

FLOW AND CONSERVATION OF ENERGY IN FORESTS

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Summary

Forests cover 35-40% of the terrestrial surface of the earth and account for the majority of the world's photosynthesis (~65%) and carbon storage (~80%). The vertical structure of forests greatly attenuates the energy capture and transformations in this dimension, greatly enhancing surface area and volume of interaction between biosphere and environment over other plant cover types. Abiotic and biotic (natural and anthropogenic) factors influence the way in which energy captured in forests through photosynthesis is released back to the environment. Conservative estimates suggest that humans now utilize 15% of the net annual primary production of forests, largely for fiber and fuel. With increasing human population, affluence, demand for energy, and

continued loss of forested land, we will soon need to critically evaluate the proportion of forest energy diversion to humans that will be sustainable in the long-term.

1. Introduction

Of the $1,368 \text{ W m}^{-2}$ of radiant energy from the sun that reaches Earth on a clear day, as much as 850 W m^{-2} penetrates the atmosphere and reaches forest canopies - less at higher latitudes. Approximately 95% of this incident energy is lost back to the environment, ~60% being reflected or transmitted through leaf surfaces, with the remainder returning subsequent to absorption via 1) long-wave radiation, 2) sensible heat or convection, and 3) latent heat or evapotranspiration. Of the latter two, convection predominates in conifer and boreal forests and those with low water availability, while latent heat loss predominates in forests with higher water availability and those composed of deciduous species.

Only 5% of energy reaching a leaf surface is absorbed by photosynthetic pigments, primarily chlorophyll, and ~ 2% of this absorbed energy is converted into chemical energy. Light energy absorbed by photosynthetic pigments is first captured in transient forms of chemical energy, namely (ATP), that along with NADPH, facilitates the enzymatic fixation and reduction of atmospheric CO_2 into sugars in the chloroplasts of leaves. Of the chemical energy and mass contained in these sugars, ~ 50% ends up in biomass, primarily cellulose in tree stems, and the other half is utilized in growth and maintenance respiration.

As trees are the longest-lived plants in a forest, and arguably the most significant long-lived multicellular organisms on earth with respect to biomass, tree stems represent the primary capacitors for energy in the biosphere. In most of the world's forests, e.g., tropical and warm forests, living or standing biomass represents the primary pool of stored chemical energy. In contrast, forests in cold regions such as in boreal regions, retain the bulk of the energy in long-lived belowground and soil-organic carbon pools. With respect to geologic time-scales, fern forests of 300 million years before present (b.p.) are the source of much of our fossil fuel energy reserves that we mine today. In fact, energy stored in the earth's current phytomass (largely forest) is roughly equivalent to the energy contained in the known reserves of coal, natural gas, and oil. Hence, forests can be viewed as the primary short, intermediate, and long-term capacitors for energy in the biosphere.

2. The Flow and Capture of Light Energy in Forests

The flow of energy in forests can be broken down into radiant versus non-radiant energy flow. Flow of radiant energy in forests is largely affected by the quantity and quality of the incident light, and the way in which this solar energy is partitioned among the photosynthetic elements in the canopy. Unless the radiant energy is converted into non-radiant forms, i.e., chemical energy, there is essentially no capacity for long-term storage. Non-radiant energy flow, e.g., the biosynthesis of tree biomass or accumulation of soil organic fractions, is typically far smaller in magnitude but of much greater significance than radiant energy storage in forest ecosystems.

2.1. Light Extinction in Canopies

Forest canopies are made up of photosynthetic elements such as foliage, with or without inclusions of epiphytes and/or vines, that attenuate solar energy in a logarithmic fashion much like a spectrophotometer cuvette containing light absorbing molecules. Thus, the absorption of light during its passage through a canopy has often been modeled and described using a modified Beer-Lambert law expression:

$$t(x) = \exp\{-K \times LAI(x)\}, \quad (1)$$

where t is the proportion of visible light incident at the top of the canopy that is transmitted to point (x) in the canopy, $LAI(x)$ is the leaf area index (m^2 leaf m^{-2} ground) above point (x), and K is an extinction coefficient which varies by tree and forest type. Forest net primary productivity typically plateaus at LAI 's of around 6, which is theoretically the LAI at which most (often taken as 95%) of the incoming radiation is effectively absorbed or utilized. Some forests appear to deviate from this relationship, apparently because of non-ideal canopy structure. For example, leaf orientation is often more vertical in the upper canopy and horizontal in the lower canopy, thus facilitating the transmittance of light energy to lower canopy positions. As light is attenuated, energy in the green part of the visible spectrum not absorbed by chlorophyll as well as in the infrared become enriched. As such, light quantity as well as quality for photosynthesis is reduced with depth in the canopy.

2.2. Light and Photosynthesis

Capture and conversion of light energy into net carbon uptake requires a minimum level of light known as the light compensation point. Leaf light compensation points have been reasonably well documented for a range of forest plant species and generally range in the vicinity of 5% of full sun. Branch, tree and forest-level light compensation points are less well studied, but are generally seen to increase from leaf to ecosystem scales. At lower points in the canopy, sunflecks, i.e., brief flashes of direct sunlight energy received in lower canopy positions, can account for up to 60% of the energy/carbon gained there. Photosynthesis generally reaches maximum values at some light level below full sunlight called the light saturation point. Light saturation points for tree leaves generally range from between 25 and 50% of full sun. However, light is not the only factor that influences energy capture, i.e., variables such as CO_2 concentration, temperature (influences respiration as well as photosynthesis), moisture, and nutrients often interact with and co-limit with light. In addition, trees and canopy layers can acclimate morphologically, physiologically and biochemically to specific light conditions in the forest. This acclimation can occur rapidly (seconds), daily, seasonally and even between years and throughout the life-span of the tree.

3. Factors Influencing Flow and Conservation of Energy in Forests

The balance of energy into and out of forests is presumed to be in balance in the intermediate time (e.g., 10^2 - 10^3 y) and spatial scales, but there may be a net influx or efflux of energy and mass at small and large scales. The precise scales of these energy balances depends on forest type and environmental and disturbance regime(s). In the

short-term, forests may exhibit an influx or efflux of energy. For example, forests are generally net sinks for energy during the day and over the growing season and sources at night and during non-growing season periods. Over intermediate-time scales, factors that lead to the release of energy from forests are either non-anthropogenic (natural) or anthropogenic in origin. Natural factors that influence the flow of energy can be classified as either abiotic or biotic, but abiotic factors such as climate are good predictors of gross biotic characteristics influencing energy capture in forests. The magnitudes and signs of steady-state energy flow can be less important than periodic flows resulting from stochastic events, e.g., fire.

3.1. Natural Factors

A variety of natural (non-anthropogenic) factors, which can be grouped into abiotic and biotic, influence energy flow and conservation in forests. However, it should be noted that there is considerable interaction between abiotic and biotic factors.

3.1.1. Abiotic Factors

In the absence of abiotic disturbance agents, and with a given forest composition, structure, and location, abiotic factors such as temperature, moisture, light, cloud, atmospheric CO₂ concentration, and soil chemical and physical properties are key variables that influence magnitude and sign of energy and mass transformations at different spatial and temporal scales. Secondary factors such as slope and aspect can strongly influence light and effective moisture availability for a location, which in turn can affect the biotic component. Specifically, the photon flux density ($\mu\text{moles m}^{-2} \text{s}^{-1}$) varies with the cosine of the angle of incidence. The angle of incidence is the angle from perpendicular to the ground surface to that of incoming solar radiation. Hence, energy flux densities are substantially lower for north-facing slopes (south-facing slopes in the southern hemisphere), increasing with latitude and slope.

3.1.1.1. Cloud

Clouds are associated with and indeed are created by many of the world's most productive forests, e.g., cloud forests of the tropics. Clouds in turn influence the light received by forests. Cloud attributes such as type, depth, altitude, and cover influence light quantity and quality. Clouds reduce light quantity by an amount largely related to the albedo of the upper cloud surface. Light attributes are further modified by photon-scattering properties of clouds, converting otherwise unidirectional sun light into diffuse/anisotropic light. Clouds further affect the spectral quality of light, ostensibly reducing the relative amounts of red and infrared light to other visible wavelengths.

3.1.1.2. Abiotic Disturbance

Major abiotic disturbance factors such as fire, wind, snow and ice, and mass movement (e.g., landslides) would in most cases be expected to result in an efflux of energy and mass from forest ecosystems, at least in the short-term. However, the sign and magnitude of the flow could depend on the state of the forest system prior to disturbance. The relative importance of these disturbance factors and the temporal and

spatial scales and characteristics over which they operate vary greatly between forest types. In addition, anthropogenic factors interact with most, if not all, natural environmental and disturbance factors in influencing energy and material flow.

Fire is one of the key 'abiotic' disturbance agents of forests, especially in drier/interior forests of the world. While fires can be natural in origin, e.g., those of lightning origin, records of human-set fires go back 1.5 million years in Africa, and at least 10 000 years in the Americas. The two main types of fires are (1) ground fires, which combust forest floor or litter and destroy seedlings, and (2) crown fires, which generally kill the tree crowns and lead to stand replacement. In the first case, little energy is dissipated, while crown fires can release substantial amounts of stored forest energy from the canopy. However, even in the latter case, much of the biomass, carbon and energy could enter 'black' carbon pools in the soil or long-lived standing or coarse woody debris pools. Such biomass pools can be very long-lived in forest systems.

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Biographical Sketch

Dr. Arthur L. Fredeen received his B.Sc. from the University of Saskatchewan in 1983, a Ph.D. in Plant Physiology from U.C., Berkeley in 1988, and was a postdoctoral fellow at the Carnegie Institution of Washington, Dept. of Plant Biology, Stanford University from 1989 to 1994. While at Stanford, Dr. Fredeen worked on physiological acclimation and adaptation in rainforest understory plants, acclimation of ecosystem physiology to elevated CO₂, and was a researcher on the BOREAS (Boreal Ecosystem Atmosphere Study) in Northern Canada.

Dr. Fredeen is currently Associate Professor in the Biology and Forestry Program at the University of Northern British Columbia in Prince George, British Columbia. His current research interests include impacts of climate change variables on gas-exchange in white spruce, effect of management on ecosystem CO₂ flux from sub-Boreal forestlands in British Columbia, and importance of epiphytes to CO₂ fixation and carbon balance in interior cedar-hemlock rainforests of central British Columbia.