tricornis, *Osteophloeum platyspermum* y *virola pavonis* (Myristicaceae). *Caldasia* 24(1): 65–94.
Kühn U and Kubitzki K (1993) Myristicaceae. In: Kubitzki K, Rohwer JG, and Bittrich V (eds) *Flowering Plants: Dicotyledons: Magnoliid, Hamamelid, and Caryophyllid Families*, pp. 457–467. Berlin: Springer-Verlag.
Nogueira BMM (1992) Anatomia foliar de *Virola* Aublet (Myristicaceae). *Boletin du Museu Paraense Emilio Goeldi-Botanica* 8(1): 57–142.
Pitman NCA, Terborgh JW, Silman MR, *et al.* (2001) Dominance and distribution of tree species in upper Amazonian terra firme forests. *Ecology* 82(8): 2101–2117.
Rodrigues WA (1980) Revisão taxonomica das especies de *Virola* Aublet (Myristicaceae) do Brazil. *Acta Amazonica* 10(1): 1–127. (Suppl.)
Russo SE (2003) Responses of dispersal agents to tree and fruit traits in *Virola calophylla* (Myristicaceae): implications for selection. *Oecologia* 136(1): 80–87.
Schultes RE and Raffauf RF (1990) *The Healing Forest*. Portland, OR: Dioscorides Press.
Schultes RE and Smith EW (1976) *Hallucinogenic Plants: A Golden Guide*. New York: Golden Press.
Ter Steege H, Sabatier D, Castellanos H, *et al.* (2000) An analysis of the floristic composition and diversity of Amazonian forests including those of the Guiana Shield. *Journal of Tropical Ecology* 16: 801–828.
Van GC and Cox PA (1994) Ethnobotany of nutmeg in the Spice Islands. *Journal of Ethnopharmacology* 42(2): 117–124.
Warburg O (1897) Monographie der Myristicaceen. *Nova Acta Academica Leopold-Caroliniana* 68: 1–680.
Wilde WJJ O de (2000) Myristicaceae. *Flora Malesiana Seed Plants* 14: 1–634.

Tropical Dry Forests

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Introduction

Tropical dry forests occur in nearly every tropical country. This forest type provides critical habitat for large mammals and migratory birds, and patches of dry forest can support a high proportion of endemic plant and animal species, as well as being highly valued for agricultural and production forestry uses. Consequently, conservation and understanding of these forests need emphasis, yet conservationists and scientists still frequently overlook this ecosystem.

Distribution and Definition

Dry forests comprise 42% of all tropical forests – the largest proportion of any forest type. They can be found as large continuous tracts, particularly in India, Mexico, eastern South America, northern Australia, and Africa, or in smaller, more local areas. Smaller tracts grow in rainshadows of tropical islands, Central America, and western South America (**Figure 1**). Coastal environments support dry forest when elevation is too low to generate rainfall from orographic uplift of ocean air masses.

Tropical dry forests occur in frost-free areas where annual precipitation is 500–2000 mm, mean annual biotemperature is $>17°C$, and potential evapotranspiration exceeds precipitation (**Figure 2**). Rain falls in one or two seasons each year, depending on the latitude of the forest, and forests experience 3–10 dry months (<50 mm rainfall) each year. The most important characteristic is the highly variable length of the dry season, seasonal distribution of rainfall, and amount of rainfall. Perhaps the only real constant from site to site is the occurrence of a dry season. Savannas often grow under the same climatic conditions as dry forests, but sparse tree cover and frequent fire in savannas allow grass to dominate.

Typically, dry forests have a closed canopy, but this may not be the case in the driest parts of their range, or if disturbance is prevalent. Due to their variability in climate and appearance, many names are applied to dry forests. These include: deciduous forest, semideciduous forest, semi-evergreen forest, woodland, and dry seasonal forests. Local names are also used: caatinga in Brazil, miombo in southern Africa, and chaco in parts of South America. Southeast Asia has a specific type of dry forest – deciduous dipterocarp forests – dominated by about six species of Dipterocarpaceae.

As a consequence of prolonged dry seasons, tropical dry forests are less complex than wet or temperate forests (**Table 1**). They have one to three canopy layers and short canopies with relatively low leaf area index (3–7) and leaf biomass (2–7 tonnes ha^{-1}). In mature forest, the stems can still be quite narrow, with common diameters in the range of 3–15 cm, and stem densities can exceed one stem per square meter. Trees are frequently multi-stemmed. Among dry forests, most structural features vary by two to ten times (**Table 1**), with the upper limits overlapping the lower limits in wetter forests, leading to inconsistencies in the scientific literature when classifying forest types. Climate features such as the amount of rainfall or the length of the rainy season can explain canopy height and biomass, but other structural characteristics, particularly stem density, are often the result of disturbance (see below).

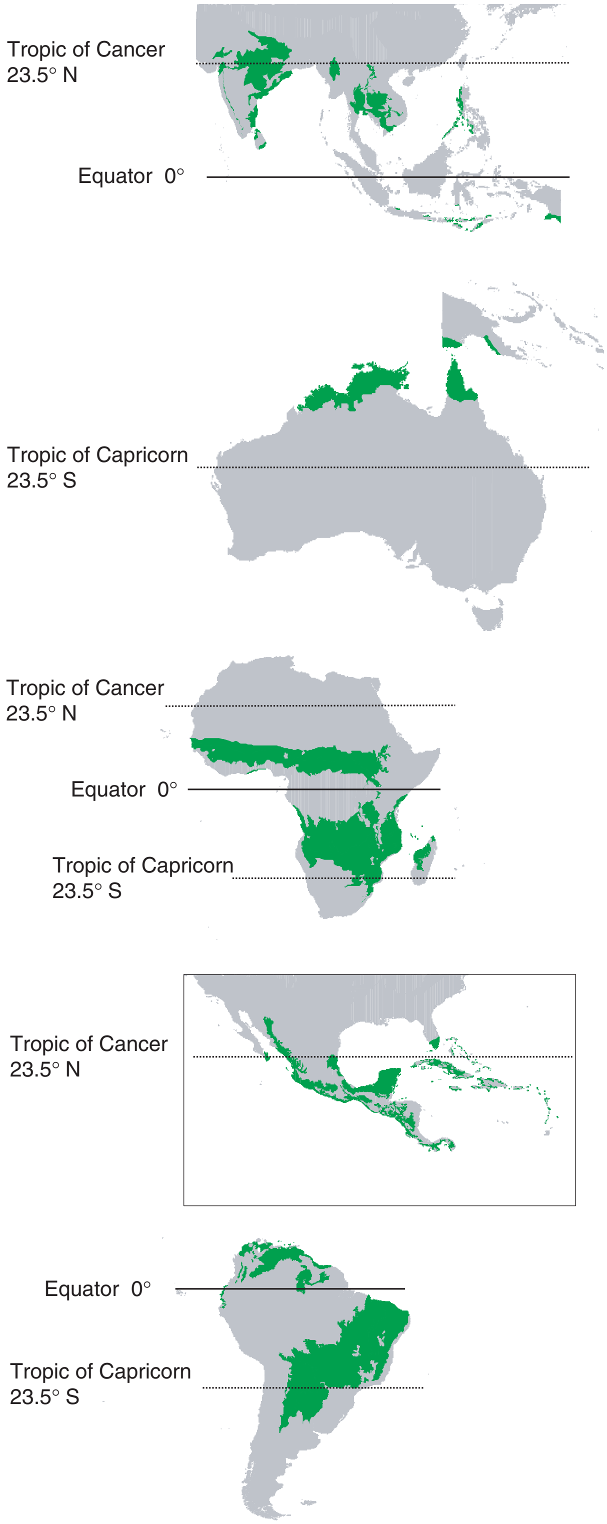

Figure 1 Global potential distribution of tropical dry forests. Highlighted areas are predominantly dry forest, but moist or open forest is interspersed in some areas. Dry forest is also found in many small tropical island nations, including American Samoa, Comoros, Cook Islands, Fiji, French Polynesia, Guam, Kiribati, Marshall Islands, Mauritius, New Caledonia, Palau, Reunion, Solomon Islands, and Vanuatu.

Components of Tropical Dry Forest

Plants

Seasonally dry forest communities worldwide contain a variety of important plant species. Trees valued for lumber include teak (*Tectona*), mahogany (*Swietenia*), sal (*Shorea robusta*), and African mahogany (*Khaya*). Commercially important fruit trees include tamarind (*Tamarindus indica*), mango (*Mangifera indica*), and cashew (*Anacardium occidentale*). Agroforestry projects have planted *Leucaena leucocephala* and *Prosopis juliflora* (mesquite) to improve soils via nitrogen fixation. *Casuarina equisetifolia* (Australian pine) and *Eucalyptus camaldulensis* are native to Australian dry forest and have been introduced in many areas for soil stabilization and wood production. In addition to these species, many others are used for firewood, construction wood, food, and medicinal purposes.

Deciduous trees are usually most common in dry forests, but evergreen species become more important at both the upper and lower limits of the rainfall gradient (**Figure 2**). The frequency of growth forms depends on climate and disturbance. Cacti and euphorbs frequent drier locations while the diversity of lianas and other vines increases with greater rainfall and following disturbances that open canopy gaps. Dry forests have more understory species than tree species but their abundance and biomass is quite low, except in open woodlands.

The high variety of growth forms and numerous physiological adaptations provide tolerance to drought conditions. Dry forest species can maintain metabolism under lower soil and leaf water potentials than temperate or moist tropical species. Dry forests average higher ratios of root to shoot biomass than moist or temperate forests. Though data on root biomass are scarce, 35–49% of root mass is below 10 cm depth as compared to 5–21% in wet forests. In dry forests, maximum root : shoot ratios range from 0.4 to 1.0. In moist forests they rarely exceed 0.25. Cacti and some deciduous tree species store water in succulent stems. The amount of water stored cannot maintain leaves, but supports flower and fruit development prior to the onset of the rainy season.

Water use is influenced by leaf habit (evergreen vs. deciduous), leaf morphology, and wood density. Compared to wetter forests, more dry tropical trees have wood specific gravity greater than 1.0. Dense-wooded and evergreen species have narrow xylem that resists cavitation under dry conditions but

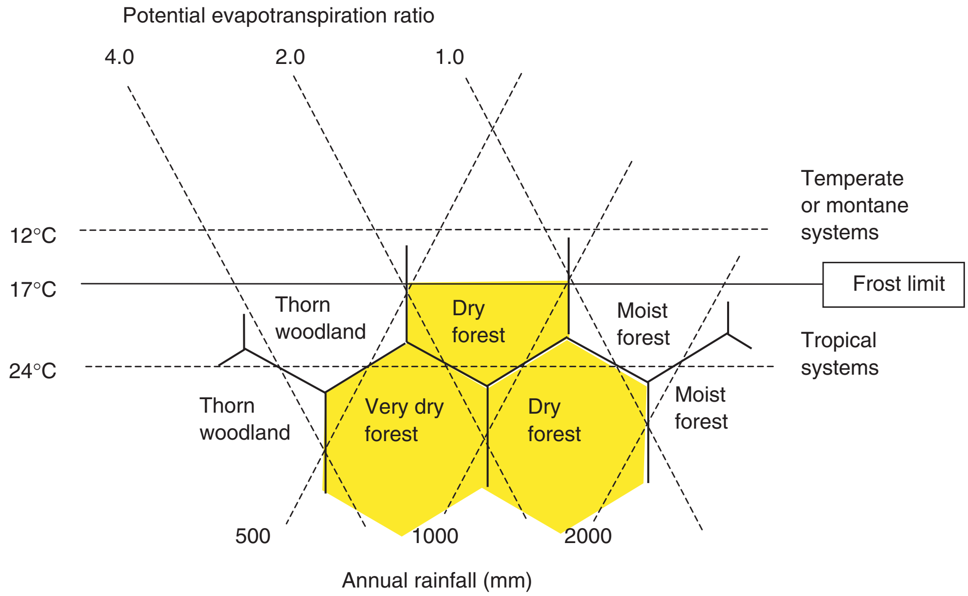

Figure 2 Climate characteristics that define tropical and subtropical dry forest life zones according to the Holdridge life zone classification system. The temperature values represent an adjusted biotemperature. PET ratio is annual potential evapotranspiration divided by annual precipitation.

transports water less efficiently. Light wooded and deciduous species have wider xylem that is more prone to cavitation and greatly reduces water conductance as the dry season progresses, but transports water more efficiently and responds faster to light rains at the onset of the rainy season. Thus, the ability to reduce cavitation during drought is traded for more efficient water conductance. Deciduous species avoid dry season water loss by shedding leaves, usually at the onset of the dry season, while the sclerophyllous leaves of evergreen species have thick cuticles and smaller internal air pockets that resist desiccation. Sclerophylly may increase in plant populations growing under drier conditions, or experiencing nutrient limitation caused by insufficient soil moisture for nutrient uptake and transport. Sclerophyllous trees frequently exhibit high nutrient use efficiency, suggesting nutrient limitation, even when soil nutrient pools are relatively high. Thus, the leaf habit of evergreen species aids in drought tolerance, while deciduousness leads to drought avoidance.

During the rainy season, dry forest trees, regardless of their particular responses to drought, exhibit many physiological similarities. For example, both drought-deciduous and evergreen dry forest species have similar values for carbon assimilation and stomatal conductance. These values equal those found in moist forest trees. When scaled by growing-season days, both dry and wetter forests have similar growth rates, suggesting they all have equally efficient productivity during favorable seasons. This may be expected because trees (with the exceptions of bamboo, arborescent cacti, and some euphorbs) all use C_3 photosynthesis, regardless of their habitat.

Phenology is closely related to the dry season in many cases, but there is a variety of patterns. Most deciduous species lose leaves at the onset of the dry season, but a few are wet-season deciduous (e.g., *Faidherbia albida* and *Jacquinia pungens*). Some species flower and fruit just before the rainy season commences, before leafing out, while others wait until after the rains have begun. Dry forest species generally flower and fruit for shorter periods than moist forest species. Often plants flower for less than 6 weeks – frequently for only the first few days following an isolated rain event or the first significant rain breaking a drought period. As annual rainfall increases on either a regional or local scale, the prevalence of species with wind-dispersed seeds decreases. In general, most species exhibit some pattern of seasonality.

Animals

Larger bodied vertebrates include elephants, large ungulates, and large felines in dry forests of Africa and Asia, jaguar in the neotropics, and monkeys in many mainland areas. In general, reptiles and birds comprise a substantial portion of dry forest fauna. In addition to the many bird species that reside in dry forests year round, dry forests in the neotropics and Africa are essential wintering grounds for many temperate species. For this reason, much of the

Table 1 Structural and functional characteristics of mature tropical dry forest

	Chandraprabha, India	*Varanasi, India*	*Ping Kong, Thailand*	*Lubumbashi, Democratic Republic of Congo*	*Chamela, Mexico*	*Guanacaste, Costa Rica*	*Rancho Grande, Venezuela*	*Veri Mer, Guyana*	*Guánica, Puerto Rico*	*North Andros Island, Bahamas*	*Wet forests*
Climate											
Annual rainfall (mm)	1050	800	1200	1273	707	1750	1140	1520	860	1300	>2000
Dry months	6–8	>6	3–4	5	6–8	6	4	3	6		<4
Mean annual temperature (°C)	26	25	25	20	24.9	25			25.1	25	>17
T/P[a]	2.5	3.1	2.1	1.6	3.5	1.4			2.9	1.9	<1.0
Vegetation											
Basal area (m^2 ha^{-1})	15–20	30.6	35.4	20–40	23.6	21.6–41.6	36.2	48.9	17.8	23	20–75
Canopy height (m)	15–20	18	10–29	14–22	10–15	10–20	20	25	9	8	20–84
Stem density (number ha^{-1})[b]	1055 (3.0)	644 (3.0)	713 (4.5)	1465 (?)	8400 (2.5)	1950–4370 (2.5)	6000 (2.5)	4000 (2.5)	12000 (2.5)	7957 (2.5)	
Total biomass (tonnes ha^{-1})	95	240	78–291	150–320	105–120				98		269–1186

[a]Temperature/precipitation × 100, used as an indicator of potential evapotranspiration.

[b]Minimum stem size (cm) in parentheses.

Data from Murphy PG and Lugo AE (1986) Ecology of tropical dry forest. *Annual Review of Ecology and Systematics* 17: 67–88; Proctor J (1989) *Mineral Nutrients in Tropical Forest and Savanna Ecosystems*. Oxford: Blackwell Scientific Publications; Quigley MF and Platt WJ (2003) Composition and structure of seasonally deciduous forests in the Americas. *Ecological Monographs* 73: 87–106; Smith IK and Vankat JL (1992) Dry evergreen forest (coppice) communities of North Andros Island, Bahamas. *Bulletin of the Torrey Botanical Club* 119: 181–191.

international conservation effort in dry forests results from concern for migratory songbirds and raptors. The relatively isolated and compact area of dry forest in western Mexico has had particular emphasis because it is the winter home for the migratory birds from the North American west coast.

Like dry forest plants, animals (both vertebrates and insects) synchronize their activities, such as reproduction, to the seasonality of their habitat. Many species enter a period of decreased activity in the dry season and some change their diets based on seasonal availability or quality of prey. For example, when living in dry forest, the northern tamandua will eat ants in the rainy season, then switch to termites in the dry season, when the termites have a higher moisture content than the ants. Aside from behavioral adaptations to seasonality, many animals have water conserving physiological adaptations as well, such as the production of dry feces.

As in other systems, animals influence plant populations. A wide variety of insects act as pollinators and specialized plant–pollinator systems are common. Vertebrates and termites disperse seed. The former transport seeds stick to their skin or fur, by caching, or in feces. Some species of termites harvest fleshy fruits to provide material for decomposition by symbiotic fungi, which the termites 'farm.' The termites usually throw unused seeds from the fruits out of the nest.

Herbivores include vertebrates and insects, particularly leaf-eating caterpillars, beetles, and leaf-cutting ants. In the neotropics, insects are the main herbivores but this may be an artifact of hunting that has reduced vertebrate populations (e.g., deer). Generally, deciduous dry forests incur greater herbivory than evergreen dry forests. Herbivory tends to be greater in the first half of the rainy season, but not because younger leaves have more nutrients or fewer secondary chemicals. Instead, herbivory decreases as the rainy season progresses, as parasite and predator populations increase, or as larval herbivorous insects mature and stop eating plants. On average, herbivory decreases leaf area from 10% to 17%. Leaf loss due to herbivory appears to decrease fruiting, fecundity, and seed viability in plants but is poorly understood. In addition, about 10% of dry forest plants incur high rates of seed predation, with some species losing nearly 100% of their seeds each year.

Termites play a vital role in dry forest dynamics. Some termite species construct majestic, meters-tall mounds that provide habitat for a suite of other animal species and, in Africa, create locally dry areas with unique tree species composition. Other species of termites live in smaller arboreal or subterranean nests. Many vertebrates and insects exploit termites as an important food source. The ability of termites to collect and process tons of dead plant material every year makes them essential to nutrient cycling in a system where many vectors of decomposition slow or cease in the dry season. Termites hasten decomposition by cutting up litter and move nutrients from place to place in the forest. They also improve soil quality by bringing up leached clay minerals from underground to build their nests.

Soil and Microbes

Dry forest soils vary widely and may be of volcanic, alluvial, or limestone origin – many are lateritic. Soil moisture content falls below field capacity for most of the year. Even during the rainy season, soil moisture drops below field capacity if rains do not occur at frequent intervals. Although leaching is less than in wetter areas, the soils are highly weathered due to their age. Similar to wet forests, the majority of dry forest soils have low nutrient supplies, particularly for phosphorus. Soils from calcareous parent material frequently have high total nutrient concentrations, but an average pH above 7.8 binds phosphorus to calcium and makes it unavailable to plants. Acid soils have high concentrations of iron and aluminum which also bind phosphorus. Conversely, some dry forest soils, particularly younger ones, have high amounts of organic matter and available nutrient pools, leading to high productivity. These soils develop mollic horizons and are found in parts of the neotropics and India. They frequently become converted to agricultural lands. The Brazilian caatinga and some forests on rocky, calcareous soil have a climate favorable for moist forest development, but the soils drain quickly, resulting in edaphically dry habitats.

Shallow or infertile soils tend to support evergreen forests, while deciduous forests generally grow on better soils. Organic matter can build up as humus in such thick litter layers that some soils have been called dryland peats. Soils with lateritic or calcareous crusts provide little habitat for grasses and herbs, supporting greater biomass in trees which can access subsurface moisture reserves.

Research on the soil microbial community of dry forests has lagged behind that in temperate or tropical wet forests, but some patterns have emerged. Like much of the rest of the living community in dry forests, microbial activity decreases greatly in dry seasons. However, termites compensate somewhat for the loss of microbial contribution to decomposition and nutrient cycling in the dry season (see above). As in other ecosystems, symbioses exist between plants and nitrogen-fixing bacteria or mycorrhizae.

Biodiversity

Diversity of dry forest plants and animals tends to be lower than in tropical moist forests, but greater than in temperate forests. Dry forests share a high proportion of their plant families and genera with moist forests, but few species overlap. Little is known about insect diversity. Larger, more mobile animals reside in both habitats, but smaller animals with limited dispersal ability or range tend to be unique to dry forests. Dry forests contain many locally and regionally endemic species of plants and animals, proportionally more than wet forests. Of the 25 hot spots identified by Conservation International as critically important for preserving biodiversity, nine contain tropical dry forest. A general trend of higher diversity in dry forests nearer the subtropics than the equator is well demonstrated in the western hemisphere. Bolivian and western Mexican forests have higher diversities of plants, reptiles, and amphibians than dry forests located at lower latitudes (**Table 2**). Subtropical African dry forests are also more diverse, with the southern region having more species than the northern.

Plant species diversity does not correspond to precipitation in dry forests, but does increase as the ratio of potential evapotranspiration (PET) to precipitation decreases. Low abundance and diversity of epiphytes further distinguish most dry forests from moist forests. Leguminous trees frequently dominate in all regions. Euphorbiaceae, Sapindaceae, and Rubiaceae are commonly found in neotropical dry forests, while Myrtaceae are common in the West Indies, Combretaceae in Africa, and Dipterocarpaceae in some Asian dry forests. The most common lianas belong to Bignoniaceae. Cacti are common in drier neotropical forests, but decrease in abundance as precipitation increases.

Lower animal diversity in dry forests can be explained in part by lower habitat diversity. Dry forests lack niches for frugivorous and semiaquatic species found in moist forests. Dry forests that border wetter forests have greater diversity as some species retreat to adjacent moist areas during the dry season. Seasonal migration of animals between forest types is common in all regions of the world.

Function of Tropical Dry Forest

Functional traits of dry and wet forests differ much less than structural differences. For example, aboveground net primary productivity (ANPP) ranges from 6–16 tonnes $ha^{-1} year^{-1}$ in dry forests and 10–22 tonnes $ha^{-1} year^{-1}$ in wet forests. Only tree growth rates separate distinctly between the two forest types. Diameter growth in dry forests averages

Table 2 Species diversity for tropical dry forests

Species diversity[a]	*Caatinga, Brazil*	*Chamela, Mexico*	*Bolivia*	*Central America*	*West Indies*	*Zambezian Area, southern Africa*	*Thailand and India*
Plants by area		94.3 (0.1 ha)	83 (0.1 ha)	67 (0.1 ha)	52 (0.1 ha)		76 (1.0 ha)
Trees by area	10–47 (0.1 ha)	80 (0.1 ha)	53 (0.1 ha)	51 (0.1 ha)	34–54 (0.1 ha)	95 (0.1 ha)	10–31 (0.2 ha) 42–50 (1.0 ha)
Endemic plants		16%		6%		Up to 35%	
Mammals (endemic species in parentheses)	86 (2)	70 (26)	110 (22)		(29%)[b]		(22%)[b]
Birds (endemic species in parentheses)	<200 (2)	270 (25)	409 (4)		(22%)[b]		(12%)[b]
Reptiles and amphibians (endemic species in parentheses)	47 (1)	173 (74)	80 (low)		(85%)[b]	? (24)	(50%)[b]

[a] Values are numbers of species unless indicated as a percentage.
[b] Regionally endemic species, may be found in either dry or moist forest.
Data from Bullock *et al.* (1995); Proctor (1989).

1–2 mm year^{-1} and occurs in one or two pulses per year. In wet forests, diameters increase 2–5 mm year^{-1} and usually grow continuously. The longer, wetter rainy season explains greater growth rates. The overlap in productivity highlights the success of dry forest species in adapting to seasonally xeric conditions.

Characteristics of nutrient cycling in tropical dry forests suggest that many sites are somewhat more fertile than moist forest. N : P ratios in dry forest leaves ($\sim$15 : 1) have lower averages than in moist forest ($\sim$28 : 1), but still exceed plants with well-balanced nutrient supply (10 : 1). Leaf N in dry forests is lower and leaf P similar to moist forests of moderate fertility. Nutrient use efficiency for nitrogen (NUE) and phosphorus (PUE) varies widely among dry forests. Many sites appear to have sufficient nutrient supplies (NUE < 130, PUE < 1600) but other dry forests exhibit phosphorus limitation (**Table 3**).

Dry forests accumulate and store nutrients in surface litter. The residence time can be about 3.5 years for N and over 5 years for P. Microbes alternately immobilize and release these nutrients. Rapid wetting of soils from the first rains burst microbial cells (plasmoptysis), leading to the greatest nutrient release at the onset of the rainy season. This type of release occurs throughout the rainy season because rainfall events are irregularly spaced. Isolated rains after the beginning of the dry season can also cause a nutrient pulse. Where soil microbes immobilize large amounts of nutrients, trees rely on greater amounts of retranslocation before leaf fall to meet nutrient demands.

Dry forest trees associate with either ectomycorrhizae (ECM) or vesicular–arbuscular mycorrhizae (VAM) or both. Mycorrhizae increase water uptake and access forms of phosphorus and nitrogen chemically unavailable to plants. In some forests, such as the dry dipterocarps, ECM species constitute only 10–15% of all plant species, but contribute 30–75% of basal area. The presence of legumes as dominant plants in many dry forests results in the potential for the improvement of soil fertility by N fixation. Limited research suggests that N-fixing trees predominate in areas with low N but can be limited by low available P. ECM are dominant in the driest areas, and both VAM and ECM are common in soils with low P, but patterns in their distribution across soils of varying N concentrations have not been clearly identified.

Disturbance

Disturbance is an important factor in tropical dry forests. Hurricanes bring destructive winds and

Table 3 Nutrient contents in leaves and litterfall and nutrient use efficiencies for a variety of tropical dry forests

Site	*Leaf*			*Leaf litterfall (kg ha^{-1})*				
	N:P	*%N*	*%P*	*N*	*P*	*Biomass*	*NUE*	*PUE*
Puerto Rico	26	1.64	0.064	44	0.7	4337	97	6056
Chamela, Mexico	11	2.96	0.28	52	2.5	2310	44	926
India	15	1.95	0.13				79	1059
Belize	15	1.50	0.10	153	9.2	12 600	82	1369
Congo	20	2.20	0.11	224	7	12 400	55	1700
Australia	27	1.66	0.06	134	12	9000	67	750
Ivory Coast				123	4	9600	78	2400
Tanzania				142	8	8800	62	1100

N, nitrogen; NUE, nitrogen use efficiency; P, phosphorus, PUE, phosphorus use efficiency.
Data from Bullock *et al.* (1995); Proctor (1989); Lugo AE and Murphy PG (1986) Nutrient dynamics in a subtropical dry forest. *Journal of Tropical Ecology* 2: 55–72; Vitousek PM (1984) Litterfall, nutrient cycling, and nutrient limitation in tropical forests. *Ecology* 65(1): 285–298.

floods to some areas, fires affect others, and prolonged or unusually severe droughts threaten all forests. The frequency and intensity of these disturbances can have important effects on dry forest structure and function. High winds from hurricanes result in defoliation and breakage of trees, with long-term consequences for forest structure. Return intervals for hurricanes range from 5 to 100 years. Mature dry forests in the hurricane-prone West Indies tend to have shorter canopies, higher stem densities, and a greater proportion of multiple-stemmed trees than dry forests outside of the hurricane belt.

Fire is a difficult feature to interpret in dry forests. In most locations, even in Africa, fire is not a frequent or severe aspect of the ecosystem. Lightning occasionally starts fires in dry forests, but they are low intensity, small scale, and usually doused by rains. Sparse understory and grass cover limit the intensity of the ground fires that burn leaf litter about every 5–10 years, returning some proportion of nutrients to the soil as ash, while losing others to the atmosphere. Forest floor heterogeneity caused by termite mounds, rock outcrops, and crusty surfaces inhibit the ability of fires to spread. During the last 50 000 years, humans have probably caused the vast majority of fires in dry forest in order to clear land, hunt animals, and burn fallow to encourage new growth for livestock. Frequent burning transforms forests into savanna, shrub, and open woodland – ecosystems more correctly associated with fire. Conversely, humans prevent burning in other forests that naturally would experience ground fires. This alters natural disturbance patterns and can lead to very destructive crown fires sparked by the build-up of litter and underbrush during long fire-free periods.

Dry forests have a particularly long history of human disturbance because they occur in climate regions that are pleasant to live in and favorable for grazing and agriculture. The dry season provides respite from rain and humidity, and reduces populations of agricultural and human pests. Livestock survive well in dry forest areas, and the relatively small trees are easy to clear for agricultural fields. Because of the desirability of dry forest climates, human population densities in these areas exceed 100 km^{-2} globally and are expected to double every 20–25 years.

Human disturbance in dry forests is primarily related to land use change and extractive activities. As in other ecosystems, there are some examples of sustainably managed dry forests, depending on political, economic, and population pressures. Large-scale logging operations affect dry forest primarily in continental locations. Some dry forest species are suitable for plantations but others grow poorly because of infestation by pests (e.g., shoot-boring insects on mahogany in monoculture). Trees are cut for firewood or charcoal production in most regions. Firewood accounts for 80–90% of dry forest harvest. Many trees coppice – an advantage when used for firewood. Unfortunately fuelwood is not regrowing quickly enough to sustain demand in many areas of Africa. The long-term effects of extraction depend on the amount and pattern of biomass removed and the degree of soil disturbance or compaction that accompanies tree harvests.

Conversion of forests to agricultural, industrial, or residential areas completely removes forest cover and disrupts roots and soil structure. Traditionally, shifting agriculture has been practiced in dry forest regions in a sustainable manner, but increasingly short fallow periods prevent re-establishment of the forest. Grazing and agriculture increase nutrient loss from the system by erosion. Grazing reduces forest biomass because cattle reduce understory growth while compacting the soil and accelerating erosion. Approximately 32% of the area that once was dry forest remains, with continuing annual losses of 0.7–1.5%. The highest deforestation rates occur in Africa, even though population densities in dry forests there are only one-fifth of those in Asia. This trend continues in most areas, but in some locations where economies have turned from agriculture to manufacturing, land is reverting back to forest. This is the case in Puerto Rico, Cuba, and the Gambia.

Response to Disturbance

The ability of dry forest to tolerate disturbance, whether natural or anthropogenic, depends on disturbance type, frequency, duration, and severity. The forest that regrows following disturbance may resemble the original, or differ greatly in terms of function and composition. In general, dry forests exhibit a high rate of resilience, defined as the rate at which a forest stand recovers from large, infrequent disturbance. Compared to other forests, succession in dry forests progresses quickly, and in some cases this can lead to expansion into other systems. In Mexico, clearing of large tracts of rainforest resulted in a drier environment that was subsequently recolonized by dry forest.

Dry forests in Puerto Rico have provided a location to compare response to natural and anthropogenic disturbances. The forest recovered similarly from the effects of a recent hurricane and small-scale tree cutting for charcoal production in the past. Both resulted in patchy loss of <25% of trees, while soil systems remained intact. Stem density increased after each disturbance, as broken trees grew from coppice sprouts. After 45 years, cut areas regained an average of 87% of mature forest structure. Post-hurricane forest will probably take about 25 years to fully recover. Neither disturbance changed the species pool. Conversely, forest recovery from abandoned agricultural and residential uses has taken much longer. After 45 years, abandoned agricultural areas had only recovered an average of 71% of mature forest structure, while residential sites were 58% recovered. The disruption of root systems had a large effect – root biomass was half or less that in mature forests and coppice growth was minimal. These areas have shifted from being dominated by native species to the invasive species *Leucaena leucocephala*, although native Puerto Rican species have begun reappearing after 40 years.

Recovery following forest conversion to agriculture or housing illustrates how a disturbance can cause a system to shift toward monodominance by a single, invasive tree species. Conversion of African dry forests to grass-dominated savanna by fire results in both a new species composition, and also dominance by a different growth form. Both of these anthropogenic disturbances have resulted in new ecosystems with different structure, though the *Leucaena* system more closely resembles the original dry forest than does the savanna.

The occurrence of multiple disturbances can have major consequences for dry forests. In the Mexican Yucatan, 10% of trees died following a hurricane, but fires subsequently burned through a portion of the forest resulting in 85% mortality, among the highest mortality rates recorded for a dry forest. On the other hand, when a hurricane hits a forest within a year following the previous hurricane, damage is usually light, as the susceptible trees have already been removed.

Characteristics of dry forests that help confer resilience include a high concentration of nutrients below ground or in litter, high root : shoot ratios, and the ability to coppice. When trees are lost, nutrient pools support regrowth and roots access nutrients and minimize erosion. Mycorrhizae and high nutrient use efficiency of dry forest trees help to keep nutrients from being leached. Dry forest trees have adapted to their natural disturbances, allowing forests to withstand drought and regrow following wind, fire, and insect damage. Dry forests absorb human activities that mimic natural disturbances but when no natural disturbance analog exists, dry forests may shift toward other systems or become susceptible to invasion by exotic species.

Conservation and the Future of Tropical Dry Forests

Loss of forest lands occurs as a function of human population density or energy use. Given the demands of increasing human population size and energy requirements from developing economies, this trend will continue in the dry tropics. On the other hand, some conservation efforts have succeeded. In Puerto Rico and India, plantations have reclaimed degraded agricultural land and fostered the regrowth of dry forest. More countries have committed to increasing forest area in parks and reserves, and about 5% of dry forests worldwide are protected. Most conservation projects fail when the needs of the local citizenry are not considered, but conservation efforts in Guanacaste, Costa Rica, have shown that local citizens can benefit from protecting dry forest. Efforts in Guanacaste have also demonstrated methods by which invasive species can be controlled and eliminated when they are detrimental to the system – this has proven to be a difficult task in any ecosystem. Future efforts in conservation should focus on taxonomically diverse locations, such as

Bolivia, western Mexico, and southern Africa, and explicitly include benefits for local citizens.

See also: **Biodiversity**: Plant Diversity in Forests. **Ecology**: Natural Disturbance in Forest Environments. **Environment**: Environmental Impacts; Impacts of Elevated CO_2 and Climate Change. **Operations**: Small-scale Forestry. **Soil Development and Properties**: Nutrient Cycling. **Tree Physiology**: Mycorrhizae; Stress. **Tropical Ecosystems**: Acacias; Dipterocarps; Eucalypts. **Tropical Forests**: Combretaceae; Tropical Moist Forests.

Further Reading

Bellefontaine R, Gaston A, and Petrucci Y (2000) *Management of Natural Forests of Dry Tropical Zones*, FAO Conservation Guide no. 32. Rome: Food and Agriculture Organization of the United Nations.

Bullock SH, Mooney HA, and Medina E (1995) *Seasonally Dry Tropical Forests*. Cambridge: Cambridge University Press.

FAO (2001) *Global Forest Resources Assessment 2000*, FAO Forestry Paper no. 140. Rome: Food and Agriculture Organization of the United Nations.

Holdridge LR (1967) *Life Zone Ecology*. San José, Costa Rica: Tropical Science Center.

Janzen DH (1986) *Guanacaste National Park: Tropical, Ecological and Cultural restoration*. San José, Costa Rica: Editorial Universidad Estatal a Distancia.

Mueller-Dombois D and Fosberg FR (1998) *Vegetation of the Tropical Pacific Islands*. New York: Springer-Verlag.

Murphy PG and Lugo AE (1986) Ecology of tropical dry forest. *Annual Review of Ecology and Systematics* 17: 67–88.

Proctor J (1989) *Mineral Nutrients in Tropical Forest and Savanna Ecosystems*. Oxford: Blackwell Scientific Publications.

Tropical Moist Forests

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Distribution of the Tropical Moist Forests

The tropical moist forests are limited by the tropics of Cancer and Capricorn (**Figure 1**). However, the distribution is not evenly dispersed across the Americas, Africa, and Asia, often being restricted by the climatic conditions surrounding the land area. The largest area of tropical forest is found in the Neotropics ($4 \times 10^6\,km^2$). The neotropical forests occur in three parts: the Amazon and Orinoco basins are the largest area, followed by a block which lies across the Andes on the Pacific coasts of Ecuador and Colombia, extending northwards through Central America as far as Veracruz in southernmost Mexico. The Atlantic coast of Brazil has a third area of rainforest, a strip less than 50 km wide on the coastal mountains, extending from Bahia in the north to Rio Grande do Sul in the south. The area has now been reduced to about 12% of its original extent.

The second largest block of tropical moist forests occurs in eastern tropics and is estimated to cover $2.5 \times 10^6\,km^2$. Centered in the Malay archipelago, it includes all of the Southeast Asian countries into the Pacific islands and in a narrow coastal strip in Queensland, Australia. In Australia, the forest extends in small pockets into New South Wales but is mainly restricted to the wettest sites with most fertile soils. In the Malay peninsula, the forests extend into Myanmar, Thailand to the southern Himalayas in upper Myanmar, Assam, and southern China. Africa has the smallest block of the tropical moist forests, with an area of about $1.8 \times 10^6\,km^2$. Centered in the Congo basin, this block extends from the high mountains at its eastern limit westwards to the Atlantic ocean, with outliers in East Africa. It extends as a coastal strip into West Africa and woodlands reach the coast at the Dahomey Gap. There are tiny patches of rainforest on the east coast of Madagascar and in the Mascarenes.

Environment of the Tropical Moist Forests

A number of interacting environmental features influence the distribution of vegetation, e.g., climate, temperature, and moisture. Tropical moist forests occur in climates where the mean temperature of the coldest month is more than 18°C. This excludes some tropical montane areas, although an alternative definition includes forests where the difference between the mean temperatures of the warmest and the coldest months is less than 5°C. Another important characteristic of tropical climates is that the diurnal range of mean daily temperature exceeds the annual range. The amount of rainfall and its distribution through the year defines different tropical climates. Rainforests develop where monthly rainfall exceeds 100 mm and short dry spells last only a few days or weeks. Where there are regular dry periods (60 mm rainfall or less), monsoon forests or tropical seasonal forests develop. Superficially, both forest formations appear similar but they have very different species compositions: tropical moist forests are species-rich with a heterogeneous physiognomy, whereas monsoon forests are relatively species-poor and have a simple structure, often containing