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The Tree and Its Environment

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The mature forest tree is an outstanding example of interaction between the hereditary characteristics of an organism and its environment. The tiny embryo of the seed of the giant sequoia *(Sequoiadendron giganteum)* contains the potential to develop into the most majestic of plants. But if the environment is unfavorable, this potential will not be realized. Thus, responses of different species to environmental influences determine in part the success of silviculture. Silviculturists must know how the environment will affect the growth and development of trees they wish to manage.

Effects of environmental factors are generally the same for all trees. Reports in this publication describe known responses of each species to specific environmental conditions. This introduction provides background information of a general nature. The information offered here cannot approach the scope of texts on forest tree physiology, such as those by Kramer and Kozlowski and by Thimann (see General Notes and Selected References). Recently, Kozlowski *(26)* outlined specific effects of some environmental stresses on tree growth and development. More information on forest ecology is available in texts by Daubenmire and by Spurr.

The Total Environment

The total environment of a tree is a complex integration of physical and biological elements. The physical elements are related to climate and soil and include radiation, precipitation, and the movement and composition of air, as well as the texture of the soil and its structure, depth, moisture capacity, drainage, nutrient content, and topographic position. Biological elements are the plant associates; the larger animals that use the forest as a source of food and shelter; the many small animals, insects, and insectlike animals; the fungi to which the trees are hosts; and the microorganisms in the soil.

Complete and exact quantification of the environment is practically impossible. Some combinations of specific conditions have been used to characterize broad environmental regions and have been related to forest cover or vegetation type. Temperature indices were the basis for one classification system in which the climate of the United States was divided into seven temperature zones, each with its characteristic forest species, minor vegetation, and animal life *(39)*. In another system the North American continent was divided into six zones on the basis of the average temperatures of May, June, July, and August *(38)*. In a more complex scheme, winter temperatures, summer and winter dryness, and relative summer temperatures were considered *(24)*. Under this classification the southeastern United States is a single zone characterized by moderate or cool winters and moist warm summers.

A more widely used classification system is based upon precipitation effectiveness (P–E), a function of precipitation and evaporation, which represents the amount of precipitation available to plant growth *(69)*. Five climatic regions are recognized: superhumid, humid, subhumid, semiarid, and arid. These are associated with corresponding vegetation types: rain forest, forest, grassland, steppe, and desert. The subhumid region, or grassland, is divided into a moist subhumid and a dry subhumid. Some ecologists believe the moist subhumid region to be a forest region from which forests have been excluded by causes other than climate.

The superhumid region in North America includes the coastal forests of southern Alaska, Canada, Washington, Oregon, and northern California; the western slope of the Cascade Range in Oregon and Washington and of the Sierra Nevada in California; and also isolated areas in the Rocky Mountains, Appalachian Mountains, and New England. Western hemlock *(Tsuga heterophylla)*, Sitka spruce *(Picea sitchensis)*, coast redwood *(Sequoia sempervirens)*, western redcedar *(Thuja plicata)*, Douglas-fir *(Pseudotsuga menziesii)*, and grand fir *(Abies grandis)* are principal tree species in the western coastal part of the region. Western white pine *(Pinus monticola)*, ponderosa pine *(P. ponderosa)*, sugar pine *(P. lambertiana)*, and white fir *(Abies concolor)* are included with other species in mountain portions of the western part of the region. In the east, Fraser fir *(Abies fraseri)*, balsam fir *(A. balsamea)*, and red spruce *(Picea rubens)* are found in the superhumid region.

The humid region in the East includes most of the forest land, aside from the small areas of the super-

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humid region described above. The humid region has been subdivided into four zones, with the oak–hickory type in the area with the lowest P–E index and the spruce–fir type in the area with the highest. In the West the broken topography of mountain ranges results in many discontinuities in the humid region. Here ponderosa pine, western larch *(Larix occidentalis)*, Douglas-fir, incense-cedar *(Libocedrus decurrens)*, and lodgepole pine *(Pinus contorta)* are typical species.

Within these broad provinces or regions, the interplay of local factors and general conditions often determines whether a species will be successful on a specific site. Thus, south-facing slopes tend to be warmer and drier than north-facing slopes, and low spots or openings in the forest may be frost pockets that restrict establishment of certain species. Soil drainage or depth is often decisive in limiting the presence or growth of trees in areas where climatic conditions are of near-critical importance.

Individual Environmental Factors

The impact of a change in environment can seldom be related directly to a single measurable factor in the total complex. Subtle interrelationships between environmental factors are usually present. Knowledge of how a plant responds generally to various individual factors is useful, however.

Temperature

Temperature directly affects the day-to-day physiological processes of plants and indirectly influences their seasonal or cyclic development. Plant processes, to the extent to which they are chemical reactions, tend to follow the van't Hoff law, namely, that the rate of reaction doubles for each temperature increase of 10° C (18° F). In such reactions the temperature coefficient is two.

In biological systems the law often operates only within narrow ranges, determined by the ability of the organism to survive. Thus, the temperature coefficient of respiration is two or more up to a temperature at which some essential respiratory enzyme is denatured. The process of photosynthesis has a temperature coefficient of less than two. Growth of cells has a temperature coefficient of about two, and even the overall growth of plants may show this response within the moderate temperature range. Because the temperature coefficient for photosynthesis is less than that for respiration, high temperatures may result in less photosynthate for growth.

For each plant there is a set of cardinal temperatures that controls its growth and development and, in fact, its existence: the minimum and maximum temperatures limiting growth and the optimum temperature for growth. For alpine plants the minimum temperature is close to 0° C (32° F), the maximum 20° to 30° C (68° to 86° F), and the optimum 10° C (50° F). For temperate plants the minimum temperature is about 4° C (40° F), the maximum 41° C (106° F), and the optimum 25° to 30° C (77° to 86° F). For tropical plants the minimum is 10° C (50° F), the maximum 50° C (122° F), and the optimum 30° to 35° C (86° to 95° F).

In a dormant or resting state, plants can endure extremes much greater than the minimum and maximum temperatures for growth. Evergreen trees endure winter temperatures of –51° to –57° C (–60° to –70° F), but temperatures of –4° to –1° C (25° to 30° F) kill twigs during the growing season. During summer in the temperate zones, temperatures may exceed 46° C (115° F), but growth is often completed before maximum temperatures occur.

Resistance to freezing temperatures, or frost hardiness, may result from a change in the protoplasm. The osmotic concentration of the cell sap increases with the hydrolysis of insoluble carbohydrates to soluble sugars *(13)*. Dehydration of the protoplasm leads to an increase in the apparent bound water content of the proteins. Frost injury results from the formation of ice crystals within the protoplasm or the dehydration of the cell by ice formation in the intracellular spaces *(34)*.

Heat resistance also appears related to a change in cellular proteins. The killing of cells by heat is brought about by denaturation of the proteins.

Thermoperiodicity

Plants not only respond to maximum, minimum, and optimum temperatures, but some also grow or develop best with an alternation of daily or seasonal temperatures. The growth of tomatoes was greatest when day temperatures were 27° C (80° F) and night temperatures were 17° to 20° C (63° to 68° F) *(73)*. Similarly, loblolly pine *(Pinus taeda)* seedlings grew most with a day temperature of 27° C (80° F) and a night temperature of 17° C (63° F) *(27)*. Several explanations have been offered for this phenomenon. The difference between the temperature coefficient of photosynthesis and that of respiration provides one explanation. Although photosynthesis increases with temperature, the rate of increase is not as great as that for respiration. Moreover, respiration continues 24 hours a day. When high day temperatures are followed by low night temperatures, therefore, more photosynthate remains for growth than when both day and night temperatures are high. Another explanation stems from an apparent decrease in translocation with increased temperature. Lower night temperatures would permit more rapid translocation of photosynthates from the leaves to meristematic tissue, favoring greater growth.

Some trees and shrubs fail to develop properly if they are not exposed to low temperatures during their dormant period. Thus, some deciduous fruit trees will not break dormancy if they are not subjected to near freezing temperatures for a minimum number of hours. Observations unsupported by controlled experiments suggest that some northern or subalpine conifers require a cold treatment to break dormancy and induce seasonal growth. It also has been demonstrated that certain nondeciduous shrubs, like camellia, show optimum blooming with cyclic temperatures *(7)*. Flower buds of camellia are initiated at temperatures of 24° to 27° C (75° to 80° F), but blooming is optimum at temperatures of 10° to 16° C (50° to 60° F).

Light

Visible light, that part of the electromagnetic spectrum with wavelengths in the range of about 400 to 760 millimicrons, plus ultraviolet and infrared light, affect the growth of trees in several distinct ways. The role of light as the source of energy for growth in photosynthesis is commonly known, but its role in regulating growth is more subtle.

Quality, intensity, and duration of light energy bear upon the photosynthetic process. Chlorophyll absorbs light more readily at wavelengths between 420 and 480 millimicrons and between 620 and 700 millimicrons. Light energy of these parts of the spectrum, corresponding to the blue-violet and the orange-red, is most efficient in the photosynthetic process. There is evidence that the color of foliage of various conifers and broadleaf trees results in differential responses to parts of the spectrum *(10)*.

Understory trees are probably exposed to light of quite different quality than overstory trees. Crowns of the overstory absorb part of the blue and red light and reflect or transmit green and yellow. Thus, light in the understory is relatively higher in green and yellow light.

Intensity of the light, or irradiance, measured in terms of energy per unit area per unit time, as gram-calories per square centimeter per minute, also affects the rate of photosynthesis. The irradiance on a clear summer day at sea level in the middle latitudes is about 1.5 g-cal per cm^2 per minute. This corresponds to an illumination value of about 10,000 foot-candles as commonly measured with a light meter.

Trees vary with respect to the light intensity at which maximum photosynthesis occurs. The rate of photosynthesis of loblolly pine increases with increasing light intensity up to full sunlight. The rate of photosynthesis of associated hardwoods, such as oaks *(Quercus)* and dogwood *(Cornus)*, however, does not increase at light intensities higher than about 30 percent of full sunlight *(28)*. Similarly, Engelmann spruce *(Picea engelmannii)* reaches near maximum photosynthesis at 4,000 to 5,000 foot-candles but lodgepole pine does not appear to be light saturated at 12,000 foot-candles *(55)*. For Japanese larch *(Larix leptolepis)*, the saturation point of light intensity is twice as high as that for white fir, Sitka spruce, or western hemlock. There is evidence that the metabolic pathway in larch may be different from that of nondeciduous conifers *(14)*.

Differences in photosynthesis among tree species are related to the arrangement of the leaves and resultant mutual shading; to the morphology of the leaves, as sun-leaves and shade-leaves; and perhaps to the chlorophyll concentration of leaves. One of the characteristics of trees termed "shade tolerant" is undoubtedly their ability to carry on photosynthesis at low levels of illumination. Seedlings of red alder *(Alnus rubra)*, a shade-intolerant tree, attain a higher rate of photosynthesis per unit of foliage weight than do seedlings of Douglas-fir, Sitka spruce, or western hemlock. Rates are similar per unit of foliage area, however. Also, the photosynthetic rate of red alder is much higher at light intensities greater than 5,100 foot-candles *(30)*.

The ability of tolerant trees to grow rapidly under low light intensities may be enhanced by the greater carbon dioxide concentration under a forest canopy. There is evidence that photosynthesis increases if the carbon dioxide concentration is more than the normal 330 parts per million found at sea level. Very high light intensities may in fact inhibit photosynthesis. Seedlings that normally develop under an overstory may not photosynthesize at a maximum rate if exposed to the full-light conditions of clearings or openings *(25)*.

There is conflicting evidence concerning efficiency in photosynthesis among provenances of various species. Genetic variation in photosynthetic efficiency was found in families of Douglas-fir seedlings; however, selection for that efficiency will be valuable only if seedling values are strongly correlated with mature growth *(9)*. Photosynthetic rates of Douglas-fir from western Oregon were higher than those from western Montana. Environmental conditions affected photosynthetic rates more than the seed source *(66)*. For jack pine *(Pinus banksiana)*, the rates of photosynthesis varied among provenances according to the time of year *(35)*. Differences in rates also were observed in Scotch pine *(Pinus sylvestris)* from Poland and from Turkey *(2)*. In Douglas-fir, rapid growth appeared to be related more to photosynthetic area than to efficiency of the foliage *(18)*.

The duration of illumination also affects the total amount of photosynthesis. Plants carry on photosynthesis continuously when exposed to light for 24 hours a day. However, the effect of the duration of illumination on photosynthesis and its resultant effect on growth probably is confounded with the temperature-regulating effect of day length on growth.

Light regulates growth and development of a tree through a number of incompletely understood reactions. One of these is the photoperiodic control of growth and flowering. Many tree species either cease terminal growth or continue to grow, depending on the duration of light within a day. A number of angiosperms and gymnosperms cease growth when exposed to only 8 hours of light a day *(11)*. Scotch pine, loblolly pine, and Virginia pine *(Pinus virginiana)* seedlings grow continuously on 14-hour days and with repeated flushes on 16-hour days. Some broadleaved trees, such as red maple *(Acer rubrum)*, birch *(Betula)*, elm *(Ulmus)*, and catalpa *(Catalpa)*, grow continuously with exposure to 16-hour days, while others, such as sweetgum *(Liquidambar styraciflua)* and horsechestnut *(Aesculus hippocastanum)*, do not.

Thus, the photoperiodic control of terminal growth of trees may be a limiting factor in the north-south movement of a species, even within its natural range. For example, under natural day length, loblolly pine from Maryland grew poorly in northern Florida compared to local loblolly pine, but it quadrupled its growth when the natural day length was extended with artificial light *(50)*. Similarly, cuttings of black cottonwood *(Populus trichocarpa)* from coastal Alaska, latitude 60° 37′ N., stopped growth about June 20 when planted near Boston (lat. 42° N.) but continued growing for 2 months more when day length was increased to match that of the source of the cuttings in Alaska *(49)*. Day length also influenced the time of bud set in western hemlock, which has a long north-south range. Because bud set precedes the onset of dormancy and cold hardiness, this species should not be moved far in a north-south direction *(31)*. Variation in height growth resulting from day length may limit the selection of provenances of white spruce *(Picea glauca)* *(53)*.

Day length, or photoperiod, also influences growth in diameter. Under long-day conditions trees produce large-diameter, thin-walled cells, resembling springwood. A change to short-day conditions results in the formation of small-diameter, thick-walled cells resembling summerwood. The transition is related to the production of growth-regulators during the period of terminal elongation *(32)*.

The transition from large-diameter cells to small-diameter cells with changing day length has been noted in a number of species, including red pine *(Pinus resinosa)* *(32)*, Monterey pine *(P. radiata)* *(19)*, Caribbean pine *(P. caribaea)* *(3)*, and European larch *(Larix decidua)* *(77)*. The content of inhibitors seems to be related to the production of thick-walled cells, whereas the content of promoters appears related to shoot growth. The amount of growth substances has been shown to be related to photoperiod *(77)*. One might speculate that the absence of definite growth rings in many tropical trees is related to a more or less constant day length.

Little evidence is available to show photoperiodic control of flowering in forest trees. Judging from the widespread occurrence of the phenomenon of photoperiodism in many plants, it is probable that such control does exist. However, flowers were borne on trees of 34 species of pine growing in California at a latitude of about 38° N., even though the trees represented pine sources ranging from latitude 15° N. to 70° N., with corresponding differences in day length *(42)*.

Unequal distribution of light may indirectly affect the form of trees. Greater development of the crown on the lighted side of the tree than on the shaded side results in asymmetrical growth of the bole. Regular spacing of trees to ensure better distribution of light thus tends to promote good form.

Light may also be a factor in epicormic sprouting. On many tree species, dormant buds on the bole are stimulated and sprouts develop after trees are exposed when surrounding trees are cut.

Moisture

Although the presence of one component of the environment is no more essential than that of another to the growth of trees, moisture is very often a limiting factor. Within the continental United States, excluding Alaska, annual precipitation to which forests are exposed varies from an average maximum of about 3550 mm (140 in) to an average minimum of about 380 mm (15 in). Rather large areas of forests, particularly ponderosa pine, grow with less than 500 mm (20 in) of annual precipitation. Silvicultural measures that make more of the total moisture available to the tree crop very likely increase growth.

Total precipitation is often used as a measure to relate productivity of forests to moisture, but it is not completely satisfactory. Moisture is available to trees primarily through the soil, although there is some evidence that they absorb atmospheric moisture under conditions of moisture stress *(65)*. The moisture-holding properties of the soil mantle are therefore of major importance.

Seasonal distribution of precipitation has a bearing upon the effectiveness of total precipitation. In forests of the Sierra Nevada in California, summer rains are rare. Nearly all the moisture available for trees is the amount held in the soil from winter and spring precipitation. In some parts of the country the highest precipitation occurs in the summer months. In much of the East, on the other hand, precipitation is rather evenly distributed throughout the year. The growth of loblolly, slash, shortleaf, and longleaf pines *(Pinus taeda, P. elliottii, P. echinata,* and *P. palustris)* has been shown to be differentially related to the amount and seasonal distribution of rainfall as well as to its retention in the soil *(59)*.

In addition to precipitation ordinarily measured as rain or snow, forests in some sections of the country obtain moisture from "fog-drip." Along the Pacific coast, the redwood forests in California and the Sitka spruce–hemlock–Douglas-fir forests of Oregon, Washington, and British Columbia undoubtedly benefit from the water condensed from fog dripping to the ground. However, fog-drip is only a part of the climatic environment of these fast-growing forests. The longer growing season, mild summer and winter temperatures, heavy precipitation, and high relative humidity (which lowers evapotranspiration rates), in addition to the fog-drip itself, certainly favor the exceptionally high forest productivity of this narrow belt along the coast.

Water available to trees is either that held temporarily in the soil mass against the force of gravity or that held between the soil particles by surface tension (capillary water). Gravitational water drains out of the soil mass following a rain. Capillary water is generally available except after rains or periods of melting snow. Water held at two other levels of energy, hygroscopic water and water of hydration in certain minerals, is not available to trees.

Water generally available to trees is held by energy forces that range from 1.1 to 15 atmospheres. The lower level approximates the field capacity of the soil, or the amount of water held against gravity. The upper level approximates the permanent wilting point, or the soil moisture level at which a plant is no longer able to obtain water fast enough to prevent wilting, from which it cannot recover unless water is added. Theoretically, plants cannot recover even when water is added if the permanent wilting point is exceeded.

The permanent wilting point is not well defined, however, for plants that have thickened rigid leaves, such as those of conifers and evergreen broadleaf trees and shrubs. There is evidence that such plants can live in a quiescent state and can extract water from the soil beyond the permanent wilting point as determined conventionally *(61)*. This enables the tree to survive temporary droughts that might cause the death of more succulent plants.

Water serves as a solvent for minerals, gases, and various organic compounds; it is a major part of the protoplasm of cells and is essential to certain metabolic processes. Most of the water taken up by a tree is transpired, however, and the benefit to a tree of such water use is not fully understood. In pine and hardwood forests in Arkansas, for example, 4.8 mm (0.19 in) of moisture was used per day from the upper 1.2 m (4 ft) of soil during the early part of summer *(79)*. The loss from the 1.8-m (6-ft) soil layer was estimated to be 6.4 mm (0.25 in) per day, or about 63 500 liters of water per hectare (6,800 gal/acre) per day.

The transpirational use of water may be of no immediately apparent benefit to a tree, but the conditions leading to transpiration are conducive to growth. The rate of photosynthesis is greater during periods of low moisture stress than when moisture stress forces the closing of the stomata. Transpiration thus may appear to be a necessary accompaniment to the availability of moisture for growth processes and the conditions promoting gas exchange and photosynthesis. There is evidence that moisture stress late in the growing season increases the cold hardiness of seedlings *(6)*.

Soil Condition

In addition to being a reservoir for moisture for trees, soil provides all the essential elements required in growth except those from the atmosphere, carbon from carbon dioxide, and some oxygen. Obviously, soil also provides the medium in which a tree is anchored. The many characteristics of soil, such as chemical composition, texture, structure, depth, and position, affect the growth of a tree to the extent to which they affect the supply of moisture and nutrients. A number of studies have shown strong correlations between productivity of site or growth of trees and various soil characteristics such as depth and position on the slope. The relationships are often indirect.

Generally, soil contains all the chemical elements essential to the growth of plants. Some elements may not be present in large enough quantity to sustain growth, however. For example, zinc, which is necessary in only minute amounts, was so deficient in western Australia that the growth of pines was inhibited *(64)*. In the United States, deficiencies of potassium, phosphorus, and nitrogen have been observed, and the application of fertilizers has resulted in increased growth, greater fruit production, and more desirable foliage color *(74)*. The effects of fertilization may continue for some time; increased growth of black spruce *(Picea mariana)* continued for 9 years after fertilization with major elements *(72)*.

The level of soil nutrients sufficient for optimum growth of most species is not known. Some guides to the adequacy of nutrient levels may be obtained from foliar analysis. Admittedly the technique has flaws, but a number of studies in the forest and in pot culture show that the optimum growth of pine occurs when adequate nutrient availability is reflected by the following foliar concentrations: nitrogen, 2 to 2.5 percent; phosphorus, 0.13 to 0.2 percent; potassium, 1 percent; calcium, 0.3 percent. In white and red spruce the transition zone from deficiency to sufficiency seems to begin at these foliar concentrations: for nitrogen, 1.3 percent; for phosphorus, 0.14 percent; for potassium, 0.30 percent; for magnesium, 0.06 percent; and for calcium, 0.10 percent *(68)*. Foliar concentrations of potassium and phosphorus were found to be correlated with growth characteristics of white fir, but no close relation was shown with most soil elements *(22)*.

In some soils the concentration of certain elements may be too high to support vigorous growth of trees. Soils derived from serpentine often contain so much magnesium that growth is poor, perhaps because the competition of the magnesium depresses calcium intake resulting in calcium deficiency.

The ability of a soil to supply water and nutrients is strongly related to its texture and structure as well as to its depth. Coarse-textured soils, the sands, are low in nutrient content and in water-holding capacity. Fine-textured soils, the clays, may be high in nutrient content and have high water-holding capacity. Aeration is impeded in heavy clays, particularly under wet conditions, so that metabolic processes requiring oxygen in the roots are inhibited.

In clay soils, percolation of water into the soil, and soil aeration, are favored by aggregated soil particles rather than by a plastic structure or cemented layers of hardpans. Silvicultural practices to prevent the destruction of organic matter and the compaction of soil can provide better conditions of soil moisture and aeration.

Air Movement

The movement of air is usually not an important environmental factor except under extreme conditions. It has a minor effect in that an increase in wind velocity results in greater evaporation and transpiration, taking water that might otherwise be used for growth. Prevailing winds from a given direction usually result in deformation of the crown of a tree and uneven development of its bole. Although the direct physical effects of wind in uprooting or breaking trees may be calamitous, adjustment of silvicultural practices to avoid such damage is not feasible. Where prevailing winds are known to be strong, however, windfirm trees can be favored and cutting patterns adjusted to minimize effects *(15)*.

Potential Effects of Climate Change

Climate (temperature, precipitation, and wind), and atmospheric chemistry (including carbon dioxide (CO_2) supply and air pollution) directly affect plant life. They also indirectly affect plants through their impact on soils and soil biota, pests and other pathogens, and other disturbances. Important changes in the Earth's climate due to increases in "greenhouse" gases are inevitable, according to most climatologists *(17,43,57,62)*. Simulation models suggest that the climate of the Earth is beginning to change at a rate unprecedented in the history of contemporary plant and animal species *(51,57)*. These changes would significantly affect reproduction, growth, and mortality of forest trees *(76)*. Thus, many of the data and relations described in this manual will be altered if climate and atmospheric chemistry change as projected.

How May Climate Change?

Mean annual global temperature is projected to rise 2° to 6° C (4° to 11° F) by the middle or end of the 21st century *(17,43,57,62)*. Most models predict the warming will be greater at higher latitudes, but there is less agreement on changes in the spatial and seasonal patterns of temperature and precipitation for areas the size of the United States *(57)*. Given the rapid rate of projected changes, plant adaptations in physiology and range will have to be made within one or two lifetimes of most tree species. This contrasts sharply with changes following the last ice age when similar temperature increases occurred over 7000 years, giving forests and trees many generations to adapt. Further, climate change will probably continue as people add more of the greenhouse gases to the atmosphere.

Natural Range

Species ranges are likely to be modified greatly if projected climate changes occur. Zabinski and Davis *(78)* projected drastic reductions in the natural ranges of eastern hemlock *(Tsuga canadensis)*, American beech *(Fagus grandifolia)*, yellow birch *(Betula alleghaniensis)*, and sugar maple *(Acer saccharum)* if CO_2 doubled as two different atmospheric general circulation models predicted. The reductions in present range varied from 20 to 70 percent, with similar expansions of potential natural range as range boundaries shifted northward hundreds of kilometers. For the western United States under a doubled-CO_2 climate, Leverenz and Lev *(33)* projected significant changes in range or importance of Douglas-fir *(Pseudotsuga menziesii)*, western hemlock *(Tsuga heterophylla)*, ponderosa pine *(Pinus ponderosa)*, western larch *(Larix laricina)*, and Engelmann spruce *(Picea engelmannii)*.

Although the natural ranges of many species will likely shift northward and upslope, some populations may not be able to expand into newly suitable areas because of the limited speed of natural migration compared to the speed of climate change *(78)* and barriers to migration, such as lowlands with inhospitable climate and agricultural and urban areas *(51,52)*.

Though mature trees may survive for long periods *(8)*, a population must be able to complete its life cycle in the new environment to survive. Populations at risk of local extinction include those near mountain tops where suitable climate may move above the mountain tops or zones of suitable soil, and those in isolated reserves. Populations that will be at low risk include those able to reproduce in the changing climate at their current sites, those far enough down mountain slopes that suitable habitat will occur upslope within dispersal distances as climate warms, those able to disperse over large distances, and those assisted by people.

Soils

Another component of environmental change, atmospheric pollution, will continue to affect trees, in part through its effect on soils. Acid deposition, including nitrate and sulfate, may acidify soils and leach nutrient cations, thus decreasing soil fertility in the long term *(5,54)*. Acidification also increases soluble aluminum that can be directly toxic to trees *(21)* and interferes with calcium uptake, reducing cambial growth, sapwood cross-sectional area, and leaf area, in turn. This latter mechanism has been suggested as a cause of red spruce decline in the northeastern United States *(58)*.

Moderate amounts of pollutant nitrogen deposition may increase available soil nitrogen *(1,5)*. In contrast, excess soil nitrogen from atmospheric pollution in the northeastern United States may have several detrimental effects on plants in addition to those already mentioned *(1)*. It may cause a decrease in fine-root biomass and energy allocated to mycorrhizal associates, leading to decreased uptake of phosphorus and water *(1)*, and it may predispose conifer foliage to winter damage *(13)*.

Soil organic matter increases markedly (up to 3-fold) from grasslands through forests on mountain slopes *(20)*. This is controlled in part by decreasing temperature. If temperature increases as projected, decomposition of litter and soil organic matter will speed up. This may cause equilibrium organic matter content to decrease in the absence of compensating increases in productivity. If this occurs, the increased nitrogen released may temporarily but significantly increase forest growth. Soil organic matter and available soil nitrogen are projected to change ± 80 percent and ± 36 percent, respectively, in some northern forests under a doubled-CO_2 climate, depending on latitude and soil water-holding capacity *(48)*.

Damaging Agents

Growth and fuel accumulations may increase in the future on sites with equivalent droughtiness because increased CO_2 fertilization often increases net photosynthesis and decreases water use *(29,67)*. Death of established trees from stresses caused by environmental change would add to these fuels. Higher fuel loadings and warmer climate would probably increase wildfire intensity. Wildfire frequency for a region may also increase as climate warms (assuming the currently widespread relation between increased drought and increased fire frequency still holds) *(36)*, and precipitation does not increase.

Pest outbreaks may increase in forests where existing drought increases *(37)*. Fertilization by CO_2, however, may partially compensate for physiological stress caused by drought and higher temperature *(29)*. Forest pests, such as the balsam woolly aphid *(44)* and pine wilt disease *(56)*, that have ranges controlled by climate will probably have range shifts. Precipitation and temperature are known to influence population of some forest pests, for example southern pine beetle *(Dendroctonus frontalis)* *(40)* and gypsy moth *(Lymantria dispar)* *(4)*, so climate changes may significantly affect magnitude and frequency of pest outbreaks.

Changes in frequencies and intensities of other natural damaging agents (high-speed winds, temperature extremes, lightning, ice storms, and droughts) may also occur with climate change and thus adversely affect forest trees *(41)*.

Continued atmospheric pollution will compound some of these effects. For example, studies have shown that pollutants can reduce the growth of ponderosa pine and increase infection and mortality from bark beetles *(16)*.

Growth and Biomass Accumulation

Simulation experiments in eastern North America suggest that doubling or quadrupling CO_2 may increase biomass of natural northern stands by 70 percent or more (50 to 80 Mg/ha (30 to 45 ton/acre)) and decrease biomass of natural southern stands by 60 percent or more, depending on specific conditions *(48, 63)*. Factors not included in these simulations, such as the potential increased ability of trees to tolerate drought under increased CO_2, may lessen growth reductions in southern stands *(11,38)*.

Increased CO_2 has also been shown to increase nitrogen fixation in black alder *(Alnus glutinosa)* and black locust *(Robinia pseudoacacia) (45)* and mycorrhizal colonization in white oak *(Quercus alba) (47)*. Moreover, carbon dioxide fertilization increases the ability of seedlings of some species to tolerate drought *(29,67)* and nutrient deficiency *(46)*.

Competition

Competition among many species may change significantly as CO_2 changes. Under high light in a greenhouse experiment with 1-year-old saplings, red oak *(Quercus rubra)* grew as fast as yellow-poplar *(Liriodendron tulipifera)* under ambient CO_2, but grew faster than yellow-poplar under doubled CO_2. Similar differences occurred with other species *(75)*. Elevated CO_2 commonly increases water-use efficiency of seedlings *(29,46,67)* but species differences are common. Water-use efficiency of water-stressed sweetgum *(Liquidambar styraciflua)* seedlings was increased more by elevated CO_2 than was that of loblolly pine *(Pinus taeda) (71)*. Thus, growth of sweetgum was reduced less by water stress than was that of loblolly pine *(70)*. This may allow sweetgum under elevated CO_2 to compete more favorably against loblolly early in succession on drier Piedmont sites. However, it is not known how these differences in seedling responses will affect competitive interactions over the lifetimes of large trees in ecosystems.

Genetics

As climate changes in some locales—for example, as temperature increases in boreal forests in Canada *(63)*—existing individuals may become better adapted and stand productivity may increase. In other areas, such as near the hot or dry limits of a species' range, existing individuals may become less well adapted *(33)* and productivity may decline *(63)*. Species with broadly adapted genetic bases, such as loblolly pine, sweetgum, and Douglas-fir, may be better able to adapt to environmental change than other forest trees *(23)*. People managing large tree-breeding programs with narrowly defined breeding zones (e.g., *60)* may find selected trees are poorly adapted to their original zones. Such programs, however, will provide an extremely large pool of measured and structured genetic diversity, potentially helpful to managers in finding trees adapted to changed climate. Determining the locales where a genotype or species will do well may be difficult, because its optimum environment will shift over the landscape if climate continues to change over a rotation. Adaptation of species to changing climate may be approached, however, by tree-breeding and silviculture programs that seek to maintain high genetic diversity within stands *(23)*, produce more heterozygous trees, and attempt to select genotypes that will be adapted to future environments.

Most of the potential responses to environmental change presented here are projections based on incomplete current knowledge, not reliable predictions. However, many projections suggest important changes in the silvical characteristics of trees and the ways we must manage them. The speed of environmental changes may cause responses, such as wildfire, that produce major change in landscapes before noncatastrophic responses cause similar alterations in established forests. Also, some of the most significant responses to environmental change will likely be surprises. So, people using this manual would do well to keep abreast of new research on expected environmental changes and impacts on trees and forests. Such information will be essential to adapt management to environmental changes, and there will be many opportunities to do so.

Conclusion

This general statement of the responses of trees to environmental factors has provided a basis for consideration of the detailed and specific information about individual species presented in the papers that follow. Knowledge of species' responses to environmental influences can guide silvicultural practices and determine their success. Thus, in efforts to favor pine in the mixed conifer forests of the west slope of the Sierra Nevada in California, it was found that white fir seedlings were very sensitive to late spring frosts, which seldom hurt ponderosa pine *(12)*. Overstory trees or understory brush can protect the firs against frost. Complete clearing, as by patch cutting, removes the protection and creates conditions in which fir regeneration cannot compete successfully with pine regeneration. In another instance, high light intensities as found in clearings inhibited Engelmann spruce but not lodgepole pine *(55)*.

Although much has been learned about environmental responses of individual species, information for some species is still extremely sketchy. Progress toward more intensive silviculture depends on our ability to fill in the gaps in our knowledge of silvics. In the words of Aristotle, the search for truth is in one way hard and in another easy. For it is evident that no one can master it fully nor miss it wholly. Each adds a little to our knowledge of nature and from all the facts assembled there arises a certain grandeur.

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