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An Overview of Forest Canopy Ecosystem Functions with Reference to Urban and Riparian Systems

Abstract

Functions of forest canopy ecosystems generally include photosynthesis; sexual reproduction of trees; light absorption, modification, and shading; nutrient cycling; atmospheric interaction; hydrologic interaction; and biodiversity. In this paper, we briefly review some of these functions and draw comparisons from two specialized systems, the urban and the riparian. Urban forest canopies abate noise, ameliorate urban tempetature increases, conserve energy by shading buildings, and capture particulate matter, pollutants, and carbon dioxide from the air, which makes cities more livable for people. Riparian and wetland forest canopies affect temperature and primary production of aquatic habitat by shading, influence productivity by controlling allochthonous inputs including coarse woody debris, and provide unique habitat for wildlife and other biota.

Introduction

The forest canopy has been called an "independent and complex subsystem" (Carroll 1979) of the forest itself, where a myriad of organisms interact with the trees to effect ecosystem function. The forest canopy is more than a simple collection of tree crowns: it encompasses the living biotic components within these crowns as well as the residues of biota, dead wood, and abiotic components such as atmospheric particulate matter and gases. Forest canopies also "work"; that is they function within the ecosystem, one example being photosynthesis-the conversion of atmospheric carbon and light energy to sugars, a primary product on which most of life on Earth depends. Until recently, forest canopies have received little detailed attention because of the obvious difficulties of access. New technologies that afford access to the canopy (Moffett and Lowman 1995) are helping improve our knowledge of this complex subsystem and thus foster a more holistic understanding of forest ecosystems.

The functioning of forest canopies is important to the forest ecosystem as a whole. Processes of individual tree crowns extend to and from the roots, from the roots to the soil, and throughout the forest floor. Ecosystem functions of forest canopies include photosynthesis; sexual reproduction; light absorption, modification and shading; nutrient cycling; atmospheric-meteorological interaction; hydrologic interactions; and biological diversity. In this paper, we provide a brief overview of these general functions of forest canopies, followed by a discussion of two unique ecosystems—urban and riparian/wetland forests—that we believe deserve special reference.

Ecosystem Functions

Photosynthesis is the primary function of forest canopies (Holbrook and Lund 1995). Carbohydrates produced by the chemical fixation of carbon dioxide in the presence of light become the energetic basis of most forms of life. Within forest ecosystems, net primary productivity is controlled by the rate of photosynthesis and respiration in the canopy, and the allocation of the photosynthate to wood, respiration, and metabolic maintenance costs of other tissues and symbiotic organisms (Waring and Schlesinger 1985). The process of photosynthesis in leaves, controls material transfers of water, carbon dioxide, and pollutant uptake between the forest canopy and the atmosphere. Thus, understanding photosynthesis at the scale of forest canopies provides insight into productivity of forests, forest health, and nutrient and carbon cycling, from local to global scales.

Sexual reproduction of trees occurs in the forest canopy. Growth and development of flowers and cones, meiosis, genetic recombination, pollination, fertilization, maturation of fruit and cones, all occur in the canopy. Therefore, the basic processes which control evolution and the success of tree species is dependant on canopy ecology.

Forest canopies absorb and modify light, and shade the forest floor. The composition and structure of the forest canopy influences these features

(Canham et al. 1990, Canham et al. 1994, Parker 1995), which has implications for growth and productivity of understory plants, within-canopy photosynthesis, plant morphogenesis, and communication between animals and between plants and animals (Endler 1993). Shading influences the temperature of the forest floor and the soil, which controls the activity rates of soil microflora and fauna and of decomposition and nutrient cycling.

The physical and biological features of forest canopies play an important role in the cycling of nutrients. The canopy is a complex structure that provides a surface for wet, dry and cloud water deposition of mineral nutrients from the atmosphere, and the type of structure can influence the rate of deposition (Lovett 1994). The biotic features of the forest canopy function to capture, transform, and cycle nutrients within the canopy as a complex and independent subsystem of the whole forest (Carroll 1979, Edmonds et al. 1991, Coxson and Nadkarni 1995). Carroll (1979) has described complex trophic structures in forest canopies in Douglas-fir forests of the Cascade Range in Oregon, based on studies of the flow of nitrogen. Nitrogen enters the subsystem via atmospheric deposition, transport from the soil, and fixation in the canopy by cyano-lichens such as *Lobaria oregana*. Micro-epiphytic fungi, yeasts, and bacteria on the surfaces of leaves and twigs absorb and concentrate nitrogen deposited from the atmosphere or leached by cyano-lichens. These micro-epiphytes are then grazed by mites and other invertebrates, which are then consumed by a host of predators. Preditors in the canopy also consume the herbivores. The resulting trophic structure, similar to that in streams or other ecosystems, acts to conserve nutrients and enhance productivity of the forest.

Coxson and Nadkarni (1995) have reviewed the role of epiphytes in nutrient cycling of forest canopies. They list five reasons that canopy epiphytes and other biota can be important components of ecosystem function:

1) pools of nutrients and organic matter generated by epiphytes contained in the canopy can be high, even exceeding host tree foliage;
2) the contribution of epiphytes to complex canopy structure may enhance wet and dry deposition by increasing the physical area of canopy surfaces for impaction and sedimentation, and by increasing the biotic uptake by nutrient-efficient epiphytic plants;
3) free-living and symbiotic biota in the canopy can fix atmospheric nitrogen;
4) certain microbial activities (e.g. nitrification) in the canopy appear to be suppressed, relative to the forest floor, which tends to foster nutrients in a form that is less mobile and leachable; and
5) pools of canopy held nutrients are by no means static: nutrients move from the canopy to the other ecosystem members by four routes: a) as litterfall via abscission and by "riding down" fallen branches and whole trees, which is subsequently mineralized at variable rates, b) as crownwash in the form of throughfall and stemflow; c) via herbivory and predation of epiphytes by vertebrates and invertebrates, and d) directly to host trees via uptake by canopy roots.

The canopy component of forests plays an important role in the hydrologic cycle as the primary surface for interaction with rain, fog, and snow. In the Pacific Northwest, where trees grow large, the canopy of a Douglas-fir/western hemlock forest *(Pseudotsuga menziesii/Tsuga heterophylla)* may hold 3 x 10^6 liters/ha of water (equivalent to 3 cm of precipitation) (Franklin et al. 1981), and summer throughfall averages 76% of gross precipitation (Rothacher 1963). Much of the water captured by the canopy returns directly to the atmosphere through evaporation, soil water reaches the atmosphere through transpiration. Fog drip, caused by condensation of wind-driven clouds on conifers can be significant in some montane forests. Harr (1982) found that gross precipitation was greater in forests of the Bull Run Watershed in the Cascade Range of Oregon than clearcuts because of this condensation, and the cutting of the forests resulted in lower streamflow.

A major function of canopies in areas of high snowfall is the interception and storage of snow and the release of snow as meltwater or water vapor (Harr 1986, Berris and Harr 1987). In the transient snow zone, where rain-on-snow events are common, coniferous forest canopies appear to reduce the peak flows of stream water compared to clearcut areas and function as a buffer for the ecosystem, reducing extremes of water release and the erosion associated with them (Harr 1986, Berris and Harr 1987).

The forest canopy is a porous, living, medium that constantly interacts with the atmosphere, exchanging water, energy, and carbondioxide and other gases, while absorbing wind energy, heat, and radiation (Nadkarni 1994, Fitzjarrald and Moore 1995, Parker 1995). Waring and Schlesinger (1985) estimate that "the equivalent of the entire atmospheric content of carbondioxide passes through the terrestrial biota every 7 years, with about 70% of the exchange occurring through the forest ecosystems." These interactions between canopies and the atmosphere influence microclimate in the forest stand, as well as local, regional, and global climate. The structure and composition of the forest canopy controls the magnitude of atmospheric interaction (Parker 1995).

Forest canopies control biological diversity by physically dominating the potential substrates and resources of the aboveground system, contributing litter and woody debris to the forest floor, and providing photosynthate that fuels the belowground system. Biological diversity in the canopy (and elsewhere) is influenced by forest canopy age, composition, and structure, particularly in the coniferous forests of the Pacific Northwest (Franklin et al. 1981). Epiphytes in Douglas-fir/western hemlock forests, for example, appear to reach highest biomass and diversity in old-growth forests, partly because the deep, vertically stratified canopy has more complex and heterogenous microclimatic conditions than younger, even-aged forests (McCune 1993, Sillett and Neitlich this issue). Wood decay and associated micro-organisms reach their greatest abundance in old-growth canopies (Parks and Shaw this issue). Microfungi act as parasites, symbionts, and microepiphytes, the diversity of which reflect the diversity of potential substrates (Stone et al. this issue). Invertebrates, especially arthropods, have more complex food webs and higher species diverisity in older canopies (Winchester and Ring this issue). Vertebrates, such as arboreal mammals (Carey this issue), bats (Wunder and Carey this issue), and birds (Sharpe this issue), find more diverse resources in older canopies than in young, even-aged canopies.

Specialized Canopy Ecosystem Functions

In the Pacific Northwest, we recognize two distinct ecosystems in which forest canopies have functions unique from the typical terrestrial canopies: urban and riparian/wetland. For example, shade is a function of canopies in all these ecosystems, but the effects of shading are different. In urban areas, the canopy shades built surfaces, resulting in less heat absorption and re-radiation, and thus cools the environment and ameliorates the heat sink effect by which urban areas contribute to global warming. In riparian forests, shade controls primary productivity in streams and the temperature of water, which has a direct influence on fish production (Franklin et al. 1981). In terrestrial environments, shade from the forest canopy directly controls the productivity of the plants on the forest floor, which influences populations of herbivores.

Urban Forest Canopies

Because of a growing human population and expanding urban areas, urban forests are increasingly important both locally in the Pacific Northwest and globally. For example, an estimated size of the potential urban forest, as the current area of incorporated cities and towns, in a four-county area of western Washington (Whatcom, Skagit, Snohomish, King), is 166,281 ha (649 square miles). One hundred and fifty years ago, this same area was relatively pristine. The urban forest is unique compositionally. For example, Seattle has more than 740 species and varieties of trees in the urban area, but the original vegetation had only about 29 species (Jacobson 1989). The extreme diversity of trees in the urban area gives urban planners and designers a plethora of options in integrating trees into the urban environment, and in a sense, engineering ecosystem functions of the urban forest.

The urban environment/ecosystem is particularly important because of the direct influence on human physical comfort, health, and use of energy resources (Rowntree 1986, McPherson and Rowntree 1993, Nowak 1993). Urban forest canopies (Figure 1) act to abate noise (Mecklenberg et al. 1972, Reethof and Heisler 1976, Mao et al. 1993); check atmospheric contaminants (Smith and Docincher 1976); shade built surfaces, which reduces the amount of radiant energy absorbed, stored, and radiated (McPherson and Rowntree 1993); modify microclimate (Federer 1976, Heisler and Herrington 1976, Oke, 1988, 1989, Wilmers 1990/1991, McPherson and Rowntree 1993, Mao et al. 1993); ameliorate the urban heat sink effect;

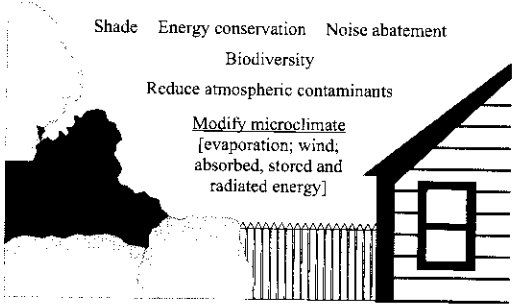

Figure 1. Characteristics of the urban forest canopy.

conserve energy (Heisler 1986, Wilmers 1990/1991, McPherson and Rowntree 1993); and influence biological diversity of urban areas (Rowntree 1986).

The modification of microclimate, saving of energy resources, and amelioration of urban heat sink are well-studied ecosystem functions of forest canopies . In addition to the cooling effect of shading, evapotranspiration converts radiant energy into latent energy, which reduces sensible heat that warms the air; air flow modification by urban forest canopies affects transport and diffusion of energy and water vapor. Temperatures in greenspaces of buildings have been shown to be as much as 3 degrees C cooler than adjacent areas outside the greenspace, and temperature differences of more than 5 degrees C have been observed between cities and more-vegetated suburban areas (McPherson and Rowntree 1993).

Riparian/Wetland Forest Canopies

Riparian forests have received considerable attention for their influence on aquatic ecosystems (Salo and Cundy 1987, Raedke 1988, Gregory et al. 1991, MacDonald et al.1991). Within the same four-county area of western Washington viewed for urban areas are 17,697 linear kilometers of mapped streams and rivers (Nooksack, Skagit, Samish, Stillaguamish, Snohomish and the Lake Washington/Cedar River watersheds). The estimation of extent of the riparian forest is complicated and depends in part on the classification of intermittent streams (Swanson et al. 1982, Gregory et al. 1991). To estimate the size of the riparian forest in this four-county area, we have estimated 100 m on either side of the rivers and streams as the riparian forest, which give about 353,934 ha.

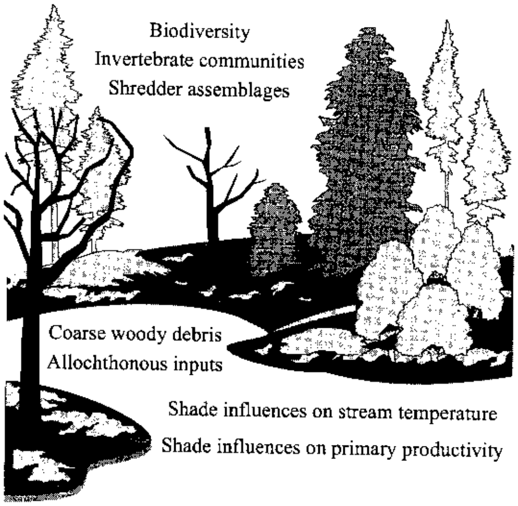

Figure 2. Characteristics of the riparian//wetland forest canopy.

Shade from riparian canopies (Figure 2), and its affect on solar radiation, has a major influence on the aquatic environment (Swanson et al. 1982, Hawkins et al. 1983, Gregory et al. 1991). Shade influences stream temperature, which influences the amount of oxygen in the water, rates of decomposition, and activity of stream animals. Shade also influences primary productivity of aquatic plants, thus affecting net primary productivity of streams (Swanson et al. 1982, Gregory et al. 1991). Direct insolation in small scale openings in streams resulted in a higher density of vertebrates presumably because of increased algae growth, increased grazing insects, and an improved food supply for fish and salamanders (Hawkins et al. 1983).

Allochthonous inputs into aquatic habitats are primarily controlled by the forest canopy. Litter quantity and quality influence communities of invertebrates, such as shredders (Swanson et al. 1982, Cummins et al. 1989) and the food webs they spawn. Coarse woody inputs into stream environments play an important role in the structure of the aquatic environment, creating a complex of pools, backwaters, ripples and eddies (Swanson et al. 1982, Gregory et al. 1991).

As in other ecosystems, the age, structure, and composition of riparian canopies directly influence ecosystem functions (Swanson et al. 1982, Hawkins et al. 1982, 1983, Bilby 1988, Gregory et al. 1991, Bilby and Bisson 1992). Gregory et al. (1991) cite the example of dense, low, overhanging canopies greatly reducing light, yet high, relatively open canopies allow more light to reach the stream.

Riparian forest canopies contribute to biologic diversity because the composition and structure of these forests is often distinct from adjacent upland forests. Microclimatic conditions associated with flowing water create distinct habitats, and a natural "edge" is created by the continual disturbance to streamside vegetation. Epiphytic communities may be more abundant and have more cyano-lichens (Sillett and Nietlich this issue), and bird communities also respond to the unique vegetation and habitats (Sharpe this issue).

Summary

Canopies form a complex subsystem in forest ecosystems. Organisms such as microbes, fungi, epiphytes, invertebrates, and vertebrates, along with the associated vegetative composition and structure interact to influence ecosystem functions. Urban forests and riparin/wetland areas illustrate the important processes and functions of forest canopies. To link canopy ecosystem functions with the objectives of ecosystem management requires a more integrated research focus on complex canopy interactions across diverse ecosystems than has been used in the past.

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