

## Forest Canopy-Atmosphere Interactions

### Abstract

Exchanges of materials (gases, nutrients, water, pollutants, and energy) between forest canopies and the atmosphere drive important ecosystem processes and influence many meteorological phenomena. Trees must exchange water, carbon dioxide, and energy with the atmosphere to survive. As new instruments and quantitative tools emerge for measuring forest and atmospheric conditions, the complexities of canopy-atmosphere interactions can be more accurately understood and modeled. Improved knowledge of canopy-atmosphere interactions is becoming more important as human activities alter both the structure and function of forest canopies, as well as the chemical and physical properties of the atmosphere. The increased scientific focus on structural and functional attributes of forest canopies in recent years promises to yield new insights into the effects of human disturbance on environments in forest canopies and the atmosphere. Important topics for future research in canopy-atmosphere interactions include: (1) the influence of elevation, forest edge, and canopy roughness on atmospheric deposition of pollutants; (2) the dynamics of carbon sequestration in forest biomass in relation to forest management practices and other disturbances; (3) the effects of anthropogenic pollutants on forest functioning and atmospheric feedbacks; and (4) the functional changes in forest canopies associated with structural changes, and consequences for watershed hydrology and nutrient cycling.

### Introduction

The forest canopy forms a major interface with the atmosphere over much of Earth's surface. Canopy-mediated exchanges of mass and energy largely define ecosystem productivity. Key interactions between the canopy and the atmosphere are influenced by environmental conditions such as climate, moisture, and nutrient availability (Mooney and Gulmon 1982, Van Cleve et al. 1983). In turn, wind velocity, energy budgets, rainfall, and other environmental conditions are variably modified by the canopy and can affect forest hydrology (Cavelier and Goldstein 1989). Forest canopies modify climates locally, regionally, and globally (Avisar and Pielke 1989, Shukla et al. 1990). Changes in the pool sizes and fluxes of nutrients, water, and carbon through forest ecosystems have important consequences not only for the prosperity of human economic systems, but also for the sustainability of life on Earth.

As a consequence of complex meteorological and biological processes, resources and microclimates within forest canopies are spatially and temporally diverse. Within these canopy "niches," specialized organisms have evolved that alter the environment for other species and iteratively form a trophic chain or "food web." Complexity and diversity at one level nurture complexity and diversity at yet higher levels. This paper explores some of the important interactions between the atmosphere and forest canopies in terms of canopy

physiology, function, and structure, with emphasis on coniferous forests. An overview of canopy-atmospheric functions and interactions is provided, including the interception, retention, modification, and conductance of energy (light, heat), gases (primarily carbon dioxide), water, and nutrients (Figure 1). Canopy interactions with wind and pollutants also are briefly discussed.

Anthropogenic disturbances such as deforestation, stratospheric ozone depletion, pollution, biomass burning, water shortages, and other factors associated with expanding human populations and industrialization pose a growing threat to forest ecosystems. A better understanding of interactions between forest canopies and the atmosphere is urgently needed to accurately assess, mitigate, and perhaps prevent negative impacts on ecosystem health from human disturbance.

### Trace Gases

Trace gases in the atmosphere range from highly reactive species with lifetimes in seconds to hours, to stable compounds with lifetimes in years or centuries. The sources, sinks, and dynamics of these gases are important for several reasons. First, many gases affect the chemistry and physics of the atmosphere and thereby can affect various natural processes, such as concentrations of tropospheric oxidants, ultraviolet absorption in the stratosphere, and the energy budget of Earth. Second, trace gases or their reaction products inter-

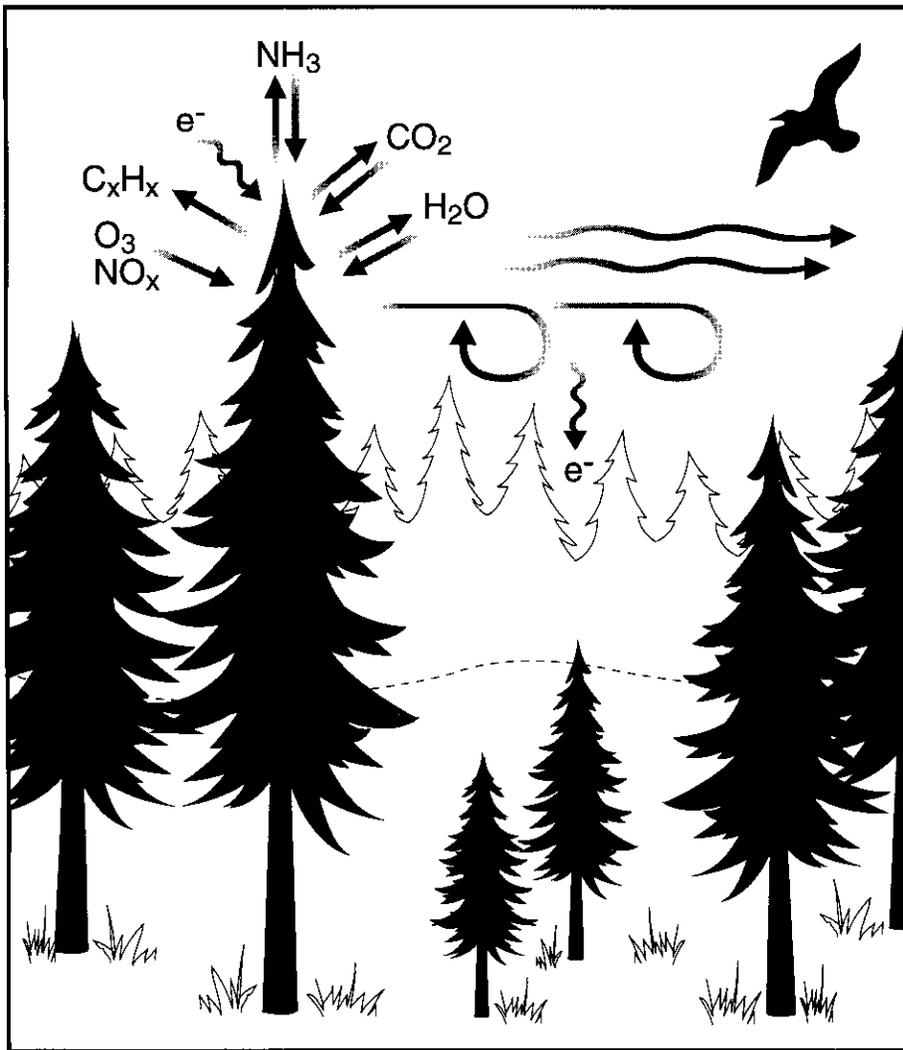


Figure 1. Complex and interacting processes influence the exchange of materials and energy between forest canopies and the atmosphere.

act with the biota to cause a multitude of effects ranging from increased productivity to heavy mortality. Third, the production or consumption of these gases serves as an important indicator of ecosystem functioning. The forest canopy is a major biologic entity interacting with the atmosphere to influence the concentrations and fluxes of trace gases. Consequently, the mechanisms of this interaction are important to understanding the dynamics of terrestrial ecosystems in relation to the atmosphere.

Excluding the anthropogenic chlorofluorocarbons, the more stable gases are generally higher

in concentration, and seasonal distribution patterns are better characterized. Long-term trends in concentrations have been documented in ice bubbles from Antarctic ice cores (Rasmussen and Khalil 1984, Pearman et al. 1986). This group of gases includes carbon dioxide ( $\text{CO}_2$ ), methane ( $\text{CH}_4$ ), and nitrous oxide ( $\text{N}_2\text{O}$ ), three stable biogenic gases that are increasing globally.

#### Carbon Dioxide

Energy to drive most processes in forest ecosystems is derived initially by the fixation of atmospheric  $\text{CO}_2$  into sugars through photosynthesis

in leaves. In photosynthesis,  $\text{CO}_2$  diffuses through small pores or stomates, into foliage where it is biochemically reduced to sugars using energy in the form of adenosine triphosphate (ATP) produced by the capture of sunlight by leaf pigments. In respiration, the breakdown of sugars to yield energy for plant growth and metabolism produces  $\text{CO}_2$  as an end product. Respired  $\text{CO}_2$  then diffuses back out of the leaf stomates into the atmosphere.

The uptake of  $\text{CO}_2$  by forest ecosystems during the daytime is controlled primarily by the response of photosynthetic rate to increasing light (photosynthetically active photon flux density, or PPF) (Hollinger et al. 1994b). The saturating response of leaf photosynthesis to light is explained by the fact that carbon uptake is limited at low PPF by insufficient electron transport and photophosphorylation, and at high PPF by insufficient carboxylation capacity (Farquhar et al. 1980, Kirchbaum and Farquhar 1984). In response to temperature, photosynthesis in many species has been found to reach a maximum between 15 - 30 °C. This results from the differential effect of temperature on the kinetics of  $\text{RuP}_2$  carboxylase-oxygenase for carbon dioxide and oxygen (Berry and Raison 1981). Other factors such as vapor pressure saturation deficit and water stress also can directly inhibit photosynthetic mechanisms, and indirectly inhibit photosynthesis by reducing stomatal aperture (Morison 1987). Similarly, the functional response of nighttime respiration to temperature dominates the production of carbon dioxide by leaves. Respiration during darkness increases approximately exponentially with the inverse of the absolute temperature.

Forest canopies differ in their productive capacities and their rates of exchange seasonally and in relation to temperature and the availability of water and nutrients. For example, humid tropical forests comprise only 6.6 percent of Earth's surface area, but accomplish 17 percent of the total net primary production. Another generalization is that young forests are a more efficient sink for  $\text{CO}_2$ ; however, older forests contain larger stores of carbon.

A recent study by Hollinger et al. (1994b) explored how environmental modifications by a forest canopy potentially alter basic patterns of ecosystem  $\text{CO}_2$  exchange compared to the current understanding of leaf gas exchange. Net flux be-

tween the ecosystem and the atmosphere was determined from the sum of the eddy flux above the forest and the change in the mean concentration of  $\text{CO}_2$  in the forest air below the canopy. The  $\text{CO}_2$  exchange patterns were similar in many ways to patterns observed at the leaf level. Seasonal changes in the relation of  $\text{CO}_2$  uptake and dark respiration varied however, with other environmental and physical characteristics that had little importance at the leaf level, such as the above-canopy spatial distribution of PPF and turbulent transport.

This and other recent studies have demonstrated that in modeling  $\text{CO}_2$  exchange, forest canopies cannot be treated as simple analogs of leaves. At the canopy level, gas exchange is controlled not only by biological processes in the leaf, but also by canopy architecture, temporal changes in the environment, site characteristics, and environmental gradients that vary spatially around vegetation (Norman 1993). Modeling efforts that attempt to scale atmospheric interactions to the level of whole canopies are described by Baldocchi (1993), Norman (1993), and Schimel et al. (1993). Modeling of gas exchange in conifer canopies is described by Price and Black (1990) and Wang and Jarvis (1990).

Approaches to modeling whole-canopy photosynthesis are reviewed by Norman (1993). The most popular approaches to estimating canopy gas exchange use the following variables: (1) absorbed, photosynthetically active radiation and leaf photosynthetic efficiency; (2) average illumination and leaf area index; (3) photosynthetic rate and total leaf area; (4) photosynthetic rate and leaf area of sun and shade foliage; and (5) leaf energy balance and environmental gradients. Particularly important research topics in canopy gas exchange include dynamic variations in turbulence and physiology.

### Methane

Tropospheric methane is increasing at about 1.1 percent per year, a substantially greater percentage increase than for  $\text{CO}_2$ . Methane is produced by specialized anaerobic bacteria that reduce  $\text{CO}_2$ . Primary sources of methane include anaerobic environments, such as wetlands, digestive systems of cattle and termites, and mining of fossil fuels (Mooney et al. 1987). Methane may have an indirect effect on forest canopies through its

influence on climate and atmospheric chemistry. A strong greenhouse gas, methane absorbs outgoing infrared radiation within the troposphere 20 times more effectively per molecule than does CO<sub>2</sub>. In addition, by reacting with hydroxyl radicals, methane can produce compounds harmful to canopy foliage, such as carbon monoxide (CO) and ozone (O<sub>3</sub>).

### Nitrogen

Although dinitrogen (N<sub>2</sub>) is the most abundant element in the atmosphere, it is also the element that most limits photosynthesis and primary production in many terrestrial ecosystems. This paradox is explained by the fact that N<sub>2</sub> in the atmosphere can be converted to biologically available forms by only a few species of prokaryotes, and because the process of nitrogen fixation is energetically expensive. Forest canopies are important sources of nitrogen fixation by both free-living and symbiotic bacteria on vegetation and epiphytes. Another form of nitrogen, nitrous oxide, N<sub>2</sub>O, is increasing globally due primarily to combustion. Nitrous oxide may affect forest canopies by contributing a small amount towards the breakdown of the stratospheric ozone layer and to global warming in the next several decades (Mooney et al. 1987).

### Reactive Gases

Reactive gases are produced biologically and by combustion, but are more difficult to quantify due to their ephemeral nature. The effects of these gases also are problematic because they can interact regionally or locally to cause the production or destruction of other gases having a major impact on atmospheric chemistry and terrestrial biota. Major classes of reactive gases include the non-methane hydrocarbons (NMHC) and CO. The NMHC, including isoprene and terpenes, are linked to the destruction of ozone and production of atmospheric CO. There is no evidence, however, that atmospheric concentrations of NMHC directly affect physiological or biochemical characteristics of foliage. Carbon monoxide has no direct biological effects at current atmospheric concentrations, but it interacts with nitrogen oxides and hydroxyl to produce tropospheric ozone, a phytotoxic compound.

Reactive nitrogen gases include oxides of nitrogen (N), referred to as NO<sub>x</sub>, which are derived

primarily from combustion and, to a lesser extent, from biological processes of nitrification and denitrification in soils. The role of NO<sub>x</sub> in atmospheric chemistry is complex - under varying conditions, it can catalyze both the production and destruction of ozone. It also is readily converted to nitric acid that forms a major component of acid precipitation downwind of industrial areas. As a fertilizer, N deposition to N-deficient forests may increase plant productivity or stimulate unhealthy changes in vegetation growth patterns and nutrition (Aber and Melillo 1991).

Although present in the atmosphere at low concentrations, ammonia sources have been augmented by intensive agriculture and livestock farming. Atmospheric ammonia can be dissolved or adsorbed by aerosols or precipitation, or be taken up directly by vegetation. In aerosols or cloud droplets, ammonia can protonate to reduce the acidity of precipitation. But if deposited ammonium is retained by vegetation or lost as nitrate, soil acidification results (Binkley and Richter 1987).

Natural terrestrial ecosystems emit an even wider array of sulfur compounds, mostly in anaerobic conditions, including hydrogen sulfide (H<sub>2</sub>S), dimethyl sulfide, methyl mercaptan, carbon disulfide, and carbonyl sulfide. All but the last compound are short lived. According to current evidence, the flux of H<sub>2</sub>S is much higher in tropical than temperate forests. Sulfur from anthropogenic fuel combustion contributes to acidified precipitation and altered nutrient cycling in forests.

Ozone in the troposphere is a strong oxidant formed by a complex set of reactions involving NO<sub>x</sub> gases, hydrocarbons, oxygen, and sunlight. Ozone can injure tree canopies by damaging leaf membranes and inhibiting photosynthesis (Bytnerowicz and Grulke 1992). In fact, on a regional scale, ozone is the only air pollutant known to be phytotoxic at ambient levels in western North America. The literature on ozone effects on forested ecosystems in the western United States is synthesized in Olson et al. (1992). Ozone monitoring data for the Pacific Northwest have been summarized by Eilers et al. (1994).

### Radiation and Heat

Radiation absorption in the atmosphere is a function of the pathlength through the atmosphere and the content of absorbing compounds, particularly water

vapor. In addition to shortwave radiation from the sun and sky, an important contribution to the radiation balance of canopies is made by longwave radiation. Longwave radiation is emitted by the gases (especially water vapor and CO<sub>2</sub>) present in the lower atmosphere. The presence of clouds increases the downward flux of longwave radiation because clouds are more effective emitters. Radiation losses from the forest canopy include thermal radiation emitted, as well as any incident radiation that is reflected or transmitted (Jones 1992).

Photosynthetic pigments in the forest canopy absorb incident light radiation mainly in the visible wavelengths (Salisbury and Ross 1985). Flux density of radiation in a canopy at a given wavelength is the sum of the direct beam and diffuse sky radiation that penetrates foliage gaps and is modified by scattering on leaf surfaces. Consequently, properties of light at any point in a canopy are dependent on conditions in the atmosphere, and the physical, chemical, and structural attributes of the canopy (Baldocchi 1993). Detailed information on physical attributes of the canopy is needed to assess the diffusive source-sink gradient and the transmission of radiation directly. The total leaf area of a canopy, species compositions, leaf spatial and elevational distribution, and angular orientation all affect the radiation environment of forest canopies. Various stresses to vegetation, including nitrogen deficiencies and moisture deficit, can affect the light absorption and reflectance properties of foliage due to changes in cellular structure and pigment functioning of foliage.

A useful approximation of radiation behavior in forest canopies is that a constant fraction is absorbed per unit distance into the canopy. This produces exponential light decay with increasing cumulative leaf area. The decay of radiative energy with distance into the canopy causes heating of the biomass and air that produces a stable density stratification in the canopy of warmer lighter air above, and cooler denser air below and partially isolates the lower canopy from the atmosphere. This effect is strongest for canopies with thick foliage near the top. At night, the canopy interferes with the loss of longwave radiation under the canopy, whereas substantial radiative cooling occurs above the canopy, and leads to strong stable layers near the top of the canopy. Temperature and humidity at the leaf surface are determined by the balance of incoming shortwave and

longwave radiation and its partitioning into sensible and latent heat exchange. When considering energy partitioning of the whole canopy, advection, and soil and canopy heat storage also must be taken into account (Baldocchi 1993). Important to note too, is that heat transport in forests can move up the gradient, contrary to expectations. This is because sporadic turbulence at scales much larger than the local gradient can produce "up-gradient" mixing.

## Water

Less than 1 percent of Earth's water is contained in the atmosphere, soil, lakes, and rivers. The atmosphere contains only 0.001 percent of Earth's water, which would amount to an average depth over the planet's surface of 20-30 mm (Mooney et al. 1987). Nevertheless, water is an important controlling factor in vegetation processes and in tropospheric temperature structure through effects on both solar and terrestrial radiation.

Water vapor transfer depends on the flows of energy that convert liquid to vapor and on molecular and turbulent diffusion that transfers water vapor molecules between the leaf and the free air. As with CO<sub>2</sub> exchange, water vapor exchange from tree canopies is dependent on all biological and structural attributes that influence local concentrations in the canopy, such as radiation, temperature, turbulence, humidity, and leaf physiological condition.

Actual evapotranspiration (AET) is the sum of all water lost to the atmosphere from the soil or vegetation surfaces (evaporation) and through plant tissues (transpiration). Potential evapotranspiration (PET) is the amount of evapotranspiration that would occur with unlimited water supply. In drier climates, AET is lower than PET. Evapotranspiration increases directly with water availability and with higher evaporative demand at the leaf surface (higher temperature and lower humidity) (Aber and Melillo 1991).

Forest canopies interact both directly and indirectly with the hydrologic cycle. Leaves, branches, and stems intercept and redirect water to the soil in throughfall or back to the atmosphere via evaporation and transpiration. Annually, as much as a third of the incoming precipitation may be intercepted by forest canopies ranging from tropical to boreal types. Structural aspects of the canopy influence the amount of intercepted ra-

diation, boundary-layer characteristics, and the amount of water available for evaporation. These influences are evident when forest cover over an entire watershed is removed and streamflow increases substantially.

Water movement from the soil through the forest canopy to the atmosphere is driven by a series of interrelated, interdependent processes. For example, the rate of water absorption by the soil is affected both by the rate of water loss from the leaves to the atmosphere and by the rate at which water can move from the soil to the root surface. Water loss and interception by tree canopies also is influenced by both the amount and duration of leaf area. For example, pine forests lose more water to the atmosphere than do hardwoods, owing to higher leaf area and to the maintenance of needles year-round. Species-specific differences in water loss also exist. Species with deep roots that can access abundant water supplies, typically sustain higher rates of evapotranspiration (Waring and Schlesinger 1985).

The quantity and distribution of water vapor controls both ecosystem and atmospheric dynamics directly. Changes in Earth's energy balance in response to greenhouse warming are expected to dramatically alter regional water budgets (Mooney et al. 1987). Hollinger et al. (1994a) recently found rapid transmittance of hydraulic pulses from the top of a *Nothofagus* tree to a mid stem and basal stem position, respectively. These pulses were induced by changes in atmospheric humidity as air of various moisture content passed over the canopy. These findings indicate that the water column is under tension governed by physical forces and that water storage plays little role. Additional research is needed to clarify the mechanisms governing evapotranspiration by forest canopies.

## Nutrients

The forest canopy is a major repository of plant and ecosystem nutrient capital. Processes within the canopy influence the retention, uptake, leaching, and redistribution of nutrients within the canopy and among the canopy, the soil, and the atmosphere. In addition to the uptake of nutrients deposited in various forms from the atmosphere to the forest canopy, canopies also are emitters of various compounds, including hydrogen sulfide, ammonia, and K-, S-, and P-containing

aerosols. During fires, large quantities of nutrients also are lost in the gases and smoke from forest canopies (Waring and Schlesinger 1985).

Ecosystem carbon and nutrient cycles are mutually linked because the chemical composition and quantity of litter supplied by the canopy modulate the processes of decomposition, mineralization, and nitrification (Fogel and Cromack 1977, Meentemeyer 1978, Melillo et al. 1982, Pastor and Post 1986). Canopy-atmosphere interactions influence these processes through changes in the carbon and nutrient ratios of foliage mediated by differences in the availability of photosynthate and nutrients. Atmospheric conditions favorable to photosynthesis may increase the foliar carbon-nutrient ratio, whereas conditions limiting gas exchange would have the opposite effect, depending also on site nutrient availability. Furthermore, the canopy influences nutrient cycling by altering moisture and temperature conditions at the forest floor.

## Wind and Turbulence

Air in the lower atmosphere is never completely still. There is usually a net horizontal motion or wind, with random movements of smaller air pockets. In free convection, air movements are caused by changes in air density, as results from heating or cooling. In forced convection, air movement is determined by an external pressure gradient causing wind. Forced convection may lead to the generation of eddies or turbulence as a result of frictional forces that develop as wind flows over an object. Characteristics of the eddies and turbulence over a forest canopy combined with attributes of the canopy boundary layer, control many aspects of mass and energy exchange with the atmosphere.

Turbulent motion has a controlling influence on the distribution and redistribution of mass and energy through forest ecosystems. Many aspects of canopy-atmosphere interactions are influenced by the fact that windflows and turbulent exchanges above forest canopies are poorly described by flat-plane boundary layer models. In addition, physical and biological influences on canopy microclimate are often complementary. For example, seed and pollen dispersal depend on a turbulent wind field, which in turn is affected by the biomass profile. Diurnal changes in canopy relative humidity affect the movements of insects and other

organisms. (Murlis et al. 1992, Fitzjarrald and Moore 1995).

Consistent with mean wind profiles, turbulent transport of horizontal momentum decays rapidly below the canopy surface; however, the degree to which the canopy is coupled to the atmosphere changes diurnally, with stronger coupling during the day than night (Fitzjarrald et al. 1988). The term "forest anomaly" has been used to describe the fact that flux profiles above rough forests are not the same as those above flat surfaces (Raupach 1979). This seems to result because the eddies are much larger than their height above the canopy, compared to turbulent flows over flat surfaces. Momentum transport to a canopy depends to a large degree on the roughness of the surface. When canopies are sparse, each tree is considered a roughness element.

### Pollutant Deposition

The processes controlling pollution deposition to forest canopies deserve special mention here. Atmospheric deposition occurs through three separate processes: (1) wet deposition in precipitation; (2) dry deposition in particles and gases; and (3) cloud deposition in droplets. Wet and dry deposition are ubiquitous, whereas cloud deposition is common in coastal and mountainous areas. Wet deposition is generally controlled by the concentration, size, and solubility of particles or gases, gas reactivity, and the meteorological processes affecting precipitation. Dry deposition is controlled by many factors, including atmospheric chemistry and meteorology; canopy structure; and physiological, chemical, and structural properties of foliage. Cloud-fog deposition is controlled by factors similar to wet deposition, though properties of the receptor surface are more important (Lovett 1994).

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Coniferous forests with fine needles are highly efficient at collecting wind-driven cloud droplets (Unsworth and Wilshaw 1989). Previously deposited pollutants on leaf surfaces can dissolve, creating more concentrated solutions than the incident cloudwater. Furthermore, moistened leaf surfaces increase deposition of particles by reducing bounce-off and resuspension, and by providing a sink for soluble gases. Diffusion through stomates is a primary pathway for entry of gases into leaves. Gases also may react chemically with leaf surfaces and remain fixed. Deposition rates for gases are thereby affected by both stomatal response and environmental effects on stomatal conductance. Stomatal closure during summer drought may afford some protection from ozone during this period. Dry deposition via minute particles is negligible, although fine sulfate particles may enter stomates.

Properties of the plant cuticle determine the interactions with wet deposition. Precipitation may be both a source and a sink for pollutants. As polluted water evaporates from the leaf surface, ion exchange may occur between the leaf interior and surface. With rapid evaporation, acid may reach damaging levels on leaf surfaces. Soluble gases also may diffuse into the water film. The most important canopy transformations of incident precipitation are the direct assimilation of nutrients by foliage, hydrogen ion buffering in the canopy, and metal cation leaching (Bredemeier 1989).

Although beyond the scope of this paper, atmospheric processes have important effects on the transport and dispersion of atmospheric pollutants. These processes have major consequences for regional patterns of pollutant deposition in mountainous areas. See Bôhm (1992) for a review of regional deposition in relation to atmospheric processes.

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