from the next clump by bare ground. The mean leaf area may therefore be comparable to that of a wet site, but the spatial distribution is quite distinct : scattered clumps, each with high leaf area, separated by nearly bare ground in the dry areas ; uniform coverage of nearly constant leaf area in the wet areas.

The method used to measure leaf area provided a means of quantifying these differences. Since 20 measurements were made on each of the eight plots per site at each of the three times measurements were made, sufficient values were available to attempt to evaluate the relative « noisiness » of the data in wet and dry areas. This was done by calculating the coefficient of variation (= standard deviation expressed as a percentage of the mean) for the 160 leaf area measurements made at each site at each time. The results are shown in Figure 3. Here the coefficient of variation is used not in its usual statistical sense to evaluate the quality of a mean value, but rather as a measure of the point-to-point variability in a canopy structure variable : leaf area index. The coefficient of variation has similarly been used on population density data (MACGUIRE 1969) and on diversity data (NICHOLSON 1970)to evaluate ecosystem stability. When applied to the leaf area data the coefficient of variation is a relatively conservative measure of canopy patchiness because the leaf area (the denominator) was higher in the wet areas ; thus, if the variances (as estimated by the standard deviations) were the same in wet and dry sites, the coefficient of variation would be lower on the wet sites. Therefore, a higher coefficient of variation on a dry site (having a lower leaf area) indicates that the corresponding standard deviation must be higher there also.

The results (Fig. 3) demonstrate that, for the first six months of regrowth, the canopy on dry sites is indeed noisier (or patchier) than on wet sites. Furthermore, with the exception of the measurements made at three months, the canopy patchiness decreases with increasing wettness. At the end of a year, however, the

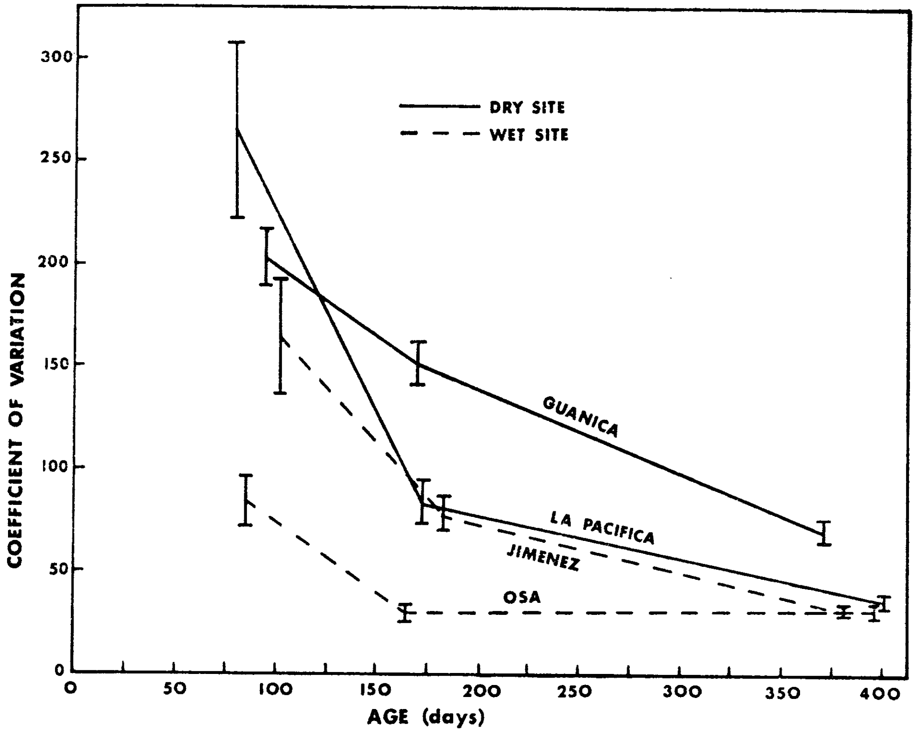

Figure 3. Canopy patchiness, as determined by the coefficient of variation of leaf area index measurements, during early succession on wet and dry sites. Bars are ± S.E.

canopies were much more uniform at all sites than they had been during earlier developmental stages. At the three wettest sites the patchiness was reduced to about 50 per cent, but it was still about 100 per cent on the driest site. The pattern which emerges is, at the ecosystem level, similar to the kinds of predictions made by HORN (1971) for the individual tree species which occur in wet and dry areas. His monolayer crowns seem to correspond to the the successionnal vegetation characteristic of wet areas, except that the vegetation consists of multiple, uniform monolayers several layers thick. These different layers may well be dominated by species of differing degrees of shade tolerance, as assumed by foresters for many decades and as more formerly restated by HORN (1971). The canopy structure in the dry areas corresponds to the multilayer structure which HORN (1971) suggested as being characteristic of species on dry sites.

Height Growth and Ecosystem Resilience

Height growth on the four youngest plots is shown, together with height data from the older successional plots, in Figure 4. Height growth was significantly faster at the wettest site (Osa), where the tallest trees averaged almost 5m tall after

13 months. One tree at this site attained a height of 9.0m in less than 13 months. Individual plants at the other wet site (Jimenez) did not grow very tall during the first year, but the average height of all plants at this site was higher than that of the drier sites, even though the tallest individuals were not taller. Data are not

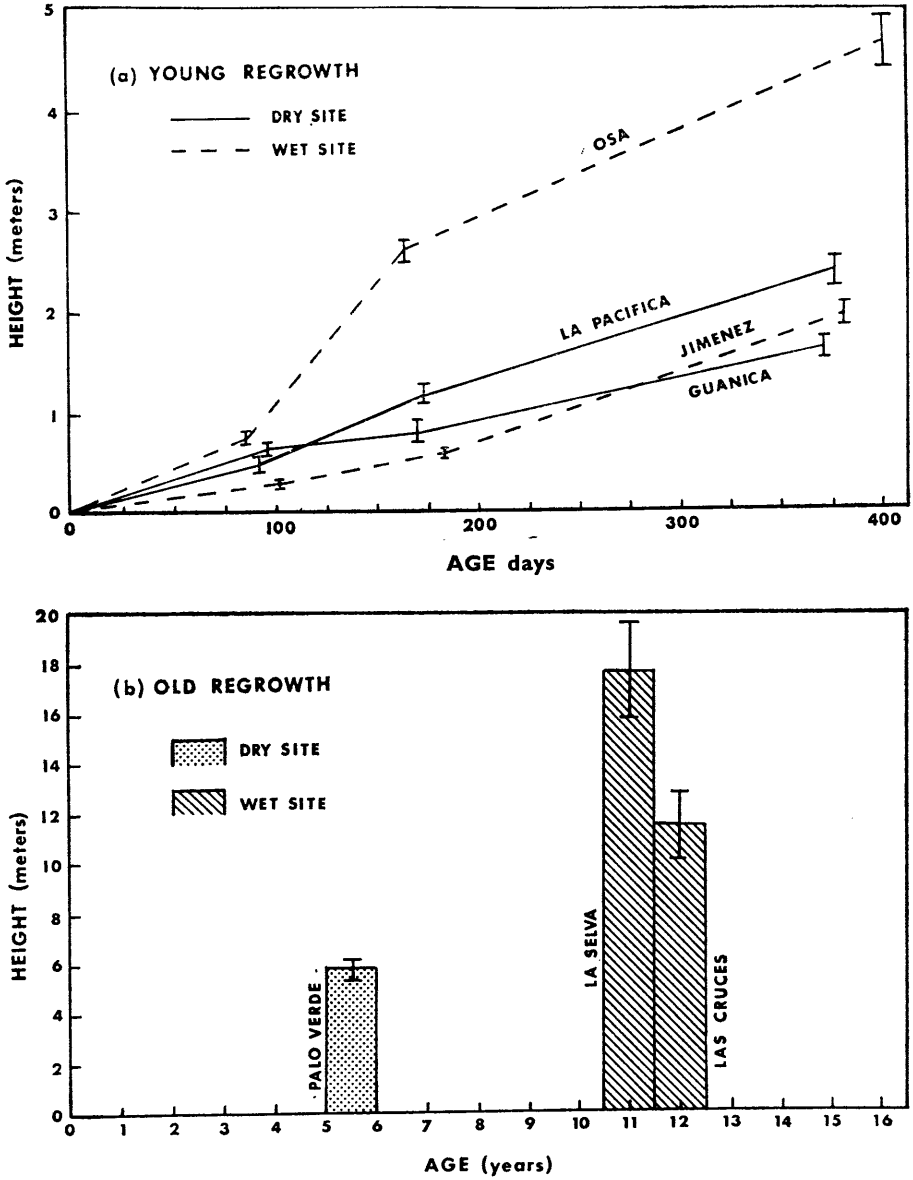

Figure 4. Height of tallest plants on young successional plots (a) and on old successional plots (b) in wet and dry environments. Bars are ± S.E.

available for older stands of the same age in both wet and dry areas, but the tallest successional trees, in a c. 11-year-old stand at a wet site, were about three times taller than the tallest trees in the 5.5-year-old dry-site stand.

That trees in a wet area should grow faster and taller than trees in a dry area is not particularly surprising. The height data can, however, be used to evaluate a general ecosystem property : resilience, or the rate at which an ecosystem tends to return to its initial condition following perturbation. This component of ecosystem stability is of considerable practical importance in that it is a measure of ability to recover ; it can, therefore, be used to rank ecosystems with respect to their long-term susceptibility to change or disturbance. In Figure 5 the successional

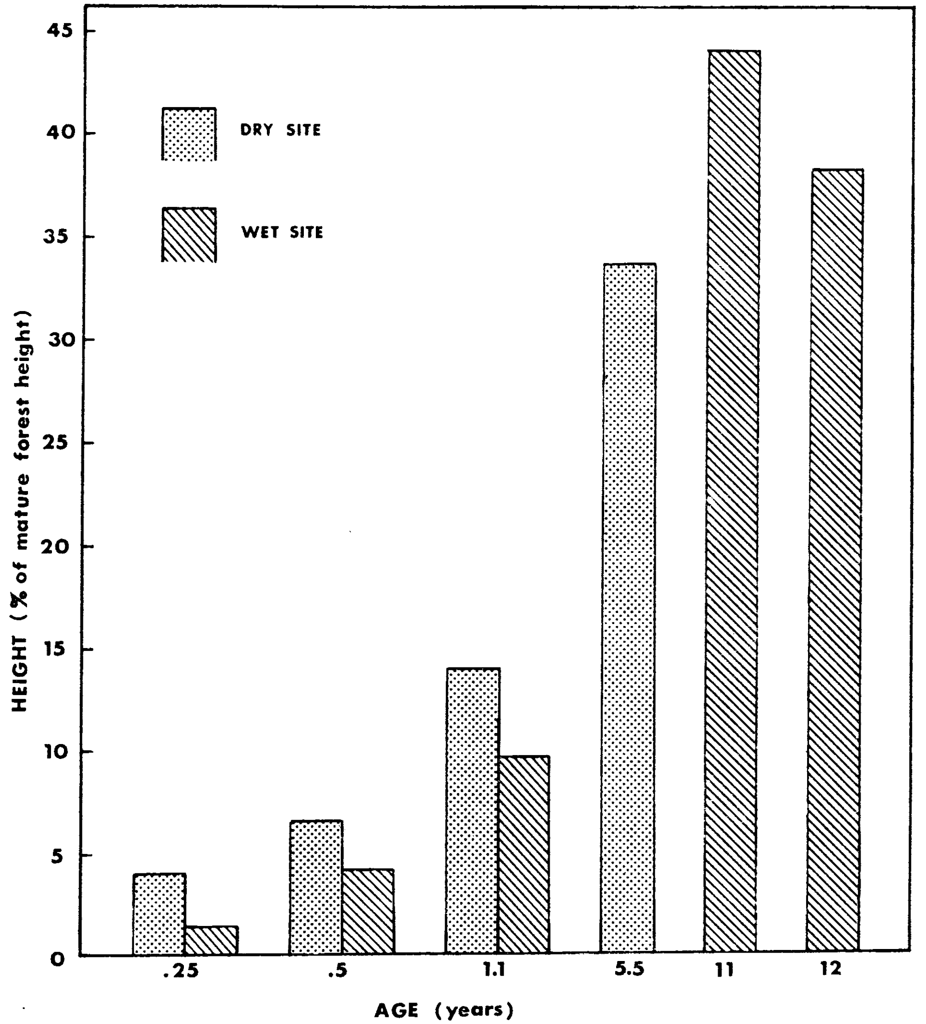

Figure 5. Resilience of successional vegetation on wet and dry sites, as measured by the rate of recovery of canopy height.

height data are expressed as a percentage of the height of the mature forest at the same site. For the young regrowth stands the values shown are averages for the two dry sites (Guanica & La Pacifica) and the two wet sites (Jimenez & Osa). Data are not available from equal-aged older second-growth in both wet and dry areas, so the conclusions which can be reached are tentative. It appears, however, that vegetation on dry sites may be more resilient than that on wet sites, even though the absolute rate of growth is slower. On dry sites the rate of height regrowth is relatively slow, but the level of the lower mature-forest canopy is approached more rapidly than is the case in wet areas. Even in the later stages of succession, the dry site trees had attained more than a third the height of the mature forest canopy after only 5.5 years, while the tallest trees on the wet forest sites, where the vegetation was twice as old, were only about 35 to 45 per cent as tall as the corresponding mature forest canopy.

That an ecosystem in a high-stress tropical environment might be more resilient than an ecosystem in a low-stress tropical environment contradicts a commonly held assumption regarding the relative stability of different kinds of tropical ecosystems. Qualitative observations made at two of the sites after the study was terminated suggest that the data summarized in Figure 5 may indeed mask an important factor in evaluating the relative stability of wet and dry tropical ecosystems. The vegetation at one of the wet sites, Jimenez, was reexamined when the plot was four-years-old. The vegetation was dense, tall, and vigorous : well on its way to becoming a forest. At the same time the vegetation on one of the dry sites, Guanica, was reexamined and its apperance was quite distinct. At that time the south coast of Puerto Rico (where Guanica is located) was undergoing a year-long drought and its effects were evident in the second-growth vegetation. Most of the young plants were dead and/or leafless ; individual plots appeared to have much less living biomass than they had four years previously. A few large (up to 6m tall) clumps of coppice dotted the 1 ha clearing in which the study plots had been located ; otherwise the vegetation was in extremely poor condition. These observations are probably not atypical of dry tropical areas. A reduction in rainfall of 200mm for one year means much more on a site where the average annual total is 800mm than it does on a site which receives 4000mm. Dry tropical climates are characteristically unpredictable and much more subject to year-to-year variability than are wet tropical climates. Thus, observations such as those made at Guanica during a drought year might indeed be the norm for the dry tropics. Germination and initial establishment are crucial stages in the life cycle of most plants, so second-growth vegetation in the dry tropics is likely to be subject to repeated setbacks during the course of succession. If such setbacks are a normal part of succession in the dry tropics, then the resistance component of dry tropical ecosystem stability might, in fact, be lower than that of wet tropical ecosystems.

Regeneration from Coppicing and Seed

When measuring the young regrowth it was observed that most of the regeneration on the dry sites originated as coppice from stumps and underground roots and stems. The majority of the individuals on the wet sites, however resulted from seed germination. At those early stages of succession it was difficult to determine whether this initial observation would hold throughout the later seral stages or wether it was simply a characteristic of the earliest stages, one which would later become unimportant as competition developed and seedlings and sprouts underwent differential mortality. Therefore the older successional stands were inventoried to determine how much coppicing was still evident in the later stages of succession and to find out if the differences which were evident between dry and wet sites during the initial seral stages were still present in later stages. The stem-to-clump ratio (Fig. 6) in these older stands indicates that succession on dry sites is

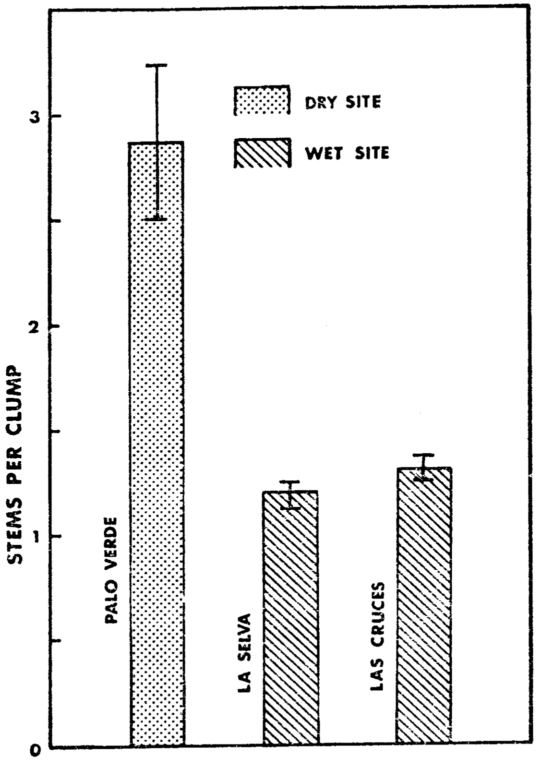

Figure 6. Coppicing in old successional stands in wet and dry environments, expressed as the number of stems originating from a common base. Bars are ± S.E.

extremely dependent upon vegetative reproduction ; each woody plant > 0.5m tall was, on the average, part of a clump of almost three stems. On the wet sites, however, the stem-to-clump ratios averaged only slightly greater than the minimum possible value of 1.0 which would have been found if each plant had been a single stem.

Because seed germination and seedling establishment are such critical stages in the life cycle of most woody plants, it is not surprising that these stages are bypassed by plants founds in harsh, unpredictable environments such as the dry tropics. Just as interesting is the question of why the data seem to indicate that these stages are not likewise bypassed on wet sites. First of all, the data do not necessarily indicate that individual trees or species in wet areas are less prone to coppicing than are those of dry areas. The data simply indicate that ratio of sprouts to seedlings is low. This could result from an abundance of seedlings interespersed among relatively few sprouting stumps. A mature, wet tropical forest contains relatively few stems, and conditions for seed germination following felling of the overstory are likely to be good. Thus, a site may be dominated by an abundance of seedlings and, even though a majority of the stumps might coppice, the stems-t-clump ratio would still be low. A second possibility is that species characteristic of dry environments are, in fact, more prolific at coppicing than are species characteristic of wet environments. Dry-site species frequently contain below-ground storage products which would serve as an energy resource during coppicing ; species characteristic of non-seasonal tropical environments are less likely to have large below-ground energy reserves. Another possibility is that the stumps and associated root system of trees in wet forests would be subject to rot, so that any regeneration which might result from sprouts would be doomed to a short life. Therefore there might be little selection for the coppicing trait in wet areas, whereas there might be such selection in dry areas, where the root system might not necessarily be so subject to decasy.

Species Richness

Diversity can be expressed in many ways, and is an important variable which might be expected to change dramatically along an environmental gradient. On young successional plots, where the number of stems is very high, where the plot size is large in relation to the size of the individual plants, and where elimination through crowding is not yet an important factor, one measure of the richness component of diversity is simply the number of species found on each plot. Table 3

Table 3. Number of vascular plant species on successional plots on wet and dry sites

Dry Sites			Wet Sites		
No. of Species per plot * (± S.E.)	Age (years)	Site **	No. of Species per plot * (± S.E.)	Age (years)	Site **
25.4 (± 2.1)	.22	L.P.	38.3 (± 2.4)	.23	O
27.4 (± 1.4)	.26	G	30.0 (± 2.3)	.28	J
28.9 (± 1.3)	.47	L.P.	36.3 (± 1.9)	.45	O
27.8 (± 1.9)	.47	G	35.5 (± 1.4)	.50	J
31.6 (± 0.8)	1.02	G	31.3 (± 1.3)	1.04	J
29.6 (± 1.5)	1.10	L.P.	35.6 (± 2.1)	1.09	O
9.8 (± 0.8)	5.5	P.V.	17.3 (± 2.1)	c.11	L.S.
			28.2 (± 2.0)	12	L.C.

* Six plots, each 5m × 5m, at P.V., L.S., and L.C. Eight plots, each 3m × 6m, at all other sites.

** G = Guanica ; L.P. = La Pacifica ; J = Jimenez ; O = Osa ; P.V. = Palo Verde ; L.S. = La Selva ; L.C. = Las Cruces.

shows the number of species per plot on the four young-regrowth sites as well as the three older stands. The young-regrowth plots at the wet sites contained about 17 per cent more species per plot than the plots on dry sites. On the older successional plots the wet sites had two-to-three times as many species per plot as did the dry sites. This large difference, however, is due, in part, to the difference in numbers of individuals on these two kinds of sites. The plots in the older second-growth were relatively small (5m × 5m) in relation to the size of the individual plants, so crowding and competition governed the number of individuals present. There were considerably more individuals per unit area on the older wet sites than on the older dry site. When the number of individuals is divided by the number of species found, the resulting ratios do not differ greatly among the three old second-growth stands. Mean values (± S.E.) for this ratio as calculated for the two wet sites were : La Selva 2.8 (± 0.3) and Las Cruces 2.0 (± 0.2) ; and for the dry site : Palo Verde 2.1 (± 0.1). Thus, although the number of species found on the wet sites was greater than the number found on the dry sites, this is partially due to the fact that dry sites support fewer individuals per unit area than do wet sites. The data do not necessarily demonstrate that the number of species that thrive on a dry site is necessarily less than the number which can thrive on a wet site, although it seems likely that this would be the case. Forest inventory data from the mature forests at La Selva (wet) and near Palo Verde (dry) certainly indicate that wet forests are richer in species (HOLDRIDGE et *al* 1971, FRANKIE et *al* 1974).

CONCLUSIONS

The conclusions which emerge from this study of wet and dry successional tropical vegetation are summarized in Table 4. Several features have direct implications regarding land use. These include the patchy canopy development in dry areas, the marked seasonality (and very rapid wet-season growth) on dry sites, the relative importance of coppice and sexual reproduction in wet and dry areas, and the susceptibility of vegetation in dry areas to the vagaries of climate. Millenia of natural selection have resulted in the evolution of two distinct strategies of succession, each presumably almost ideally suited to the physical and biological conditions characteristic of wet and dry sites respectively. It is not unreasonable to assume that these two strategies exist because they have conferred adaptive value upon the individuals (and ultimately, therefore, the populations, communities, and ecosystems) found there. If this is so, then surely these patterns of ecosystem development can teach us a great deal about the design of ecosystems suitable to different kinds of tropical environments. Successional tropical ecosystems can serve as living models of the kinds of structural and functional properties which we should design into those ecosystems modified by humans to satisfy our food and fiber needs.

ACKNOWLEDGEMENTS

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Table 4. Comparative summary of some of the difference between wet and dry successional tropical ecosystems.

Characteristic	Wet Tropics	Dry Tropics
Structural Development		
cover	rapid soil coverage	spotty development of cover
leaf area	develops uniformly on site	extremely high in patches, with bare ground in between
height growth	rapid ; small annual pulse	rapid during rainy season, but not continuous
canopy patchiness	low ; smooth canopy of uniform leaf area	patchy, with great point-to-point variation in leaf area
Stability		
resilience (as measured by canopy height recovery rate)	low	high
resistance (subject to environmental perturbations during covery)	high	low
Regeneration		
coppice	present, but not extremely important	very important
seed	more important than coppice	less important than coppice
species richness	many potential colonizers	numerous potential colonizers, but fewer than on wet sites

Puerto Rico. Field studies there were supported by Atomic Energy Commission contract AT—(40-1)—4150 with H.T. ODUM, who offered many helpful suggestions throughout this study. Field sites and logistical support in Costa Rica were provided by the Tropical Science Center, W. HAGNAUER of Finca La Pacifica, the Costa Rican Forestry Department, Osa Productos Forestales, Inc., and the Organization for Tropical Studies, Inc., through Pilot Grant 69-12 and course 75-2. D. POOL assisted in field work on all of the older regrowth sites in Costa Rica. R. MYERS assisted in the field at Las Cruces. K.C. EWEL assisted in the field at all of the young regrowth sites. Computer time was provided by the Northeast Regional Data Center, University of Florida.

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