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2.2 Ecosystems of the World

E. F. BRUENIG

2.2.1 DEFINITION

An ecosystem is a community of organisms and their physical and chemical environment interacting as an ecological unit. It represents all biological and abiotic components, including man, within a defined and delimited biotope, and is characterized by distinct ecological biocoenotic features of structure and functioning. The ecosystem relates to many different scales. At the lowest end of the scale, the ecosystem may comprise a rock, a fallen tree, or a certain layer in a plant community (pico-ecosystem, as described by Ellenberg, 1973). At the largest end of the scale it relates to life support media and covers oceanic, terrestrial, limnic, or urban ecosystem categories (mega-ecosystem). The present description is restricted to terrestrial ecosystems and focuses in particular on potential natural vegetation. Centred on the plant formation, it classes natural forests and woodlands in hot and cold climates at macro-ecosystem level. The description is structured by classifying the forests and woodlands at micro-ecosystem (formation group) level according to major physiognomic, phenological, and growth features in relation to the site and environmental conditions. These units correspond roughly to the bioclimatic life zones of Holdridge (1967). The description is patterned on the serial structure of the physiognomic-ecological classification of plant formations of the earth (Müller-Dombois and Ellenberg, 1974, pp. 466–488) commonly quoted as the UNESCO Classification.

2.2.2 NATURAL VEGETATIONAL ZONES

2.2.2.1 Latitudinal Zonation

The characteristic features of the zonal vegetation in each latitudinal zone are primarily determined and shaped by climate. In hot climates, vegetation physiognomy and phenology express the effects of the change from weak seasonality near the equator to pronounced radiation and rainfall seasonality around the tropics. The climatic equator is straddled by the Predominantly Evergreen Humid Tropical Forest, which extends north and south of the tropics along major paths of tropical cycles (Figure 2.2.1). This humid to supersaturated forest ecosystem belt is broken on land by considerable gaps in Africa and India. In West Africa, the gap is caused by wind circulation and barrier effects which allow relatively dry conditions to develop seasonally. Similarly, the pattern of atmospheric circulation caused by orography together with the effects of human activity combine to create semideserts, dry woodlands, and man-made savannas in East Africa and south India.

To the north and south of the Predominantly Evergreen Humid Forest lies a fragmented mosaic of Predominantly Deciduous Humid to Subhumid Forests and replacement vegetation, such as various forms of man-induced savannas, dry woodland, and scrub. Agricultural land, extensively used grazing land, and increasingly degraded wasteland occupy large portions of the Predominantly Deciduous Humid to Subhumid Forests and the semi-arid zone. The boundaries between these two zones are indistinct, interlocked, and fluctuating, generally moving towards more xeric conditions in the course of advancing desertification. The tropical and subtropical semideserts and deserts occupy relatively small areas in the neotropics, but cover larger areas elsewhere, where oceanic and atmospheric circulation and the effects of topography cause more xeric conditions.

In contrast to the tropics, the vegetation in the cold climates is primarily determined physiognomically and phenologically by the short period in which sunlight and temperatures suffice to achieve a positive net photosynthesis and assimilation balance, as well as by the severities of the long winter. The latitudinal vegetation zones in the cold climates in the northern coniferous forest and tundra biomes are of varying widths in America and Eurasia. Figure 2.2.1 shows the extent of the Boreal Coniferous Forest (close stipples) and Tree Tundra (wide stipples), the latter becoming treeless tundra and cold deserts further north. The climate diagrams in Figure 2.2.2 show typical examples for the lowland climate in the equatorial evergreen forest, the predominantly deciduous moist tropical forest, and the oceanic and continental boreal forest. The tropical and boreal forest and woodland vegetation represents 80% of the world forest and woodland area (Table 2.2.1); the tropical forests and woodlands alone represent 50% of the world's wooded land.

2.2.2.2 Altitudinal Zonation

The general features of the altitudinal zonation of the natural vegetation are shown in Figure 2.2.3, excluding hot semideserts and desert. The change of physiognomy and phenology is primarily determined by the decrease of temperature with increasing altitude, interacting with the simultaneously changing moisture and radiation regimes. In the tropics, temperature decreases by 0.5–0.6 C° per 100 m, while rainfall increases up to the cloud belt, which

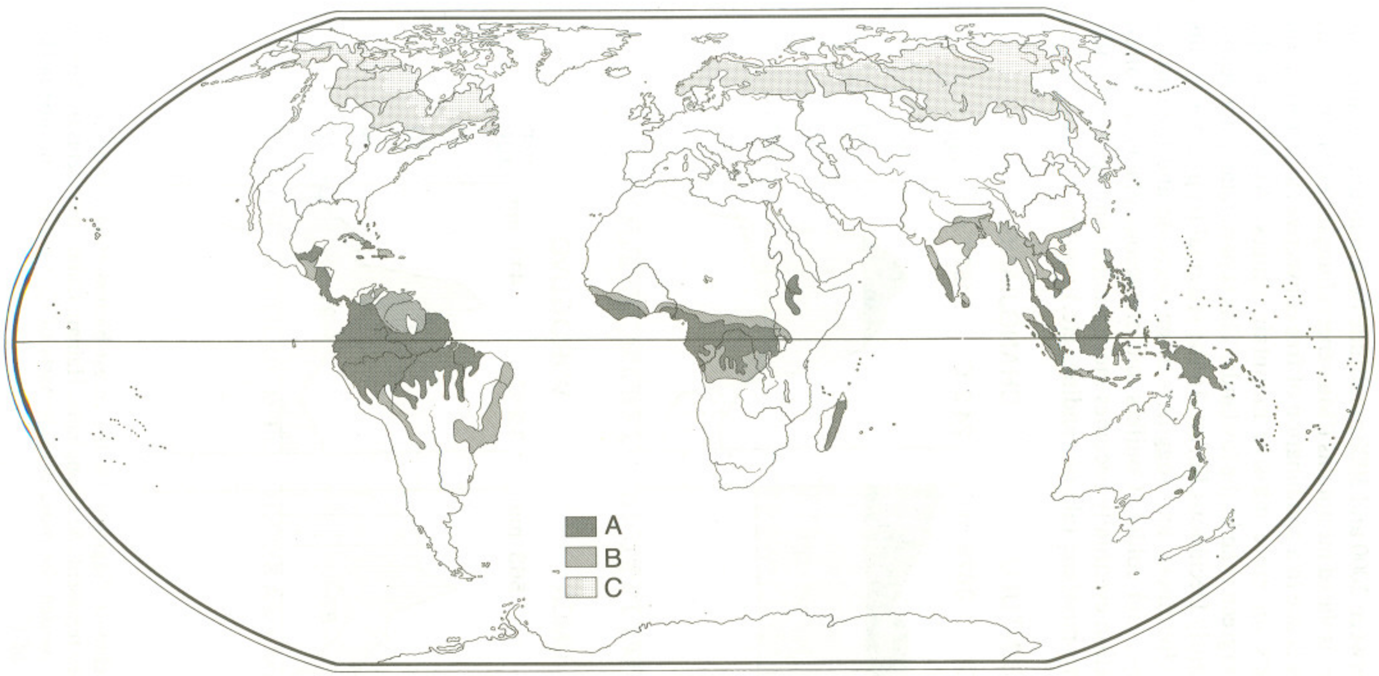

Figure 2.2.1 World Distribution of: (A) the Predominantly Evergreen Tropical Humid Forest Biome (including perhumid to saturated life zone); (B) Predominantly Deciduous Tropical Forest (including outliers in subtropical areas); (C) Boreal Coniferous Forest (taiga); and Tree Tundra

frequently centres between 2000 and 3000 m altitude on mountain massifs, but may be lower on more isolated mountains ('Massenerhebungseffekt'). Increased humidity with altitude is due to a combination of free convective cloud formation and of barrier effects on more massive mountain ranges. As a result the vegetation is more evergreen than in the lowlands. This is particularly noticeable above the Predominantly Deciduous Forest. In the seasonal tropics above this cloud belt, rainfall, cloudiness, and fogginess often decrease and the climate is sunnier, more xeric, and colder. Conifers and ericaceous plants are often common. The vegetation eventually becomes more stunted and sparse, finally degenerating into alto-montane (alpine, andine, etc.) tundra.

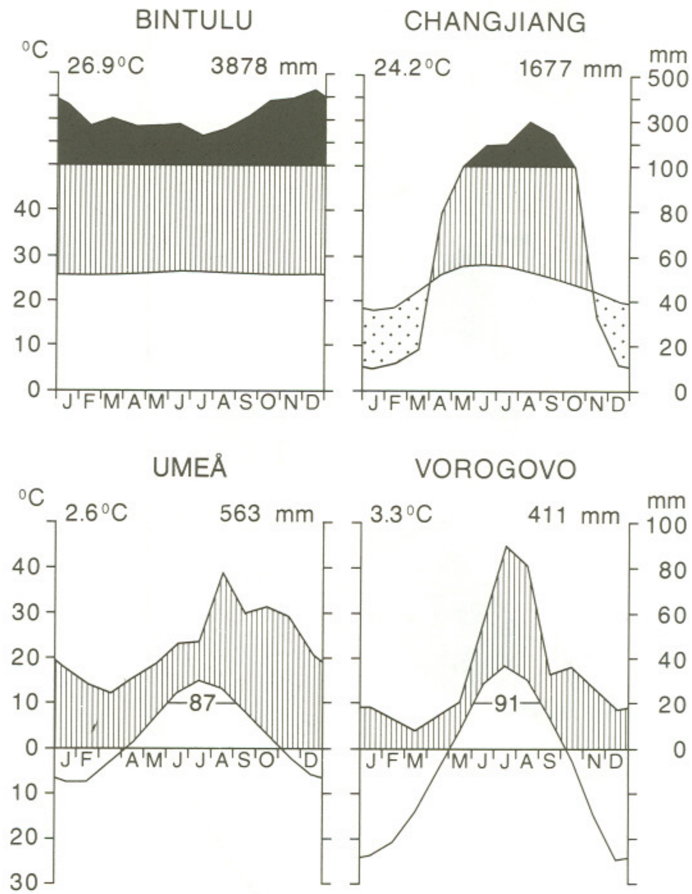

Figure 2.2.2 Typical climate diagrams for the forest biomes shown in Figure 2.2.1. Bintulu, Sarawak, Borneo represents A; Changjiang, Hainan, China, represents the humid section of B; Umeå in Sweden the more oceanic parts of C; Vorogovo in Siberia the more continental parts of C

Table 2.2.1 a = optimistic prediction; b = pessimistic prediction. Compiled from Lanly (1982) and World Resources Institute and IIED (1986)

Forest formation class	Area (10^6 km^2)				
	1965	1975	1985 a	2000 a	2050 a
1. Closed virgin and modified high forest equatorial-tropical predominantly evergreen; wet to moist; (saturated/humid)	5.5	5.0	4.4	4.0	3.0
Tropical predominantly deciduous; moist to dry; (humid to subarid)	7.5	6.5	6.0	5.5	4.5
2. Open virgin and modified natural high forest and woodland; deciduous and evergreen; dry to parched; (semi-arid to arid)	7.5	6.5	6.0	5.5	4.5
Sum natural high forest					
a	20.5	18.0	16.4	15.0	12.0
b	20.5	17.0	15.0	12.5	8.0
Tropical tree plantations					
Forestry	0.04	0.05	0.08	0.16	?0.30
Agriculture	0.20	0.25	0.27	0.28	?0.50
3. Natural and man-made forests and woodlands					
Subtropical	7.6	3.6	3.7	3.7	3.8
Warm/cool temperate	2.6	2.6	2.7	2.7	2.8
4. Cold temperate (boreal) virgin and modified					
High forest	6.0	5.9	5.7	5.5	?5.0
Open tundra woodland	> 6.0	6.1	6.3	6.5	?7.0
5. Total world forest and woodland					
a	38.2	36.0	34.5	33.7	30.6
b	38.2	35.5	33.0	29.0	26.6
World population ($\times 10^9$)					
a	–	4.0	5.0	5.8	?
b	–	4.2	5.3	6.6	>11.0

The zonation of altitudinal belts in the tropics is not analogous to the latitudinal zonation of vegetation in the lowlands. One very obvious difference is the increasing seasonality of moisture and temperature at higher latitudes. The diurnal pattern of temperature, wind, precipitation, and cloud becomes less regular and the free convective component of the moisture regimes becomes relatively less important than in the tropics. This influences the physiognomy of the various vegetation belts, although the effect is obscured by the general dominance of evergreens at higher altitudes (Figure 2.2.3).

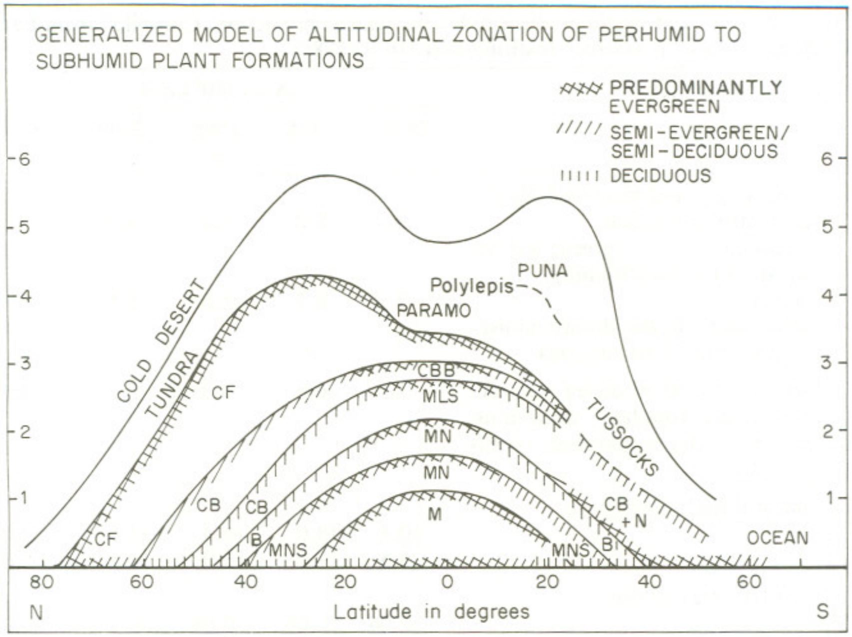

Figure 2.2.3 Generalized model of altitudinal and latitudinal zonation of perhumid to subhumid plant formations and latitudinal on big mountain massifs. The predominant physiognomic vegetation formations are: CF = conifer forest, mainly boreal and temperate-montane; CB = mixed conifer-broadleaved, mainly temperate and subtropical; CBB = mixed conifer-broadleaved with bamboo, tropical, and subtropical alto-montane; B = broadleaved forest, predominantly noto-mesophyll deciduous forest; M = mesophyll forest, mainly tropical evergreen and deciduous; MN = meso-notophyll forest, tropical montane; MNS = meso-nanophyll sclerophyll, australo-pacific forest; NMS = noto-microphyll sclerophyll forest; MLS = micro-leptophyll sclerophyll forest, tropical montane and australo-pacific forest; N = notophyll broadleaved forest, australo-pacific forest. Adapted from Troll, 1948

2.2.3 EDAPHIC ZONATION

Within each ecological vegetation zone and altitudinal belt, different physical and chemical soil conditions are associated with differences of physiognomic and functional features of plants and vegetation. These could be interpreted as adaptations along the edaphic gradient similar to the changes which occur along the latitudinal and altitudinal gradients. These edaphic gradients often have a pattern of repetitive catenas primarily determined by variations in soil moisture and nutrients, and by correlated biological activity on and in the soil. At one end of the nutrient gradient are nutrient-rich soils, while at the other end of the gradient are the oligotrophic soils. The edaphic moisture gradient runs from permanently wet and water-logged, through mesic conditions, to alternating wet and dry, and finally to permanently dry conditions. In addition the soil texture, structure, and organic matter content modify the effects of any conceivable combination of moisture and nutrient regimes. In the humid tropical climate, rates of weathering of parent materials, leaching, mass wasting, and acidification of soils, as well as the intensity of biological activity in the soil, are generally high, and in any event higher than on sites with corresponding soils in other climatic zones. But this relatively high intensity of soil-forming processes in the humid tropics has not led to any uniformity of edaphic conditions. On the contrary, even on very old land surfaces, tropical soils are at least as heterogeneous and diverse as temperate soils, over both small-scale and large-scale areas.

2.2.4 TIME-RELATED TRENDS

Structure and processes in the natural forest ecosystems are subject to changes over time. Natural ecosystems are not in a state of homeostasis, and at no stage do they function as closed systems. Long-term successional phasic development, processes of build-up of biomass, storage and release of nutrients, and change of species, are combined with short-term processes of regeneration, maturing, and mortality caused by small- to large-scale perturbations, disturbances, and, in extreme cases, full-scale catastrophies. Disturbances over small areas prevail in climatic climax tropical forests. Small gaps are created continuously and provide the mechanism by which structural complexity and species diversity are maintained.

By contrast, natural monocultures in the tropics, such as *Shorea albida* peatswamp forests in Sarawak, Borneo, and in the Boreal Coniferous Forest Zone are liable to large-scale catastrophic collapse from insect pests, windthrow, or fire. The ecosystem reverts over large areas to almost initial stages of succession. Reconstruction involves the early phases of pioneer vegetation.

While the effect of small-scale perturbance and disturbance on chemical cycles and organizational structure is small and ephemeral, large-scale destruction profoundly disrupts ecosystem functions and causes drastic changes in stocks, turnover rates, and organization. Figure 2.2.4 gives an impression of the factors and structural changes involved in the case of evergreen lowland tropical forest. This figure gives a generalized illustration of the hypothetical course of forest development as a result of successional dynamics; the cycles of regeneration, growth, and mortality; and the effects of perturbations caused by biotic and abiotic agents. To be added are the effects of inputs of gaseous, dissolved, and solid substances from the atmosphere and the discharges into it. In the example man-made or spontaneous fire (or landslide) is incorporated as a completely destructive exogenous factor to initiate a new successional sequence. Perturbations by climatic damage, pest, and disease, and by pollinating, dispersing, and consuming organisms are essential components of the ecosystem's dynamics and its capacity to adapt and survive.

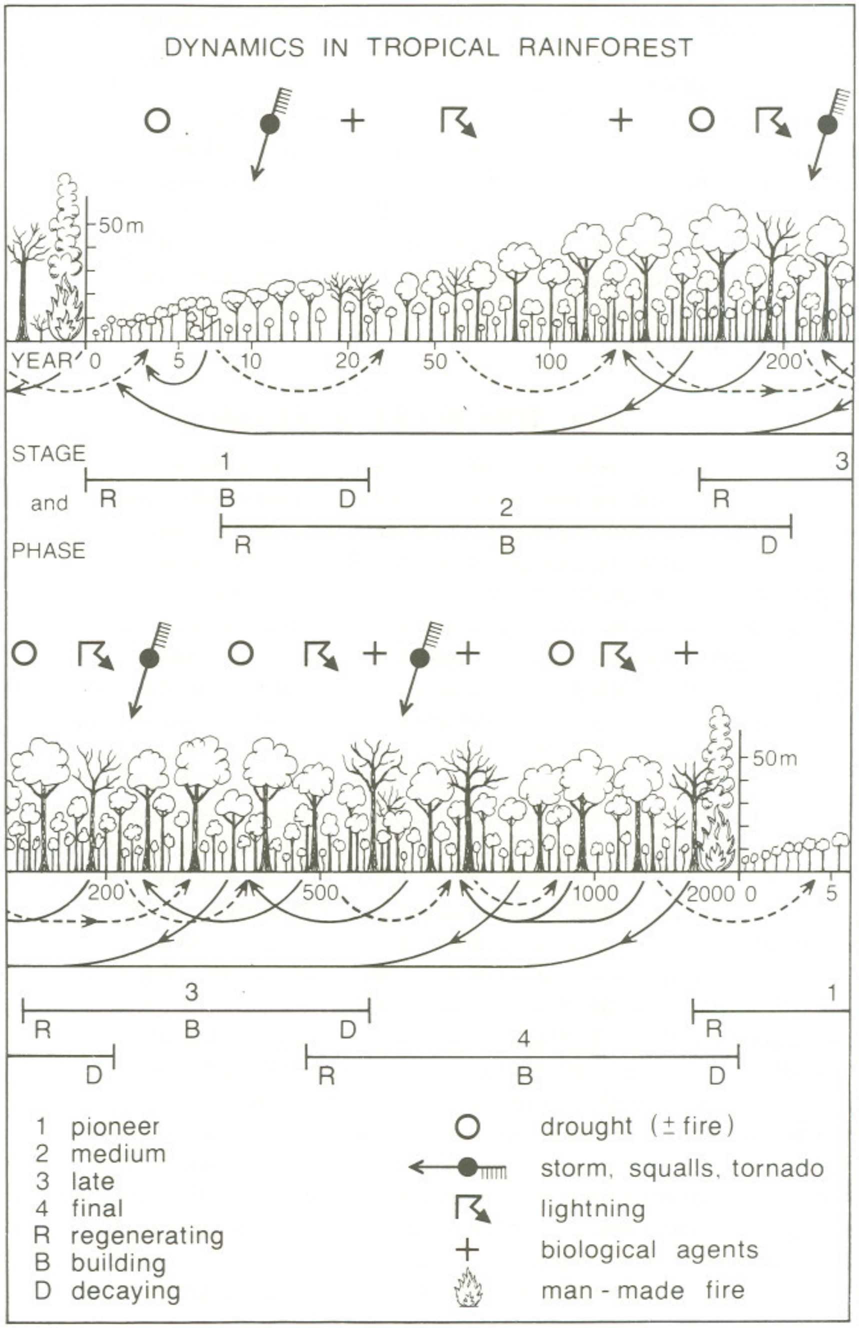

Figure 2.2.4 Dynamics in tropical rainforest

To generalize, the following processes are characteristic components of time-related trends of vegetation dynamics:

(a) energy fixation and negentropy formation;

(b) build-up of structure to the limits of the site carrying capacity;

(c) build-up of architectural and organizational complexity to the limits set by floral and faunal richness interacting with environmental growth and disturbance factors.

The natural terrestrial ecosystems are thermodynamically open systems in which dynamical change; rates of input, throughput, and output; internal cycling; and growth and decay are closely linked with the architectural structure and the floristic and faunal richness and diversity.

2.2.5 STRUCTURAL ADAPTATION TO ENVIRONMENTAL FACTORS

Prevailing minimum factors for primary productivity in the humid tropics are mainly edaphic: low absorptivity of the soils; low mineral nutrient contents; and poor aeration of the soil. In the subhumid tropics and subtropics, aeration is a critical factor only in certain hydromorphic soils. In the semi-arid tropics moisture supply is the major limiting climatic factor, with downward leaching being replaced by upward accumulation. Critical factors are water availability, high potential evapotranspiration, and soil salinization. In the boreal zone, minimum factors are the length of the growing season, low temperatures, and consequently low biological soil activity, which causes a tendency for the accumulation of dead biomass on the soil and hence soil acidification.

The structure, physiognomy, biochemistry, and dynamics of natural vegetation are designed to use site resources efficiently under the average climatic conditions, but at the same time to reduce risk of damage in the event of extreme conditions. Sporadic extreme events must be endured with resilience or elasticity. Catastrophic collapse under strain must be overcome by the capability to restore organization by structural reconstruction and build-up of biomass and self-regulating mechanisms. The architectural, biochemical, and biological features of the vegetation canopy as an active-exchange surface layer between earth and atmosphere determine the intensity of the processes of change and in fact the stability of the ecosystem itself. The illustration of the water balance in a tropical rain forest and in a temperate mixed forest demonstrates the high rates of input, turnover, and output in the complex, aerodynamically rough tropical evergreen lowland rainforest (Figure 2.2.5).

Greater aerodynamic canopy surface roughness is associated with:

(a) greater interception and absorption of radiation and matter;

(b) greater penetration of irradiance into the canopy;

(c) greater crown surface area which absorbs and re-radiates energy;

(d) greater turbulence, deviation, and vertical speed of airflow;

(e) more rapid exchange of moist air within the canopy with drier air from above;

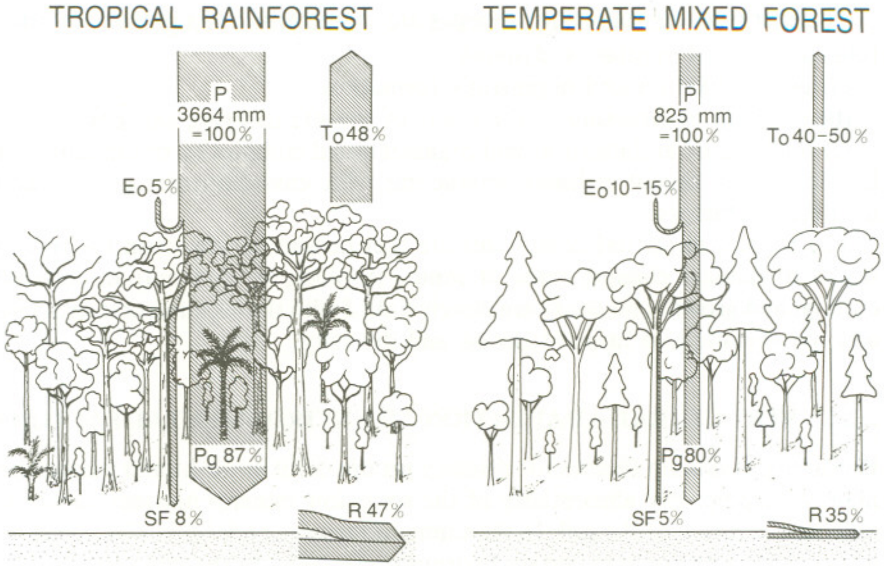

Figure 2.2.5 The water balances of the lowland rain forest in the Amazon Ecosystem Research Area at San Carlos de Rio Negro, Venezuela, and of average cool-temperature mixed forest in Central Europe. This illustrates the comparatively very high rates of input, throughput, output, and runoff of water in the tropical rain forest. Similar relations characterize the energy balance. Both are vital for the system to function effectively, but also put heavy stress on it. P = precipitation; Pg = precipitation reach ground; E_o = evaporation from overstorey; T_o = transpiration from overstorey; SF = stemflow; R = runoff

(f) greater potential and actual evapotranspiration;
(g) greater potential primary gross productivity and greater associated rates of respiration from greater leaf area and crown volume.

Lesser aerodynamic canopy surface roughness is associated with:

(a) lesser absorption of radiation and greater reflection at low sun angles; therefore greater albedo;
(b) lesser turbulent air exchange and kinetic wind energy absorption;
(c) greater or lesser penetrability and transfer resistance to light, humidity, heat, and air, depending on leaf and foliage features.

The vegetation can adjust to the opportunities and risks of the site by a suitable combination of features, such as canopy surface roughness, crown architecture, foliage density, leaf size, leaf orientation, pigmentation, leaf surface characteristics, and internal diffusion and conductance capacities (Bruenig, 1970; 1971).

Higher species richness and diversity increase differences of albedo, surface temperature, and emission of latent and sensible heat in the canopy, and thereby the tendency to free convection and lower canopy diffusion resistance. Greater species richness and diversity is associated with more complex organization of food chains, self-regulating mechanisms and functions. Consequently, the ecosystem is likely to react to impacts by change, but to maintain its functionality by diversion (Bruenig, 1973).

However, the ecological interpretation of features of the physiognomy of natural ecosystems is complicated by the fact that many site factors interact and that individual, seemingly adaptive, features are compensatory, and that adaptation to certain physical, chemical, and biotic stress and strain factors can be achieved in various ways. However, certain common features of physiognomy and structure of natural ecosystems along the ecological gradients of temperature, moisture, and, to some extent, nutrients and solar radiation, can be recognized.

Outward from the perhumid and humid tropical lowlands on medium soils (ferrasol, acrisol, oxisol, ultisol) and on medium sites the stature, complexity, and species richness and diversity of the natural ecosystem decline toward super-saturated and xeric sites in the equatorial zone and the drier, seasonal subhumid and semi-arid tropical zones. This is accompanied by a decline in the gross primary productivity, in the respiration and decomposition rates, and also in the speed of chemical processes and intensity of turnover of matter and energy.

This general trend continues beyond the arid and hyperarid subtropics as the latitude increases. Here again in each zone, vegetation stature, physiognomy, and functions follow similar trends along the gradients of moisture, temperature, and nutrients.

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