

## **Temperate Coniferous Forests**

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# Temperate Coniferous Forests

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*Temperate coniferous forests include representatives of the most massive forms of terrestrial life on Earth. In the coastal redwood (*Sequoia sempervirens*) forests of northern California, trees may reach heights >100 m and accumulate biomass in excess of 3000 t ha<sup>-1</sup>. In the more extensive Douglas fir (*Pseudotsuga menziesii*) forests of the Pacific Northwest, USA and Canada, biomass in older stands frequently reaches 1000 t ha<sup>-1</sup>, with an additional 500 t ha<sup>-1</sup> of standing dead and fallen trees. Above-ground biomass ranges widely, however, as does above-ground growth. Temperate coniferous forests produce an average of about 5 t ha<sup>-1</sup> year<sup>-1</sup> of above-ground biomass but in climatically diverse areas production may range from <1 to >20 t ha<sup>-1</sup> year<sup>-1</sup> (Runyon et al., 1994).*

*Because of their high growth capabilities, favorable wood structural properties and columnar form, temperate coniferous forests play a disproportionate role in meeting global demands for lumber and fiber. As a consequence, the geographic range of temperate conifers has been extended beyond the native ranges of many species.*

*In this contribution we focus on the attributes of temperate evergreen coniferous forests that distinguish them from their major competitors, deciduous hardwoods. This differentiation should help us anticipate the future role and importance of temperate coniferous evergreen in relation to rising levels of air pollution, atmospheric carbon dioxide (CO<sub>2</sub>), and changing climate.*

## EVOLUTION

Conifers bear naked seeds, unlike angiosperms, and differ from other gymnosperms by having the seeds arranged inside cones. During the Carboniferous period (300 million years ago), conifers represented a minor group of gymnosperms, but they evolved rapidly as conditions became drier and colder during the Permian (286–240 million years ago). Temperate coniferous forests were most widely distributed during the Tertiary period (90–15 million years ago), with coastal redwood (*Sequoia sempervirens*) and dawn redwood (*Metasequoia*) distributed throughout both Eurasia and North America. Today, conifers are the dominant representatives of gymnosperms with about 50 genera and 550 species, predominantly in the Northern Hemisphere (Raven et al., 1986).

Conifers are well adapted to arid and cold conditions. The surfaces of needle-shaped leaves are protected by waxes

and sunken stomata and a large proportion of their stems consists of sapwood that serves as a storage reservoir, as well as a conduit for transport of water from roots to leaves.

## GEOGRAPHIC DISTRIBUTION

Today, temperate evergreen coniferous forests cover approximately  $2.4 \times 10^6$  km<sup>2</sup> (Melillo et al., 1993; Landsberg and Gower, 1997). Conifers dominate the montane forests in North America, Europe, and China. Smaller areas of temperate conifers are located in montane regions of Korea, Japan, Mexico, Nicaragua, and Guatemala. In Europe, the distribution of native and introduced conifers has been expanded into areas more climatically favorable to hardwoods. Pines (*Pinus*), represented by more than 90 species, are the most widely distributed conifer and their range has increased by widespread planting in the Southern Hemisphere. Other important genera include the firs (*Abies*), spruces (*Picea*), hemlocks (*Tsuga*), false-hemlocks (*Pseudotsuga*), larches (*Larix*), cypresses (*Cupressus*), cedars (*Chamaecyparis*, *Thuja*, *Libocedrus*) and juniper (*Juniperus*). In the yews (*Taxus*), the seeds are not borne in cones but are enclosed within a fleshy structure. Additional conifer genera (*Araucaria*, *Fitzroya*, *Austrocedrus*) are present in the Southern Hemisphere, where they were once more widely distributed (Axelrod et al., 1991).

## ECOLOGICAL DISTRIBUTION

The potential ecological niche of temperate conifers falls within regions of >250 mm in annual precipitation that experience subfreezing conditions, down to, but not below –45 °C, which is the limit for supercooling of water. Only boreal tree species, which include some pines and spruces, are adapted to temperatures below this limit (Waring and Running, 1998). In regions where precipitation is well distributed throughout the growing season, deciduous hardwoods usually dominate over temperate conifers. Following major disturbances, however, conifers can become established and achieve temporary dominance (Landsberg and Gower, 1997).

In the Pacific Northwest region, where summer drought is common, the situation is reversed and many long-lived conifers replace earlier established hardwoods (Waring and Franklin, 1979). To explain these shifts in dominance requires an appreciation of how resources are captured by temperate evergreen conifers throughout the year.

## PHYSIOLOGICAL AND MORPHOLOGICAL ADAPTATIONS OF CONIFERS

Conifer leaves are more clumped and narrower in cross-section than the foliage of most angiosperms, and the

branch structure is much less extensive. These properties allow light to penetrate more deeply through conifer canopies than through hardwood forests with comparable leaf area. As a result, the maximum surface area of conifer foliage, often expressed as  $\text{m}^2$  of (projected) leaf area per  $\text{m}^2$  of ground surface, may reach 10–12, while hardwood forests rarely exceed half these values. In addition, conifer canopies reflect only about 5–10% of intercepted solar radiation, whereas hardwoods reflect 15–25%. In combination, these differences in canopy properties permit coniferous forests to absorb a greater proportion of incoming solar radiation than forests composed of hardwoods (Jones 1992).

Although conifers absorb a larger fraction of intercepted radiation than hardwoods, they are less prone to suffer damage from elevated temperatures because the needle-shaped foliage dissipates heat efficiently, even under unventilated conditions. Consequently, conifers conserve water under conditions where broad-leaf species must transpire at higher rates, wilt, or shed foliage to prevent temperatures from rising above  $45^\circ\text{C}$ , when enzymes begin to become unstable.

Another foliage characteristic that distinguishes most conifers from other evergreen vegetation is the duration that leaves remain functional. Conifers generally hold some foliage for 3–5 years, although a few species maintain functional leaves for 30–40 years (Landsberg and Gower, 1997). The fact that temperate evergreen conifers can maintain dense, needle-leaf canopies, composed of multiple-age classes of foliage, affects many ecosystem processes including the capture of water, nutrients, and pollutants from the air, and the rates of decomposition, nutrient release, and soil organic matter accumulation.

Anatomically, long-lived foliage is characterized by an epidermis covered with a thick waxy cuticle, above one or more layers of compactly arranged, thick-walled cells, which in turn surround a structurally reinforced vascular system. The result is that nutrient concentrations in conifer needles may be only half those in deciduous hardwood leaves of equivalent mass. Lower nutrient concentrations in individual leaves translate into lower demand, yet long-lived foliage provides a greater store of nutrients available for transfer during peak growth periods than is available in deciduous hardwoods.

In addition, in environments where mineral weathering rates are slow and nutrient availability limited, evergreen conifers can take up nutrients from the soil as long as conditions remain above freezing. Photosynthesis can also continue under these conditions. As a result of nutrient uptake and photosynthesis during the dormant season, stored reserves (starch, sugars, amino acids) are available to activate symbiotic fungi on tree roots that efficiently scavenge nutrients. In contrast, deciduous trees, which also have symbiotic root fungi, are restricted to taking up nutrients when foliage is present.

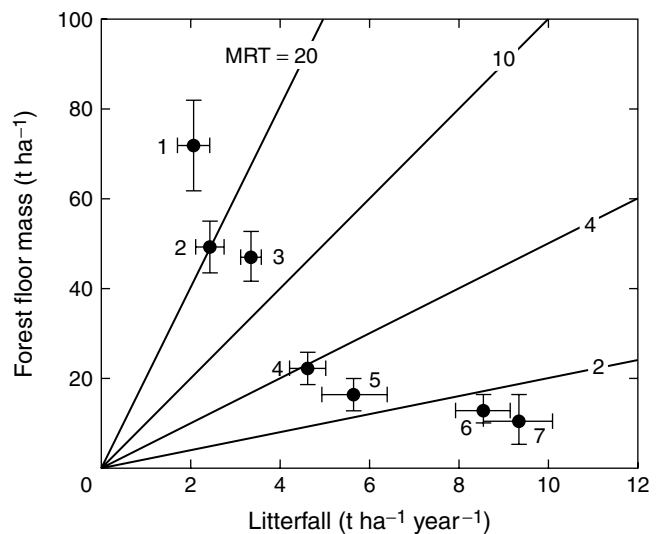
The evolutionary advantages that conifers have on infertile soils can place them at a disadvantage on more fertile sites. On infertile soils, most available nitrogen (N) is in the form of ammonium ( $\text{NH}_4^{+1}$ ), which conifers take up selectively in preference to nitrate–nitrogen ( $\text{NO}_3^{-1}$ ). As nitrate–nitrogen becomes more available, conifers are disadvantaged in competition with hardwoods (Smirnov and Stewart, 1985).

## ECOSYSTEM RESPONSES OF TEMPERATE CONIFEROUS FORESTS

### Decomposition

Leaf litter, wood, and root materials produced by evergreen conifers usually contain twice the amount of carbon (C) in relation to nitrogen found in corresponding materials produced by deciduous angiosperms. As a result, the decomposition of coniferous litter is usually 3–4 times slower than hardwood litter, leading to a greater accumulation of forest floor litter under conifers (Figure 1).

With time, as litter decays, soils under coniferous forests maintain high C–N ratios and serve as storage sites for amounts of carbon that far exceed above-ground biomass, and have turnover times of centuries and millennia. This



**Figure 1** Average forest floor mass plotted against litter-fall for (1) boreal needle-leaved evergreens, (2) boreal broad-leaved deciduous, (3) temperate needle-leaved evergreen, (4) temperate broad-leaved evergreen, (5) temperate broad-leaved deciduous, (6) tropical broad-leaved evergreen, and (7) tropical broad-leaved deciduous trees. Assuming the forest floor is at steady state, the average mean residence time (MRT, years) can be calculated as forest floor mass/litterfall mass. The lines indicate that forest floor litter of temperate needle-leaved evergreens take about 15 years to turnover whereas other temperate hardwoods turnover in <4 years. (Reproduced from Landsberg and Gower, 1997)

property of coniferous forest ecosystems, combined with their potential rapid growth, makes them an attractive vegetation type to manage for the sequestration of large amounts of atmospheric carbon dioxide (CO<sub>2</sub>).

### Hydrology

The potential of evergreen coniferous forests to maintain dense, well ventilated canopies throughout the year significantly increases the annual water vapor transfer from their canopies, relative to deciduous forests. As a result, evergreen coniferous forests reduce stream flow by an average of 15–25% in comparison to deciduous hardwoods in similar environments (Waring and Schlesinger, 1985). The dense, finely dissected canopies of evergreen conifers also have the propensity to condense water (and pollutants) from clouds, leading to fog drip, which can increase the effective precipitation at high elevations substantially in windy environments (Harr, 1982).

Water stored in the sapwood of conifer trees can serve as a temporary buffer against drought. During the day, this reservoir may contribute up to a third of the water transpired, with refilling taking place during the night. In general, the ratio of sapwood mass to leaf area increases in conifers with harshness of the environment (Waring and Running, 1998); the total volume of sapwood determines the reservoir of water. Thus, a 50 m tall Douglas fir forest with about a quarter of the stem composed of sapwood may hold 30 mm of stored water whereas a 15 m tall pine forest, with stems composed largely of sapwood, can hold 20 mm of stored water (Waring and Running, 1978; Waring *et al.*, 1979). In a few species, such as redwood, the voluminous heartwood also plays an important role as a reservoir.

### RESPONSE OF TEMPERATE CONIFEROUS FORESTS TO AIR POLLUTION

In clean environments, nitrogen deposition is usually <5 kg ha<sup>-1</sup> year<sup>-1</sup> whereas in heavily polluted areas, nitrogen additions exceed 50–70 kg ha<sup>-1</sup> year<sup>-1</sup>. Much of this excess nitrogen ends up as nitrate, which is easily leached in soil solution. The negatively charged nitrate ions extract calcium, magnesium, and other positively charged nutrient from soil cation (+) exchange sites. Because weathering rates are slow, the lost nutrients are often replaced with positively charged acid radicals (H<sup>+</sup>) and toxic forms of aluminum (Al<sup>3+</sup>). As a result, a nutrient imbalances may arise where the availability of nitrogen is in excess to that of other elements, creating conditions where plants become more nutritious, and less resistant to attack from a variety of organisms (Waring and Running, 1998).

In areas where hydrocarbons released by the combustion of fossil fuels interact with sunlight, ozone (O<sub>3</sub><sup>-3</sup>) is

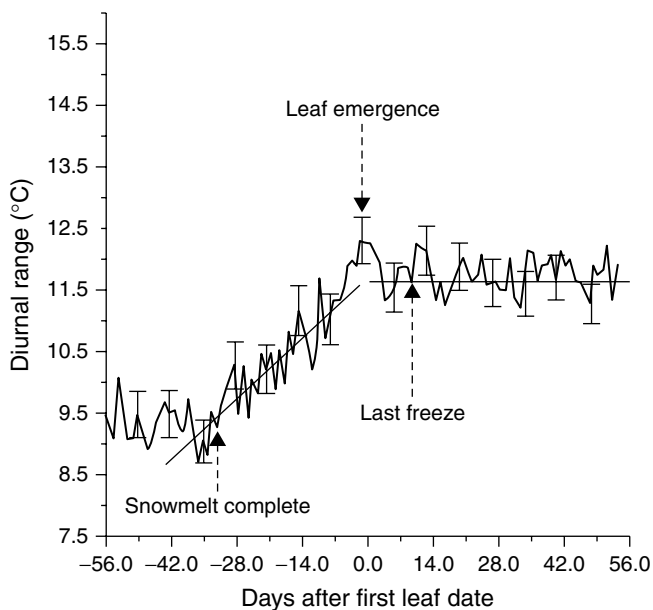
formed. Ozone is a highly reactive oxidizing agent that diffuses through stomatal pores on leaf surfaces when they are open and injures the photosynthetic machinery inside. Over a single growing season, conifer foliage suffers less damage than deciduous hardwoods because gas exchange rates through stomata are only about half those of deciduous hardwoods for an equivalent surface area (Reich and Amundson, 1985). With continued exposure, however, older foliage on conifers sustains accumulated damage and is shed prematurely (McLaughlin, 1985), leading to reduction in tree vigor and a greater likelihood of disease and insect outbreaks (Waring and Running, 1998).

### RESPONSE OF TEMPERATE CONIFEROUS FORESTS TO CLIMATIC CHANGE AND INCREASING ATMOSPHERIC CO<sub>2</sub>

We might expect temperate coniferous forests to be favored over deciduous hardwoods if climatic conditions during the dormant season become more favorable and those during the growing season less so. Thus, if minimum temperatures rise during the winter, the constraints exerted by subfreezing and suboptimal temperatures on photosynthesis will be reduced (Runyon *et al.*, 1994; Landsberg and Waring, 1997). The relative importance of warmer conditions during the winter can be assessed by considering the seasonal shifts in potential radiation available at different latitudes, aspects, and slopes to evergreen conifers (Running *et al.*, 1987; Waring and Running, 1998). If warming is combined with more frequent storms, without necessarily any increase in total precipitation, the associated increase in cloud cover may substantially reduce solar energy available to melt snow or drive photosynthesis.

On the other hand, if climatic warming extends throughout the year, the growing season will be lengthened. A higher frequency of storms in this case could moderate summer temperatures by allowing vegetation to maintain transpiration at near maximum rates and reduce the fraction of energy going into heating the air (Figure 2). More frequent wetting of surface litter and soil would also foster more rapid decomposition and release of nutrients, while reducing the likelihood of forest fires. This climatic scenario would favor replacement of conifers by hardwoods.

To factor in the response of vegetation to rising atmospheric CO<sub>2</sub> concentrations is more of a challenge. In general, increases in CO<sub>2</sub> should result in elevated rates of photosynthesis because carbon dioxide is a limiting resource for all tree species. Moreover, a rise in CO<sub>2</sub> should reduce photorespiration and increase the efficiency of photosynthesis, particularly if conditions become warmer. Because stomatal adjustments in most tree species maintain CO<sub>2</sub> concentrations within their leaves at about 75% of the value in ambient air, we might conclude that rising



**Figure 2** Average daily surface temperature amplitude (maximum–minimum), measured before and after spring leaf emergence of local vegetation for 12 sites across the north-central United States. The rapidly warming spring temperatures generate progressively larger temperature amplitudes during the 2–3 week period prior to leafing out; the amplitude is dampened, however, by leaf emergence as partitioning of incoming solar radiation is shifted as a result of cooling by rapidly transpiring vegetation. (Reproduced from Schwartz and Karl, 1990; Waring and Running, 1998)

atmospheric CO<sub>2</sub> will result in a net reduction in transpiration per unit leaf area, and thus increased carbon gain per unit of water lost. This may be generally true for many hardwood species, but there is less evidence that conifer stomata respond similarly (Norby *et al.*, 1999). In fact, in one field experiment where ambient CO<sub>2</sub> levels were artificially elevated for more than two years, no shift in pine stomata behavior was recorded (Ellsworth, 1999).

If net photosynthesis were to increase significantly, canopy leaf area index would reach a higher value, assuming sufficient nutrients were available. An increase in leaf area would affect the water balance by increasing canopy interception, evaporation, and transpiration under a stable climate. On the other hand, if climatic conditions were to warm without a corresponding increase in precipitation, drought could reduce photosynthesis, growth, and canopy leaf area.

In summary, although changing patterns of climate and atmospheric CO<sub>2</sub> concentration together are likely to have subtle effects on tissue biochemistry and the allocation of resources, forest growth and composition could be dramatically altered as a consequence of disturbance from outbreaks of fire, diseases, and insects.

## FOREST MANAGEMENT OPTIONS

With increasing demand for forest products, and increasing appreciation of other values derived from forests, there is considerable controversy and concern over how forests, on both public and private lands, are to be managed. Temperate coniferous forests have tremendous value to human societies, so there is justified concern about their management. Ancient coniferous forests have long been appreciated by many cultures as places of beauty, often with religious significance. Many groves have been designated as sacred and others set aside as natural wonders to be preserved in parks. The value of forests for maintaining clear running streams and high quality drinking water has also been long appreciated. Recently, modifying the structural characteristics of young coniferous forests to create properties more typical of mature stands has gained acceptance as a means of creating more favorable habitat for rare and endangered species commonly associated with extremely old forests. At the same time, ways of increasing the amount of carbon stored in biomass and soils are being developed. These carbon-sequestering techniques affect site preparation and harvests as well as the design, use, and recycling of forest products.

It is clear that young plantations will play an increasing role in providing lumber and fiber: whether these plantations replace native species or reclaim marginal farmland, however, will make a difference in the extent that plant and animal biodiversities are affected. Similarly, the fraction of the landscape occupied by plantations will alter the likelihood of fire, water runoff, and the potential for outbreaks of insects and diseases.

The challenge associated with more active management for wood, water, biodiversity and carbon storage, is the need to anticipate the extent to which disturbances may occur across broad landscape and ownership patterns. The introductions of exotic organisms into native forests is a particular concern because exotic insects and pathogens can result in replacement of native trees and open the environment to invasion by noxious weeds and other organisms.

General models that employ computer and satellite technology to compare projected changes with those that can be observed across broad landscapes and regions can provide a valuable aid to decision making. Remote sensing technology by itself permits us to monitor the state of the Earth's vegetation and the extent of change in vegetative cover over the last three to four decades.

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