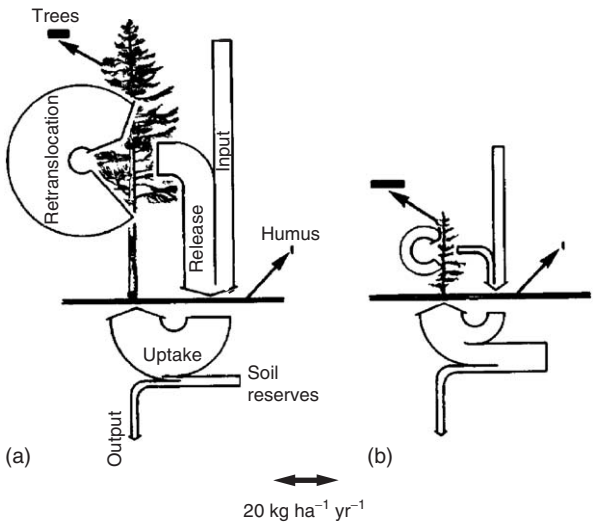


Figure 2 Patterns of *K* cycling in (a) 40-year-old and (b) 10-year-old *Pinus nigra* plantations. This diagram illustrates the change in sources and sinks of nutrients as a tree grows. The older trees here had about half the annual requirement for K as the younger trees. Most of this requirement was met by retranslocation and cycling through the litter layer, in contrast to a younger tree that relied heavily on soil reserves. Reproduced with permission from Miller H (1984) Dynamics of nutrient cycling in plantation ecosystems. In: Bowen GD and Nambiar EKS (eds) *Nutrition of Plantation Forests*, pp. 53–78. London: Academic Press.

reactive forms. Nutrient retranslocation occurs to meet the demands of an expanding canopy and some nutrients are conserved by withdrawal from leaves during senescence; these processes are quite pronounced in trees. Numerous physiological mechanisms are under some degree of genetic control, the elucidation of which will be a major focus of investigation for the next few decades. In contrast to non-woody plants, trees can to some extent store nutrients in sapwood under very high nutrient supply regimes and later withdraw these nutrients during periods of insufficient supply from soil.

See also: **Soil Biology and Tree Growth**: Soil Organic Matter Forms and Functions; Tree Roots and their Interaction with Soil. **Soil Development and Properties**: Nutrient Cycling; Nutrient Limitations and Fertilization. **Tree Physiology**: A Whole Tree Perspective; Physiology and Silviculture; Root System Physiology; Shoot Growth and Canopy Development; Stress; Xylem Physiology.

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Canopy Processes

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Introduction

A forest canopy is the aggregate of the leaves of trees that typically forms a layer overhead. It may also include the leaves of vines, epiphytes, and parasitic plants when they are present. A canopy can have large gaps, allowing plentiful light to reach the forest floor, or be closed and dense, with almost no light penetrating below it. The primary purpose of the forest canopy is to capture solar energy needed for photosynthesis. A number of factors can reduce the potential carbon gain of forests by preventing the

achievement of a high leaf surface area in the canopy or by reducing the rate of net photosynthesis of leaves. A forest canopy also releases a large amount of water into the atmosphere in the process of transpiration. The amount of water transpired from a forest is closely associated with the leaf surface area of the canopy.

Canopy Photosynthesis

Within-Canopy Environmental Characteristics

Attributes of the canopy are the sum of the functions of all the leaves that make up the canopy. Through the process of photosynthesis each leaf creates carbohydrates from atmospheric carbon dioxide (CO_2). Leaves within a canopy photosynthesize at different rates, depending on available resources and microclimate at specific canopy positions. The most important rate-controlling factors are solar radiation, temperature, CO_2 concentration, vapor pressure deficit (an index of the dryness of the air calculated from relative humidity and temperature), available soil moisture and acquired nutrients. During the daytime, microclimatic conditions, temperature, humidity and CO_2, can vary within the canopy, with higher temperatures, lower humidity and near-atmospheric CO_2 concentrations occurring near the top of the canopy, and lower temperatures, higher humidity and lower CO_2 concentrations occurring near the bottom of the canopy. These trends tend to reverse at night. If the canopy is open, allowing wind to penetrate throughout, there is little appreciable difference in temperature, humidity, or CO_2 concentration among canopy positions.

Of the environmental factors affecting photosynthesis, the one that varies to the largest extent within the canopy is solar radiation. Only a portion of the solar spectrum is used in photosynthesis, between wavelengths of 400 and 700 nm. This portion of the spectrum is called photosynthetically active radiation (PAR). Most of the radiant energy found in longer wavelengths, i.e., heat, is reflected or transmitted through the leaves, while most of the PAR is absorbed by the leaves. This creates variations in light quality above, within and below the canopy. Often 80–95% of the incoming PAR is absorbed in a well-developed forest canopy, allowing little solar energy to pass through to the plants in the understory. Plants below the canopy respond to this light stress by developing thin leaves that efficiently photosynthesize in low light conditions (high quantum yield) and have growth patterns that are characterized by long internode lengths that minimize mutual shading and shading from competing plants.

The amount of PAR received at different depths within the canopy can be approximated using Beer's law:

$$I_z = I_0 \exp(-kL_z) \quad (1)$$

where I_z is the average solar radiation at height z within the canopy, I_0 is solar radiation above the canopy, k is the light extinction coefficient, and L_z is the leaf area index for that portion of the canopy above height z. The light extinction coefficient varies with species and forest type. Typical values of k for coniferous forest canopies range between 0.4 and 0.65, and between 0.5 and 0.8 for broadleaf deciduous forest canopies. In most cases, in coniferous and deciduous forests the value of k falls between 0.5 and 0.6. The pattern of solar radiation through hypothetical forests with different values of k (**Figure 1**) illustrates the effectiveness of light absorption by the canopy and the reduction in available light with depth within the canopy. It should be noted that the application of Beer's law assumes that the canopy consists of leaves that are randomly distributed throughout the canopy. This is never the case in actual forests because the foliage is always arrayed on branches and often clumped near the end of the branch. Clumping is particularly evident in conifers and this results in more light transmission through the canopy than would be predicted by Beer's law. In coniferous forests, discrepancies of 30% or more in calculated light transmission through the canopy can be attributed to nonrandom spatial variation in the foliage. This error is often lower in deciduous species.

Within-Canopy Foliar Characteristics

Leaf morphology changes dramatically in most tree species as a consequence of changing light conditions from the top to the bottom of the canopy. The most limiting factor to photosynthesis at the bottom of the canopy is solar radiation, and leaves at that level show an acclimation to this limitation by developing a high specific leaf area (SLA, defined as the surface area-to-mass ratio of a leaf) meaning they are very thin, often with only two or three cell layers capable of photosynthesis. This improves their ability to efficiently fix carbon at low light levels, and the photosynthetic light compensation point is lowered, although the maximum light saturated rate of photosynthesis is also reduced. Leaves near the top of the canopy are not light limited, but are often water- and heat-stressed. In this portion of the canopy the leaves have multiple photosynthetic cell layers in the mesophyll, and therefore a lower SLA, are smaller, reducing the boundary layer, and can

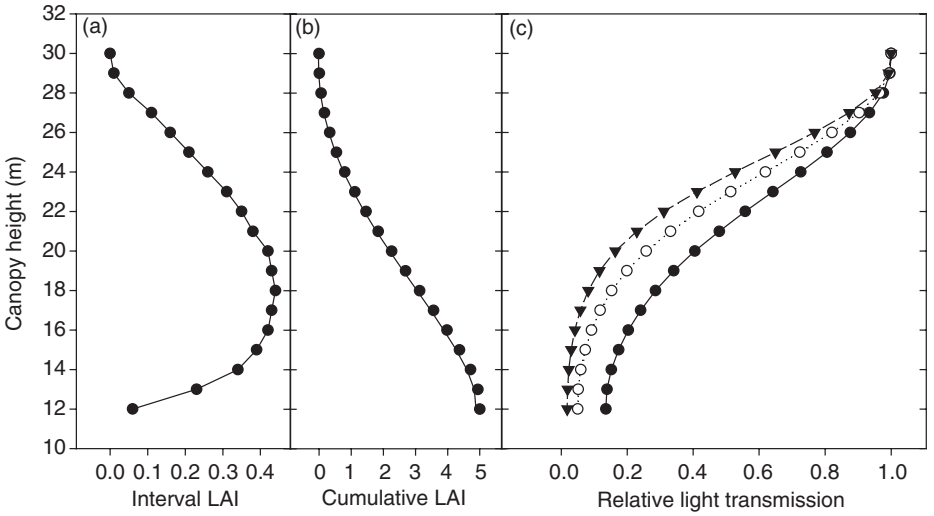


Figure 1 (a) Projected leaf surface area profile by 1-m intervals within a typical (hypothetical) forest canopy with a leaf area index (LAI) of 5 ($m^2\,m^{-2}$). (b) Cumulative LAI with canopy depth. (c) Relative light transmission through the canopy calculated from Beer's law (eqn [1]) assuming light extinction coefficients of 0.4 (triangles), 0.6 (open circles), and 0.8 (filled circles).

have lower stomatal density, all attributes that make them more able to conserve water and/or dissipate heat. In broadleaf species, leaf orientation also tends to shift from canopy top to bottom, with leaves in their most horizontal position at the canopy bottom and in their most vertical position at the top. This improves light absorption at the bottom of the canopy and reduces the heat load on the leaves at the top of the canopy.

Between the top and bottom of the canopy a continuous gradient of changing SLA usually can be found as the microenvironment changes. Values of SLA can double from the top to the bottom of a forest canopy. The SLA of a leaf is inversely related to the daily sunlight under which the leaf developed within the canopy. The light saturated rate of net photosynthesis of the leaf is also inversely correlated to its SLA. On the other hand, there is a direct positive relationship between SLA, the nitrogen content of the leaf, and physiological activity. Higher levels of nutrients, in particular nitrogen, are found in regions of the canopy that receive the highest amounts of solar radiation, and also have the highest SLA, i.e., the leaves found at the tops of trees and the upper third of the canopy. Most, if not all, quantifiable aspects of leaf metabolism decrease from top to bottom of the canopy, including maximum rates of photosynthesis and respiration, number of mitochondria and chloroplasts, and chlorophyll, starch, and sugar contents.

Leaf Area Index

A forest canopy consists of thousands of individual leaves arrayed in complex patterns. Leaf shapes, sizes, and longevities as well as branching patterns vary tremendously among tree species. However, there are effective ways of making useful comparisons between forest types at the scale of the canopy by reducing variation in measurements of these attributes. One of the most widely used bases for comparison of canopies is the measurement of leaf area index (LAI). To calculate LAI, the surface area of the leaves is summed and divided by the ground surface area that they occupy. Both areas are measured in the same units, e.g., $m^2\,m^{-2}$, so LAI is dimensionless. The 'projected' leaf area of the leaves in the canopy is often used to determine LAI. Projected leaf area is the surface area of a leaf that intercepts a direct beam of light. In the case of a flat leaf of a deciduous broadleaf species, it is simply the area of one side of the leaf. For more complex leaf shapes, such as conifer needles, it is the area of the leaf that intercepts a direct beam of light projected onto a flat surface. Projected leaf area provides a measure of the surface area of leaves that can absorb direct beam solar radiation. The use of projected leaf area as the basis for comparison among species minimizes variation by reducing the myriad complex leaf shapes into the effective absorbing surface area. Occasionally when comparisons of LAI are made, total surface area of leaves (all-sided leaf area) is used instead of projected leaf area. The reader is cautioned that these values of LAI will be two to four times greater than those based on projected leaf area. The difficulty in accurately measuring leaf area in conifers has sometimes led to the substitution of leaf biomass for leaf area. This is suitable for comparisons made within a species, but can introduce unwanted

variation when comparisons are made across species with a wide range of SLA.

When maximum LAI values (projected leaf area basis) of forests growing in fertile and moist conditions are compared, they are typically between 5 and 7. Assuming that 95% of the incoming solar radiation is the practical maximum that can be absorbed by a canopy, then with a light extinction coefficient (k) of 0.5, using Beer's law (eqn [1]) full interception would occur at LAI = 6. If the value of k was 0.4 or 0.8, then the LAI value for full interception would be 7.5 and 3.8, respectively. Although unusual, occasionally LAI values for forests have been reported to be substantially higher, in the range of 10 to 20. One possible explanation is that in these cases the foliage was highly clumped. Clumping has the effect of reducing the effectiveness of interception of solar radiation by individual leaves. In turn, to maximize intercepted radiation the trees would have to produce substantially more leaves than in a less clumped forest canopy.

As a young forest approaches canopy closure, its maximum leaf area will exceed the stable LAI value. In favorable conditions this transient LAI could temporarily exceed 7. This reflects the high degree of competition between trees that occurs at this point of stand development. However, such a high LAI cannot be sustained and the highest long-term average LAI is usually around 5. Lower maximum LAIs are very common, and reflect site resource limitations to tree growth. The LAI of a forest is not constant, and will tend to fluctuate yearly due to differences in seasonal weather patterns, drought, or perturbations that the forest may experience such as fire, insect infestation or disease. If the stress is severe, the LAI will be reduced within the year. Drought and insect defoliation, for example, can have this effect. However, more commonly, a stress or decrease in resource availability will result in a lower leaf area in the subsequent year. Similarly, an increase in resources will increase the LAI in the current year in a forest that contains tree species with recurrent or continuous flushing patterns, and will cause an increase in LAI in the following year in all species. The increase in LAI in the subsequent year is due to the development of more leaf initials within the dormant period bud and the acquisition and storage of resources, particularly carbohydrates and nutrients, to support the additional leaves.

Intercepted Solar Radiation

For a given species, LAI and leaf biomass have strong positive correlations with most measures of stand growth or productivity across sites or treatments. These same relationships, while generally remaining positively correlated, are more variable when comparisons are made among species because LAI does not adequately account for how effectively solar radiation is absorbed by the canopy. Absorption is a function of the total amount of leaves in the canopy and how those leaves are displayed. The latter is determined by canopy and branch architecture, and leaf distribution and orientation. The depth of the canopy, branch pattern and orientation, leaf size, shape and arrangement on the branches, and overlap among leaves and branches within the canopy all affect how much solar radiation a canopy can absorb.

The quantity of solar energy absorbed by the canopy determines to a large extent how much carbon is gained through photosynthesis, and this in turn, defines the productivity of the forest. A generalized relationship between absorbed radiation and forest growth can be seen in **Figure 2**. This diagram illustrates that the general relationship between stand growth and the amount of intercepted solar radiation is usually linear. Over short time periods, for example days or weeks within a single growing season, there could be substantial nonlinear variation in this relationship, but over longer time

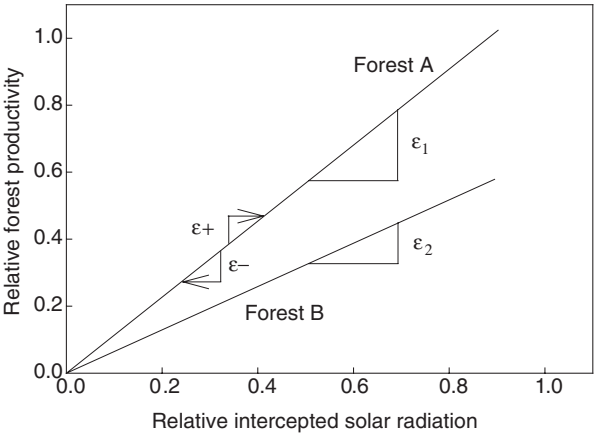


Figure 2 Idealized relationships between intercepted radiation and forest productivity. The two lines represent forest types with a high dry matter : radiation quotient (ε_1, Forest A) and a low dry matter : radiation quotient (ε_2, Forest B). When comparing between forest types, a higher canopy photosynthesis (ε_1 versus ε_2) results in greater carbon gain per unit of intercepted radiation. However, within the same forest type short-term changes in ε caused by increased resource availability ($\varepsilon+$) or environmental stress (ε–) produce adjustments in canopy leaf area, so that over time forest productivity for a given forest type tends to remain linearly related to intercepted radiation. Adapted and modified with permission from Jarvis PG and Leverenz JW (1983) Productivity of temperate, deciduous and evergreen forests. In: Lange OL, Nobel PS, Osmond CB, and Ziegler H (eds) *Physiological Plant Ecology, vol. 4, Encyclopedia of Plant Physiology New Series 12D*, pp. 233–280. Heidelberg, Germany: Springer-Verlag.

periods, such as growing seasons and years, variation is greatly reduced and a linear relationship becomes evident. The linear nature of this relationship holds within and across species, which is an indication that it is a more robust measure of canopy carbon gain than LAI. Different types of forests and species will produce relationships with different slopes due to inherent differences in physiological processes, including photosynthetic capacity of the leaves.

The slope of the relationship, ε, has been termed the dry matter : radiation quotient and is determined by a wide range of factors. It is important to remember that the term ε is an amalgamation of many important physiological attributes that contribute to growth, including photosynthesis, respiration, carbon allocation and plant responses to environmental stresses. The maximum potential value of ε can be estimated based on the following information: (1) a tree requires 20 mole quanta of solar energy to assimilate a mole of CO_2, (2) there are 2.3 mole quanta per MJ of absorbed solar radiation (or 4.6 mole quanta per MJ of PAR), (3) the mass of a mole of CO_2 is 44 g, and (4) an estimated conversion factor from mass of CO_2 to mass of dry matter is 0.5. The maximum potential conversion of solar radiation to dry matter in a plant is $(2.3/20)(44 \times 0.5) = 2.5\,g\,MJ^{-1}$ (total solar) or $5.0\,g\,MJ^{-1}$ (PAR). Typical values of ε for crops range from 1.1 to $1.7\,g\,MJ^{-1}$ (total solar) while for forests values have been reported from 0.2 to $1.4\,g\,MJ^{-1}$. This range in reported values indicates that the dry matter : radiation quotient of forest canopies of different species or species mixtures can vary greatly. However, the ε for a single species or a group of species, on a single site or on similar sites, will be nearly constant, because, in large part, the pattern of carbon allocation among leaves, roots, and stem is controlled principally by soil resources, especially nitrogen and water availability, and the genetic characteristics of the species. Likewise, the inherent photosynthetic and respiratory capacities of the foliage and woody tissues are fixed.

On a single site, in any given year, conditions that affect photosynthesis of the leaves will vary. When conditions are less favorable, the trees allocate more carbon to roots, and, because there is less carbon remaining for leaves, fewer, or smaller, leaves are produced. When conditions are more favorable for photosynthesis, more, or larger, leaves, are produced, and less carbon is allocated to the root system. In the short term, this produces temporary shifts to higher or lower values of ε. However, over longer time periods, such as a growing season or year, the changes in carbon availability and proportions allocated for root and leaf growth result in a strongly linear relationship between intercepted radiation and aboveground stand growth.

Since we know that many factors affect the rate of photosynthesis of leaves, why is intercepted solar radiation so strongly correlated with forest productivity? While there is still more research needed to fully understand these phenomena, the current explanation is that tree species in general utilize a similar strategy for growth and survival, which is to grow more leaves when more resources are available, rather than increase the photosynthetic capacity of a fixed amount of leaves. For example, on droughty or low-fertility sites, the carbohydrate and nutrient supply is limited, allocation favors roots, and fewer leaves are produced; thus, the amount of solar radiation intercepted is low. On resource-rich sites, available carbohydrates and nutrients are used to create more leaves, which in turn intercept more radiation and produce higher levels of carbohydrates for export to the rest of the tree. An individual species that is naturally occurring or planted across a wide variety of sites can often be defined by a single line (**Figure 2**) that represents its long-term productivity as a function of intercepted radiation. In other words, ε remains relatively constant for a species. On resource-rich sites, more leaves are produced in the canopy and more radiation is absorbed by them, while on the resource-poor sites, fewer leaves can be produced, and growth is proportionately reduced.

Measurement Approaches

Canopy carbon gain has been estimated in a number of ways. It has been inferred from changes in biomass, modeled by integrating the rates of physiological processes over time, and measured by micrometeorological techniques. The recent development of relatively reliable and robust instrumentation for eddy covariance measurements (a micrometeorological technique that measures the CO_2 concentration in eddies of air allowing the calculation of the flux of CO_2 into and out of an ecosystem) has made this an important method for estimating total net CO_2 uptake or release by a forest ecosystem. Usually eddy covariance measurements are only made above the canopy, so this technique cannot discern where within the ecosystem (soil, plants, animals) the CO_2 is being absorbed or released. As a result, unless it is combined with more measurements, it only provides an estimate of net fluxes of all photosynthetic and respiratory activity. However, this is a very useful approach for characterizing whole ecosystem carbon dynamics, and provides insight into canopy processes. One result of these measurements has been to establish that the rate of CO_2 uptake of canopies in

response to PAR is very similar to the light response curves of individual leaves.

Transpiration

All plants lose water through their stomata as they absorb CO_2 from the atmosphere. When the stomata are open during the day, a tremendous amount of water can be lost from the forest canopy. Water loss through stomata is linearly related to stomatal aperture, which is estimated by measuring stomatal conductance. The average stomatal conductance of all the leaves in the canopy is called canopy conductance. Light in visible wavelengths is required for the stomata to open. As a result, transpiration occurs mostly during daylight hours. Only about 5–10% of water loss occurs at night. This loss results from stomata that do not always close fully, particularly as leaves age, and a small amount of diffusion through the leaf cuticle.

Canopy water loss depends on soil water availability, canopy leaf area and environmental conditions, especially PAR and vapor pressure deficit. Vapor pressure deficit (VPD) describes the dryness of the air, and more specifically, the potential gradient for water movement from the leaf to the atmosphere. A high VPD indicates that there is a large water vapor gradient from the leaf to the atmosphere that will cause rapid diffusion of water from the leaf when the stomata are open. The rate of transpiration is closely correlated with VPD, especially under conditions of plentiful soil moisture. Mitigating factors that cause the stomata to close, such as leaf water stress, modify the rate of transpiration and its relationship with VPD.

Estimating Evapotranspiration

Evapotranspiration (E_t), i.e., the combined total of transpiration and evaporation, from a forest has been estimated in many ways. Micrometeorological methods such as the Bowen ratio (the ratio of sensible heat flux to latent heat flux computed from vertical gradients of air temperature and water vapor) and eddy covariance, can be used to estimate evapotranspiration from a forest. Physiologically based methods, including sap flux, porometry, and lysimeters, as well as stream flow from catchments and soil water depletion have been used as well. One of the most proven and widely used approaches is the Penman–Monteith equation:

$$E_t = sA + (c_p \rho_a D g_a)/\{\lambda[s + \gamma(1 + g_a/g_c)]\} \qquad (2)$$

where s is the rate of change of saturation vapor pressure with respect to air temperature, c_p is the specific heat of dry air of density ρ_a, D is vapor pressure deficit of the air, g_a is boundary layer conductance for water vapor, λ is the latent heat of vaporization of water, γ is the psychrometric constant, and g_c is canopy conductance.

In the case of aerodynamically rough canopies, such as in coniferous forests and other forests made up of small leaves, g_a is usually large in relation to g_c. The small leaf size and large boundary layer conductance results in close coupling between leaf and air temperatures, allowing the equation to be simplified to:

$$E_t = (c_p \rho_a / \lambda\gamma) D g_c \qquad (3)$$

Particularly in the simplified form, the dependence of E_t on VPD and canopy conductance is clear. For conifer and other narrow-leaf tree canopies, stomata play an important role in controlling the rate of transpiration. In contrast, in broadleaf canopies, transpiration is much more closely related to the input of solar radiation, and less dependent on canopy conductance. However, there is no notable distinction between daily or hourly maximum rates of E_t in canopies of coniferous, deciduous, or mixed species stands.

Daily Evapotranspiration

Estimates of E_t of forests range from less than 1 to as much as 7 mm day^{-1}, although maximum values are usually reported in the range of 5–6 mm day^{-1}. The low values will occur during drought, or conditions of high atmospheric humidity or low solar radiation, or in forests with very low LAI. The high values indicate that forests can be very effective at absorbing solar radiation, and very well coupled to the atmosphere, because these represent values that are at the theoretical maximum for evaporation. In full sunlight a maximum of 380 calories day^{-1} of energy are available at the earth's surface. As 570 calories are required to evaporate 1 cubic centimeter of water, this is equivalent to a maximum of 6.6 mm day^{-1} of evaporation. Although LAI values indicate that leaf surface area is many times larger than the unit ground surface, water loss cannot exceed that of an equal surface area of water receiving the same amount of energy. Values of E_t that exceed the maximum rate are uncommon, but can occur if an additional source of energy is available, for example from advection.

In summary, when considered from a physiological perspective, a forest canopy is a system for harvesting solar energy. Leaves are displayed throughout the canopy for this purpose as efficiently as possible, within the constraints of the morphology and branch

architecture of the tree species that contribute to the canopy. If unconstrained by a lack of site resources for growth, the canopy captures a very large proportion of the sun's available energy. Due to the close coupling between resource acquisition and canopy development, LAI and intercepted radiation are excellent indices of forest productivity. This is because improvements in resource acquisition that increase canopy photosynthesis in the short term lead quickly to increased leaf growth. Likewise, when fewer resources are available, decreased canopy carbon gain causes a subsequent reduction in leaf growth. Forest canopies can also lose appreciable amounts of water through the process of transpiration. Canopy transpiration is positively correlated with LAI, canopy conductance, and available energy. At high values of LAI, the rate of transpiration of forest canopies is comparable to that of open water, providing another example of the effectiveness of forest canopies in absorbing solar energy.

See also: **Biodiversity**: Plant Diversity in Forests. **Ecology**: Forest Canopies. **Environment**: Carbon Cycle. **Hydrology**: Hydrological Cycle. **Tree Physiology**: Physiology and Silviculture; Stress.

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Stress

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Introduction

Throughout their lives trees are exposed to a range of stressful conditions. If they are to survive, they must adapt by modifying their metabolism (physiology), cellular structure (anatomy), and form (morphology). Adaptation to a wide range of stresses, however, limits growth and the ability to compete in more favorable environments. The trade-offs are important to recognize in selecting trees that might grow best in a particular environment and in modifying the environment to reduce stressful conditions.

The nomenclature for defining physiological stress is derived from physics with the idea that a force upon a body causes a strain in the opposite direction. The strain is elastic if completely reversible following removal of the stress, or plastic if only partly reversible. How long it takes a plant to recover following exposure to a particular stress or whether the stress is fatal are questions that can be answered by careful observation. Survival following exposure to one stress, however, often increases a plant's susceptibility to another. On the other hand, repeated exposure to one kind of stress can lead to adaptations that increase a tree's ability to tolerate or to avoid the stress.

A brief analysis is presented below of the kinds of tolerance and avoidance mechanisms that trees have evolved to withstand specific stresses. To demonstrate how seasonal variation in climatic conditions imposes stresses on common processes, such as photosynthesis, a simulation model is introduced, and the performance of pine and eucalyptus is