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.

Further Reading

Holbrook NM and Lund CP (1995) Photosynthesis in forest canopies. In: Lowman MD and Nadkarni NM (eds) *Forest Canopies*, pp. 73–108. San Diego, CA: Academic Press.

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.

Kozlowski TT and Pallardy SG (1997) *Physiology of Woody Plants*. San Diego, CA: Academic Press.

Kramer PJ and Boyer JS (1995) *Water Relations of Plants and Soils*. San Diego, CA: Academic Press.

Landsberg JJ (1986) *Physiological Ecology of Forest Production*. London, UK: Academic Press.

Lassoie JP and Hinckley TM (1991) *Techniques and Approaches in Forest Tree Ecophysiology*. Boca Raton, FL: CRC Press.

Parker GG (1995) Structure and microclimates of forest canopies. In: Lowman MD and Nadkarni NM (eds) *Forest Canopies*, pp. 73–108. San Diego, CA: Academic Press.

Russell G, Jarvis PG, and Monteith JL (1989) Absorption of radiation by canopies and stand growth. In: Russell G, Marshall B, and Jarvis PG (eds) *Plant Canopies: Their Growth, Form and Function*, pp. 21–40. Cambridge, UK: Cambridge University Press.

Smith H (2000) Plant architecture and light signals. In: Marshall B and Roberts JA (eds) *Leaf Development and Canopy Growth*, pp. 118–144. Boca Raton, FL: CRC Press.

Squire GR (2000) Plant and canopy diversity. In: Marshall B and Roberts JA (eds) *Leaf Development and Canopy Growth*, pp. 280–309. Boca Raton, FL: CRC Press.

Stenberg P, DeLucia EH, Schoettle AW, and Smolander H (1995) Photosynthetic light capture and processing from cell to canopy. In: Smith WK and Hinckley TM (eds) *Resource Physiology of Conifers*, pp. 3–38. San Diego, CA: Academic Press.

Waring RH and Running SW (1998) *Forest Ecosystems*. San Diego, CA: Academic Press.

Whitehead D and Jarvis PG (1981) *Water Deficits and Plant Growth*, vol. 6. New York: Academic Press.

Stress

R H Waring, Oregon State University, Corvallis, OR, USA

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

compared in an environment where neither species is native. Then, some general biochemical and structural indices of tree stress are introduced. These stress indices change not only in response to variation in climate and soil conditions but also in response to competition among trees. The stress indices are useful in assessing tree susceptibility to attack from insects and disease. In the last section, procedures for separating climatically induced stress from other types are discussed that apply at the landscape level.

Tree Adaptations to Specific Stresses

Trees may alter their biochemistry to tolerate a particular stress that occurs infrequently but the metabolic cost is high for such temporary adjustments. Frequent exposure to a particular stress leads to avoidance mechanisms that may permanently change a tree's physiology, anatomy, and morphology. Tolerance and avoidance mechanisms differ depending on the kind of stress but both types of adaptations may reduce the amount of resources available for above-ground growth under more favorable conditions. If an environment is sufficiently harsh, however, trees that can adapt encounter little competition. Examples of tolerance and avoidance mechanisms are presented in this section in relation to radiation, drought, flooding, temperature extremes, mechanical forces, toxic compounds, and nutrient deficiencies.

Radiation

Solar radiation includes a wide spectral range in wavelengths. The sun's ultraviolet (UV) radiation (200–400 nm) can destroy chemical bonds, whereas its visible light (400–700 nm) is essential for photosynthesis, and its infrared radiation (700–2500 nm) heats plant and soil surfaces. Trees produce a series of phenolic compounds that absorb particular parts of the UV spectrum or they may adapt by producing waxes and whitish hairs on leaf and stem surfaces that reflect a large amount of radiation.

Trees growing in shaded environments can increase photosynthetic pigments that absorb light, such as chlorophyll. Leaves in the upper canopy, however, are exposed to varying light intensities, sometimes greater than their photosynthetic capacity. Under such conditions, many species have evolved the ability to generate special pigments that cycle from absorbing to reflecting modes throughout the day. The shapes of leaves exposed to high radiation are generally smaller, more dissected, and less directly oriented to absorb sunlight than leaves adapted to more shaded conditions. Leaf thickness also generally decreases from the top to the bottom of a forest canopy in response to available light.

Drought and Flooding

Drought and flooding represent extremes in water availability. To avoid drought, vascular plants have evolved the ability to grow roots that can extract water from >10 m depth in the soil and transport it through a series of connected, dead, woody (lignified) cells to leaves situated more than 50 m above the ground. Gymnosperms, represented by pines (*Pinus*), spruces (*Picea*), firs (*Abies*), *Araucaria*, and *Ginkgo*, transport water through specialized (bordered) pits on the connected side walls of tracheids, whereas angiosperms, represented by evergreen and deciduous hardwoods such as *Magnolia*, beech (*Fagus*), maple (*Acer*), and ash (*Fraxinus*), have vessels with perforated plates at each end. The bordered pits and perforated plates reduce the possibility of air being introduced into the conduits when under tension and, if air is introduced, they are designed to remove it.

As tension on water columns increases due to high evaporative demand or drought, stomata are induced to close before irreversible damage to the vascular system results. Trees adapted to periods of seasonal water stress also have the ability to increase solute concentrations in living cells, to reduce the size of vessels and tracheids, and the amount of leaf area supported by a unit of vascular tissue, while at the same time increasing their root systems.

To adapt to periodic flooding, water tupelo (*Nyssa aquatica*), black ash (*Fraxinus nigra*), and other swamp hardwood species have developed metabolic systems that permit root growth and photosynthesis to continue under anaerobic conditions. In addition, baldcypress (*Taxodium distichum*) and other species exposed to chronic flooding have adapted anatomically to allow diffusion of air through specialized tissue to their roots.

Temperature Extremes

Plants adapted to high or low temperatures differ in the biochemical composition of their cellular membranes. These differences influence the ease that chemical elements, organic compounds, and water can be absorbed and transferred from roots to shoots. Tropical trees are adapted to high temperatures but withstand little frost, whereas temperate trees can adjust their cellular structure, when in a dormant state, to prevent ice crystal formation down to −45°C, and boreal trees can, when fully preconditioned, withstand temperatures approaching absolute zero.

Plants adapted to subfreezing temperatures reduce their photosynthetic activity before conditions become unfavorable in response to shorter day length. If climatic conditions become warmer, low-temperature adaptations are a disadvantage. At the other

extreme, some broad-leafed tree species, when exposed to high radiation when their stomata are closed, initiate the production of volatile isoprene compounds, which protect the photosynthetic machinery within the leaf, and create haze that reduces solar radiation.

Mechanical Forces

Snow, ice, and wind exert mechanical stress on leaves, branches, and stems. Trees species have adapted by folding leaves, by developing flexible stems and branches, by increasing the density of their wood, by shortening and altering the orientation of branches, by increasing the taper of stems, and the proportion of growth allocated to large-diameter roots. In unstable soils, the shape of stems and extension of surface roots may be quite asymmetrical, serving to buttress trees against the forces of gravity.

Mechanical stresses are also induced by feeding and other activities of animals that remove leaves, branches, and bark. Adaptations to herbivory vary from the development of thorns, and prickly leaves to biochemical defenses.

Toxic Compounds

Toxic compounds are widely dispersed in the environment in the form of gases, such as ozone, and as heavy metals such as lead, chrome, nickel, and selenium. Ozone diffuses through stomata into the chloroplast and injures the photosynthetic machinery as well as a tree's ability to transport photosynthate from leaves. Species that are conservative in their use of water maintain less open stomata and therefore take up less ozone over a given period. On the other hand, species that shed their foliage annually suffer less damage per leaf than more drought-adapted species that have long-lived evergreen foliage. To repair ozone-damaged cells requires expenditure of photosynthate and other resources that might otherwise go toward growth or defense.

Heavy metals interfere with the enzyme reactions essential for plant growth and development. Some tropical trees can store toxic compounds in vacuoles that do not disturb cell metabolism; others adapt by producing metal-binding peptides that keep heavy metals out of solution. The synthesis of these compounds is metabolically expensive, and again, like other specific adaptations to stress, reduce a species' ability to compete in environments lacking heavy metals.

Nutrient Deficiencies

Nutrient limitations can reduce growth and increase a tree's susceptibility to other stresses. Trees differ in their demands for specific nutrients, but exhibit a similar optimal balance. At slow growth rates, the overall demand for nutrients is low, and optimal balance can be achieved through selective uptake of scarce nutrients by roots and symbiotic (mycorrhizal) fungi. Some trees species also have symbiotic associations of bacteria that can fix atmospheric nitrogen gas (N_2) into ammonium (NH_4^+), a form available to the host tree as well as to other species. The fixation of nitrogen and acquisition of other nutrients via symbiotic bacteria and fungi, or through production of exudates that stimulate free-living microbial activity to release nutrients from decomposing litter, require a high expenditure of metabolic energy, reducing resources that could go into growth and defense. In many areas once limited by nitrogen, atmospheric depositions have increased from <2 to $>50 \, kg \, ha^{-1} \, year^{-1}$. This increased availability of nitrogen favors above-ground growth, even when other nutrients are in less than optimal supply. As a result of imbalanced nutrition, plants expend energy and create tissues less tolerant to a variety of other stresses.

Process Modeling to Integrate Stress Effects

Trees are exposed throughout their lives to a wide range of different stresses. The question arises, which species might grow best? To assess species performance under a wide range of environmental conditions, physiologically based process models have been developed that have a common structure (**Figure 1**). The maximum rate of photosynthesis is determined by the nutritional status of leaves and the amount of light they absorb. Additional environmental constraints are imposed by frost, drought, high evaporative demand, suboptimum temperatures, and nutrition (and by additional stresses if important, e.g., wind stress, insect defoliation, and ozone). The models take account of interactions among stresses as they affect photosynthesis, respiration, and growth.

If *Pinus ponderosa* and *Eucalyptus globulus* were selected for planting in a cold, drought-prone region of Argentina, *P. ponderosa* would be predicted to photosynthesize and grow nearly four times as well as *E. globulus*, largely because of differences in performance at temperatures between 0°C and 10°C (**Figure 2**). Both species have similar responses to humidity deficits but because the pine grows more foliage it extracts more water from the soil and experiences somewhat more drought stress during the late summer than eucalyptus.
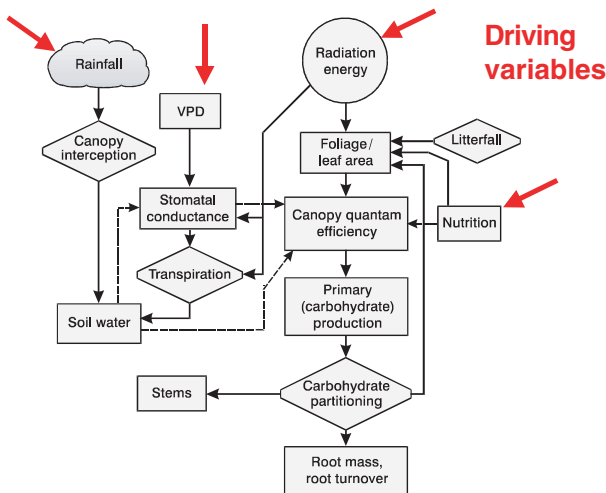
Figure 1 Structure of a physiologically based tree growth model where photosynthesis is constrained by environmental factors that also affect respiration and allocation of resources to growth. VPD, vapor pressure (humidity) deficit. Reproduced with kind permission of Natural Resource Modeling, published by the Rocky Mountain Mathematics Consortium.
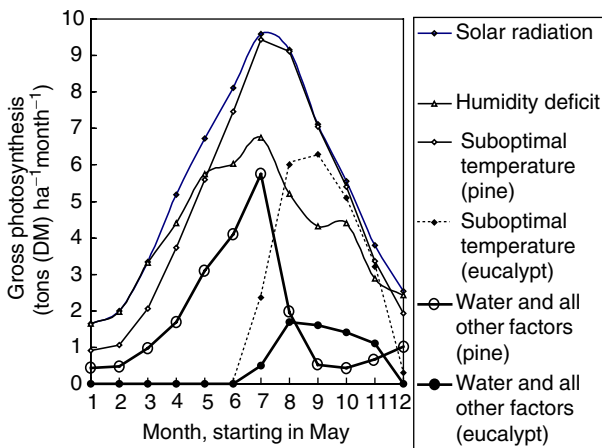

Figure 2 *Eucalyptus globulus* is predicted to grow at less than one-third the rate of *Pinus ponderosa* because it is more poorly adapted to temperatures between 0°C and 10°C that occur frequently at 750 m elevation near Bariloche, Argentina (41° S latitude). Drought and high evaporative demand (humidity deficits) reduce photosynthesis and growth for both species well below limits set by absorbed radiation. DM, dry matter.

The photosynthetic component of process models is well developed and capable of analyzing the impact of rising atmospheric carbon dioxide. Some process models keep track of seasonal changes in storage reserves and predict timing of budbreak, shoot and root elongation, and dormancy. A major challenge remains: to predict competitive relationships in forests composed of many species, some of which fix nitrogen, have roots that access ground water, are tolerant to toxic compounds, or to attack from herbivores and pathogens.

General Indices of Stress

Biochemical Indices

Both biochemical and structural features of trees have been used to assess tree vigor and susceptibility to attack by insects and pathogens. In many cases, specific biochemical compounds have been identified that attract or repel attack. These secondary plant metabolites include alkaloids, nonprotein amino acids, ligans, lipids, phenolic acids, phytoalexins, quinones, terpenes, and steroids.

In a search for general biochemical indicators of stress, physiologists have focused on the storage of starch, an energy source, and amino acids, the building blocks of protein. The seasonal variation in both of these resources can be large so comparisons are generally made during the dormant season. When starch reserves drop below normal, trees become more susceptible to disease. Also, when amino acid concentrations increase with tissue N content, that too is an indication of increased susceptibility. The energy required to store excess amino acids reduces that available for production of defensive compounds. Thus, in Scots pine (*Pinus silvestris*), the concentration of defensive compounds (procyanidins) decreased by 45% while the fraction of arginine in the amino acid pool increased by nearly 400% as foliar N concentrations changed from 1.4% to 2.1%. Expressed as a ratio, a threshold of susceptibility can be identified when leaf N% is in excess of 1.5%. Biochemical ratios of defensive compounds to sugars have also been used to define threshold susceptibility to injury from pathogens (**Figure 3**).

Structural Indices

Wood growth is greatly reduced under stressful conditions but differs with tree size. Physiologists take into account differences in size by calculating partitioning coefficients that express the relative allocation of resources to roots, stems, branches, and foliage. With the knowledge that sapwood cross-sectional area at breast height is correlated with a tree's leaf area, and that stem growth can be related to annual increment in diameter, a general index of tree vigor (growth efficiency) can be defined. Following establishment of a plantation of trees, growth efficiency drops rapidly as the canopy develops and natural mortality (self-thinning) begins. In regions where extensive forests of a particular species exist, outbreaks of insects are
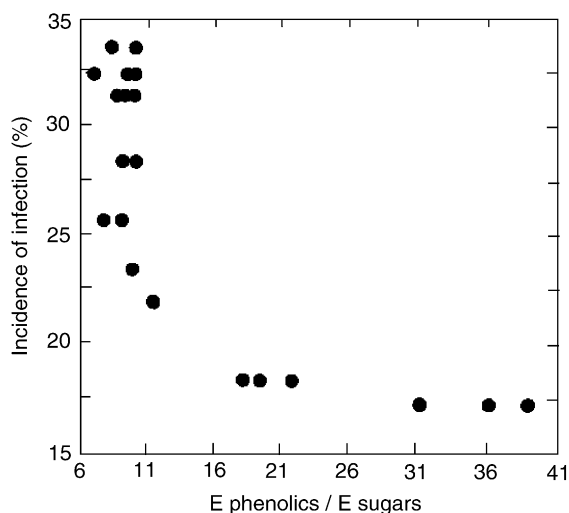
Figure 3 Incidence of infection by a root pathogen, *Armillaria*, on Douglas-fir increased when the ratio of energy (E) required to metabolize defensive compounds (phenolics) in reference to the energy available in sugars drops too low. Reproduced with permission from Waring RH and Running SW (1998) *Forest Ecosystems: Analysis at Multiple Scales*, p. 192. Copyright (1998) Academic Press, San Diego, CA.
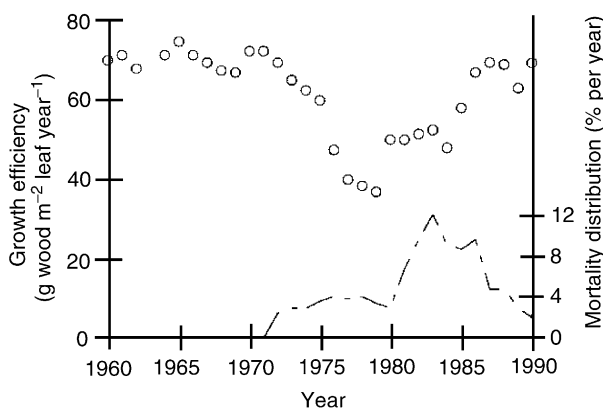

Figure 4 A spruce budworm outbreak in a balsam fir (*Abies balsamea*) stand in Quebec, Canada indicates that tree mortality (dashed line) recorded between 1972 and 1990 restored average tree growth efficiency (circles) to values recorded before the outbreak. Reproduced with permission from Waring RH and Running SW (1998) *Forest Ecosystems: Analysis at Multiple Scales*, p. 192. Copyright (1998) Academic Press, San Diego, CA.

associated with periods when stand growth efficiency drops below normal. The resulting mortality improves the growth efficiency of surviving trees (**Figure 4**). The growth efficiency index, combined with knowledge of the density of bark beetle attack, provides a basis for predicting survival or death of individual trees. Although unusual weather conditions can cause stress, it is often possible to improve tree vigor and biochemical defenses through thinning and application of fertilizer.

Separating Climatic from Other Stresses

Process models, provided with climatic data as well as information on stand structure, can provide monthly and annual estimates of photosynthesis, growth, and growth efficiency. With weather satellites in orbit around the earth, it is possible to obtain estimates of cloud cover and thereby to estimate incoming solar radiation. On clear days, it is also possible to estimate ambient air temperatures, humidity deficits, and periods of drought. With some simplifying assumptions, global variation in terrestrial primary production has been predicted exclusively from weather satellite-derived data. New satellite systems provide 8-day estimates of photosynthesis, and more accurate estimates of changes in canopy leaf area and annual above-ground production. In the future, remote sensing systems already tested from aircraft are being designed to provide improved estimates of changes in forest structure (leaf area and biomass) and canopy biochemistry (lignin and nitrogen concentrations).

With frequent monitoring of the forest condition via remote sensing, it is possible to distinguish disturbances caused by fire, insect outbreaks, logging, and wind storms from those associated with gradual changes in climate and pollutant loads. If conditions shift permanently, trees adapted to the previous environment should experience more stress and eventually be replaced by others better adapted to the new environment.

See also: **Genetics and Genetic Resources**: Genetic Aspects of Air Pollution and Climate Change. **Health and Protection**: Biochemical and Physiological Aspects. **Tree Physiology**: A Whole Tree Perspective; Canopy Processes; Physiology and Silviculture.

Further Reading

Evans J (ed.) (2001) *The Forest Handbook*, vol. 1. Oxford: Blackwell Science.

Franklin SE (2001) *Remote Sensing for Sustainable Forest Management*. New York: Lewis.

Landsberg JJ and Gower ST (1997) *Application of Physiological Ecology to Forest Management*. San Diego, CA: Academic Press.

Levitt J (1980) *Responses of Plants to Environmental Stresses*. vol. 1. New York: Academic Press.

Mitchell CP, Ford-Robertson JB, Hinckley T, and Senner-by-Forsse L (eds) (1992) *Ecophysiology of Short Rotation Forest Crops*. Dordrecht, Netherlands: Kluwer Academic.

Waring RH and Running SW (1998) *Forest Ecosystems: Analysis at Multiple Scales*. San Diego, CA: Academic Press.