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TREE PHYSIOLOGY

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Physiology and Silviculture

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Introduction

Physiology is the study of how plants function. Ecophysiology is the study of how a community of plants, animals, and microorganisms function together. Environmental ecophysiology is the study of how factors such as light, temperature, atmospheric carbon dioxide concentration, wind, relative humidity, soil water, and nutrients affect community function. Silviculture is the science and art of using environmental ecophysiology, wittingly or unwittingly, to manage forests.

The physiological processes observed in trees are common to most plants. As with other species in the plant kingdom, trees are found across a range of environments and therefore display a very wide

range of adaptation to environment. In this article we examine the basic physiological processes that govern tree function and indicate how this information can be applied to silviculture.

Silvicultural practices are directed towards a management objective. These include ensuring adequate regeneration, promoting some species over others, making trees grow faster, improving the quality of wood, protecting the trees from pests and diseases, sustaining water supply and soil chemical and physical properties, and conserving biodiversity. Many traditional silvicultural practices were developed before there was little physiological awareness of how trees grow. However, there is ample evidence that an understanding of environmental ecophysiology can assist in improving current, and developing new, silvicultural practices.

For convenience we consider the relationships between physiology and silviculture in the context of (a) the aboveground (aerial) environment and (b) the belowground (soil) environment.

The Aboveground Environment

The leaves, their structural properties and display, and their interaction with environmental variables determine photosynthesis, the process that drives all plant growth and therefore all biological systems. The environmental variables include quantity and quality of light intercepted by the foliage, atmospheric carbon dioxide concentration, air temperature, vapor pressure deficit, and wind. Based on an understanding of the relationships between photosynthesis and environment, silviculturalists manipulate the forest to achieve a particular management objective.

Leaves

The leaves of trees vary considerably in their size and shape. There are well-defined differences in the period of time that they remain functional. This is in part related to the architecture of the tree including whether the species is evergreen or deciduous. Size and longevity of leaves are affected by environmental stress. These properties are concerned with leaf expansion, retention, and senescence, and determine the size and extent of the canopy. Leaf structure and angle vary with depth in the canopy. These properties are dynamic and driven by the immediate light environment, and related to the physiological activity of the leaves (*see* **Tree Physiology**: Canopy Processes).

Leaf growth   Leaves grow by expanding their surface area and increasing their mass. Their potential for expansion is determined by the extent of cell division and their size by the capacity of those cells to expand. In the absence of stress, rates of growth and leaf size at maturity are primarily determined by temperature and nutrition. Cell expansion is a function of leaf turgor (see Water relations below) and quite sensitive to water stress. Cell division and the rate of emergence of leaves are less sensitive to stress but have a large demand for the products of photosynthesis (assimilates). Growth requires an irreversible increase in cell volume that occurs above a threshold or critical value of turgor. Foliar nitrogen (N) has a large effect on final leaf size.

The period as well as the rate of expansion of leaves can vary considerably within and between species. In tropical species, rates of leaf extension can be as high as 18 mm day^{-1} and growth can be completed in 2 weeks. In conifers, needle extension can continue for several months. In eucalypts, a genus with a naked bud habit that allows continuous growth if conditions remain favorable, leaf size will be reduced while water stress develops or at the end of the growing season where low temperatures limit growth.

Leaf longevity   Leaf longevity is the period that a leaf remains functional between initiation and fall. The period can vary up to three orders of magnitude between species. Longevity is often related to patterns of growth and levels of stress experienced by species in their native habitats. In the very slow-growing and long-lived bristlecone pine (*Pinus longaeva*), leaves have a lifespan of up to 45 years; in early-successional rainforest species lifespan may be just 50 days. Coniferous leaves have a longer lifespan than evergreen broadleaves while that of deciduous species is largely dictated by the length of the growing season. In tropical deciduous species, leaf longevity is strongly seasonal and largely determined by the levels and intensity of water stress that induce earlier leaf senescence and leaf fall.

Leaf longevity affects fluctuations in the extent of the canopy. However, the physiological activity of leaves across a range of species is closely related to their longevity. For example, a coniferous needle over a 5-year lifespan can fix two to three times the amount of CO_2 in photosynthesis than a deciduous leaf in one growing season, but at a lower rate of photosynthesis per unit leaf area. Leaf longevity is associated also with adaptation to stress. Plants that have leaves with a long lifespan minimize investment in new foliage but the leaves are suited to survival, for example through being structurally and chemically more robust in order to deter herbivory.

Photosynthesis

Photosynthesis converts solar (light) energy into dry mass and occurs in the leaves. The biophysical and biochemical processes that constitute photosynthesis are located in the mesophyll tissue, layers of cells that contain chlorophyll and other pigments, and enzymes. These processes involve both light and dark reactions. In the light reactions, solar energy in the spectrum between 400 and 700 nm is absorbed by chlorophyll and converted to chemical energy which is stored as phosphorylation potential (ATP) and as reducing power (NADPH). The dark reactions then lead to the reduction of carbon dioxide (CO_2) and its conversion to simple carbohydrates (CH_2O, sugars). The biochemical cycle that drives photosynthesis is the Calvin or photosynthetic carbon reduction cycle. Trees use this cycle only for photosynthesis and are C_3 plants. The enzyme (that catalyzes a reaction between two substrates, ribulose 1,6-*bis*phosphate and CO_2; see **Figure 1b**) involved in the first reducing step is ribulose 1,6-*bis*phosphate carboxylase, commonly referred to as Rubisco. It is present in leaves at high concentrations but these vary widely according to incident levels of light on the leaf, and the availability of nutrients (as Rubisco, a protein, has a high demand for nitrogen-based resources) and water. Photosynthesis is commonly measured as the amount of CO_2 fixed per unit leaf area per unit time. The photosynthetic capacity or maximum rate of photosynthesis varies widely between tree species, from <5 to around 25–$30 \mu mol$ $CO_2 m^{-2} s^{-1}$. Species with higher photosynthetic capacity are usually associated with higher rates of growth. Leaf photosynthesis is commonly measured using gas-exchange analysis; micrometeorological techniques are used over whole canopies (*see* **Tree Physiology**: Canopy Processes).

Gas exchange   In order to absorb CO_2 for photosynthesis, leaves expose a wet surface to a drier atmosphere. The evaporative loss of water that occurs results in cooling that assists maintaining equable temperatures for photosynthesis. To prevent dehydration, the epidermis has a relatively impermeable cuticle and turgor-operated valves called stomata. Changes in turgor lead to the opening and closing of the stomata. This regulates the diffusion of water vapor out of, and of CO_2 into, the leaf in a process referred to as gas exchange. The driving force in gas exchange is the concentration difference between the external atmosphere and, for CO_2, the concentration within the leaf; for water it is the saturated vapor pressure at the leaf temperature. The (stomatal) conductance is a measure of the degree of opening of the stomata.
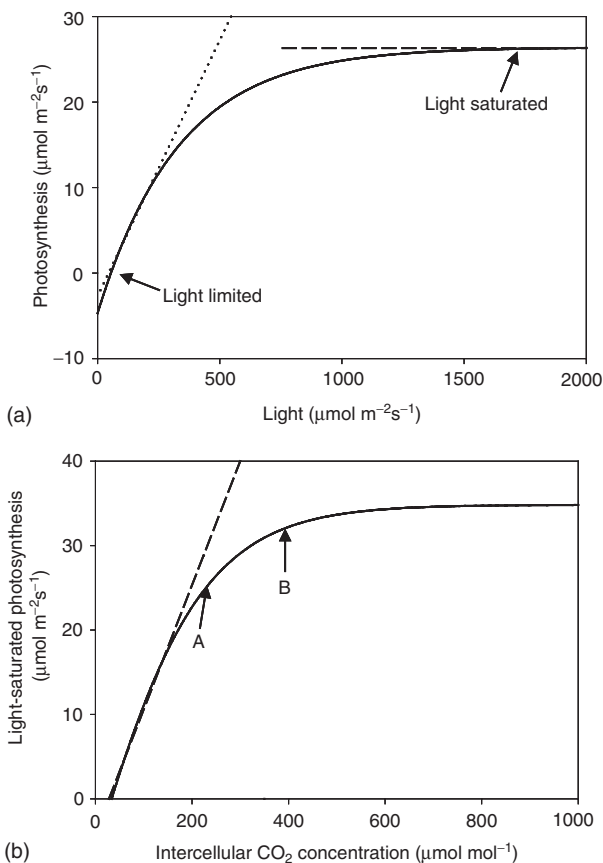

Figure 1   (a) The response of photosynthesis to increasing levels of light. At very low light levels, photosynthesis is negative as the rate of dark respiration (which results in the release of CO_2) is greater than the rate of photosynthesis. Photosynthesis then increases rapidly, the dotted line representing the initial slope of the response or quantum yield ($\mu mol\,CO_2$ fixed per μmol incident or absorbed light). At high light levels, photosynthesis becomes light saturated (broken line). Full sunlight varies with season but is approximately $2000 (\mu mol\,m^{-2}\,s^{-1})$. (b) The response of light-saturated photosynthesis to intracellular CO_2 concentration, a measure of the concentration in the internal spaces of the leaf that is available to be fixed in the mesophyll cells. The broken line measures the carboxylation efficiency and indicates that photosynthesis is RuBP (ribulose 1,6-*bis*phosphate) saturated. As CO_2 concentration increases, photosynthesis becomes limited by the regeneration of RuBP in the Calvin cycle. Point A represents the rate of photosynthesis that occurs at atmospheric CO_2 concentration; point B the rate if there was no stomatal limitation.

Environment and photosynthesis   Light and CO_2 are essential to photosynthesis as explained above. Light varies both diurnally and seasonally, and in a tree canopy the levels of light incident on a leaf will vary with position and orientation of the leaf. Leaves adapt to their incident light environment but have a characteristic light-response curve (**Figure 1a**). When light levels are low, photosynthesis is limited by light. When light levels are high in C_3 plants, photosynthesis is light-saturated.

Carbon dioxide and water (see below) are the essential substrates of photosynthesis. Photosynthesis is CO_2 limited at low levels of CO_2 concentration but the process becomes saturated at high concentrations (**Figure 1b**). The average atmospheric CO_2 concentration today (in 2004) is approximately $370\,\mu mol\,mol^{-1}$. Thus rates of photosynthesis will continue to increase if anthropogenic release of CO_2 into the atmosphere continues at current rates. This will lead to further increases in photosynthesis assuming no change in other factors that affect the rate of photosynthesis, for example temperature. As trees are the major terrestrial global sink for CO_2, this has environmental as well as biological significance.

Temperature is closely associated with photosynthesis as we are dealing with a biochemical process where rates of reaction increase with temperature, approximately doubling with each $10^{o}C$ increase in temperature. Thus photosynthesis varies both diurnally and seasonally. However, as pointed out above, leaf initiation and shedding are also driven by the availability of water. Thus photosynthesis tends to be most active over the middle range of temperatures, that is the response curve is parabolic, and decreases at very low and very high temperatures that are often associated with stress. Extremes of temperature are often associated with photoinhibition and photorespiration (see below). Seasonal shifts in temperature result in adaptive changes that are defined by the slope of the line relating the optimum temperature for photosynthesis and the acclimation or ambient temperature. Species from a continental climate and a more variable diurnal temperature range tend to have a broad temperature maximum to maximize uptake of CO_2 in photosynthesis whereas in species from a coastal environment, where diurnal changes in temperature are moderate, uptake of CO_2 has a more dynamic response to changes in temperature.

Rates of photosynthesis are also limited by nutrient and water stress (see below). Given that nitrogen and phosphorus are essential components of the photosynthetic process (Rubisco, ATP, and NADPH) positive associations between photosynthetic capacity and leaf nitrogen and leaf phosphorus are observed. However the effects of atmospheric and soil water stress on photosynthesis are primarily caused by changes in response to leaf water status and vapor pressure deficit on stomatal conductance.

Stomatal conductance   Stomata are powerful regulators of gas exchange and linear relationships between rate of photosynthesis and stomatal conductance are often observed in trees. This relationship may become nonlinear at high conductance as the rate limitation may no longer be diffusion of CO_2 into the leaf but reside in the activity of photosynthetic processes in the mesophyll. As with rates of photosynthesis, there is a considerable variation in maximum stomatal conductance between species where low conductance is often associated with low photosynthetic capacity and vice versa.

Stomata open and close as a result of increases and decreases in turgor, respectively, of guard cells that surround the stomatal pore. However these changes in turgor are driven by active mechanisms that involve the transport of ions, in particular potassium. The regulation of stomata is complex but in general they open in response to light, have a parabolic response to temperature and close in response to atmospheric (vapor pressure) and leaf (soil) water deficits (**Figure 2**). The sensitivity of stomata to these variables varies between species, and as with photosynthesis, there is adaptation of stomatal conductance to the ambient environment. Trees are tall crops and the leaves are closely coupled to the atmosphere (*see* **Tree Physiology:** Canopy Processes). As a result, stomatal conductance of trees is often observed to be quite sensitive to vapor pressure deficit.

Effects of age   The photosynthetic capacity and maximum stomatal conductance of leaves changes during their development, maturation, and senescence. On tree species that have several cohorts of leaves, for example conifers, there may be considerable stratification of physiological activity, the lowest being associated with the oldest leaves. Trees are perennial crops and some are very long-lived. There is evidence that tree aging is associated with a decline in photosynthetic capacity though this is linked to changes in other areas of physiological activity.

Photoinhibition   Photoinhibition is associated with the absorption of light by plants in excess of that required for photosynthesis and is manifest in a reduced photosynthetic capacity. Photoinhibition occurs when leaves are under stress, for example during conditions of low temperature or water stress, such that the rate at which enzymes function in the Calvin cycle is limited. Sustained decreases in the efficiency of photosynthesis and quantum yield, a measure of the efficiency of conversion of light to biomass, are observed that can be detected by chlorophyll fluorescence and are associated with prevention of damage to the photosynthetic system. If light is absorbed in excess but not dissipated, oxidative damage occurs. Prevention of damage is associated with the xanthophyll cycle, an interconversion of carotenoid pigments that results in the harmless dissipation of light as heat energy, and a range of other potential mechanisms, some unproven.
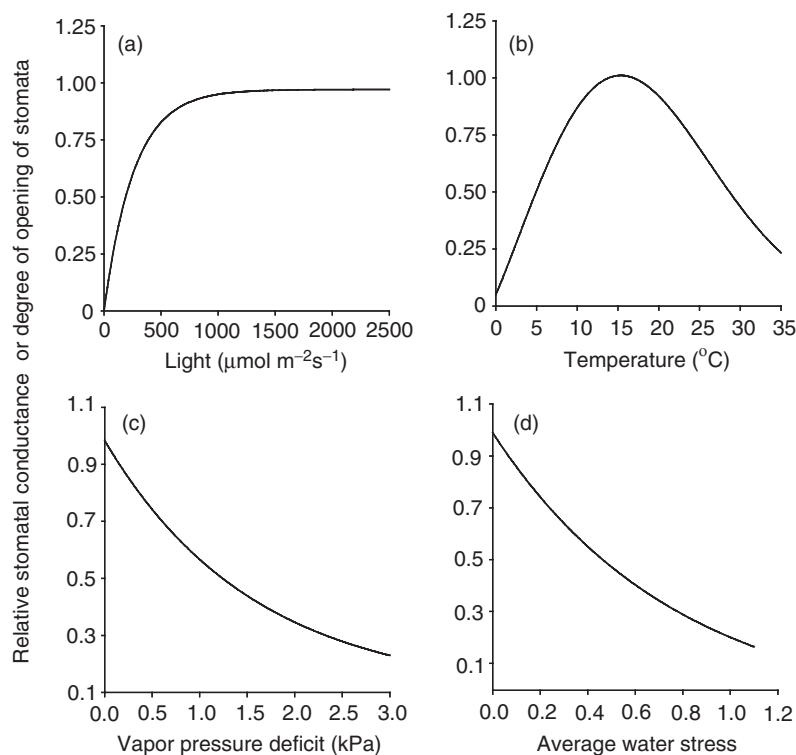
Figure 2 Stomatal respond to their environment. Stomata open rapidly in response to increasing light levels (a). Stomata also open in response to increasing temperature but are observed to close at high temperatures (b). However this is often because the stomata are sensitive to increasing vapor pressure deficit (the difference between the saturated vapor pressure at the air temperature and the actual vapor pressure) (c) and vapor pressure deficit increases with temperature. Stomata are also responsive to the water status of the leaf (d); this is measured by considering the water stress history (measured as the pre-dawn water potential) that the leaf has experienced. The stomata of tree species differ in their response to these environmental variables.

Respiration   Respiration is a process that consumes oxygen and releases CO_2, water, and energy. Most respiration is independent of light and produces energy to support growth. However, photorespiration occurs only in the light and competes directly with photosynthesis in a process where both oxygen and CO_2 compete for ribulose 1,6-*bis*phosphate and Rubisco. This reduces the efficiency of utilization of CO_2 in the Calvin cycle and causes photosynthesis of C_3 plants to saturate at lower values of light and photosynthesis than in C_4 plants. (C_4 plants can largely overcome the negative effects of photorespiration by using anatomical and biochemical mechanisms to deny access of oxygen to Rubisco.) Photorespiration is most active at high light intensities and temperatures and acts, along with photoinhibition, to reduce photosynthesis.

Silviculture

Several tools are available to silviculturalists to manipulate the aboveground environment. Choice of species, stocking density, the use of monocultural or mixed-species plantings, shelter belts, pruning, and thinning are some. Application of fertilizer and

irrigation, although altering the belowground environment in the first instance, change growth rates and canopy size, thereby altering also the aboveground environment. Some of the ways these actions affect physiological activity will now be explored.

Light   The classical silvicultural systems in natural forests are single-tree selection, group selection, shelterwood, and clear-cut. This series represents a progressive increase in the amount of light reaching the forest floor to promote regeneration. The appropriate system is determined to a large extent by the photosynthetic properties of the trees. Although clear-cuts are considered by many to be environmentally unfriendly, there are circumstances in which this system is the most appropriate. In native forest, many 'clear-cuts' that arise from natural disturbance (e.g., by fire) are essential for regeneration and replacement of the same forest type. For example, *Eucalyptus regnans* is a major forest type in southeastern Australia which often occurs as a single species of the same age. This age is determined by the timing of the fire event that destroyed the previous forest and provided a large seedbed out in the open. Physiologists call *E. regnans*

a 'sun' or 'shade-intolerant' plant. Conversely, in the rainforests of northeastern Australia, *Alocasia macrorrhiza* grows as an understory species and regenerates and persists under low light. *A. macrorrhiza* is a popular indoor plant. Physiologists call it a 'shade' or 'shade-tolerant' plant. The photosynthetic properties of sun plants and shade plants are shown in **Figure 3**.

It can be seen that sun plants (e.g., *E. regnans*) typically grow faster than shade plants (e.g., *A. macrorrhiza*) but only if there is plenty of light reaching the leaves. *Eucalyptus regnans* grows very poorly under shade and indeed will only regenerate and grow satisfactorily in the open. *Alocasia macrorrhiza* grows much slower than *E. regnans* but it can establish and persist at lower light levels. The light compensation point (the light level at which net photosynthesis is zero) is considerably less in *A. macrorrhiza* than in *E. regnans*. Thus use of a silvicultural regime that shades *E. regnans* regeneration is likely to fail. Pioneer species that are intolerant of shade (like *E. regnans*) are usually very productive and readily establish on bare sites. Successful plantation trees are often pioneer species that occur naturally as even-aged monocultures. By contrast species with photosynthetic properties adapted to growth under shade are not suited to being regenerated in the open and attempts to use these species in plantations often fail.

The manipulation of light in forest plantations through stocking density at planting and thinning during the rotation are used to optimize the amount of light intercepted by an individual tree and therefore its size, at the same time maximizing the quantity of wood produced per unit area, and the quality of the wood required for a particular end-use. High initial stockings in all types of forest promote height growth, straight and single-stemmed trees,

and prevent the development of large branches. Thinning reduces between-tree competition and allows increased growth of remaining trees. Pruning reduces the size of the knotty core and allows the development of knot-free clear wood by removing the lower branches, often in a series of progressive lifts.

Pruning and thinning are associated with changes in the photosynthetic activity of leaves. Green pruning that removes live branches reduces the total number of leaves per tree; thinning changes the distribution of light incident on the leaves of the retained trees. A quantitative understanding of the physiological responses to both practices is used as a basis for management. The reduction in canopy size with green pruning significantly increases the rate of photosynthesis of the residual leaves throughout the crown. There is also an increase in the rate of leaf development and delayed senescence of existing leaves. The magnitude and duration of these responses is related to the severity of pruning. Thus an increasing capacity for photosynthesis at tree level is offset by an increasing reduction in crown size. The balance point is the pruning severity beyond which reduction in growth is observed. The enhanced levels of light-saturated leaf level photosynthesis observed following thinning are related to the increase in the fraction of incident light penetrating to the middle and lower parts of the canopy compared to that in unthinned stands. The magnitude of this response increases with time from thinning and is associated with increased levels of leaf nitrogen concentration and changes in its distribution commensurate with its allocation according to the prevailing light environment. Thinning is also associated with increases in tree-growth efficiency, the amount of stemwood produced per unit leaf area.
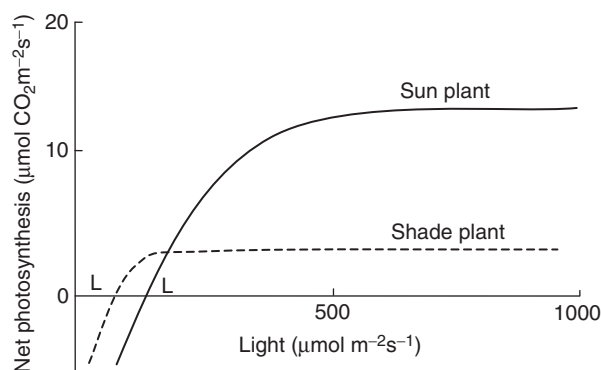
Carbon dioxide   As CO_2 is a primary reactant of photosynthesis, increases in its concentration in the atmosphere have the potential to increase growth rates. Indeed, artificial enrichment of CO_2 concentrations in nurseries has been used to that effect. The concentration of CO_2 in the atmosphere has been increasing exponentially for over 100 years, mainly from burning fossil fuels but also from the clearing and burning of vegetation, including forests which historically have been very large sinks for CO_2. If not already occurring, it is expected that climates will change as a result of increased CO_2 concentrations in the atmosphere and that the consequences of this will be largely negative for human welfare. Forests, however, all other things being equal, may be more productive, though any increase in average

Figure 3   A typical relationship between net photosynthesis and light for single unshaded leaves of sun plants and shade plants. L is the light compensation point.

temperatures and the distribution and quantity of rainfall will change species boundaries.

While changes in atmospheric CO_2 concentration are beyond their control silviculturalists can manipulate CO_2 to their advantage by increasing the stomatal conductance of CO_2 from the atmosphere into the leaves through the stomata. Silviculture is used in a broad sense to maximize photosynthesis in this way. For example weed control, the removal of competition for resources, i.e., light, nutrients, and water, ensures that these are used to support uptake of CO_2 by the tree crop only. This is particularly important when any one resource is a major factor limiting plant growth.

Air temperature Very low temperatures can 'damage' the physiological integrity of plant tissue. This is, in particular, a silvicultural issue in nurseries where seedlings are raised under conditions that are mild compared to those at the planting site. Two types of damage may occur. Physical frost damage is caused by the freezing and expansion of intracellular fluid that result in cell breakage. Photodamage associated with photoinhibition is caused when more light is absorbed than can be dissipated harmlessly. This leads to reactions that destroy cell membranes. Silviculturalists impose 'hardening' in the nursery to make the seedlings physiologically more resistant to frost and low temperature after transplanting. These include progressive exposure to lower temperatures that leads to improved resistance because the seedlings increase the osmotic concentration of cell contents, thereby decreasing their freezing point. Low temperature and nutrient starvation increase resistance to photodamage by stimulating the activity of physiological processes that dissipate light energy. In addition, shadecloth is used to reduce the levels of incident light on seedlings. The pattern of regeneration of tree seedlings in native forest is affected by the degree of cold-induced photoinhibition and greater exposure increases the intensity of a frost event. Shelterwood systems reduce exposure and increase average minimum temperature, thereby supporting seedling survival.

Wind A boundary layer of relatively still air at the leaf surface contributes to the resistance to transfer of CO_2 into, and water vapor out of, the leaf. However forests with high canopies are aerodynamically rough and the atmospheric climate comes very close to the leaf surface. Consequently boundary-layer conductance is very high and reinforced by wind mixing up the air close to the leaf surface. Photosynthesis is increased in gentle to moderate winds but severe winds can accelerate water loss, promoting stomatal closure and a reduction in photosynthesis. Strong winds can also cause mechanical damage to trees. Planting patterns are used to promote shelter within a stand, and belts of trees planted strategically to reduce wind speed across the stand.

The Belowground Environment

Plants require water and nutrients for growth and these are obtained in the main by absorption through roots. Thus the physiological condition of the aboveground parts of the plant are reliant on soil properties, and processes that control root development and the exploration of the soil (*see* **Tree Physiology**: Root System Physiology) and the acquisition, translocation, and storage of nutrients (*see* **Tree Physiology**: Nutritional Physiology of Trees). Conversely root systems are reliant on the translocation of assimilates from leaves for their growth and energy requirements. Changes in soil water content can have a profound effect on physiological activity and are associated with reductions in water potential and water content throughout the plant.

Water Relations

The amount of water used directly in the biochemical reactions of photosynthesis is very small compared to that transpired by leaves. Changes in water status strongly influence tree growth through their effect on leaf expansion and shoot and root extension. As water status decreases, turgor is reduced, stomata close, and direct effects of water stress on chloroplast processes reduce the rate of photosynthesis. There is evidence that hormonal signals transmitted between the root surface and leaves can trigger changes in stomatal conductance in response to the current level of water supply.

Water content, water potential, and water transport Water status can be measured gravimetrically as tissue water content, most often relative to its saturated or turgid weight. Water moves along gradients of water potential (that has units of pressure) which is defined as the potential energy per unit volume of water with reference to pure water at zero potential. Water in most biological systems and in soil has less potential energy than pure water. Consequently values of water potential are negative and water moves along negative potential (pressure) gradients. A key measurement of leaf water potential is made pre-dawn to determine the minimum level of water stress. This value is taken when there is little or no net flux of water through the tree and therefore estimates the water potential at the soil–root interface.

The water potential of a leaf (shoot or root) is the sum of two components, a negative osmotic potential arising from the presence of dissolved solutes in the cell and a positive turgor potential arising from the pressure exerted on the cells by their walls. These variables, and a measure of the elasticity of the cell walls, can be derived from the relationship, referred to as the pressure–volume curve, between water potential and water content.

In response to the demand for water at the evaporating surface, leaf water potential becomes more negative to increase the potential gradient. As the soil dries and soil water potential becomes more negative, a strategy for maintaining the same flux of water through the plant is to further lower leaf water potential to maintain the potential gradient. Trees are observed to adopt a range of strategies to deal with water stress including an inherently low osmotic potential, lowering of leaf osmotic potential that is referred to as osmotic adjustment, and elastic tissues that allow the maintenance of turgor over a wider range of tissue water contents. Trees with high osmotic potentials and inelastic tissues that promote rapid loss of turgor are associated with a high stomatal sensitivity to leaf water status and drought avoidance. Conversely, trees with low osmotic potential and elastic tissues are associated with a low stomatal sensitivity and drought tolerance.

Sapwood   The major conducting pathway for water between the roots and the leaves is the stem sapwood. The sapwood consists of a network of interconnecting pipes which in trees is made up of xylem vessels or tracheids. This 'pipe model' link between sapwood and leaves implies a causal relationship although the direction of causation remains unclear. Thus stem sapwood area can be an accurate scalar for estimating leaf area due to its role in supplying water to the transpiring foliage (*see* Tree Physiology: A Whole Tree Perspective).

Silviculture

The growth and function of roots is influenced by soil water, soil nutrients, soil air, soil strength, soil temperature, soil salinity, soil acidity, soil sodicity, and soil toxicity. Silviculturalists can manipulate these environmental factors to their advantage, using techniques such as cultivation, including mounding and deep ripping, or by species selection. A soil environment that promotes root development does not necessarily mean that the growth of roots will be greater than that of the stem, branches, and foliage. Indeed it is usually the

opposite. Thus if the soil has plenty of water and nutrients but the aboveground environment is in some way deficient, e.g., there are low levels of incident light, then the tree will partition more assimilates to aboveground growth in a bid to capture more light.

When dealing with an interface between soils and roots, there is a knowledge boundary and exploitation of a physiological understanding of root behavior requires close cooperation with soil scientists as well as silviculturalists.

Water   Irrigation is not usually an option for the silviculturalist, except in nurseries or in disposal of treated sewage effluent (*see* **Soil Development and Properties**: Waste Treatment and Recycling). However there are silvicultural strategies that can conserve scarce soil water and ensure that it is used most efficiently in growth. The most fundamental is avoidance of dry sites but as these are often unsuitable for activities other than forestry, an option is a tree species that will grow and survive at such a site. Trees vary in their response and ability to adapt to soil water stress. They also vary in their ability to close their stomata in response to the dryness of the atmosphere (measured as the vapor pressure deficit). Water-use efficiency, a term that measures biomass produced per unit of water transpired varies a limited amount and is not commonly used as a selection tool in forestry. In environments that have higher levels of water supply but where water stress is still the major factor limiting tree growth, one strategy is to deliver the soil water to the crop trees only. This can be achieved by reducing the evaporation of water directly from the soil by using mulches or retaining litter. In addition, spacing and thinning the tree crop reduces the total transpiring area. Besides increasing tree survival, this option can be used to maximize the growth of the retained trees and provides a basis for the sustainable use of available soil water across rotations. As pointed out above, weed control is an essential part of management on dry sites.

Eucalypts provide an example of where insufficient knowledge of tree physiology has resulted in poor silviculture and created a potential environmental weed. Australia is a large and predominantly dry country dominated by genus *Eucalyptus*. This genus includes some very fast-growing species and the inference was made that some of these species might be successful on sites with low rainfall. However the fast-growing species are native to wetter sites and are not physiologically well adapted to severe water stress. Thus many early plantings of eucalypts outside of Australia on dry sites failed

because of inappropriate species selection. When these same species escaped to sites with higher water supply, they became aggressive weeds and suppressed the growth of more desirable species. An understanding of the physiology of water use would have foreseen these eventualities. A general strategy among plants for conserving soil water is to close stomata, but this will also reduce growth rates because photosynthesis will also be reduced. However several eucalypt species tolerate drought and do not close their stomata so much as the soil dries or as the vapor pressure deficit increases (**Figure 4**). This means that when eucalypts are grown in competition with more conservative and slower-growing species, they transpire more water and exhaust the soil water supply faster. Eucalypts often survive by dropping their leaves and then regenerating their foliage from dormant buds when the conditions are again favorable for growth, a strategy that also makes them highly competitive species in some exotic environments.

Nutrients   The elements essential for growth were established by physiologists in the early twentieth century and mineral nutrition is now relatively well understood in the context of the processes that drive plant growth. Application of fertilizer to forests is an established silvicultural practice. For example rates of canopy development and canopy size are strongly dependent on the supply of nitrogen. Fertilizers are also used to correct nutrient imbalances which can impair the functioning of processes that are crucial to acceptable growth and form. However, there are other ways of managing forest nutrition. Cultivation, residue retention, elimination of burning, organic matter maintenance, prevention of erosion, use of legumes, application of treated municipal wastes,

and the promotion of mycorrhizal infection of roots are all forms of management of nutrition, and in all of these cases a knowledge of the underlying physiological processes helps in defining the most appropriate regimes.

Small amounts of nutrients can also enter foliage and soil through atmospheric deposition and this can be critical to the welfare of certain ecosystems. However, nutrient inputs from air pollution can be significant. Soils in southern Sweden have been estimated to receive approximately $30 \, kg \, ha^{-1}$ of free nitrogen from the combustion of coal and other fossil fuels in Germany. This, combined with increased CO_2 concentrations in the atmosphere, has resulted in higher growth rates. However, air pollution is not recommended as an acceptable silvicultural practice!

Soil air and soil strength   Roots need oxygen for respiration and growth. Oxygen can be reduced to critical limits in situations where the air-filled pore space in the soil is reduced, such as in clay soils, in waterlogged soils, and in compacted soils. Reduced soil air will impair membrane function and therefore can reduce the uptake of water across the root endodermis. This means that a soil with too much water can actually cause water stress in the tree. Waterlogged soils can be mounded and compacted soils can be ripped.

In order for roots to grow they need to overcome the mechanical resistance offered by the soil. This mechanical resistance or impedance is related to the strength of the soil. Root growth rates decrease exponentially with increasing soil strength (**Figure 5**). Ripping the soil can reduce soil strength but it is better to have soil management regimes that do not cause soil compaction in the first place. The strength of a particular soil increases with soil bulk density (a measure of soil compaction) and decreases with soil water content. This means that root growth in a drying soil will be reduced because of both the lower water potential in the soil and the increased soil strength. Thus soil cultivation can alleviate water stress in plants in compacted soils to some extent.

Cultivation   Soils are cultivated (by plowing, mounding, ripping) as part of plantation establishment to control weeds, to release nitrogen, to improve access to soil water and drainage, and to reduce soil strength. Cultivation regimes are usually based on empirical trials. Silvicultural practices informed by empirical trials or trial and error must by their very nature be blunt tools. The tendency has been to assume a worst-case scenario and
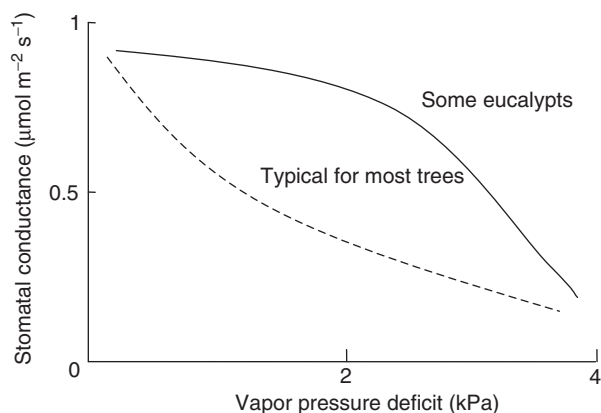

Figure 4 The typical relationship between stomatal conductance and vapor pressure deficit for most trees compared to that of some eucalypts.
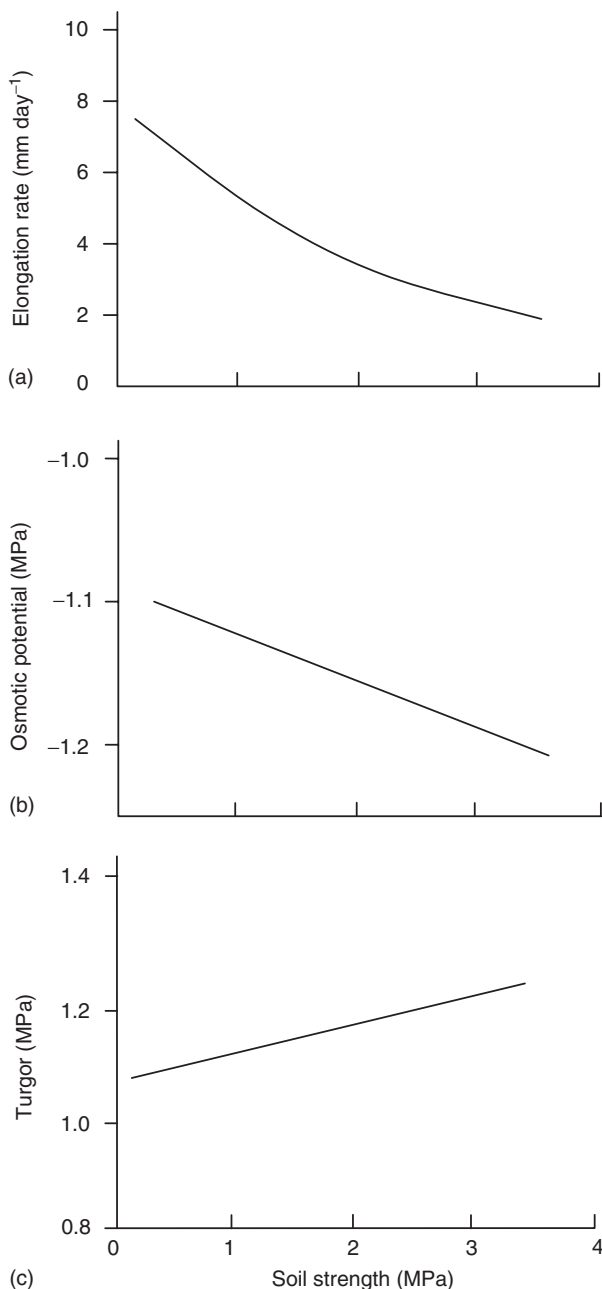
Figure 5 The effect of soil strength on (a) the rate of elongation of roots of radiata pine, (b) the osmotic potential of the cells in the root elongation zone, and (c) the turgor of the cells in the root elongation zone. Part (a) shows that the rate of root elongation decreases exponentially with increasing soil strength; (b) demonstrates that elongating cells reduce their osmotic potential (osmoregulation) in response to increasing soil strength which results in an increase in turgor (c) which can compensate in part for the increasing mechanical impedance of the soil. Adapted with permission from Zou C, Sands R, and Sun O (2000) *Tree Physiology* 20: 1205–1207.

consequently to overcultivate in order to be sure that an effect is realized. Thus knowledge of root physiology can assist the silviculturalist in making a more informed decision.

Process-Based Models: A Synthesis and Conclusion

There has been considerable effort in recent years to inform silviculture through process-based models. These are complementing and extending the use of empirical models. Empirical models can only be used to predict growth for the sites, environments, and conditions on which they are based, i.e., they are site specific.

Physiological relationships of the type described in this article form the basis of process-based models that can describe forest growth. These models are 'process-based' because growth is predicted from a knowledge of how physiological processes respond to environment and to silviculture. The advantage of these models is that they can be used across a range of environments where a species is grown although the parameters of the model, for example light-saturated photosynthesis or resistance to uptake of water by roots, may change with species. These models are becoming very sophisticated and dynamic such that they can now be used for predicting responses to silviculture and growth in future rotations based on an understanding of the resources used to support the current rotation.

The lines of communication between physiologists and silviculturalists have been improved but there is still a long way to go. It is essential that Schools of Forestry teach tree physiology in order for silviculturalists to be able to communicate with physiologists. It is perhaps equally important that silviculture be taught as applied environmental ecophysiology in an economic and social context.

Further Reading

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