Figure 5 Rainforest has been cleared for timber and agriculture in this subsistence farm in Providencia, Antioquia, Colombia. Credit: Robert B. Waide.

Hunting of large animals may have insidious effects on forest structure, as the populations of prey species may explode when released from predation. Increased populations of small mammals, for example, may have severe effects on other organisms, leading to the breakdown of whole ecosystems over time.

Because the issues facing tropical rainforests vary considerably from one place to another, generic conservation solutions are not practical. However, the major elements of a conservation strategy for tropical rainforests will include the creation of reserves to protect biodiversity, the regulation of exploitative use of tropical rainforest products, the engagement of traditional societies, the development of sustainable use strategies that will address the issue of poverty, and an increased effort by developed countries to form partnerships with developing countries.

See also: Tropical Seasonal Forest.

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Tropical Seasonal Forest

E G Leigh Jr., Smithsonian Tropical Research Institute, Panama, Republic of Panama

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Definitions and Distinctions

Tropical seasonal forest is defined here as lowland tropical forest (mean annual temperature $\geq$20 °C, mean temperature of the coolest month $\geq$18 °C) which averages $\geq$1600 mm yr^{-1} of rainfall and $\geq$100 mm for at least seven months of the year, with a single severe dry season averaging <175 mm for the year's driest quarter and <100 mm for at least 3 consecutive months. Its wetter counterpart, tropical rainforest, which is almost entirely evergreen, averages $\geq$1750 mm yr^{-1} of rainfall and $\geq$100 mm nearly every month (no 2 consecutive months average <100 mm). Its drier counterpart, tropical dry forest, where most trees lose their leaves in the dry season, averages 800–1800 mm yr^{-1}of rain with $\geq$5 consecutive months averaging <100 mm (Table 1). Evergreen seasonal forest averages $\geq$2500 mm yr^{-1}, with a single, long dry season with 6 or more consecutive months averaging <100 mm.

Most rainforest occurs near the equator, where the midday sun is within 18° of zenith all year round (normally, the nearer the midday sun to zenith, the higher the rainfall 6 weeks later). Rainforest also occurs at higher latitudes near the base of east-coast slopes facing trade

Table 1 Sample rainfall régimes for different forest types. Average rainfall for each month, the year (total), and the driest quarter (P_3), and Walsh's index[a]

Forest type	*Everwet (rain)*	*Seasonal forest*	*Dry forest*
Site	Pasoh, Malaysia	BCI, Panama[b]	HKK, Thailand[c]
Latitude	2° 59′ N	9° 9′ N	15° 38′ N
January	94 mm	71 mm	6 mm
February	109 mm	32 mm	30 mm
March	153 mm	23 mm	39 mm
April	167 mm	106 mm	82 mm
May	162 mm	245 mm	226 mm
June	125 mm	275 mm	120 mm
July	115 mm	237 mm	123 mm
August	120 mm	322 mm	155 mm
September	162 mm	309 mm	278 mm
October	189 mm	364 mm	360 mm
November	224 mm	360 mm	47 mm
December	168 mm	202 mm	10 mm
Total	1788 mm	2551 mm	1476 mm
Driest quarter	356 mm	131 mm	46 mm
Walsh's index	11.5	12.5	− 1.5

[a]To calculate Walsh's index, add + 2 for each month averaging > 200 mm of rain, +1 for each month averaging 101–200 mm, −1 for each month averaging 51–100 mm, −2 for each month averaging ≤50 mm, and 0.5 for each month averaging ≤100 mm following a month averaging >100 mm.
[b]BCI stands for Barro Colorado Island
[c]HKK stands for Huai Kha Khaeng.
Data from Losos EC and Leigh EG (2004) *Tropical Forest Diversity and Dynamism. Findings from a Large-Scale Plot Network.* Chicago, IL: University of Chicago Press.

winds, as in Puerto Rico's Luquillo Mountains (18° N), La Selva, Costa Rica (10° N), Las Tuxtlas, Mexico (18° N), and most of the east coasts of Madagascar and the Philippines. Seasonal forests flank equatorial forests to north and south. Most of the African forest block, including Makokou (Gabon), Korup (Cameroun), and the Congo's Ituri forest, as well as the forests of Ghana, the Ivory Coast, and Liberia, are seasonal. Large blocks of southern and southwestern Amazonia are seasonal, including Cocha Cashu in Peru's Parque Nacional Manú (12° S). Seasonal forest also extends northward from roughly 7° N, near the Thai–Malaysian border, into the Isthmus of Kra, where Khao Chong is located, and seasonal forest formerly covered most of lowland Java. The best-studied seasonal forest, Panama's Barro Colorado Island (Figure 1), is at 9° N, but in Central America, seasonal forest extends to Belize (18° N). Dry forest occurs at higher latitudes than most seasonal forest, as does Thailand's Huai Kha Khaeng (16° N), and in rainshadow, as on Madagascar's west coast (the location of Kirindy Forest, 20° S), and on the west coast of Central and North America from Costa Rica's Parque Nacional Santa Rosa (11° N) to Chamela, Mexico (19° N) and beyond. Evergreen seasonal forest occurs at 13–15° N in India's Western Ghats.

These distinctions reflect major differences in flora and vegetation. On the Isthmus of Kra between the Malay Peninsula and Thailand, rainfall during the year's driest quarter declines from >300 mm at 5° N to 112 mm at 9° N. On this isthmus, 200 plant genera reach their

Figure 1 View of old-growth seasonal forest on Barro Colorado Island, Panama, facing southward, downslope from the island's central plateau. From left to right, the canopy trees are *Prioria copaifera* (Leguminosae), an epiphyte-laden *Anacardium excelsum* (Anacardiaceae), and *Quararibea asterolepis* (Malvaceae). Drawing by Daniel Glanz.

southern limit where seasonal forest ends, near 7° N, whereas 375 genera reach their northern limit at this same latitude, where rainforest ends. In the rainforest of Pasoh Reserve at 3° N in the Malay Peninsula, trees of species that also grow in seasonal forest north of 7° N grow more slowly and die faster, on the average, than trees of species restricted to the rainforest. All forest along the Panama Canal is seasonal, but from its Caribbean to its Pacific end, annual rainfall declines from 3285 to 1747 mm and rainfall during the year's driest quarter declines from 167 to 71 mm. Over this 80 km gradient across the Isthmus of Panama, flora and vegetation change markedly. The proportion of canopy species that include at least some deciduous trees increases from 14% on the Caribbean side to 41% near the Pacific. In a census conducted by Richard Condit and co-workers for the Smithsonian's Center for Tropical Forest Science in 1997, the ten most common tree species on a 5 ha plot near the canal's Caribbean end included 1191 of its 2492 trees ≥10 cm in trunk diameter, but only one species was represented by trees this large (just four such trees) on a 4 ha plot near the Canal's Pacific end. Similarly, the ten most common species on the Pacific-side plot included 690 of its 1083 trees ≥10 cm trunk diameter, but none of these species was represented by a tree this large on the Caribbean-side plot.

Nonetheless, this article's definition of seasonal forest is arbitrary. First, most forest characteristics vary continuously with the severity of the dry season, without 'natural divisions'. Second, other measures, such as Walsh's index (**Table 1**), which are more sensitive to total rainfall, are better predictors of some distinctions between different forest types. Finally, rapidly draining soils that hold little water support tree species typical of drier climates, whereas soils better able to hold water, which release it slowly enough that plants can still extract some water at the height of dry season, support tree species typical of wetter climates.

What Difference Does a Dry Season Make?

A dry season ≤4 months long leads to increased leaf area (thanks to the more abundant light) and presumably increases production of lowland tropical forest. Water shortage, however, limits productivity of dry forest. Although some trees of seasonal forests lose their leaves during the dry season, in Barro Colorado's seasonal forest most canopy trees can reach soil water throughout a normal dry season. In both seasonal and everwet climates, 1 ha of mature forest supports about 7 ha of leaves and the total cross-sectional area of its tree trunks ≥10 cm in diameter is near 30 m^2. On average, this hectare of forest annually photosynthesizes a total of about 30 metric tons of carbon, and drops about 7 metric tons dry weight of leaves. In this range of climates, soil fertility is the primary influence on forest structure and wood production. On poorer soils, trees are designed to minimize waste of mineral nutrients, and they devote more of their resources to root-making. Accordingly, their forests produce less wood, and trees and their leaves are built to last. Tree trunks have denser, stronger wood, leaves are thicker and tougher, and leaves and tree crowns are designed to limit transpiration and restrict leaf overheating.

Severity of the dry season, however, limits tree diversity, whereas soil infertility does not except when extreme. In some everwet forests, a hectare has over 200 species of trees ≥10 cm trunk diameter. A hectare of dry forest supports <80 tree species, whereas a hectare of seasonal forest supports 80–150 tree species (**Table 2**).

Table 2 The relation of tree diversity to dry season severity. Number N of trees ≥ 10 cm dbh, number S of species among them, average annual rainfall P, and average rainfall P_3 for the year's driest quarter at selected sites

Site	*N*	*S*	*P*	P_3
Kirindy, Madagascar	788	45	711	14
Huai Kha Khaeng, Thailand	438	65	1476	46
Khao Chong, Thailand	482	141	2718	160
Pasoh, Malaysia	531	206	1788	346
Lambir Hills, Malaysia	637	247	2664	498
Santa Rosa, Costa Rica	354	56	1614	10
Barro Colorado Id., Panama	429	91	2551	131
BDFFP, Amazonia, Brazil	578	247	2600	346
Yasuni, Amazonia, Ecuador	702	251	3081	594

Data from Losos EC and Leigh EG (2004) *Tropical Forest Diversity and Dynamism. Findings from a Large-Scale Plot Network.* Chicago, IL: University of Chicago Press, except Kirindy, Madagascar, which is from Abraham J-P, Benja R, Randrianasolo M, *et al.* (2004) Tree diversity on small plots in Madagascar: A preliminary review. *Revue d'Écologie* 51: 93–117; Santa Rosa, Costa Rica, which is from Burnham RJ (1997) Stand characteristics and leaf litter composition of a dry forest hectare in Santa Rosa National Park, Costa Rica. *Biotropica* 29: 384–395; and BDFFP, Amezonia, Brazil, which presents an average of 6 control hectares (first sensus) tabulated by Gilbert B, Laurance WF, Leigh EG, Jr., and Nascimento HEM (2006) Can neutral theory predict the responses of Amazonian tree communities to forest fragmentation? *American Naturalist* 168: 304–317.

In rainforests, energetic activities such as leaf flush, flowering, and fruiting occur during the warmest, sunniest time of year, but in seasonal forests the dry season plays a larger role in shaping the annual rhythms of forest activity. Severe dry seasons depress insect abundance. In the tropical dry forest of south India, with 1200 mm yr^{-1} of rain and a 6-month dry season, trees flush edible new leaves several weeks before the rains begin, thereby reducing losses to insect herbivores. By the time rains bring out the insects, these leaves are tougher and harder to eat. The same is true, to a lesser degree, for seasonal forests. In rainforests, however, the dry season is too weak to limit plant activity or to desiccate most insects, so leaf flush, flowering, fruiting, and insect activity peak throughout the sunnier dry season, when light is least limiting.

Indeed, the coming of the rainy season to seasonal forest is like the coming of spring. Although some seasonal forest plants, including big trees with colorful flowers, depend on dry season rains to trigger synchronous flowering, many more plants, especially those with small flowers pollinated by small, easily desiccated insects, flower after the rains begin, when small insects become abundant. Many trees bear fruit and/or flush leaves at or soon before the rains. Although most canopy trees in seasonal forest can reach water even at the height of the dry season, the same is not true of seedlings. In the seasonal forest, most seedlings germinate soon after the rains begin, to have time enough to sink deep roots before the next dry season. The onset of the rainy season is also a season of abundance for vertebrate herbivores, the most favorable season for bearing and rearing the young.

See also: Leaf Area Index; Mangrove Wetlands; Seasonality; Temperate Forest; Tropical Ecology; Tropical Rainforest.

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