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ECOLOGY OF TROPICAL DRY FOREST¹

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INTRODUCTION

According to the Holdridge system of life zone classification (42), dry tropical and subtropical forests and woodlands occur in frost-free areas where the mean annual biotemperature is higher than 17°C, where mean annual rainfall is 250–2000 mm, and where the annual ratio of potential evapotranspiration (PET) to precipitation (P) exceeds unity. The many types of woodland and forest ecosystems that fall within this climatic envelope are widespread, usually transitional between semidesert or savanna and moist forest.

About 40% of the earth's tropical and subtropical landmass is dominated by open or closed forest. Of this, 42% is dry forest, 33% is moist forest, and only 25% is wet and rain forest (*sensu* Holdridge, 42; 15). We will never know the true original or potential extent of dry forest because many savannas and scrub or thorn woodlands are thought to be derived from disturbed dry forest. Walter (110), for example, considers most or all of the grassland in India to have been derived from seasonal or dry forest. Some of the processes that cause this conversion are addressed later in this review. The largest proportion of dry forest ecosystems is in Africa and the world's tropical islands, where they account for 70–80% of the forested area. In South America they

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represent only 22% of the forested area but in Central America almost 50% (14).

Although literature has proliferated concerning the ecology of certain types of tropical ecosystems, such as savanna (12, 47, 99) and rain forest (39a, 101, 103b, 114), far less attention has been given to tropical and subtropical dry forest and woodland. Our focus is on this relatively neglected category of ecosystems, which we refer to in the collective sense as tropical dry forest. Our emphasis is on the plant, as opposed to animal, component of the system.

SEASONALITY AND VARIABILITY IN THE DRY FOREST CLIMATE

The climate of tropical dry forest was defined above according to the average annual conditions of temperature and rainfall. But most tropical forests, even wet or rain forests, are to some extent seasonal with respect to rainfall (111), a factor of significance to ecosystem structure and function. Whereas the seasonality may be subtle in the wetter forests, it may be extreme in other cases, such as the monsoon forests of southern Asia where monthly rainfall may vary from near 0 to over 2500 mm (111). The timing, frequency, and duration of dry periods (*sensu* Holdridge, 42) depend largely upon latitudinal position, with the shortest and least severe dry periods found at or within several degrees of the equator. With increasing distance from the equator, the pattern of a short (several-week- to one- or two-month-long) dry period during the summer months and a long (two- to six-month) dry period during the winter months becomes increasingly prominent (95). Areas near the latitudinal limits of the tropics may have only one pronounced dry season, but it may be up to eight months in duration. In some areas, factors other than latitude—such as proximity to warm or cold ocean currents or exposure to monsoon or monsoon-like air mass movements—have a dominant role in determining seasonality. In equatorial Africa, for example, the marked seasonality of the eastern part of the continent (relative to the more uniform humid climate of the western half) can be attributed to differences in hemispheric air mass flow.

Rainfall seasonality becomes a dominant ecological force when temporal patterns of biological activity such as growth or reproduction become synchronized with the availability of water or when the geographic distributions of plant or animal taxa are constrained by moisture limitations during certain times of the year. In India, the more humid forest types are differentiated from each other by the duration of their dry periods whereas the driest ecosystems, such as thornbush savanna or desert, exhibit characteristic differences based more on the total amount of annual rainfall (110). Although similar analyses are not available for other regions, it appears that the various types of dry forest, such as those considered in this review, are largely determined by both

annual rainfall and the seasonality of rainfall distribution [cf the findings of Walter (110) in India]. While some dry forests may experience only two months of adequate moisture annually, those that border tropical moist forests (*sensu* Holdridge, 42) may receive eight or more months of adequate rainfall. Generally, it appears that as few as two or three dry months are sufficient to alter significantly the composition and structure of an ecosystem which might otherwise qualify as moist, wet, or rain-forest. The effects of seasonality on forest functioning are discussed later in this review.

Another temporal aspect of climate that is not within the realm of extant climate-vegetation models is year-to-year variability. Variability in the annual amount of rainfall and variability in the intensity and timing of wet and dry periods are often considerable in tropical areas. Whereas the coefficient of variation for annual rainfall in temperate regions approximates 15%, it is more often in the range of 30% in tropical areas (97). Variability is significant for ecosystems near threshold levels of water supply, that is, systems that include numerous plant or animal components near the margins of their tolerance relative to moisture. The high levels of water stress that occur during dry years—a common cause of tree mortality (23, 93)—suggest that the extreme years, rather than the average years, may be of most significance in molding overall structural, compositional, and functional properties of dry forest ecosystems. But in the absence of more longterm studies and information, the inclusion of extreme values of environmental parameters is as yet beyond the scope of existing climate-vegetation models.

DRY FOREST STRUCTURE AND FUNCTION

As is the case in other climatic areas, the continua of vegetation types that occur across environmental gradients in the tropics are not easily divided into meaningful subunits for purposes of classification. Consequently, one of the major problems in attempting to draw generalizations about tropical dry forest ecosystems is the plethora of designations that exist in the literature for the many types of these systems (e.g. 7, 79, 110).

The diversity of classification systems clearly reflects reality. Of the studies reviewed for this paper, no two sites can be thought to represent very similar—much less, identical—ecosystems either in vegetation composition and structure or in macro- or micro-climate. The inherent variability of dry forest ecosystems, coupled with the sparseness of the environmental data available, allows only coarse generalizations regarding the ecological characteristics of dry forest, relative to other tropical forest types.

Among the research sites employed in ecosystem level studies of dry forest (Table 1), the annual rainfall averages from 600 to 1800 mm, distributed over 4–9 months. In most instances, sites are characterized by two dry periods, one

major and one minor. Ratios of mean annual temperature (T) to mean annual precipitation (P) are used in the table because the data necessary to calculate PET/P ratios accurately are unavailable for most sites (see discussion of T/P ratios in Brown & Lugo, 15). Ratios range from $4.1 \times 10^{-2} \text{C/mm}$ on the driest site, a subtropical deciduous forest in India, to $1.4 \times 10^{-2} \text{C/mm}$ on the site with most favorable moisture conditions, a dry forest in Costa Rica. In addition to climatic and other environmental differences, the sites differ markedly with respect to degree of disturbance, or vegetation maturity, but in most cases this factor is not quantified.

Table 1 Dry forest study sites, arranged according to increasing annual precipitation

Forest type, location	Mean rainfall (mm/yr)	Mean temp. (°C)	T/P ^a ratio	Dry months	Selected references
Deciduous forest (Udaipur, India) 24°35'N, 75°49'E 587 m elevation	603	25	4.1	>6	35, 108
Deciduous forest ^b (Chamela, Jalisco, Mexico) 19°30'N, 105°05'W Upland site	748	24.9	3.3	6–8	17, 31, 73
Semideciduous forest ^b (Chamela, Jalisco, Mexico) 19°30'N, 105°05'W Arroyo site	748	24.9	3.3	6–8	17, 73
Mixed deciduous forest (Varanasi, India) 25°20'N, 83°01'E 350 m elevation	800	25	3.1	>6	5, 81, 94
Semideciduous forest ^c (Guanica, Puerto Rico) 17°57'N, 65°52'W 160 m elevation Successional and mature sites	860	25.1	2.9	6	24, 26, 27, 29, 65, 66, 67, 86a, 86b
Dipterocarp savanna forest (Ping Kong, North Thailand) 16°30'N, 101°00'E	1200	25	2.1	3–4	88
Monsoon forest-savanna ecotone (Ping Kong, North Thailand) 16°30'N, 101°00'E	1200	25	2.1	3–4	88
Dry monsoon forest (Ping Kong, North Thailand) 16°30'N, 101°00'E	1200	25	2.1	3–4	88
Deciduous savanna forest (Calabozo Plains, Venezuela) 08°48'N, 67°27'W	1200	27.1	2.2	4	78
Mixed dry forest (Ibadan, Nigeria) 07°26'N, 03°48'E	1230	25	2.0	6	69
Muhulu ^d , dry evergreen forest (Lubumbashi, Zaire) 11°37'S, 27°29'E 1244 m elevation	1270	19.2	1.5	6	70, 71, 72

Table 1 (continued)

Forest type, location	Mean rainfall (mm/yr)	Mean temp. (°C)	T/P ^a ratio	Dry months	Selected references
Miombo ^d , deciduous woodland (de- graded muhulu) (Lubumbashi, Zaire) 11°37'S, 27°29'E 1244 m elevation	1270	20	1.6	6	25, 70, 71, 72
Monsoon forest ^e (Kakadu/Kapalga, North Australia) 12°25'S, 132°00'E	1400	26	1.8	6	113
Dry forest (Santa Rosa, Costa Rica) 10°50'N, 85°40'W 0–300 m elevation	1500	25	1.7	6	34, 46, 51, 52, 53, 54, 55
Seasonal forest (Ivory Coast) 05°00'N, 05°00'W	1500	27	1.8	3	82
Semievergreen forest (Sri Lanka) 07°56'N, 81°00'E	1671	27	1.6	3	22
Dry forest (Palo Verde, Costa Rica) 10°20'N, 85°20'W 5–100 m elevation	1750	25	1.4	6	27, 53
Dry forest (La Pacifica, Costa Rica) 10°26'N, 85°08'W 45 m elevation Successional and mat- ure sites	1800	25	1.4	6	27, 50, 53, 56, 90

^aT/P, (mean annual temperature, °C / mean annual precipitation, mm) × 100

^bUnpublished information was provided by S. H. Bullock.

^cAdditional information is available in the final report submitted to the National Science Foundation in 1985 by P. G. Murphy and A. E. Lugo; Grant DEB-81-10208.

^dBecause of their elevation, these sites are within the premontane moist forest life zone (*sensu* Holdridge, 42).

^eAdditional information is available in an unpublished collection of abstracts from a 1983 symposium on the ecology of the wet-dry tropics; CSIRO, Darwin, Australia.

In view of the major differences among sites, including their wide geographic distribution, it is not surprising that representative values of important structural and functional traits for tropical and subtropical dry forest are highly variable (Table 2). In large part, the dry forest values presented in the table are based upon the sites and studies listed in Table 1. Values for wet forest are included in Table 2 for comparison.

Structural Traits

Generally, dry tropical forests are smaller in stature and less complex floristically and structurally than wet tropical forests (Table 2). Because of differences in sample size, in the taxonomic groups included, and in plant size, comparisons of species diversity among different tropical forests are difficult to make or limited in meaning. However, on the scale of several hectares or less, dry forests average about half or less the tree species of wet forests. The

same applies to larger areas as well, where the number of species increases along a moisture gradient (86a). The lower values are found in the driest areas and particularly in insular forests, such as that in southwestern Puerto Rico near Guanica where are found 30–50 tree species per hectare (86a). The only wet forests with comparably low values for tree species diversity are those on swampy or unusually infertile sites, or where the elevation is high. In his studies of the more diverse (87 tree species) dry forest of Guanacaste Province in Costa Rica, Hubbell (46) found that tree species were either clumped or randomly dispersed, with rare species more clumped than common ones. He therefore rejected the generalization that in tropical forests, mature individuals of a species tend to be relatively widely spaced.

Table 2 Structural and functional characteristics of tropical and subtropical dry forest^a relative to tropical and subtropical wet and rain forest^b

Trait	Forest type		References
	Dry ^a	Wet ^b	
<u>Structural traits, community level</u>			
Number of tree species ^c	35–90	50–200	8, 11, 46, 53, 86a, 91, 95, 103a, 105, 106
Complexity index ^d	5–45	180–405	41, 42, 43
Canopy height, <i>m</i>	10–40	20–84	5, 11, 22, 33, 46, 53, 70, 86a, 88, 95
Number of canopy strata	1–3	3 or more	5, 27, 88, 95
Leaf area index ^e , m^2/m^2	3–7	5–8	77, 86a, 88
Ground vegetation cover ^e	low-high	<10 %	63
Basal area of trees ^f , m^2/ha	17–40	20–75	5, 16, 35, 70, 73, 81, 86a, 108
Plant biomass, <i>t/ha</i>			5, 16, 38a, 70, 76, 81, 86a, 88
Stems and branches	28–266	209–1163	
Leaves	2–7	7–10	
Roots	10–45	11–135	
Total	78–320	269–1186	
Root biomass as % of total	8–50	<5–33	
<u>Functional traits</u>			
Net primary productivity, <i>t/ha yr</i>			5, 58, 67, 69, 73, 77, 78, 81, 82, 84, 85

Table 2 (continued)

Trait	Forest type		References
	Dry ^a	Wet ^b	
Aboveground	6-16	10-22	
Roots	2-5	3-6	
Total	8-21	13-28	
Fine litter production ^c , t/ha/yr	3-10	5-14	13, 77
Tree diameter growth ^c , mm/yr	1-2	2-5 or more	10, 83, 112
Growth periodicity ^c	1-2 pulses annually	continuous or intermittent	30, 83
Foliage persistence ^c	deciduous & evergreen	primarily evergreen	23, 34, 48, 56, 59, 76, 110
Reproductive phenology ^c	seasonal & aseasonal	less seasonal	20, 23, 34, 49, 59, 115
<u>Successional traits</u>			
Resistance to disturbance	low	high	27, 28
Resilience, overall	high	low	27, 28
As % original height ^c , 1 yr	9-14	7-10	27, 28
Taxonomic recovery rate ^c	high	low	24, 28, 90
Overall recovery, years	150+	1000	90
Plant ht. growth ^c , m, 1 yr	1-3	2-5	27, 28
Leaf area index ^c , m ² /m ² , 1 yr	2-3	4-5	27, 28
Leaf area index uniformity ^c	patchy	more uniform	27, 28
Vegetation cover ^c , %, 1 yr	90	100	27
Importance of coppicing ^c	high	less	27, 28, 86a
Soil seed pool longevity ^c	short to long	relatively short	40

^aAnnual rainfall 500-2000 mm; strongly seasonal; annual PET/P normally >1.

^bAnnual rainfall >2000 mm; little or moderate seasonality; annual PET/P normally <1.

^cBased upon surveys of 1-3 ha; includes trees at least as small as 10 cm dbh.

^dCalculated as the product of number of species, basal area (m²/0.1 ha), maximum tree height (m), and number of stems/0.1 ha, times 10⁻³ in a 0.1 ha plot (41, 42, 43).

^eUnpublished information on Guanica forest, Puerto Rico, is available in the final report submitted to the National Science Foundation in 1985 by P. G. Murphy and A. E. Lugo; Grant DEB-81-10208.

^fUnpublished information for Chamela, Mexico was provided by S. H. Bullock.

The degree to which tree species are shared between wet and dry forests appears to be low. In Costa Rica, Frankie et al (34) found that only 11 tree species, out of a sampled total of 298, were found on both wet and dry sites. In Puerto Rico, where wet and dry forests grow in close proximity, none of the 33 tree species within our dry forests sample plots occurs in wet forest nearby, although about a third are found in moist (but not wet) forest of the limestone hills on the north coast (86a). These sites tend to be edaphically dry.

The relatively simple structure of the dry forest is manifest in the complex-

ity index derived by Holdridge et al (41, 42, 43; Table 2). Complexity index values for dry forest are only a fraction of those for wet forest (Table 2). In dry forest, canopy height averages about 50% and basal area 30 to 75% that of wet forest. Whereas most wet forests have three or more canopy strata, many dry forests have only one or two. Similarly, the leaf area index of most dry forests is only about half that of wet forests, although maximum values on favorable sites, particularly those in monsoonal regions, may be as high as those of many wet forests. The more open woodland of savanna may have leaf area index values for the tree stratum well below one, but such systems are not included in this review. Generally, ground cover is inversely proportional to canopy cover and is, therefore, typically higher in dry forest than in wet forest.

Reflecting the overall smaller structure of dry forest is its low biomass, relative to that of wet forest (Table 2). Moisture (expressed as a T/P ratio; see Table 1) is a major determinant of biomass in tropical forests (15). Generally, biomass is maximum on moist, rather than dry or very wet, sites. Within the dry forest climatic zone, only the moister sites, with limited dry periods, support biomass levels comparable to those of the smaller rain forests. Because of the scarcity of data, only limited comparisons of belowground biomass can be made. However, dry forests generally have a larger proportion of root biomass than do wet forests (Table 2). The highest proportion (50%) of root biomass yet recorded in a dry forest was for subtropical dry forest of small stature in Puerto Rico (86a). In this forest, 21% of the root mass was composed of roots less than 1 mm in diameter, and 40% was less than 5 mm. More than 90% of all roots were in the upper 40 cm of soil, but some penetrated to depths in excess of a meter. The difficulty in extracting the fine, or deep, root components suggests that the smaller values of root biomass reported for some dry forests may, in part, reflect incomplete recovery.

Functional Traits

Gross primary productivity of dry forest in southwestern Puerto Rico correlated with soil moisture (66). The net primary productivity (NPP) of dry forest averages 50–75% that of wet forest (Table 2), a proportion approximately equivalent to the portion of the annual cycle with suitable growing conditions in most dry forest environments. A similar pattern applies to fine litter production (Table 2). In Guanica forest (Puerto Rico), we found that peaks in litter production closely reflect seasonality and occur during the major and minor dry seasons when the fall of leaves and fine litter is maximum. In this forest the ratio of leaf fall to live leaf biomass decreased exponentially with increasing soil moisture; this reflects the sensitivity of leaf turnover to changes in water availability (66). Overall, NPP correlates with annual rainfall and/or duration of the wet seasons, although other factors such as soil and topography induce considerable variability in the relationship.

Because of the shorter growing period, annual diameter growth in dry forest trees is also about half that of wet forest trees. In the dry forest environment, periods of wet season growth may alternate with periods of dry season shrinkage (e.g. 20, 61—our unpublished data for Guanica forest, Puerto Rico). Although such growth periodicity may produce visible banding or rings in some species, the annual growth increment is so small (usually less than 2 mm) and the wood commonly so dense that it is usually not possible to identify growth increments of an annual or even seasonal nature, particularly since there are typically two growth periods each year. Daubenmire (20) found that annual growth could not be determined accurately from increment cores from dry forest trees in Costa Rica. Other authors, however, consider the use of rings to be feasible for age determination in some tropical species (30).

Perhaps because water plays such a dominant role in the regulation of structure and the dynamics of tropical dry forest, very little attention has been given to the important role of nutrients. Although the relation between dry forest productivity and nutrient status has not been established, it is known that plantation yields in irrigated arid soils improve with increasing soil fertility (2). Furthermore, nutrient content affects the drought tolerance of plants by helping to maintain osmotic pressure in their leaves (92).

A study of N, P, and K cycling in Guanica dry forest in Puerto Rico (67) showed conservative recycling of P relative to N and K. Phosphorus cycling was characterized by: a high proportion of storage in soil (98% of total); low rates of uptake but high rates of retranslocation prior to leaf fall (65% of the phosphorus needed to satisfy aboveground NPP was retranslocated); a small fraction of the total inventory cycled at any given time; slow release through litter decomposition; and high concentrations in dead roots. The within-stand efficiency of phosphorus use (mass of litter fall/mass of nutrients in litter fall; *sensu* Vitousek 107) was among the highest reported for tropical forest (6057 vs >3000 for highly efficient forests). High stores of N and K were also found in the soil (91% and 96%, respectively), but their movement through the system was faster and less conservative, which suggests that they were not limiting to forest function. A similar study of the N cycling of a seasonal forest in Belize (3) also showed a low within-stand efficiency of nitrogen use.

The phenology of the tropical dry forest is not well understood. The variation among species, as well as the variation among individuals of the same species, is great with regard to most if not all phenological events, including stem growth, leaf loss, leaf initiation, flowering, and fruiting. The relationship apparent between growth (vegetative and reproductive) and the season of water availability strengthens with aridity (23). However, the available information suggests that no single environmental factor is responsible for the type or timing of phenological events in tropical species. While water stress is most frequently cited as a primary factor (1, 34, 49, 59), the

mechanisms of its action remain obscure. Other factors of probable significance include day length and plant age (62), internal growth correlations (9), and combinations of biotic and abiotic factors (34).

One of the most conspicuous seasonal events is leaf turnover, which varies along a moisture gradient. Provided that moist forest receives at least 2500–3000 mm of rainfall per year, it can tolerate drought periods of up to 2.5 months in the evergreen condition (110). As annual rainfall diminishes, or drought period increases, the upper tree stratum becomes deciduous and the forest becomes semievergreen. Further reductions in rainfall cause deciduousness in the lower, as well as upper, strata. In the drier environments, deciduous and evergreen species coexist in different proportions, depending upon moisture and soil conditions. Except for the evergreen *Eucalyptus*-dominated monsoon forests of north central (tropical) Australia, most such forests are composed of numerous facultatively or obligately deciduous species. In the dry forest of Costa Rica's Guanacaste Province, for example, 60–75% of all trees are deciduous (34, 46).

In a general way the timing of leaf fall and flushing can be related to temperature and moisture seasonality (48). There are few experimental studies on regulation of leaf shedding in tropical trees (76), but leaf fall generally occurs earlier in dry years and later after a good rainy season (110). Normally, leaf emergence is not correlated with the onset of the rainy season but rather precedes it, often coinciding with flowering (110). In dry forests of Ghana, however, leaf flushing is entirely limited to wet seasons, although not all species or individuals produce new leaves each wet season (61). Leaf fall occurs in the dry season (61). Walter (110) suggested that the trigger for leaf emergence may be an increase in temperature, rather than rain. Medina (76) also mentioned the possible role of photoperiod and/or increasing night temperatures at the beginning of the wet season. In those ecosystems where the dry season is the warm season, i.e. a Mediterranean climate, the vegetation tends to be sclerophyllous and evergreen because most woody plants are incapable of producing foliage during seasons of temperature decline. Although leaflessness in most deciduous species coincides with the dry season, this is not always the case. A shrub (*Jacquinia pungens*) of Costa Rican dry forest loses leaves during the wet period and flushes during the dry season, apparently in synchrony with the changing light conditions controlled by the upper forest canopy (50, 56). Soil characteristics can also be important determinants of forest composition with respect to the proportion of deciduous and evergreen species. In some climatic areas where dry deciduous forest would be expected, oligotrophic soils may instead support savanna or evergreen scrub (76). With respect to another aspect of leaf turnover, severe herbivory and defoliations occur with many plant species in various seasons or years in Costa Rican dry forest (52).

Leaf structure does not always correlate well with specific environmental

variables (76). Generally, dominant leaf size decreases both with increasing aridity and altitude (77). Additionally, compound deciduous leaves become more prevalent in dry environments (37, 76). But mesophytic leaf types frequently dominate arid tropical environments, while sclerophylls are common in ecosystems with adequate water supply but with oligotrophic soils (32, 75). On relatively fertile soils, however, the degree of water deficit during the dry season can be estimated from the proportion of deciduous microphyllous to nanophyllous tree components, compared with evergreens (76). Also, deciduous tree leaves average higher in specific leaf area and total nitrogen content than evergreen leaves in dry tropical deciduous forest (75, 77).

Although there are only limited measurements of photosynthesis in dry forest trees, the available data suggest that photosynthetic capacity is lower in evergreen trees than in deciduous trees, possibly because of the higher nitrogen content of deciduous leaves (77). Trees with sclerophyllous leaves may be more tolerant of water stress; in arid areas they do not wilt, they show relatively low water potentials, and their vacuolar sap shows low osmotic potential. However, when the dry season is too long and the water table is below the rooting zone, they can not compete effectively with deciduous trees (76), in part because of their relatively slow growth rates. Studies of gas exchange in Guanica forest (Puerto Rico) demonstrated a rapid response of plant photosynthesis to increased moisture, and a wide range of photosynthetic response strategies within a small forest area (66). For example, on the drier sites plants with nocturnal carbon uptake (e.g. arborescent cacti) become abundant.

The variation among and within species with respect to reproductive phenology in tropical dry forest is comparable to that for vegetative phenology. On any site a wide variety of phenological patterns may be evident (23, 34, 61). However, although population biologists place considerable emphasis upon the occurrence of flowering during the periods of leaflessness (20, 49), the mechanisms by which these processes are regulated are almost totally unknown (23). Zapata & Arroyo (115) found that three species in tropical dry premontane forest in Venezuela flowered between the end of the dry season and the middle of the wet season. In tropical dry forests of Ceylon, flowering occurred as soil moisture reserves were depleted, particularly on the drier sites (59). In Costa Rican dry forest, Frankie et al (34) recognized two peak periods of flowering activity. One extensive period occurred during the long dry season and a second peak period corresponded to the onset of the rainy season. In the dry forest of southern Puerto Rico, we found that no more than 50% of the 33 tree species we observed were ever in fruit at the same time. About half the species produced fruit at least twice per year, whereas 25% bore fruit more or less continuously (at least every other month). The largest number of species fruit at the end of the spring and fall wet seasons, with

fewer than 10% in fruit during the winter dry season. Lieberman (61) found that in Ghana dry-fruited species fruit principally in dry seasons while fleshy-fruited species do so in either wet or dry seasons. She concluded that moisture deficit limits all phenological activity (flowering, fruiting, leaf production, leaf fall, and tree growth), although patterns vary among species.

Successional Traits

Because of the more rigorous and less predictable environment, dry forests are more vulnerable to stress during the successional process than are wet forests. Furthermore, succession is generally a slower process, in terms of plant growth and other developmental features (Table 2), in dry tropical environments than in wet areas (27). However, because of the relative simplicity and small structure of many mature dry forests, and because of the predominance of coppicing, dry forests have the potential to recover to a mature state more quickly than do wet forests, and they may, therefore, be considered more resilient (27). Projecting from known rates of change in mean seed weight in successional vegetation, relative to mature examples, Opler et al (90) estimated recovery times of 1000 years and 150 years for wet and dry lowland forest ecosystems, respectively. Coppicing is the primary regeneration mechanism in dry sites that have been cut, with stumps and roots remaining in place (27, 86a). Although wet forest tree species may, on average, have comparable potential to sprout when cut, the ratio of sprouts to seedlings in wet forest recovery plots is considerably less than in dry forest plots (27). A consequence of this is the very patchy development of dry forest in the early stages of succession and the development of a long-lived stage characterized by a large density of very small tree stems, a condition that may inhibit the rate of attainment of mature structure (86a). The recovery characteristics of dry forest on long-disturbed sites with an absence of root systems of dry forest species has not been studied. In Puerto Rico, we found no evidence of a long-lived seed pool in the dry forest soil and litter. Presumably, therefore, recovery rates in such sites would be largely dependent upon seed dispersal and, consequently, distance from a seed source. In a 1-ha cut site in Puerto Rico, Dunevitz (24) was unable to find a relation between abundance of seed germination and distance to surrounding forest, but in larger disturbed areas the effect should be measurable.

THE TROPICAL DRY FOREST IN RELATION TO PEOPLE

A Preferred Life Zone

In the tropics people apparently prefer environments where the PET/P ratio is near unity (i.e. the dry and moist humidity provinces, sensu Holdridge, 42).

The warmer it is, the greater the tendency for selection of environments with a PET/P ratio in excess of unity, i.e. dry.

A plot of population density by life zone for five countries in Central America (Figure 1), based on data from Tosi & Voertman (104), shows that 79% of the people live in the dry and moist life zones (PET/P = 0.5–2.0), with 15% living in the very dry forest life zone (PET/P = 2.0–4.0). Only 5% live in the wet life zone (PET/P = 0.25–0.50), and fewer than 2% in the rain forest life zone (PET/P = <0.25). Furthermore, 19 of the 20 capitals of the tropical American republics fall within dry or moist life zones (42). Only in recent times, concurrent with human population expansion, have significant population concentrations developed in the wetter life zones, often with major difficulties, as in the case of the Brazilian Amazon (102).

Why the affinity of humans for the dry and moist, rather than wetter, life zones? Although some of the reasons may relate to political history, many of the reasons are probably biological or ecological. For example, compared to rain forest, dry forest is generally smaller in stature and thus easier to clear for agriculture. The dry forest climate is also more suitable for livestock. Furthermore, dry forest soils are often more fertile, because less leaching occurs in the subhumid environment, and weeds and successional vegetation tend to be less aggressive in dry forest climates. The impact of human diseases may also be less in dry environments.

Forest Utilization and the Impact of Humans

Because they are associated with large population centers, dry forests have been exploited for thousands of years for many different purposes. It is

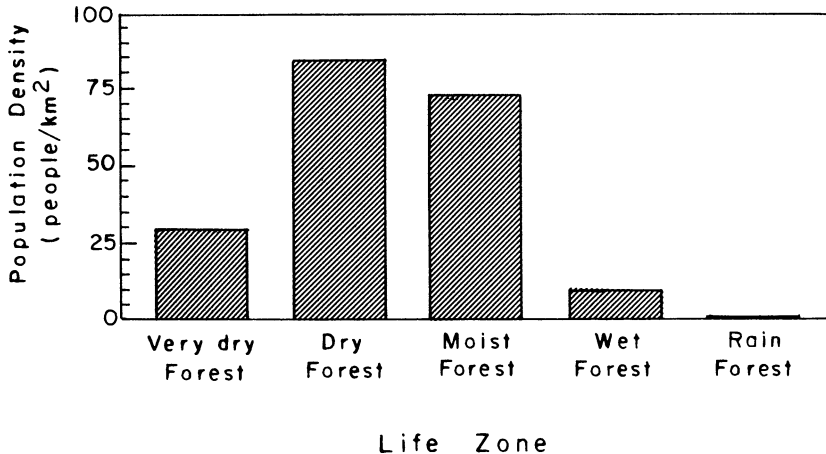


Figure 1 Average population density by life zone (sensu Holdridge 42) in five Central American countries. Based on data from Tosi & Voertman (104).

unlikely that there is a single remaining dry forest that has not been used at least as a source of firewood or for charcoal production. In the tropics, an estimated 80% of all the harvested wood is used for fuel purposes, and the proportion is higher (90%) in the African tropics, where dry forests are predominant (64, 109). But most tropical dry forests have been exploited for more than just fuelwood. They have been cut, burned, grazed, and recut, many times. And the situation is only getting worse. In Africa, it appears impossible that firewood needs can be met even into the near future. Norman (87) reported that an estimated 5–20-fold increase in tree plantings will be needed if requirements are to be met on that continent. Unfortunately, many of the forests are already degraded, and much of the land is needed for food production. The outcome can only be greater stress on the dry forest and woodland that characterize 34% of the tropical and 81% of the subtropical life zones of Africa (15). New approaches to wood production are needed.

Stemwood production of tropical forests is in the range of 2–11 t ha⁻¹ yr⁻¹ in the moist life zone (15, 58), but it is only about 2 t ha⁻¹ yr⁻¹ or less in the dry tropics (15, 67). Low rates of wood production in dry forests, coupled with high human demand for wood products, is one of the causes of wood shortages in these environments. Plantation forestry provides an alternative source of wood to satisfy these demands because plantation species are selected for greater wood yields of known quality. The dry tropics are known for their fine hardwoods. For example, mahogany (*Swietenia macrophylla*) reaches its optimum development in tropical dry forest life zones (60). Other mahogany species (*S. mahagoni* and *S. humilis*) are similar in this regard. Teak (*Tectona grandis*) is characteristic of dry and moist life zones (e.g. 100), but in plantations measured in India, it appears to have its highest yields in the dry life zone (Institute of Tropical Forestry, unpublished data).

As in natural forests, production of hardwoods in plantations is limited by water availability (68). While plantations in moist and wet environments can accumulate stemwood biomass at rates that range from 10 to 30 t ha⁻¹ yr⁻¹ (Institute of Tropical Forestry, unpublished), those in tropical dry climates do so at 4–18 t ha⁻¹ yr⁻¹ depending on the species (Figure 2). Plantations in thorn woodland life zones (with less than 500 mm rainfall per year) must be irrigated. With irrigation, plantation yields increase significantly over the expected yield of natural vegetation, but management is complicated and expensive (2). Lugo et al (68) found a fourfold increase in stemwood biomass production (up to 11 t ha⁻¹ yr⁻¹) of irrigated plantations over the expected yield of rainfed plantations. However, stemwood biomass production of irrigated plantations rarely exceeds 10 t ha⁻¹ yr⁻¹ for young plantations (less than 10 yr), and this decreases with age (2). An exception is plantations of *Shorea robusta* in India which increase in biomass production up to the age of 40 years (21).

Biomass or energy plantations in the dry tropics are characterized by a high

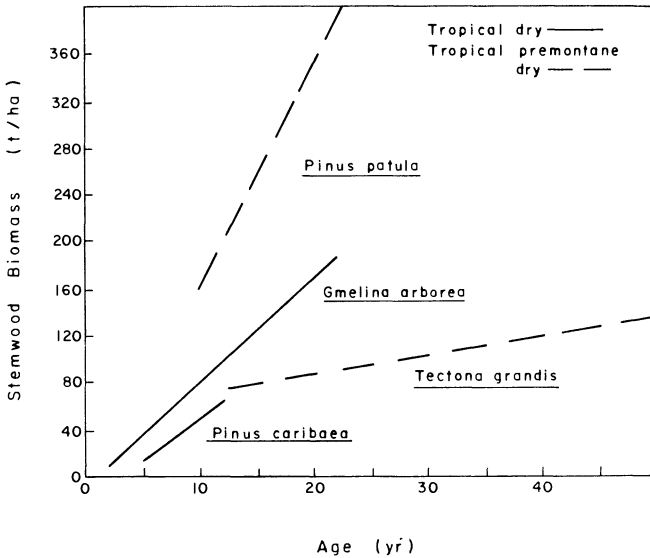


Figure 2 Stemwood biomass accretion in tree plantations of tropical dry and tropical premontane dry life zones (sensu Holdridge, 42). Data compiled by the Inst. Trop. For., Rio Piedras, Puerto Rico.

proportion of branch wood production (as much as 50% or more of total aboveground production), high wood density, and propensity for coppicing. These characteristics are suitable for fuelwood production, and some of the favored tree genera used for this purpose are *Prosopis*, *Eucalyptus*, *Leucaena*, *Cassia*, *Casuarina*, and *Albizia*. Total biomass yields of young plantations of these species may exceed $20 \text{ t ha}^{-1} \text{ yr}^{-1}$, but it is not clear if these yields can be sustained through many rotations. Maxfield (74) and Jennings (57) have provided estimates of fuelwood potential for the dry forests of the Dominican Republic. One forest was estimated to contain the energy equivalent of between 54 and 102 barrels of oil per hectare (74).

Numerous food crops are more productive in the drier and more seasonal tropical regions. In tropical and subtropical areas of Africa, for example, maximum yields of pearl millet, sorghum, maize, soybean, *Phaseolus* bean, and sweet potato are attained in areas with a 150–180 day growing period (89). The yields fall to 10–25% of that maximum in areas with a continuous growing season (i.e. wetter areas).

Shifting cultivation is a major mode of agriculture in the dry tropics. However, the dry tropics are characterized by shifting cultivation systems with relatively long cultivation periods (3.7 yr vs 1.8 yr in moist climates) and relatively short fallow periods (7.6 yr vs 9.9 yr in moist climates) (97). In fact, the relatively high ratio of cultivation to fallow causes agronomists to

rank many dry land cultivation systems as semipermanent fallow systems, rather than shifting cultivation (97). This can be interpreted in different ways, but in part it reflects the fairly good soil conditions. It also reflects the heavy population pressure on the land and indicates that dry forest landscapes are under great stress from human activities. Under such conditions the maintenance of full productive potential can hardly be anticipated. It must also be assumed that the potential of such landscapes for recovery to a more natural state upon abandonment is greatly curtailed, partly because of substrate degradation and partly because of the reduction or even elimination of seed pools.

Fire is commonly associated with human activities in the tropics. In the savannas of Africa, intentional burning has occurred for at least 50,000 years (18, 36, 96). The effects of fire on the overall character and geographic distribution of dry forest are not well understood. Under unusually dry climatic conditions, even wet or rain forests are subject to occasional fires (6, 98). Under normal conditions, however, major fire does not appear to be a frequent occurrence in even the drier tropical forest types (45, 70). Malaisse (70) found that most fires associated with African miombo (woodland) ecosystems are started by people during the dry season; fires caused by lightning usually are extinguished by rain. The most vulnerable dry forests are those that adjoin savanna vegetation, although even these are seldom subject to major fire impact, primarily because of the sparseness of the ground vegetation under the forest canopy (45). In southwestern Puerto Rico, fires are not uncommon along the disturbed margins of Guanica dry forest, particularly near highways, but there is no record or evidence of significant burning within the forest itself during the 50-year period that it has been protected from human activity.

An assessment of the role of fire is complicated by the effects of other human-related disturbance and of grazing. Farms within dry forest areas near savanna vegetation tend to be invaded by savanna grasses during the fallow period. If the fallow is burned, the density of grasses may be increased at the expense of woody, dry forest species. Ultimately, if burning is frequent enough, the abandoned farm patches may be converted to grassland or savanna (45). It is largely through this process that savanna may invade dry forest areas in some regions, such as in Africa, where the savanna boundary has been extended by 500 km in some areas (45). Sites with shallow soil on rocky parent material, or with heavy clayey soils, occasionally survive as dry forest because of their unsuitability for agriculture. Consequently, the border regions between savanna and dry forest are sometimes characterized by a mosaic of forest patches, grassland, savanna, farms, and fallow (45).

The actual transition between forest and savanna is often very abrupt, sometimes occurring over a distance of 50 m or less, as in southwestern Nigeria (19). In some areas where fire is not frequent and where grazing is

limited or nonexistent, forest may advance upon savanna, primarily by shading out heliophilic herbaceous plants at the forest margin. This has been observed at various locations in Africa, where rates of forest advance have been estimated at 2.5–3.5 m yr⁻¹ (44, 80).

Hopkins (45) concluded, contrary to Aubreville (4), that it was doubtful whether fire alone can change moist forest to savanna. But Hopkins did concede that dry forests and woodlands ecotonal between moist forest and desert, were probably much more widespread in Africa in the past; probably they had been converted to savanna and other degraded vegetation types by fire in association with the types of disturbance described above.

A model of dry forest response to human-related disturbance (Figure 3) is

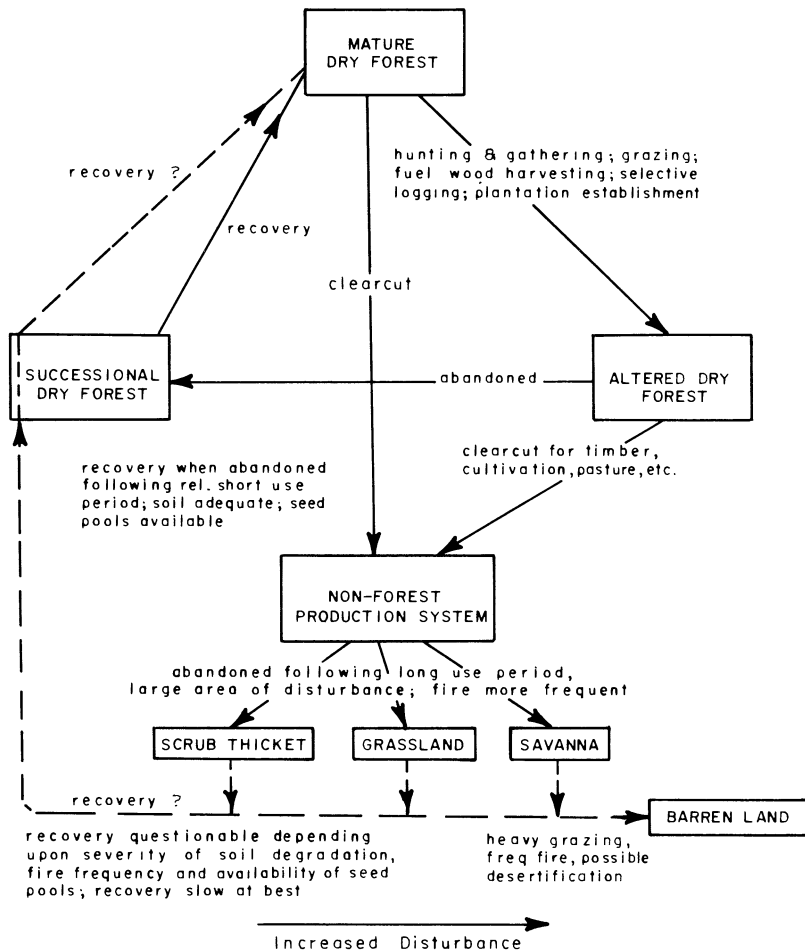


Figure 3 Hypothetical response of dry forest to human impact.

based on few data concerning the pathways shown. The diagram is largely hypothetical, based primarily upon our personal observations and qualitative observations in the literature. The details of the model's composition would vary according to geographic setting, climate regime, taxonomic composition, forest complexity, and other factors of a local character. In this sense, the diagram is an effective statement of research needs concerning the recovery dynamics of dry forest under utilization. Among the parameters in most need of study are: the pathways and rates of forest conversion; the rates and pathways of forest recovery subsequent to different levels (intensity, area, duration) of disturbance; the threshold disturbance levels beyond which recovery is greatly curtailed or even precluded; and other factors relating to the overall resilience of natural and altered dry forest relative to disturbance.

Only with substantially more data than are currently available, including more information on the effects of unusually stressful periods, such as severe drought, can a better understanding of dry forest dynamics be developed. Long-term studies of representative sites will be essential to attaining this goal. In view of the importance of the dry forest and the dry forest environment to people throughout the tropics, such studies should be considered of high priority.

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