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Forest ecology

The forest canopy is the layer of the forest ecosystem that is photosynthetically active, and is an important interface between the atmosphere and the biosphere. The structure of the canopy determines the diversity of habitat and food resources for associated plants and animals. Canopy interactions with the atmosphere contribute to forest health, air quality, and climate.

Canopy structure. Canopy structure develops as forests age, often culminating in dense, multilayered canopies that may exceed 225 ft (70 m) in height in temperate and tropical rainforests. Forest canopies in less favorable environments are more open, as a result of wider tree spacing, and often reach only a few meters in height. Canopy structure is determined primarily by resource availability and disturbances.

Effect of resources. Canopy structure reflects tree adaptations to acquire adequate water and light. Water availability and snow accumulation influence tree crown height, shape, and spacing. The conical shape of boreal conifers is an adaptation for shedding snow and reducing winter breakage; the funnel shape of crowns in xeric forests is an adaptation for channeling water to roots; the arching form of rainforest trees is an adaptation for shedding water.

Forests with closed canopies or foliage characteristics that limit light penetration have shallower canopies than do forests with open canopies. Similarly, forests at low latitudes with high sun angles (tropical forests) maximize interception of light from above with shallowly domed crowns (**Fig. 1**). Subcanopies form at heights where cones of light penetrating shallow upper canopies intersect to form a zone of adequate light intensity. By contrast, trees at high latitudes and low sun angles (boreal forests) maximize light interception from the side with narrow crowns (boreal conifers). Light penetration under these conditions is insufficient for subcanopy development.

Effect of disturbance. All forests periodically experience disturbances that alter canopy structure. Catastrophic disturbances, such as wildfire, landslides, and hurricanes, remove the canopy over relatively large areas every 50–500 years and initiate canopy development. Small-scale disturbances that injure or kill individual trees or small groups of trees are more frequent; such disturbances include wind and storm damage, drought, breakage under the weight of snow or accumulated epiphytes, factors that increase competition for light and other resources, and infestations of insects and pathogens.

All tree species are adapted to survive some adverse conditions that kill or suppress other tree species. For example, shade-adapted tree species tolerant of low light intensities will be favored in gaps that are small relative to sun angle or canopy height; shade-intolerant tree species requiring full sunlight will be favored in large gaps. In the absence of further disturbances or other limiting factors, shade-intolerant species are eventually replaced, through the process of succession, by shade-tolerant species that can germinate and grow under the canopy. Therefore, disturbances tend to maximize forest diversity by maintaining a patchwork of varied canopy structures.

Canopy composition. Half of all known organisms may inhabit forest canopies. Older, more complex canopies with moderate temperature and humidity are especially diverse. Epiphytic plants intercept water and nutrients, and provide additional food resources and, in many cases, aquatic habitats. Small pools in tree cavities and epiphytic bromeliads are protected habitats for many amphibians and invertebrates. A variety of vertebrate and invertebrate herbivores, predators, and decomposers also make their homes in forest canopies and influence forest processes. Insects are especially well represented, with perhaps several million species in tropical canopies.

Most canopy organisms are highly specialized and rarely, if ever, are seen living near the forest floor. Many are restricted to particular tree species or canopy layers (**Fig. 2**). In turn, the importance of a tree species to canopy structure and function often reflects the presence of associated species that affect pollination, seed dispersal, growth rate, or branching pattern.

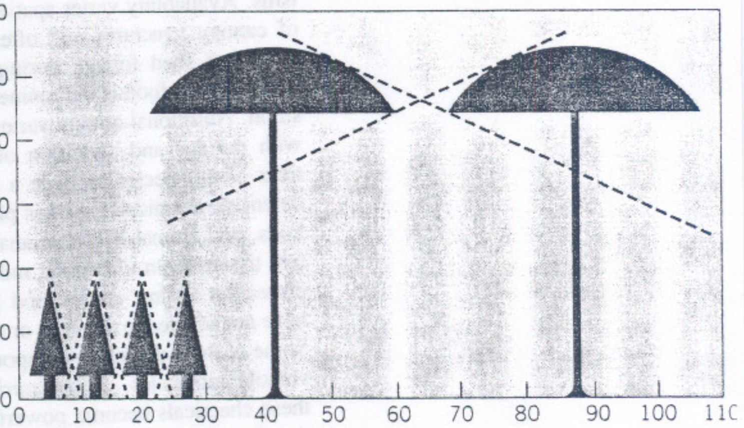

Fig. 1. Schematic representation of the canopy of a boreal forest (left) and a tropical forest (right) drawn to scale. The limiting angle for light penetration through the boreal canopy is 15° from the vertical, and for the tropical canopy 60°. 1 m = 3.3 ft. (*From J. Terborgh, The vertical component of plant species diversity in temperate and tropical forests, Amer. Natural., 126:760–776, 1985*)

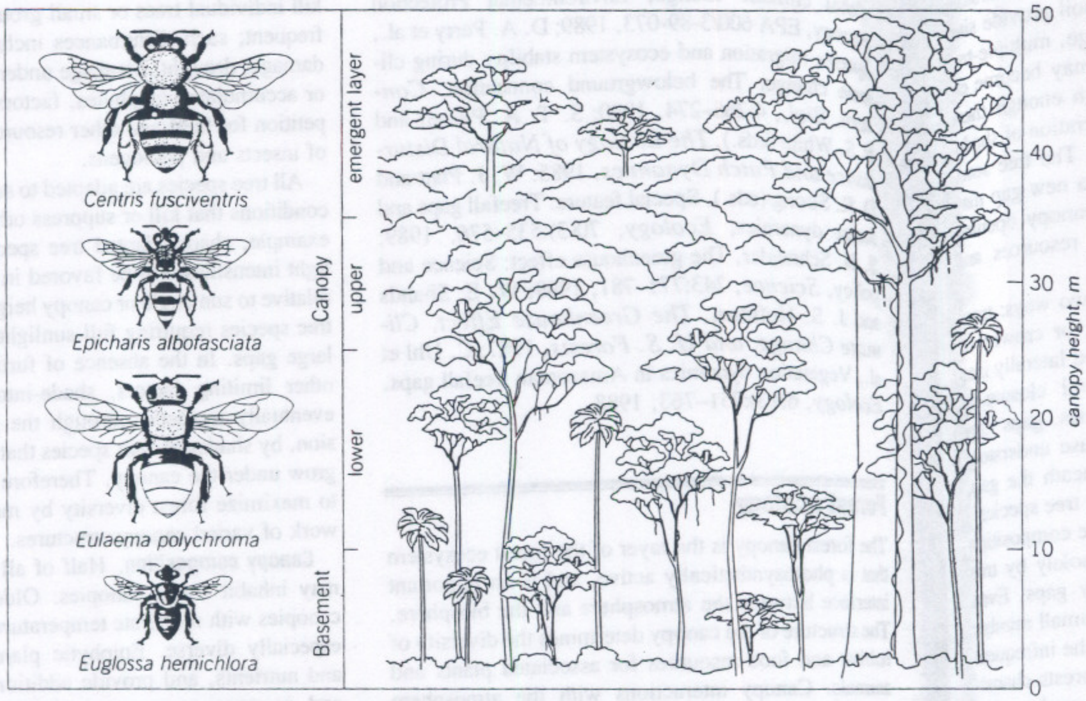

Fig. 2. Layering of environments in the rainforest. Each level of the forest has its own array of plants and animals, including pollinating insects. The two bee species at the top left were found only at the upper margin of the canopy, and the lower two species only in the forest below. 1 m = 3.3 ft. (*From D. R. Perry, The canopy of the tropical rain forest, Sci. Amer., 251(5):138–147, 1984*)

Nutritional quality and density of foliage and other plant tissues, size and orientation of branches, depth of bark crevices, and size of sunlit openings vary widely, especially in older forests. The variety of these resources determines the diversity of associated plant and animal species. For example, large epiphytes with high moisture requirements are restricted to large branches low in the canopy; insects that feed on young, succulent foliage occur on the outer margins of the canopy.

Canopy resources vary in availability, suitability, and visibility as food or habitat for associated organisms. Availability varies spatially over the patchwork of canopy structures and often varies seasonally in trees that shed foliage during unfavorable periods. Suitability as food is determined by chemical composition. Nutritional quality varies with tree species and with the age and condition of the foliage. Healthy trees of all species produce a characteristic array of defensive chemicals (such as phenols, terpenes, alkaloids, and animal hormone analogs) to protect sensitive tissues from ultraviolet radiation, and to provide protection against animal and pathogen species that have not adapted to detoxify or avoid these chemicals. Some of these defensive compounds are small, highly volatile molecules. When carried on the airstream, these chemicals become powerful signals that advertise plant location to adapted animal species that track host aerosols.

Feeding pressure by organisms adapted to plant defenses favors plants that produce new compounds. The biochemical diversity found in canopy plants and other organisms is gaining increased attention. Animals produce their own array of biochemicals, used to detoxify host chemicals, attract mates, and deter predators. Although the potential wealth of canopy compounds has barely been tapped, chemical screening, especially of tropical species, is yielding promising new pharmaceutical chemicals and natural pesticides. Natural products may regain attention as petroleum-derived products become more expensive.

Canopy function. Forest canopies are recognized for their importance to photosynthesis, evapotranspiration, and reduced soil disturbance and erosion. Research on canopy function has been limited by the difficulty of canopy access. However, development of canopy access and remote sensing techniques in the 1980s has stimulated canopy research. Elaborate rope-and-pulley systems suspended among neighboring trees have increased canopy access from the ground, permitting the first detailed observation of canopy communities. Sky cranes (tall structures with revolvable booms) are being used to access larger canopy areas, to map canopy structure, and to install monitoring equipment. Remote sensing via satellite and laser imagery now permits studies of canopy productivity, evapotranspiration, thermal flux, and foliar and atmospheric chemistry over extensive areas. As a result of these new techniques, canopy processes contributing to forest health, air quality, and global climate are becoming better understood. Figure 3 summarizes these canopy processes.

Forest health. The diversity of canopy species functions to maintain forest health and minimize disruption of ecological processes. Ground cover by the canopy reduces precipitation impact and erosion, and maintains the moderate environment essential for survival of many key species. The vast surface area of tree foliage and epiphytes serves to intercept water, nutrients, and other particulate materials from the atmosphere. Some epiphytic lichens, algae, and bacteria capture and convert atmospheric nitrogen, a critical and often limiting nutrient, into usable organic nitrogen through the process of nitrogen fixation. Decomposition of dead plant and animal tissues within the canopy makes nutrients available for canopy processes. Nutrients eventually reaching the forest floor increase soil fertility.

Even herbivorous insects, which are often viewed as pests, contribute to long-term forest health by pruning plant tissues that are photosynthetically inefficient or poorly defended, and releasing nutrients from these tissues. Nutrient availability and forest productivity can be enhanced for decades following insect population outbreaks.

Diverse and healthy canopies tend to prevent outbreaks of particular species. Because many canopy organisms are restricted to a particular tree species, a diverse canopy limits species ability to increase population size and exhaust resources. Necessary resources are widely scattered, chemically defended, and hidden by mixing of host and nonhost aerosols in the airstream. In contrast, forest canopies composed of one or a few tree species provide abundant resources for adapted organisms. Adverse conditions stress most trees simultaneously in such forests, increasing the likelihood of pest outbreaks and forest decline.

Canopy processes are essential to the long-term health and stability of forest ecosystems. Disruption of these processes through crop species selection, reduced biodiversity, canopy removal, and other management practices can reduce soil fertility and forest productivity, exacerbating adverse conditions and leading to forest decline.

Air quality. The filtering capacity of the canopy is instrumental in removing particles, including pollutants, from the air. Deposition of atmospheric particles on canopy surfaces augments other sources of essential nutrients. Filtering of fog and rain removes additional materials from the atmosphere; conifer forest canopies may intercept and filter as much as 30% of bulk precipitation, and broadleaved canopies 20%.

Unfortunately, this filtering capacity also aggravates canopy vulnerability to atmospheric pollutants. Acid deposition and toxic chemicals affect a substantial portion of the canopy during air passage through the forest. Toxic aerosols and acid precipitation deposited on foliage or absorbed through stomata destroy plant tissues and disrupt photosynthesis. Air pollutants have been implicated in forest declines in industrial areas of Europe and eastern North America.

Climate. Forest canopies have a substantial effect on local and global climate. Shading provided by the canopy reduces soil temperature and convective radiation, stabilizing diurnal and regional temperatures. Evapotranspiration further cools the forest and contributes to cloud formation and regional rainfall and humidity. Deforestation can raise regional temperatures and reduce precipitation.

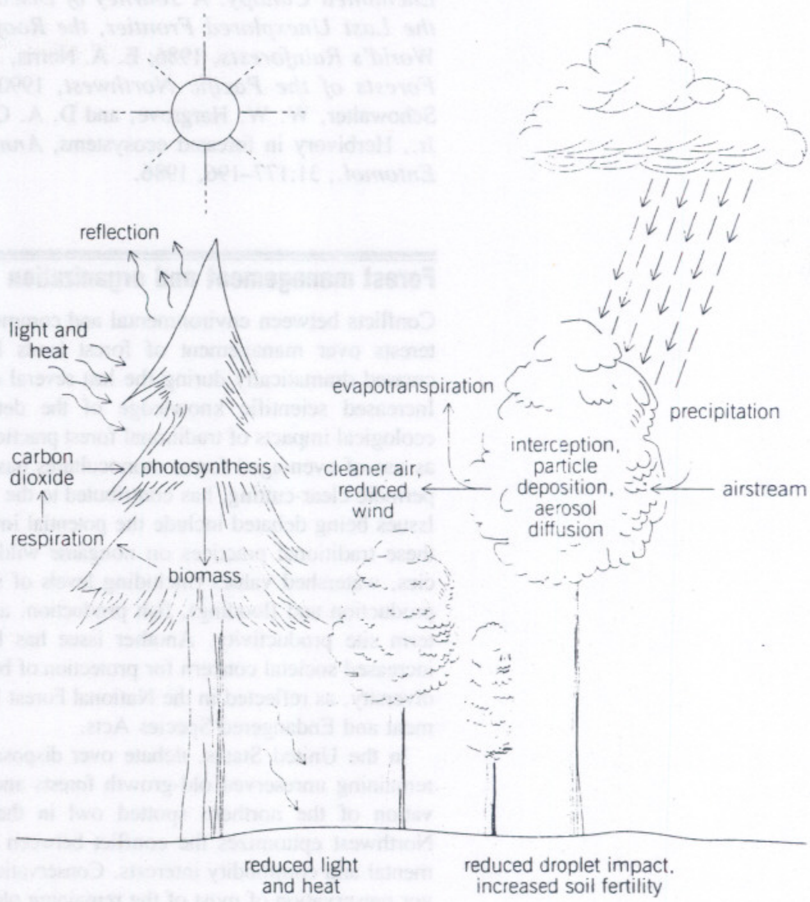

Fig. 3. Canopy processes influencing interactions between the biosphere and the atmosphere. The net result of the process of photosynthesis and respiration is reduced atmospheric carbon dioxide.

Incorporation of atmospheric carbon dioxide, a greenhouse gas, into forest biomass through photosynthesis in the canopy regulates the absorption of infrared radiation by the atmosphere. Forest biomass accounts for at least 60% of global organic carbon storage. Young trees are more efficient photosynthetically than are older trees, leading some resource managers to contend that conversion of older forests to younger forests will reduce atmospheric carbon dioxide. However, young forests harvested every 50–100 years cannot accumulate as much carbon dioxide as is released by harvest, burning, or conversion of older forests. Hence, harvest likely will increase the carbon dioxide content of the atmosphere. Increased atmospheric carbon dioxide, in the absence of cooling factors, is projected to increase global temperatures.

For background information *SEE* EVAPOTRANSPIRATION; FOREST AND FORESTRY; FOREST ECOLOGY in the McGraw-Hill Encyclopedia of Science & Technology.

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Forest management and organization

Conflicts between environmental and commodity interests over management of forest lands have increased dramatically during the last several decades. Increased scientific knowledge of the detrimental ecological impacts of traditional forest practices, such as use of even-aged forest monocultures based upon periodic clear-cutting, has contributed to the conflict. Issues being debated include the potential impacts of these traditional practices on nongame wildlife species, watershed values (including levels of sediment production and flooding), fish production, and long-term site productivity. Another issue has been the increased societal concern for protection of biological diversity, as reflected in the National Forest Management and Endangered Species Acts.

In the United States, debate over disposal of the remaining unreserved old-growth forests and preservation of the northern spotted owl in the Pacific Northwest epitomizes the conflict between environmental and commodity interests. Conservationists favor preservation of most of the remaining old-growth forests for their environmental and recreational values. One major environmental concern is maintenance of old-growth forest habitat for species such as the northern spotted owl, which was recently listed by the U.S. Fish and Wildlife Service under the Endangered Species Act as a threatened species. The forest products industry, on the other hand, favors logging of the remaining unreserved old-growth forests, arguing that sufficient acreage of old-growth forests is already preserved in National Parks, National Wilderness, and other reserved areas.

Traditionally, such conflicts have been resolved by allocating lands to primary or single uses, such as intensive timber production or preservation. New approaches to forest management that better integrate maintenance of ecological values with commodity production, sometimes called New Forestry, have emerged as an alternative to allocation. Although many of the specific practices advocated under New Forestry have their historical roots in traditional forestry, there are many differences. New Forestry incorporates an ecosystem view of the forest and provides tools that allow a more balanced weighting of ecological values with commodity values.

Scientific basis for New Forestry. New Forestry draws heavily on modern ecological concepts to design forest practices that retain ecological values while providing for production of wood products. The ecosystem paradigm, which recognizes the forest as a biological system with many essential and highly integrated parts, is one critical concept. For example, natural forests typically have high levels of spatial heterogeneity and structural diversity (including trees varied in size, species, vigor, and soundness). This richness in structural characteristics is one of the major reasons that natural forests provide habitat for a wide variety of organisms and exert great influence on ecological processes, such as those involved in regulation of nutrient and hydrologic cycling. For example, the immense surface areas of the multilayered canopies of the old-growth forests provide condensing surfaces for moisture and other atmospheric materials.

A second concept, biological legacies, relates to the recovery of natural forests following catastrophic disturbances, such as wildfire and windstorm. There are typically large legacies of living organisms in forms ranging from mature and seedling trees to spores and seeds found in the forest floor and fossorial animals. Extensive legacies of dead organic materials, including large structures, such as logs on the forest floor and standing dead trees (snags), also carry over from the ecosystem before the disturbance to the recovering ecosystem after the disturbance. For example, wildfire typically kills trees but does not consume much of the wood. Because of these legacies, natural young forests are typically diverse ecosystems with high levels of structural and compositional diversity rather than simply communities of young trees. SEE FOREST AND FORESTRY.

Consideration of large spatial scales, or landscapes, and longer temporal scales is a third concept underpinning New Forestry. This concept addresses the critical importance of issues such as patch sizes and arrangements, edge phenomena, corridors to wildlife, and the size of watersheds. Increasing evidence of ecological dysfunction at the landscape level, such as cumulative negative impacts on water quality from excessive cutting or fragmentation of forest cover, has spurred the interests of scientists and managers in landscape ecology.

Application of concepts at stand level. A basic principle of New Forestry at the level of the forest stand is maintenance of structural and compositional diversity within stands managed primarily for wood production. This contrasts with traditional forest practices that have emphasized simplification of forests, for example, creation of even-aged monocultures.

Many techniques that will promote greater species richness and structural diversity can be applied to young managed stands. An aggressive effort to establish mixtures of tree species, rather than monocultures, is one approach. For example, hardwood trees can be included within a stand dominated by conifers; or soil-building coniferous species, such as members of the Cupressaceae, can be added to plantations. Early successional plant and animal species can also be retained for longer periods by using wide spacings to delay tree canopy closure.

Maintaining a continuous supply of coarse woody debris (large standing dead trees and downed logs) is one technique increasingly used to provide structural diversity within managed forest stands and associated