

LECTURES 5 and 6: Tropical Biomes -- Equatorial Evergreen Forests, Tropical Deciduous Forest and Savannas

I. Climates

A. Definition:

The best way to define tropical climates is as those where the mean daily fluctuation of temperature equals or exceeds the variation in monthly means. This definition stresses the lack of temperature seasonality in the tropics, rather than the fact that mean temperatures are usually high; we regard even a snowfield in the central Andes or on Mt. Kenya as having a tropical climate.

B. Causes of Tropical Climate Patterns

High solar radiation, and small seasonal variation in day length and sun angle cause the temperature relations of our definition. Rainfall patterns are much more variable in tropical climates than temperature patterns. The ITCZ, Inter-Tropical Convergence Zone, with its high rainfall moves north and south with the seasons. The equatorial regions, generally beneath the ITCZ all year, have either constant rainfall or a double peak in rainfall. Further north and south, the influence of the ITCZ is present only in that hemisphere's summer, giving contrasting wet and dry seasons. As the Subtropical High Belt, between 20° and 35°, is approached, the rainy season gets shorter, and the peak rainfall diminishes.

Exceptions to typical tropical patterns occur in the monsoon areas of East Asia where the effects of the huge Asian Continent cause a very strong summer rainy season to occur further north than usual. The heating of Central Asia causes a deep low pressure area that sucks warm tropical maritime air masses from the Indian and Pacific Oceans into the continent. Exceptions also occur where mountains create rain shadow or cold offshore currents weaken the ITCZ. Coastal Peru has both effects, and is extremely dry almost to the equator. The rains only come when the notorious El Niño replaces the Peru Current with the warm water of the Equatorial Counter-current. Mountains have special climates that we will consider in a later lecture.

C. Climate Diagrams

Figure 5.1a shows climate diagrams for the typically very rainy Equatorial Climate and Figure 5.1b shows a series of increasingly drier summer rain situations from the Indian Monsoon region. A climate diagram from the Peruvian Desert is also shown in Figure 5.1.

II. Introduction to Tropical Biomes

The tropics are dominated by two main biomes, the Evergreen Forest, Biome I, associated with ever-rainy climates and the Tropical Deciduous Forest, Biome II, associated with the high but seasonal rainfall outside the strictly equatorial regions. These two biomes grade gradually and unobtrusively into one another. The ecotone between the Deciduous Forest and Subtropical Desert, Biome III, is more dramatic, being marked by large expanses of Savanna (mixed trees and grass) that once supported large concentrations of big game (and still do in parts of Africa).

Large tracts of savanna also occur in the tropics because of edaphic and anthropogenic effects in areas that would otherwise support deciduous forests. Other special communities of interest in the tropics include various kinds of seasonally flooded habitats, because mean rainfall is high and because so much of Africa and South America are relatively flat.

III. Evergreen Forest -- Biome I

A. Typical Climate

1. Driest month with 100 mm of rain, no drought period.
2. Total rainfall 2,000 mm.
3. Mean Annual temperature 25°C.
4. Range of monthly means 3°C.
5. Warm nights (20°C), moderately hot days (32°C), very humid.

B. Soils

1. Hot, wet climate causes extreme leaching and rapid weathering typically forming Latosol.
2. Acidity high - basic minerals like CaCO_3 (limestone) removed.
3. Clays are broken down to iron and aluminum oxides; silicates leached, thus mineral nutrient holding capacity is much reduced.
4. Low organic matter content due to rapid mineralization.
5. Typical soils very old - Amazon basin and African shield have been very stable geologically for many millions of years.
6. Exceptional soils:
 - a. recent alluvium along rivers, Amazon, Congo, etc.
 - b. volcanic soils, Central America, Java.

C. Vegetation (See Figures 5.1 and 5.2)

1. Tree layer strongly dominant (70% of species)
 - a. ample water and warm temperatures favor evergreen broadleaf trees.
 - b. intense shade limits shrubs and herbs.
 - c. extremely diverse - 300 species per community.
2. Multi-layer structure
 - a. overstory - solitary giant trees.
 - b. canopy - closed, dense layer of smaller trees.
 - c. subcanopy - sparse because of light limitations.
3. Specialized growth forms that are rare in other habitats:
 - a. lianas - climbing plants that compete for light by exploiting the bioenergetically expensive trunks of the trees (California grape and poison oak do this sometimes).
 - b. epiphytes - plants that grown on the branches and in the crotches of the trees, without soils. Bromeliads and orchids are common examples of epiphytes. Epiphytes are drought adapted because even one day without rain exhausts their "soil" water reserves (our "Spanish moss," a lichen, is an analog).
 - c. stranglers - plants that begin as epiphytes, but put down roots that gradually take over and constrict the host's trunk preventing the host's growth.

4. Typical adaptations:
 - a. Strong differentiation of sun and shade leaves - high radiation intensities make the exposed overstory habitat susceptible to strong evapotranspiration stress, resulting in thick, leathery, often small leaves. The house plants Philodendron and Ficus show the thick leaf adaptation. Leaves are usually "entire," having smooth margins.
 - b. shallow root systems are common because water is less a problem than nutrients. However, the absence of extensive or deep roots makes the trees subject to falling over (see the next adaptation).
 - c. "Buttress" trunks - Base of trunks on some trees develop lateral supports that act as tension cables to brace the trees.

D. Animals

1. Grazing and browsing guild very restricted because of the high canopy.
2. Fruit and seed-eating guilds very well developed -- monkey, parrots, pigeons, hornbills, etc.
3. Herbivorous insects very diverse, reflecting the diversity of the vegetation.
4. Pollinator guild dominated by large, strong flying animals because of the rarity of their individual hosts and the seasonality of flowering -- bats, hummingbirds, bumblebees, hawk-moths.
5. Termite and ant faunas very well developed.
6. Predators -- few large predators. Medium sized cats common (leopard, puma), feeding on monkeys and other arboreal herbivores. Trophic webs based on insects are important (amphibians, small mammals, snakes).

E. Ecosystem function

1. Very high primary production due to warmth, rainfall, and high light intensities, but also high respiration. Typical figures: gross production 55 tons/ha, respiration 40 tons/ha, net production 15 tons/ha, standing crop 300 tons/ha.
2. Soils have very poor nutrient-holding capacity because of clay weathering.
3. The shallow root systems of the trees are equipped with mycorrhiza (symbiotic fungi) which transfer nutrients from decaying litter directly into the vegetation. The vast bulk of the nutrient stores of the ecosystem are in the vegetation, not in the soil. Very effective nutrient recycling necessary to support high rates of carbon fixation.
4. Some decomposers move out of the soil in order to compete with bacteria and fungi -- termites.
5. Relatively low flows of production to consumers. Most plants are well equipped with anti-herbivore defenses, and the fact that tree leaves are held up out of the reach of large, efficient herbivores like the ungulates (cow-antelope-deer) greatly reduces herbivore attack. The biomass of animals on the order of 0.001% of the plant biomass, and over half the animals are detritivores. Many of the herbivores depend on fruit or nectar, and relatively few attack leaves.

F. Human uses

1. Rainforests support small human populations.
 - a. A few hunters in the forest -- Siriono, Pygmies, still exist because the deep forest is so unsuited to other uses.
 - b. Cultivators largely confined to better soils (Amazonian Varzea, riverbank areas with alluvial soils, volcanic soils of Central America, etc.).
 - c. A few swidden horticulturalists penetrate areas with better soils and enough dry season to burn the vegetation.
2. Specialized jungle products.
 - a. hardwoods
 - b. rubber
3. Rainforest is difficult to convert to intensive uses -- clearing results in catastrophic loss of nutrients and very slow recovery, except on rare good soils. Ecologists fear that clearing large areas of Amazonia will increase the world's CO₂ burden, alter climates over wide areas and globally, and not be successful in creating long lasting farms or plantations.

IV. Deciduous Forest -- Biome II

A. Typical climate

1. 3-4 months with rainfall under 100 mm, 3-4 months with rainfall over 200 mm.
2. total rainfall 900 mm (much more in the monsoonal variant).
3. Mean annual temperature 20°C.
4. Range of monthly means 6-7°C, no frost.
5. Cool nights, hot days, particularly in the dry season. (In much of Africa, Biome II climates are not desperately hot because the African plateau has a little elevation - 700-1,000 m).

B. Soils

1. Latosols, as in Biome I, typical.
2. Slightly less intensely leached.
3. Sometimes fairly good soils persist on weathered limestone parent material - Cuba, Zambia - or when young soils are produced by stream deposition, volcanic ash, etc..

C. Vegetation (Figures 5.1 and 5.2)

1. Usually, a gentle gradient.
 - a. Broad ecotone with some deciduous, some evergreen trees.
 - b. Core Biome II, all trees deciduous.
 - (1) distinct seasonality of flowering and fruiting.
 - (2) facultative leaf shedding in response to variable rains.
 - (3) consistent pattern of long very dry season followed by long very wet season with no frost favors deciduous broadleaf habit. There is time to form leaves at the onset of the growing season and still use most of the available water during the rainy season. Later, we will contrast this adaptation with the evergreen-sclerophyll habits of the Mediterranean biome which is also seasonally rainy and not extremely cold.
 - c. At the poleward margins, the forest becomes more open and gradually becomes savanna.
2. Tree diversity drops along the gradient, other life forms increase in importance.
3. Rainforest specialists, such as lianas, epiphytes and stranglers drop out of the vegetation.
4. As forest opens, competition for light becomes less intense, the stature of the forest diminishes, and buttressing disappears.

D. Animals

1. Gradual invasion of the forest by a community of ground-dwelling large herbivores. First, the ground-dwelling primates such as Mandrills become important. Finally, elephants, rhino and other big game invade as browse and graze plants increase.
2. Seasonality begins to favor more generalized, often migratory animals. Some plants (e.g. bamboo) use mast producing adaptation, the production of huge volumes of seed, at annual or longer intervals, to saturate and escape seed predators.

E. Ecosystem function - presumably similar to rainforest in the wetter examples, except for the seasonality and less extreme nutrient leaching. Not much comparative work is available yet.

F. Human Uses

1. Deciduous forests often support substantial populations of swidden horticulturalists (and once probably fair populations of hunters).
 - a. Dry season permits extensive burning.
 - b. long fallow systems well adapted to this zone.
 - (1) fields burned and cultivated for 1-3 years.
 - (2) "bush fallowed" for 10-30 years.
 - (3) during fallow, weed species are shaded out by secondary forest, nutrients recover.
 - c. permanent cultivation possible only on good soils, in small plots where manuring is practical, or with heavy inputs of labor and artificial fertilizer.
 - d. often converted to grazing where human populations less dense (Brazil, Bolivia).

2. Forest valuable for lumber and firewood, but these uses become secondary as populations increase.
3. One of the most human altered biomes of all because of its suitability for extensive swidden cultivation. Problems occur especially when fallow cycles are shortened by too large a human population. Agricultural productivity drops, and catastrophe can ensue. Raising food production on typical Biome II soils is one of the world's most pressing and difficult problems.

V. Savannas - Biome IIA

A. Savannas are tropical vegetation dominated by grasslands, but with a good admixture of trees. They are widespread as the ecotone between Biomes II and III and also within Biome II for edaphic and anthropogenic reasons.

B. Controlling factors (see Figure 5.3)

1. Savannas result from some factor that balances the competition between grass and trees. Normally, these plant forms are strong competitors. Trees can usually out-compete grasses if rainfall is high enough that they can close the canopy and prevent enough light from reaching the ground. Where rainfall is from 100-200 mm and the soil has reasonable water holding capacity above a meter or so depth, the intensive root systems of the grasses use up all the water. Therefore, trees cannot get enough water to survive the dry season. The advantage of grasses is effective competition for shallow water, that of trees is competition for light.
2. Climatic savannas occur where rainfall is about 400 mm. See Figures 5.1 and 5.3. Enough water seeps below the root zone to support scattered trees that compete for the minimal quantity of excess water. Climatic regions favorable for savannas will lack them if the soil is too stony (water sinks so deep that the extensive roots of trees and shrubs get most of it) or too heavy (water doesn't penetrate deeply enough, and much is lost by capillary conduction and evaporation at the surface). Note that savanna-like communities occur in California at the lower elevations, from sea level to about 500 m. Rainfall is also roughly 400 mm in our savannas too!
3. Edaphic savannas. The latosols of the tropics often solidify into a hard, concrete-like layer, laterite. If there is a shallow soil layer above the laterite, grasses will grow in it, and the trees will be restricted to the cracks in the laterite where their roots can escape competition with grasses. Large areas, with climates that should support deciduous forests, have savanna under this regime, including huge areas in Venezuela and Brazil. Similarly, regions with seasonally flooded soils are unfavorable to trees, and savanna vegetation can occur on them -- trees on the drier sites and grasses in the depressions. The Okavango Delta is such an area in N.W. Botswana.
4. Fire induced savanna. Anywhere Tropical Deciduous Forest is thin enough to permit an understory that can carry fire, grassland and savanna can often expand against the forest. Humans are probably responsible for considerably expanding grassy habitats in the tropics (and temperate zone too) by burning to encourage game and cattle and from simple pyromania.
5. Grazing also will often affect the balance between grasses and trees.

C. Ecosystem Function

Savannas are most notable for their ability to support a very high herbivore biomass. High production, concentrated in a low growing plant, provides ample forage for large, efficient herbivores. Grasses resist grazing mainly by having their growing point at ground level and tolerating heavy herbivore pressure on the mature leaves. Thus, the primary production per unit biomass is very high, and as much

as 30% of gross production is consumed by the herbivores. In forests, much more production is used just to maintain the high biomass of the trees, so herbivores get only about 1% of gross production. A great variety of herbivore specializations arise to exploit different vegetation situations in savannas. In Africa, elephants and giraffes exploit the trees, antelopes, bovids, and equids the grasses and forbs of various species and various growth stages, pigs the subterranean plants, and so forth. Formerly, the world's other grasslands and savannas supported equally spectacular herds.

D. Human Uses

Most savannas are too arid, or have soils poorly adapted, for cultivation. Hunting must once have been very good on them, and some of the world's remaining hunters still use the poorer examples in Africa and Australia. However, most savannas make good cattle pasture, and pastoralism or ranching have evicted the game and the hunters. Africa's big game herds have survived the last few thousand years in large part because endemic sleeping-sickness-like diseases exclude stock raising from tsetse-infested areas. Overgrazing is the commonest abuse of these habitats, along with destruction of game for meat, skins and ivory. Tourism is a non-trivial industry in Africa, of course.

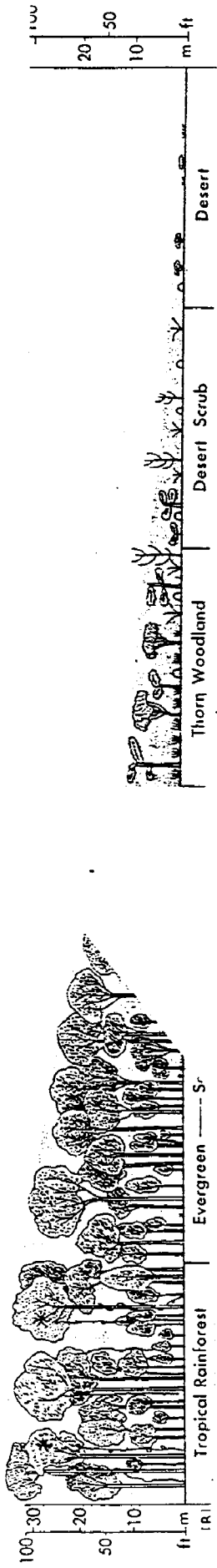


Figure 5.1b

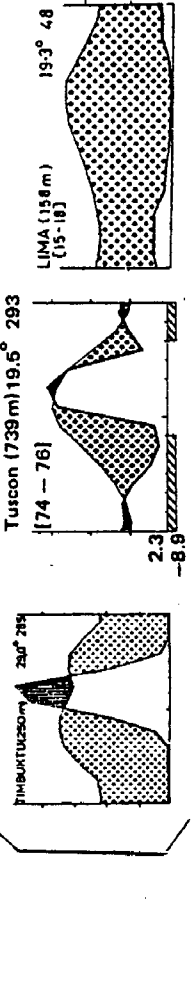
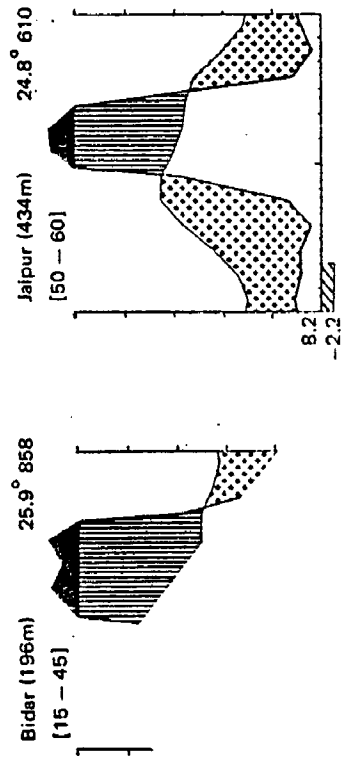
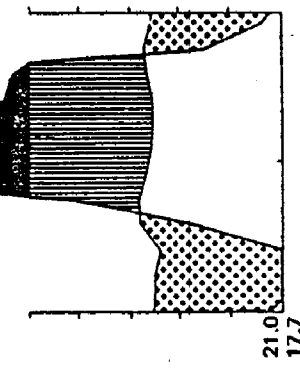


Figure 5.1a



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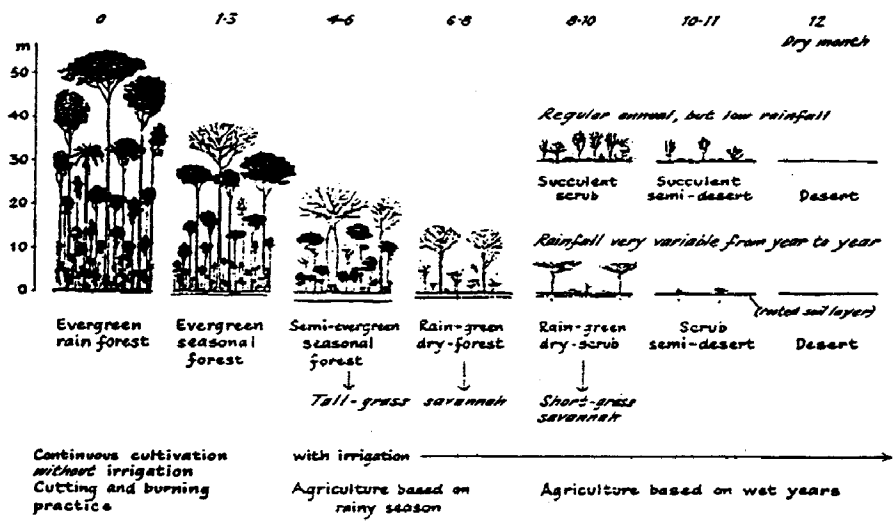


FIG. 124. Schematic representation of the different forest types in the tropical zone of Peru in relation to increasing length of dry period and decreasing rainfall (after Ellenberg). Savannah communities after burning, and comments on general suitability for agriculture have been added.

Figure 5.2

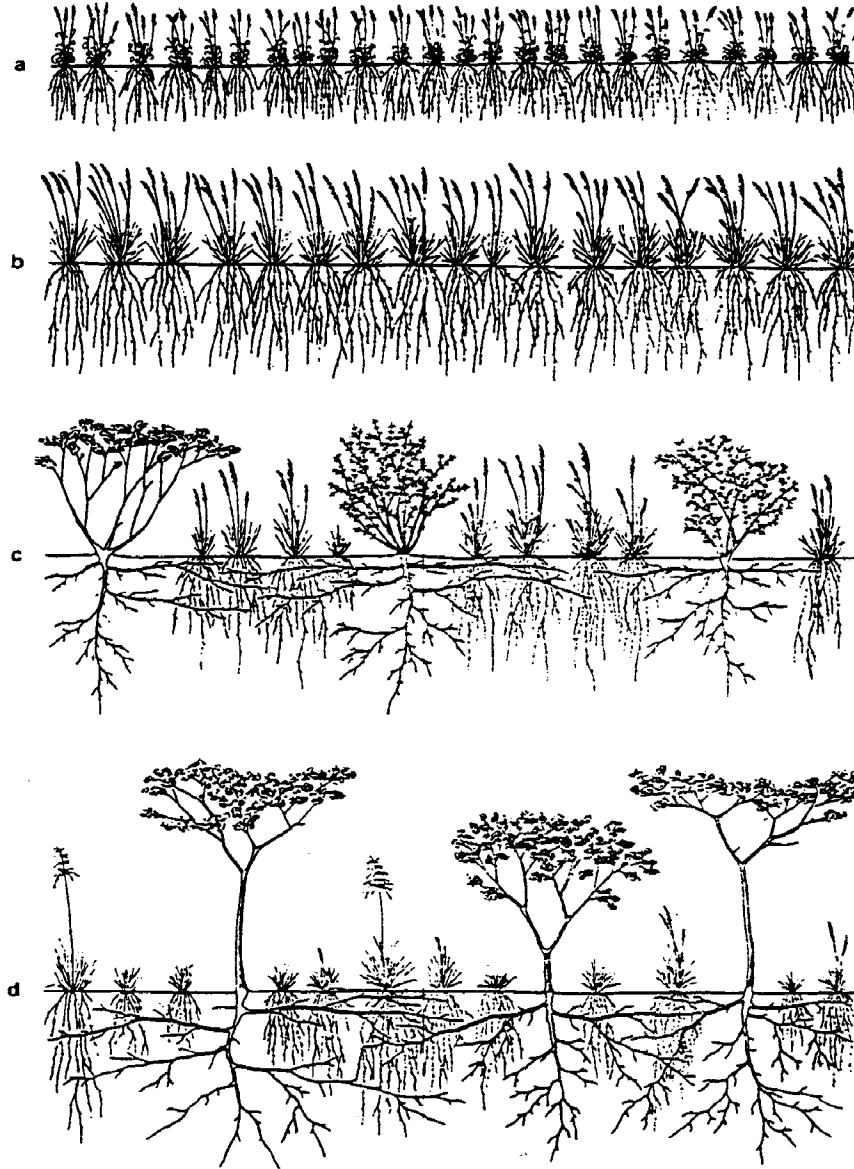


Fig. 29. Schematic representation of the transition from grassland (a and b) to savanna (c) and to dry woodland (d). Explanation in text.

Figure 5.3

Lecture 5: Discussion Questions

1. Why do trees grow in the wet tropics to the exclusion of most other growth forms? What are the advantages of the tree growth form relative to its costs?
2. Why are tropical habitats so diverse?
3. Does our definition of tropical climates in terms of fluctuations of daily and monthly means of temperature make intuitive sense?
4. Tropical soils are quite different from temperate zone soils. Why?
5. Do you think that tropical forests can or should be extensively colonized for human use? Similarly, big game on the savannas.