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Physiological Activity in Douglas-Fir

J. P. Lassoie

INTRODUCTION

Primary producers form the cornerstone on which all life is ultimately dependent, since they provide the means by which energy is supplied to drive the biosphere. Therefore, an understanding of those processes related to carbon fixation in green plants is paramount to the overall understanding of the mass and energy transfer within a terrestrial ecosystem.

Trees as stationary terrestrial organisms have adapted in order to tolerate or avoid the rigors imposed by the highly variable atmospheric and edaphic components of the ecosystem. As living interfaces between these two components, trees are controlled by those abiotic factors that regulate their physiological processes and eventually determine the distribution and abundance of species throughout the terrestrial biosphere. Trees, as do all autotrophic plants, utilize water, nutrients, carbon dioxide, and sunlight as the building blocks on which growth, maintenance, defense, reproduction, and, ultimately, survival depend. The biotic and abiotic factors that govern the processing and utilization of these building blocks have always received considerable attention from tree physiologists (for example; Walker et al. 1972; Larcher 1975; Bannister 1977; Kramer and Kozlowski, 1979).

This chapter elucidates the abiotic and biotic control of those tree physiological processes felt to be of major importance to the functioning of the western coniferous forest biome. Specifically, emphasis is on temporal and spatial variations in, and interrelations between, net photosynthesis, tree water relations, meristematic activities, and biomass accumulations. Furthermore, owing to their ecologic and economic dominance throughout the biome, large, field-grown Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) are considered primarily in the following discussion.

Presented here is an integrated view of whole-tree physiological processes in Douglas-fir. The approach is based on a wide variety of interrelated physiological data and is viewed in reference to the functioning of the entire coniferous forest biome. Though there has been continuing interest in tree physiol-

ogy since the work of Hales (1727), such an approach in the past has been confined primarily to European studies (for example, Ellenberg 1971). Also presented is physiological support for other chapters in this volume (for example, Chapters 3 and 5) and physiological reasoning behind the distribution and abundance of Douglas-fir throughout the coniferous forest biome is illustrated. In addition, voids are identified in the understanding of Douglas-fir physiology and future research needs and directions are suggested.

Numerous techniques were used by investigators at different study sites throughout the U.S. coniferous forest biome in order to produce the data on which this chapter is based. The techniques and approaches are summarized in Table 6.1 and no attempt will be made to discuss the methodologies. Readers needing specific information should consult the references cited in the table.

PHYSIOLOGICAL ACTIVITY AND ITS CONTROL

Physiological activity in forest trees is controlled by certain intrinsic and extrinsic factors. Various physiological steps are involved in the accumulation of tree biomass; specifically, net photosynthesis, the internal flow of carbon and its incorporation into biomass constituents, and the cell growth process. These phenomena are complex and precise quantification currently is not possible. The following presentation should yield at least a qualitative understanding of the physiological connection between carbon dioxide uptake at the needle and biomass accumulation throughout the aboveground portions of conifers, particularly Douglas-fir.

Net Photosynthesis Rates

Higher plants differ in their primary mode of fixing carbon dioxide. All forest trees seem to be C_3 plants, which fix carbon according to the classic Calvin cycle. Maximum net photosynthesis rates for C_3 plants generally range between 15 and 40 $mg \cdot dm^{-2} \cdot h^{-1}$ and most studies suggest that rates in conifers are generally lower than those in deciduous trees (Jarvis and Jarvis 1964; Larcher 1969, 1975; Black 1973). However, some evidence suggests that photosynthetic capacities in conifers and deciduous trees may be similar but that the needle arrangements on conifer branches promote mutual shading, which lowers total photosynthesis (Krueger and Ferrell 1965; Krueger and Ruth 1969; Ludlow and Jarvis 1971; Norman and Jarvis 1974, 1975).

Limiting Factors

As an outgrowth of Liebig's law of the minimum, the concept of limiting factors states that a biological process (for example, photosynthesis or growth)

TABLE 6.1 *Summary of important techniques used in various investigations of physiological activity in Douglas-fir within the coniferous forest biome.*

Factor	Technique and reference(s)	Investigators ^a	Units	Study locations ^b
Net photosynthesis rate	Infrared gas analysis (Sěsták et al. 1971, Zelawski and Walker 1976)	I, N	mg CO ₂ · dm ⁻² · h ⁻¹	WA
	Steady-state mathematical model	K	mg CO ₂ · dm ⁻² · s ⁻¹	WA
	Curve-fitting model	B	mg CO ₂ · dm ⁻² · d ⁻¹	OR
Transpiration rate	Gravimetrically: lysimeter (Fritschen et al. 1973)	C, D, H	mm H ₂ O	WA
	Humidity sensors: gas exchange (Salo 1974)	I, N	g H ₂ O · dm ⁻² · h ⁻¹	WA
	Heat-pulse velocity (Swanson 1967)	F, H	cm/h	WA
	Tritiated water (Kline et al. 1970)	E	liters/h, liters/d	WA, OR
	Low-resolution simulation model	J	g H ₂ O/cm ²	OR
Photosynthate translocation	¹⁴ CO ₂ labelling (Webb 1977)	O	%C-14 assimilated/d	OR
	¹⁴ CO ₂ labelling (Ross 1972)	L	%C-14 assimilated	WA

Cambial growth	Automated band dendrometers (Dobbs 1969)	F	mm ²	WA
	Direct measurement (also shoot growth)	A	mm, cm	OR
Stomatal activity	Diffusion porometer (Turner et al. 1969, Kanemasu 1975)	G, M	s/cm	WA, OR
	Infiltration pressures (Fry and Walker 1967)	F, G, H	MPa	WA
	Calculation based on transpiration (Holmgren et al. 1965)	I, N	s/cm	WA
	Regression models	J, M	s/cm	OR
Xylem pressure	Pressure chamber (Ritchie and Hinckley 1975)	B, F, H, I,		
		J, M, N	-MPa	WA, OR

Note: See primary references for information on environmental measurement techniques.

*Primary reference: A = Emmingham 1977; B = Emmingham and Waring 1977; C = Fritschen and Doraiswamy 1973; D = Fritschen et al. 1977; E = Kline et al. 1976; F = Lassoie 1973, 1975, 1979; G = Lassoie et al. 1977b; H = Lassoie et al. 1977c; I = Leverenz 1974; J = Reed and Waring 1974; K = Reed et al. 1976; L = Ross 1972; M = Running 1976; N = Salo 1974; L = Webb 1975a b.

^bStudy location: WA = Washington, primarily the A. E. Thompson Research Center; OR = Oregon, primarily the H. J. Andrews Experimental Forest.

is controlled by that factor present in the least amount relative to its minimum requirement (Blackman 1905). The concept has had a tremendous impact on the course of biological studies (Kramer and Kozlowski 1979; Spurr and Barnes 1980). Though this is a relatively simplistic way to examine complex physiological processes, investigations of net photosynthesis lend themselves quite readily to such analysis.

Typically, when net photosynthesis rates (or many other physiological processes) are monitored under field conditions and plotted against a single controlling independent variable, a scatter diagram results (see Figure 6.1). The exact configuration of the diagram depends on the variable involved, but obviously net photosynthesis is not neatly related to any single plant or environmental variable.

Faced with this variability, how can one separate the various factors that control net photosynthesis? Three primary methods exist. Webb (1972) and Jarvis (1976) have suggested the use of boundary-line analysis in interpreting single variable relations. Thus, if an adequate number of measurements are taken in order to fill a variable data space, the upper limit of the scatter diagram will delineate the response of net photosynthesis to a particular independent variable when other factors are not limiting (Figure 6.1). Values below this line, therefore, represent control by other limiting factors. Most commonly such analysis is used with measurement of net photosynthesis under fluctuating ambient environmental conditions (for example, Lassoie and Chambers 1976; Leverenz 1981a).

Under controlled environmental conditions, another type of limiting factor analysis is possible. With some gas exchange systems it is possible to alter one environmental variable artificially while the others are kept at optimal levels

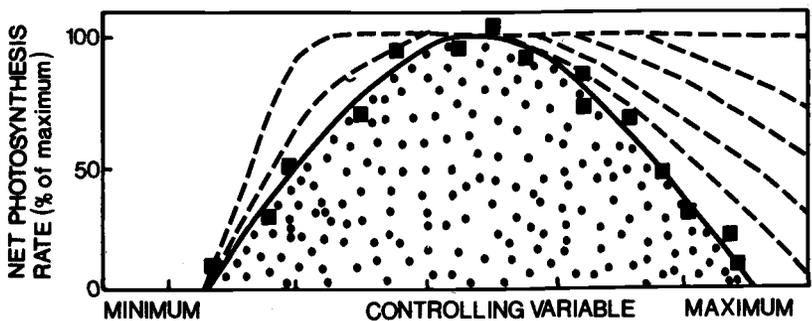


FIGURE 6.1 Idealized relation between net photosynthesis rate and a controlling plant (for example, leaf conductance of carbon dioxide) or environmental (for example, temperature) factor; actual shape of the curve (dashed lines) depends on the variable involved. The curve represents either a boundary line when data (●) were collected under field conditions or a least-squares fit line when data (■) were collected under controlled environmental conditions.

(for example, Salo 1974; Dougherty and Hinckley, 1981). A least-squares fit is then used in order to generate the response curve (Figure 6.1).

A third approach to separating the various factors that affect net photosynthesis is available in studies producing large data sets. It is then possible to examine the data in specific temperature, light, vapor pressure deficit, and plant water potential classes, thereby better identifying the control actions of different variables on net photosynthesis (Hallgren 1978; Leverenz 1981b).

Larcher (1969) has listed and discussed numerous variables that can affect net photosynthesis; they include radiation, temperature, ventilation, carbon dioxide concentration, water supply, relative humidity, soil, genetic characteristics, stage of phenological development, types of special adaptations, and chlorophyll. However, Reed et al. (1976), used only light, temperature, carbon dioxide concentration, and stomatal resistance in successfully modeling net photosynthesis in yellow poplar (*Liriodendron tulipifera*). In this model, stomatal resistance integrated the effect of tree water balance on gas exchange at the leaf-air interface. The following discussion concentrates on the controlling functions of these four factors. Other limiting factors are discussed only in relation to their effect on stomatal activity.

Temperature. Temperature response curves for net photosynthesis in conifers generally have seasonal optima between 10° and 20°C (Larcher 1969; Pisek et al. 1973; Bauer et al. 1975). Temperature optima are usually very broad, often spanning 10° to 15°C. For example, with Douglas-fir under controlled environmental conditions, the temperature response curve at near optimal light levels (in excess of 500 $\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$; 1 $\mu\text{mol} = 2.37 \times 10^1$ joules) is quite flat between 2° and 25°C; the optimum is 10°C (Figure 6.2). Controlled light and temperature studies under field conditions during the summer support this 10°C optimum (Salo 1974). Field studies by Leverenz (1981a, b), however, suggest that the optimum temperature range is 20°C or below. J. A. Helms (pers. comm.) has found that optimum net photosynthesis in Douglas-fir growing at 1000 m in the Sierra Nevada Mountains of California occurred over a broad temperature range of 15° to 30°C.

The optimum temperature range for maximum net photosynthesis in Douglas-fir of between 10° and 25°C is well supported by the work of others (Pharis et al. 1970; Sorensen and Ferrell 1973). The variability often expressed reflects genetic variability as well as differences due to environmental factors in addition to temperature. For example, temperature optima are light dependent (Figure 6.2; Brix 1967; Webb 1971) and perhaps vapor pressure deficit dependent (Ng 1978).

The high temperature limit for positive net photosynthesis is determined by effects on respiration and the dark reactions of photosynthesis (Bauer et al. 1975). This temperature maximum ranges between 36° and 45°C in Douglas-fir (Helms 1965; Krueger and Ferrell 1965; Salo 1974; Leverenz 1981b).

The rate of photosynthesis is directly reduced by cold temperatures, which lower the activity of enzymes involved in the dark reaction. It is indirectly

retarded by mechanical injuries resulting from ice formation and by abnormally low leaf water potentials that follow the freezing of the sapwood (Salo 1974). Minimum temperatures for assimilation activity are generally between -3° and -5°C (Pisek et al. 1973). It is interesting to note that with Douglas-fir, net photosynthesis at 0°C is still 70 percent of that occurring at 10°C (Figure 6.2).

Light. Solar radiation is probably the single most important environmental factor regulating net photosynthesis. Light is necessary for photosynthetic phosphorylation, stomatal activity, and photorespiration. In Douglas-fir, net photosynthesis rates typically increase rapidly with increasing light levels; high rates occur at about $600 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ (about 3500 ft-c; 1 ft-c = 10.764 lx) with little increase thereafter, under both controlled environmental conditions (Figure 6.2) and in the field (Figure 6.3). This value for the light saturation of the photosynthetic machinery is within the range reported for other conifers (Larcher 1969; Walker et al. 1972). However, because of the mutual shading of needles on and between individual twigs composing a sample (Leverenz and Jarvis 1979), net photosynthetic rates often tend to increase slowly as more

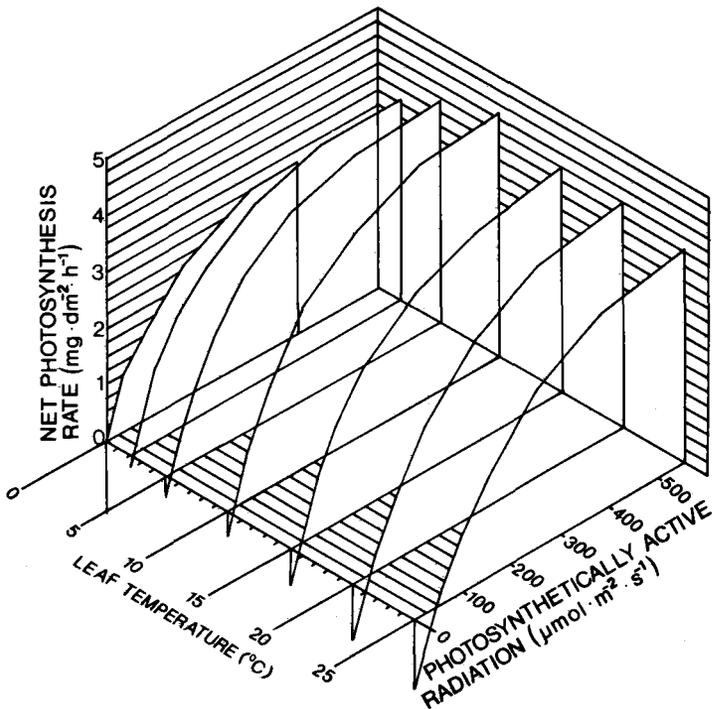


FIGURE 6.2 Net photosynthesis rate as a function of leaf temperature and photosynthetically active radiation during autumn studies conducted under controlled environmental conditions with ten-year-old, garden-grown Douglas-fir (after Salo 1974).

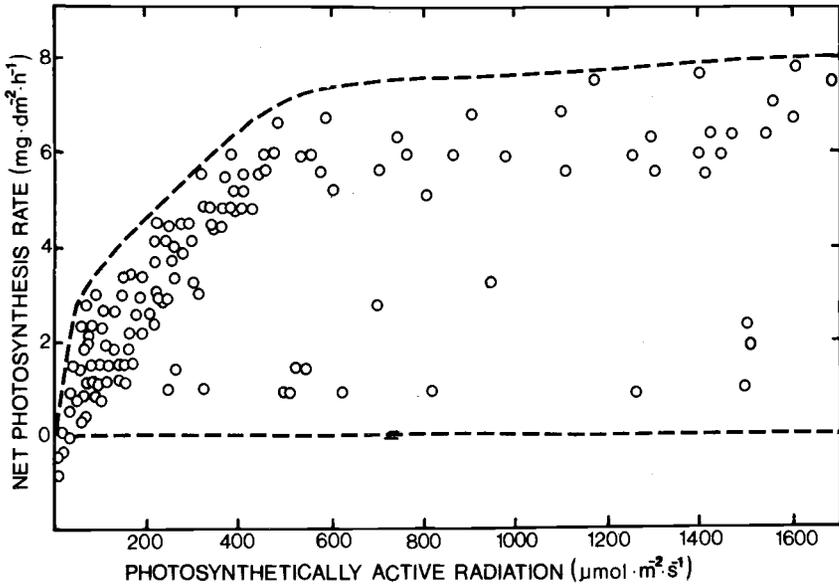


FIGURE 6.3 Net photosynthesis rate as a function of photosynthetically active radiation for current-year foliage near midcrown in a forty-year-old, twenty-seven-meter, dominant Douglas-fir under a variety of environmental conditions during late summer (after Leverenz 1974).

needle surfaces become illuminated at light levels above $600 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ (Figure 6.3). Furthermore, because of the three-dimensional nature of tree crowns and the mutual shading between branches, the concept of light saturation cannot be clearly extended to the entire crown.

As mentioned earlier, net photosynthesis rates at light saturation are also temperature-dependent, with rates decreasing on either side of a 10°C optimum (Figure 6.2). Regardless of temperature, maximum rates at saturating light intensities were higher with forest-grown trees (Figure 6.3) than with garden-grown trees (Figure 6.2). The garden-grown trees, however, had a relatively high ratio of leaf surface area to dry weight, which is typical of shade-adapted needles (Drew and Ferrell 1977). When net photosynthesis rates were expressed on a dry weight basis, they were similar to those of field material reported in the same units (for example, about $5 \text{ mg CO}_2 \cdot \text{g dry wt}^{-1} \cdot \text{h}^{-1}$; Salo 1974).

Water and stomatal activity. The influence of water deficits (that is, water stresses) on net photosynthesis rates is exerted primarily through a decrease in stomatal conductance of carbon dioxide (Hsiao 1973). Stomatal activity is complex, however, and is influenced by a variety of factors including light, leaf water potential, soil water potential, vapor pressure difference between leaf and air, leaf temperature, various plant hormones, and internal carbon dioxide concentration (Jarvis 1976; Tan et al. 1977). The following

discussion considers the control of stomatal conductances in Douglas-fir by such factors. More inclusive reviews may be found in the works of Jarvis (1976) and Hinckley et al. (1978).

Douglas-fir stomata typically open rapidly with increasing light levels, and maximum leaf conductance is usually reached at about $200 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ or less (Figure 6.4a; Tan et al. 1977; Leverenz 1981a). This light level is about 10 percent of full sunlight, a level causing similar stomatal responses in numerous hardwoods (Davies and Kozlowski 1974; Federer and Gee 1976) and in other conifers (Running 1976). Running noted that leaf conductance maxima differed between eight conifer species but that most were in the range between about 0.2 and 0.4 cm/s, a range similar to that for numerous hardwood trees (Federer 1977; Körner et al. 1979). Douglas-fir had a total range from 0.003 to 0.333 cm/s (Running 1976). Salo (1974) has reported maximum leaf conductances in dominant Douglas-fir to be between 0.20 and 0.33 cm/s, which are similar to maxima reported for seedlings (Drew and Ferrell 1979). Maxima reported by Salo (1974) and Running (1976) were generally higher than those illustrated in Figure 6.4a since the latter accounted for the diffusion coefficient for carbon dioxide (Jarvis 1971).

Stomata are generally closed in the dark. During late fall, winter, and early spring, however, when evaporative demand is low and tree water deficits are minimal, Fry (1965), Hinckley (1971); Running (1976) and Blake and Ferrell (1977) all have observed Douglas-fir stomata staying open all night. Similar results were noted by Hinckley and Ritchie (1973) in Pacific silver fir (*Abies amabilis*) and are also suggested in Figure 6.4a.

The effect of temperature on leaf conductance is difficult to separate from other variables affecting stomatal activity. Specifically, care must be taken in interpreting the effects of temperature on stomata, since increases in leaf temperature lead to larger vapor pressure differences unless compensating changes are made in the ambient humidity (Neilson and Jarvis 1976). In Douglas-fir, leaf conductance for carbon dioxide seems to be maximum at about 20°C, dropping rapidly at higher temperatures (Figure 6.4b). J. A. Helms (pers. comm.) found that optimal leaf conductances for water vapor occurred at 10°C, slowly decreased between 10° and 25°C, and then rapidly decreased as leaf temperatures approached 40°C. The decrease at higher temperature is no doubt also influenced by concurrent changes in vapor pressure gradient between the leaf and the air, which affects mesophyll (Stålfelt 1962) and peristomatal transpiration rates (Lange et al. 1971), which in turn influence guard cell turgor.

In Sitka spruce (*Picea sitchensis*) leaf conductances to water vapor have been observed to drop on either side of 15°C (Neilson and Jarvis 1976). Therefore, though no data are presented in Figure 6.4b below 15°C, lower conductances might be expected as temperatures approach 0°C. Freezing air temperatures do seem to promote stomatal closure in Douglas-fir (Reed 1968; Drew et al. 1972; Salo 1974). Drew and Ferrell (1979) noted a decline in leaf conductances in the winter with Douglas-fir seedlings that was independent of

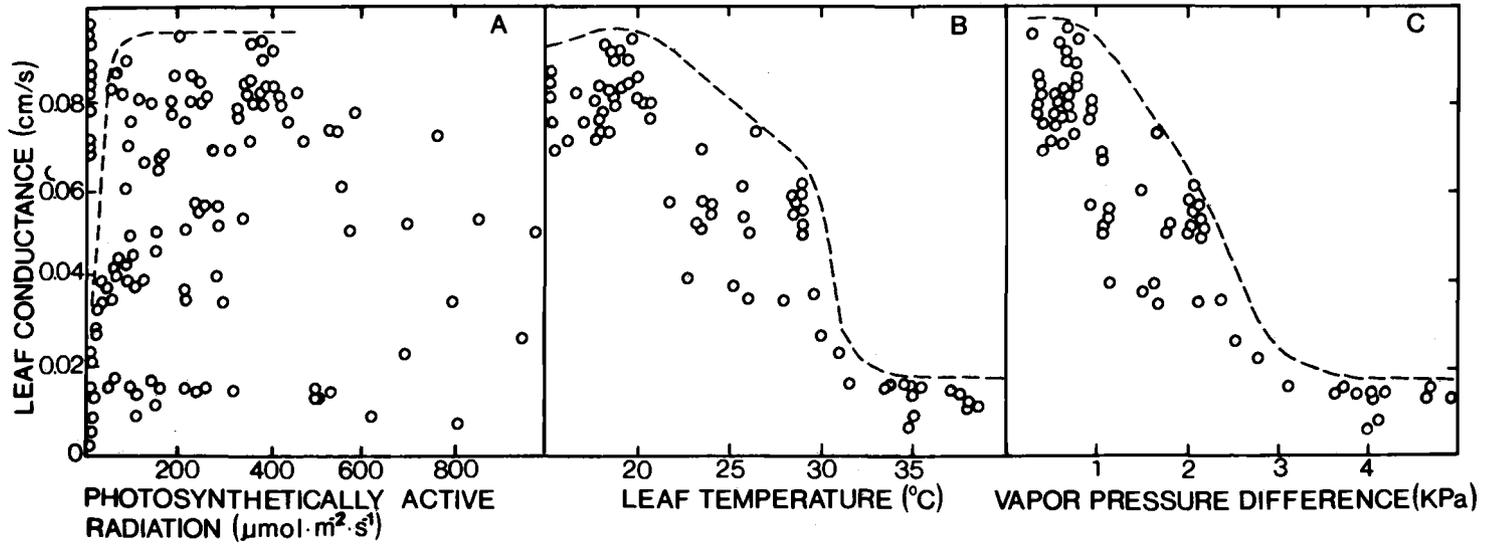


FIGURE 6.4 Calculated leaf conductance of carbon dioxide as a function of (A) photosynthetically active radiation, (B) leaf temperature, and (C) vapor pressure difference between the leaf and the air at light levels greater than $200 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. Measurements were taken on current-year foliage near midcrown in a forty-year-old, twenty-seven-meter, dominant Douglas-fir under a variety of environmental conditions (after Leverenz 1974).

leaf water potential but simultaneous with the onset of subfreezing air temperatures. In addition, lower than expected conductances following freezing or chilling have been observed in other conifer species (Kaufmann 1976; Running 1976; Lassoie et al. 1977a; Fahey 1979). Care must be taken when evaluating the effect of freezing on stomatal activity, however, as the temperature effect may actually be mediated through its effect on internal water deficits (Salo 1974, Lassoie et al. 1977a).

The impact of humidity on stomatal activity is equally difficult to separate from those effects associated with temperature. In Douglas-fir, rapid decreases in leaf conductances occur as leaf-to-air vapor pressure gradients increase to about 3.5 kPa (Figure 6.4c). Many other studies with both hardwoods and conifers have noted a leaf conductance to atmospheric humidity relationship similar to that reported for Douglas-fir (Schulze 1970; Davies and Kozlowski 1974; Hinckley et al. 1975; Kaufmann 1976; Lassoie and Chambers 1976; Running 1976). Neilson and Jarvis (1976) and Watts et al. (1976) have also observed a strong correlation between stomatal conductance and vapor pressure deficit for Sitka spruce. Leverenz (1981b) has reported a synergistic interaction between the response of stomatal conductance to humidity and temperature. This probably results in the apparent lack of response of conductances illustrated in Figure 6.4c at vapor pressure differences above 3.5 kPa (Leverenz 1981a). A similar interaction between humidity and temperature has been shown for Scotch pine (*Pinus sylvestris*) and discussed by Hall et al. (1976).

The exact mechanism by which atmospheric humidity controls stomata is not yet clear. Some investigators have hypothesized that stomata react primarily to turgor changes in the bulk leaf (for example, Meidner and Mansfield 1968), while others feel that the actual transpirational loss of water directly from and around the guard cells (peristomatal transpiration) reduces their turgor causing closure (Lange et al. 1971; Hall and Kaufmann 1975; Tyree and Yianoulis 1980; Leverenz 1981b).

Obviously, only turgor pressure differences in guard cells and associated epidermal cells directly affect stomatal apertures. Most commonly, these turgor pressures are inferred from leaf water potentials measured using thermocouple psychrometers (Brown and Van Haveren 1972) or estimated using the pressure chamber (Ritchie and Hinckley 1975). Running (1976) and Tan et al. (1977) have found that an abrupt midday stomatal closure in Douglas-fir saplings was triggered by branch xylem pressure potentials reaching a threshold of about -2.0 MPa. Waring and Running (1978) reported a threshold of -2.2 MPa in a 40-m Douglas-fir while closure was initiated near -1.7 MPa in seedlings. Work by Drew and Ferrell (1979) confirmed this -1.7 MPa threshold for Douglas-fir seedlings during the fall. However, during the summer the threshold increased to about -1.0 MPa, possibly indicating seasonal osmotic adjustment in order to maintain needle conductances at maximum levels (Cline and Campbell 1976). In addition, seedlings grown at low light levels had lower thresholds for stomatal closure, thus making them less drought resistant than seedlings grown under full sunlight.

Different coniferous species have different thresholds generally ranging between about -1.2 and -2.5 MPa (Lopushinsky 1969; Puritch 1973; Running 1976). However, as suggested above, these thresholds may vary depending on the specific environmental conditions and on the season.

It should be emphasized that if the threshold water potential is not reached by the tree, leaf conductance is then controlled by base (predawn) leaf water potential (Figure 6.5) and/or humidity (Figure 6.4c). When base xylem pressure potentials are very low, stomata are relatively closed all day as hydraulic considerations almost completely override the photoactive response illustrated in Figure 6.4a (Salo 1974; Zobel 1974; Lassoie and Salo 1981; Figure 6.5).

Stomata of some species are reported to be very responsive to the concentration of carbon dioxide near the inner walls of the guard cells (Allaway and Milthorpe 1976). However, several investigators have concluded that the influence of changes in internal carbon dioxide levels on stomatal functioning is often overridden by other limiting factors (for example, Hall and Kaufmann 1975; Schulze et al. 1975). Thus no strong relations have been observed between calculated internal carbon dioxide concentrations and stomatal activity in Douglas-fir (Fry 1965; Leverenz 1974, 1981a) or Sitka spruce (Neilson and Jarvis 1976; Beadle et al. 1979). Such results illustrate the current lack of knowledge concerning the exact control of guard cell movement by both inter-

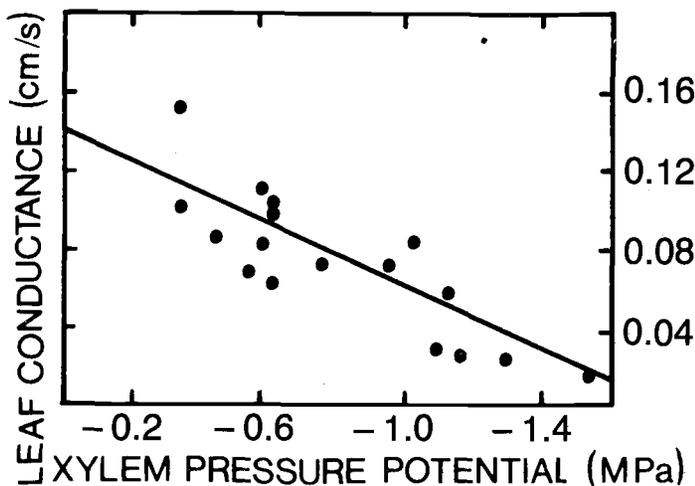


FIGURE 6.5 Regression of maximum morning leaf conductance of water vapor as a function of base (predawn) xylem pressure potential (coefficient of determination [r^2] = 0.71). Each data point represents the average of at least nine conductance measurements taken before 0900 h in the canopy of various one- to three-m Douglas-fir growing in the field (after Running 1976).

nal (for example, hormones) and external (for example, carbon dioxide) factors (Burrows and Milthorpe 1976).

Considerable interest has recently been directed toward the possible role of abscisic acid in inhibiting stomatal opening, inducing stomatal closure, and reducing gas exchange rates. Unfortunately, little of this work has examined the dynamics of endogenous abscisic acid levels in tree species (see reviews by Livne and Vaadia 1972; Hsiao 1973; Meidner and Willmer 1975; Wright 1978). In a study with drought-stressed Douglas-fir seedlings, Blake and Ferrell (1977) noted that as the soil dried and xylem pressure potentials decreased (that is, plant water deficits increased), abscisic acid concentrations increased; when a threshold in the abscisic acid level was reached (at about 1700 ng/g dry wt), stomata began to close both in the light and the dark (Figure 6.6). Similar results have been observed in balsam fir (*Abies balsamea*) and white spruce (*Picea glauca*) (Little and Eidt 1968; Little 1975), and suggested by work with transplanted Sitka spruce (Coutts 1980). Therefore there seems to be a possible connection between the diurnal development of internal tree water deficits and the promotion of stomatal closure by enhanced abscisic acid levels; however, this interesting phenomenon has yet to be fully clarified.

Of course, as has been suggested, environmental and biological factors controlling stomatal activity never act independently from one another under

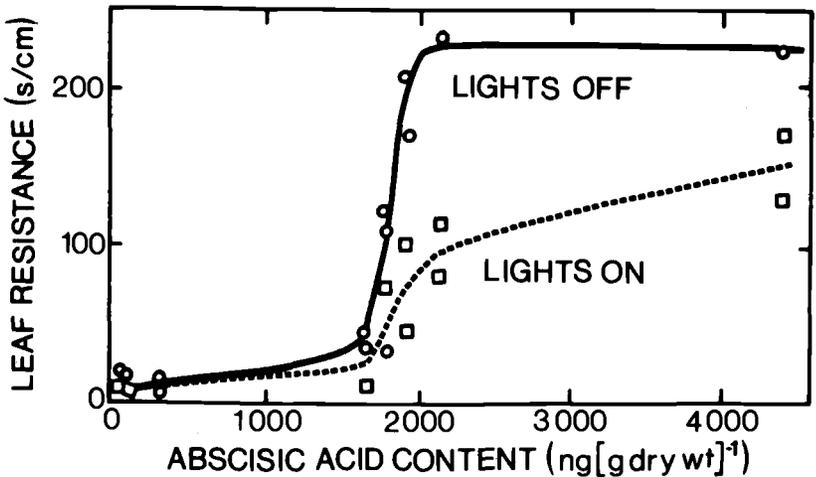


FIGURE 6.6 The association between leaf resistance (the reciprocal of conductance) and abscisic acid content in progressively stressed two-year-old Douglas-fir seedlings (unwatered for about thirty days with base xylem pressure potentials exceeding -3.0 MPa). The rapid rise in leaf resistance was associated with an abscisic acid content of about 1700 ng/gram dry wt and base xylem pressure potentials between -1.0 and -1.2 MPa. Relation is shown under both light and dark conditions (after Blake and Ferrell 1977).

field conditions. Though independent relations can be defined using boundary line analyses (for example, Figure 6.4), they do not illustrate how various controlling factors interact to simultaneously influence the stomatal mechanism. For example, it was shown earlier that the maximum conductance attainable during a day by Douglas-fir needles was linearly related to the base xylem pressure potential (Figure 6.5). When similar data are separated based on the absolute humidity deficit, however, a more complex relation results (Figure 6.7; Tan et al. 1977). Thus Douglas-fir stomata will remain relatively closed on days when atmospheric evaporative demand is high even though base xylem pressure potentials are high. The contrast seems true on more humid days, even those marked by low soil moisture levels. Such "fine tuning" to evaporative demand by Douglas-fir stomata may possibly be an adaptation strategy to prevent excessive water loss on days when soil moisture levels might otherwise promote stomatal opening.

The preceding discussion illustrates the need for further studies to identify the controlling influence of multiple factors on leaf conductance. To date it may be best to assume that synergistic interactions do not occur and that limiting factors are simply multiplicative; that is, less than additive (for example, two factors that independently reduce leaf conductance to 80 percent of maximum may, in combination, cause a reduction to 64 percent of maximum; Jarvis 1976). However, there are a few reports of synergistic interactions occurring (for example Ng and Jarvis 1980; Leverenz 1981b) and the preceding remarks may soon need to be revised.

Ambient carbon dioxide concentration. Carbon dioxide at normal ambient concentrations (about 320 $\mu\text{l/liter}$) is below the level required for maximum net photosynthesis rates in forest trees (Fry 1965; Ludlow and Jarvis 1971; Green and Wright 1977; Dougherty and Hinckley 1979). The slight carbon dioxide gradient between the ambient air and the chloroplasts and the resistances to transport in the leaf-air boundary layer and through the stomata and mesophyll seem to be the regulating forces involved (Larcher 1969; Reed et al. 1976; Leverenz 1981a). With Douglas-fir seedlings maintained at 2400 ft-c (1 ft-c = 10.764 lx; about one-fourth full sunlight), Salo (1969) observed a 100 percent increase in net photosynthesis as the carbon dioxide concentration was increased from 200 to 500 $\mu\text{l/liter}$. Furthermore, this relation seems to be quite light-dependent, with carbon dioxide concentrations above the ambient level exerting their greatest control at relatively high light intensities (Figure 6.8). Carbon dioxide concentrations may also affect stomatal activity, making the actual relation between net photosynthesis and high carbon dioxide concentrations difficult to assess accurately (Jarvis 1976).

Carbon dioxide concentrations below about 250 $\mu\text{l/liter}$ greatly limit net photosynthesis in Douglas-fir (Figure 6.8). Under normal field conditions, however, where adequate air mixing occurs, ambient carbon dioxide concentrations normally remain between 360 and 380 $\mu\text{l/liter}$ (Woodman 1968; Leverenz 1974; Doraiswamy 1977). Thus, when proper gas exchange tech-

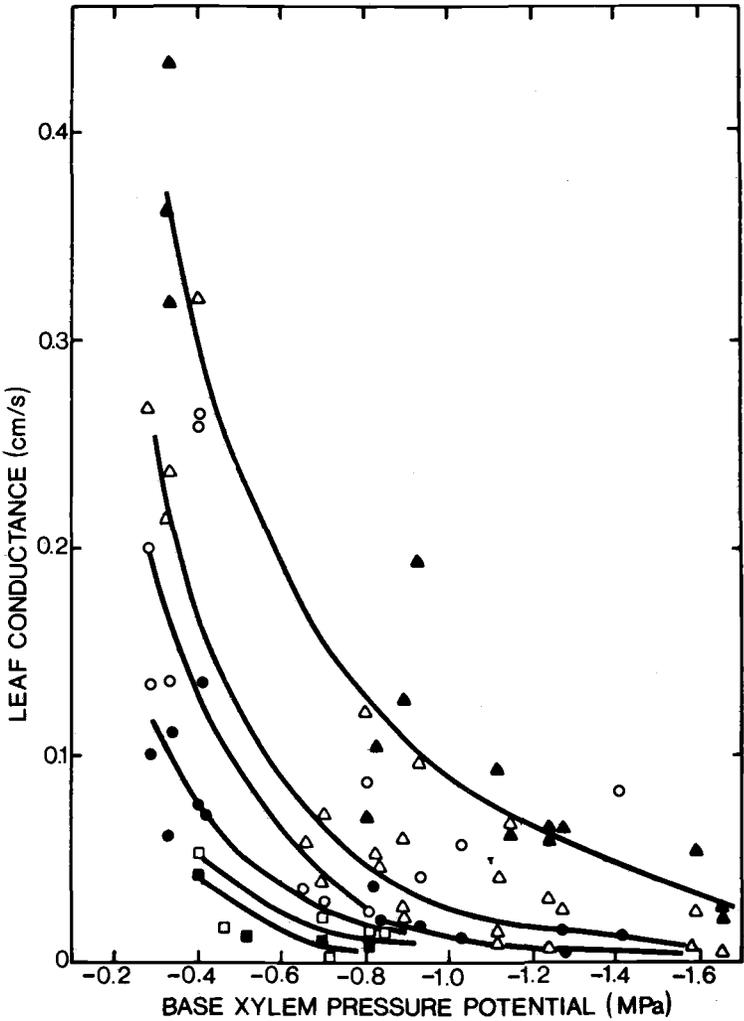


FIGURE 6.7 Relation between leaf conductance and base (pre-dawn) xylem pressure potential in various Douglas-fir seedlings. The data were separated into six ranges of absolute humidity deficit and were collected on twenty days. Each data point represents the mean of seven to fifteen measurements (after Hallgren 1978). Key: Absolute humidity in grams per cubic meter: ▲ = 3 to 6, △ = 6 to 9, ○ = 9 to 12, ● = 12 to 15, □ = 15 to 18, ■ = 18 to 21.

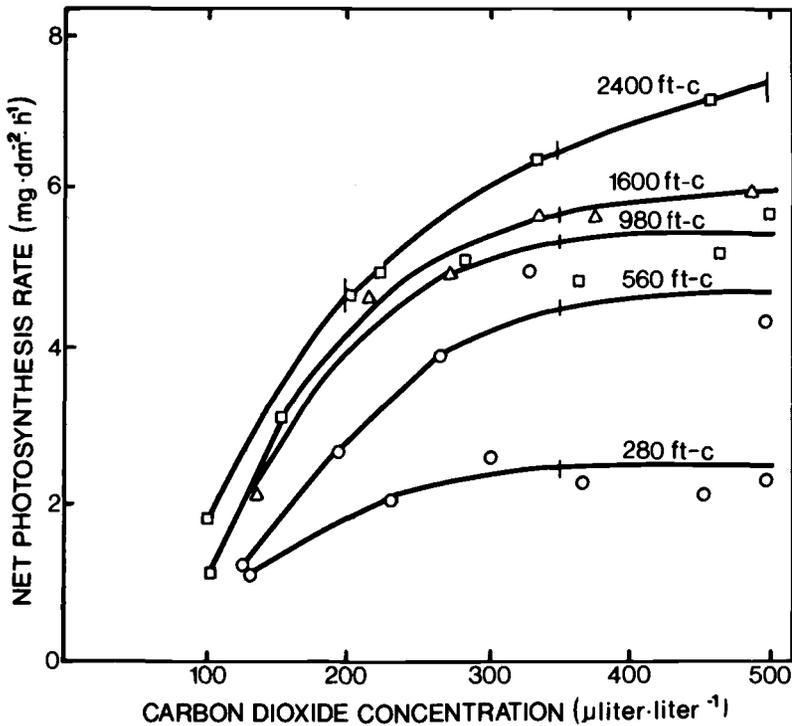


FIGURE 6.8 *The influence of carbon dioxide concentration on net photosynthesis rate in Douglas-fir seedlings at different light intensities (2400 ft-c is about one-fourth full sunlight) under controlled environment conditions (after Fry 1965).*

niques are used in the tree canopy studies, the carbon dioxide concentrations in the ambient air normally need not be considered a limiting factor (Larcher 1969).

Internal Carbon Flow and Incorporation

Understandably, there must be a close relation between carbon fixation and biomass production in forest trees (see Chapters 3 and 5); however, in order to relate net photosynthesis to growth, the distribution of photosynthates to the respective carbon sinks in the tree must be known (Ledig 1969). The relation between carbon uptake and growth involves the translocation of carbohydrates that are intermediates in a number of metabolic pathways. Their concentration in any tissue reflects the balance between the rates of photosynthate influx and efflux, or conversion of storage constituents (lipids) to soluble products. The

use of radioactive carbon-14 to label photosynthetic products has greatly advanced the understanding of the pattern and control of photosynthate distribution in Douglas-fir seedlings (Webb 1975a,b) and saplings (Ross 1972). Since the work of Ross (1972) involved an examination of temporal and spatial source-sink relations for photosynthates, such information will be presented later in this chapter.

Webb (1975a,b) examined the accumulation rates of photoassimilated carbon relative to total tissue carbon in various tissues of two-year-old Douglas-fir seedlings just after bud set (Figure 6.9). Results support the source-sink concept; that is, actively growing sites accumulate carbon at the highest rates. Differences in source strengths existed between old and new needles and followed phenological development of these tissues (Gordon and Larson 1968; Ross 1972; Chung and Barnes 1980a,b). The accumulation rates illustrated in Figure 6.9 represent growth and carbon storage in the respective tissue respiration (Webb 1975b). Differences can be attributed to the separate carbon requirements of different tissues for maintenance and tissue construction (Chung and Barnes 1977; 1980a,b) and to differences in accumulation rates due to the lags inherent in the translocation process. Needles all had positive y -intercepts while other tissues had negative values, indicating that a lag was occurring before carbon was translocated into the stem; the lag was intensified for the roots (Figure 6.9). Roots received photoassimilated carbon later than the stem but accumulated carbon faster, which represented a flux of carbon through tissue with a low carbon requirement (the stem) into tissue with a higher requirement (the roots).

In order to estimate the steady rate accumulation of photoassimilated carbon in the various tissues, Webb (1975a) developed a compartment model of carbon flow in Douglas-fir seedlings. The model illustrated the transient condition of carbon flow during the first six days of the experimental period (Figure 6.10). After this point, photoassimilated carbon was increasing at essentially constant rates in all tissues (Figure 6.9, Table 6.2). The constant increase represented the real accumulation of carbon resulting from the uptake and distribution pattern instead of the apparent rates, which were obtained directly from the tracer results (Figure 6.9). Roots received the most carbon per day followed by new needles, old needles, new shoots, and then stems (Table 6.2). These rates were the average accumulation rates for each tissue and reflected the total average carbon in each tissue as well as the demand of each for photoassimilated carbon on a per-unit-of-tissue basis. When accumulation rates were adjusted based on the total amount of carbon present in the various tissues, new and old needles accumulated carbon at the highest rates (that is, milligrams photoassimilated carbon per day per milligram of total tissue carbon), followed by roots, new shoots, and then stems. Generally, the lower rates for roots, stems, and new shoots, compared with needles, reflected the much higher metabolic activity (unit weight basis) in the needles. Thus needles were

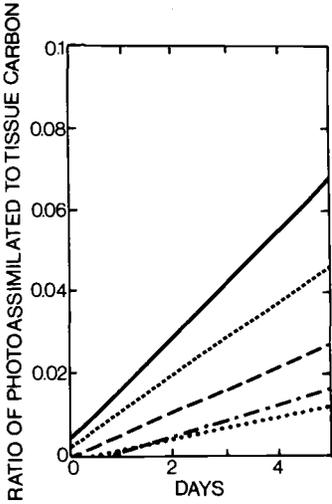


FIGURE 6.9 *The accumulation of photoassimilated carbon relative to tissue carbon in Douglas-fir seedlings (after Webb 1975a).*
 Key: Solid line = new needles; square dotted line = old needles; dashed line = new shoots; dot-and-dashed line = roots; round dotted line = stem.

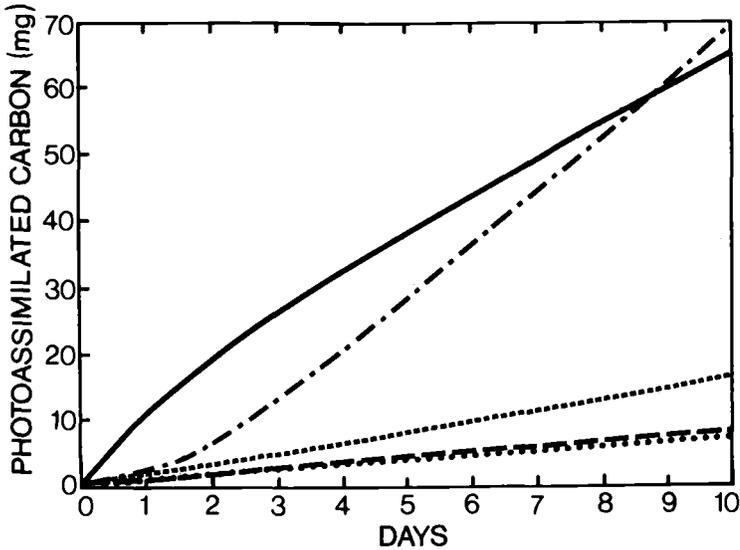


FIGURE 6.10 *Model calculations of accumulated photoassimilated carbon in Douglas-fir seedlings (after Webb 1975a).*
 Key: Solid line = new needles; square dotted line = old needles; dashed line = new shoots; dot-and-dashed line = roots; round dotted line = stem.

TABLE 6.2 *Steady rate increase of photoassimilated carbon in Douglas-fir seedlings.^a*

Tissue type	Average total carbon (mg)	Increase of photoassimilated carbon (mg/d)	Increase of photoassimilated/total carbon
New needles	573	5.39	0.0094
Old needles	157	1.79	0.0114
New shoots	192	0.73	0.0038
Stem	445	0.71	0.0016
Roots	1592	7.98	0.0050

^aFrom Webb 1975a.

clearly a major sink for photoassimilated carbon as well as the major source. Ross (1972) has presented a similar conclusion for ten-year-old Douglas-fir saplings under field conditions.

Though the source-sink concept seems to explain adequately the internal flow of carbon in forest trees, the relation between carbon dioxide uptake, assimilation, and biomass yield still remains vague for Douglas-fir. In order to address this relation adequately, Chung and Barnes (1977) noted that information is needed in three main areas: (1) the temporal and spatial distribution of biomass formation (Chapter 5); (2) the temporal and phenological fluctuations in biochemical composition of various portions of the tree; and (3) the metabolic pathways involved in, and substrate and energy requirements for, biosynthesis of constituent compounds. Most commonly, ratios of carbon dioxide uptake to biomass production are calculated. Woodwell and Botkin (1970) estimated that this ratio was 1.0:0.614 based on the assumptions that 1 g of carbon dioxide produces 0.682 g of glucose and that 1 g of glucose forms 0.900 g of biomass (that is, anhydroglucose $[C_6H_{10}O_5]_n$). Chung and Barnes (1977), however, have indicated that this assumption is not completely correct as biomass consists of much more than merely hexose polymers; their carbon dioxide-to-biomass ratio for loblolly pine (*Pinus taeda*) was 1.0:0.433. This ratio compared favorably with the 1.0:0.55 ratio derived for balsam fir by Loach and Little (1973).

Shoot and Cambial Growth Processes

The cellular growth process, utilizing photosynthates synthesized in the needles, results in the formation of biomass that is of considerable ecologic and economic importance in the coniferous forest biome (see Chapter 5). Because of the relative magnitudes and the obvious economic implications involved, the greatest amount of interest has been in stemwood production. In this respect,

the correlation between total seasonal net photosynthesis and stemwood production is surprisingly close (Chapter 3; Emmingham and Waring 1977).

The meristematic activity responsible for major aboveground biomass accumulation in large Douglas-fir is reviewed briefly here, with particular focus on the processes related to diameter and height growth arising from cellular division occurring in the cambial and apical meristems, respectively. It must be noted, however, that the tree growth process, leading to total stand biomass accumulation, also involves roots, needles, and reproductive structures. Though extremely important, the growth dynamics of these structures are not considered herein, and readers are directed to the texts of Kozlowski (1971a,b) for such information. In addition, a more recent review of tree root structure, distribution, and growth is also available (Hermann 1977).

Shoot Growth

Douglas-fir have preformed shoots; that is, overwintering buds are telescoped shoots that contain the primordia of all the needles that will expand during the next growing season. Thus the growth potentials of shoots are essentially fixed in the apical buds. Shoot growth is also seasonally determinate, meaning that after the terminal shoots elongate, there is a period of inactivity until new terminal buds form and can expand; usually the expansion phase occurs only once a year.

The environment controls shoot growth by influencing the production of new primordia, which will expand the next spring. Since the photosynthetic and growth processes are inseparably linked, the environmental control factors discussed earlier for net photosynthesis also influence the production of new buds and their subsequent growth (Kozlowski 1971a). In general, late-summer environmental stresses do not greatly restrict current-year elongation of preformed, predetermined shoots as they usually complete most of their expansion before that time. Late-season stresses, however, affect shoot growth the following spring by reducing the number of primordia produced in the new, unopened bud. Thus bud size is a prime indicator of shoot growth potential (Clements 1970).

When unusually severe environmental stresses occur during the growing season, the full growth potential of the preformed buds is not realized (Kozlowski 1971a). For example, during the installation of a weighing tree-lysimeter at the Thompson site in the summer of 1971 (Fritschen et al. 1973), the tree was periodically subjected to abnormally severe internal water deficits with base xylem pressure potentials often decreasing below -1.8 MPa (R. B. Walker and D. J. Salo, pers. comm.). Severe water deficits coupled with mineral deficiencies during the elongation growth phase resulted in the 1971 shoots' being uncommonly short but covered with numerous, closely spaced needles. In addition, the 1972 shoots were relatively sparse, presumably be-

cause of a reduction in the number of leaf primordia formed in the new buds at the end of the 1971 growing season. These effects strongly suggest "transplanting shock," (Coutts 1980) which became morphologically undetectable by the 1973 growing season.

Cambial Growth

Diameter growth in stems, roots, and branches arises from the meristematic activity of their cambiums and accounts for the major proportion of the standing biomass in Douglas-fir (see Chapter 5). The term "cambium" actually denotes a zone of cells between the secondary xylem and phloem that undergoes periclinal cell divisions. This zone is composed of various types of initiating cells producing an assortment of derivatives. In conifers, fusiform initials give rise to tracheids and various axial parenchymal cells toward the inside and sieve and parenchymal cells to the outside. The width of the cambial zone is greatest in fast-growing trees and hence proportionately greater amounts of phloem and xylem tissue are associated with such individuals (Grillos and Smith 1959).

After their production by xylem mother cells, daughter cells go through three distinct phases before becoming functional tracheids (Wodzicki 1971): (1) radial enlargement, characterized by the uptake of water into the vacuole, increases in turgor pressure, and cell expansion; (2) maturation, which involves secondary wall synthesis and lignification; and (3) cellular differentiation, which often lags considerably behind cell division. New xylem cells, during their enlargement phase, can exchange water with the transpiration stream and fluctuate in size, thereby becoming involved in the internal storage of water and in the reversible stem shrinkage phenomenon (Dobbs and Scott 1971; Lassoie 1973, 1979).

Tree water balance seems to play an important role in the differentiation of xylem derivatives and is therefore involved in the transition from earlywood to latewood within the annual ring of conifers. Variations in tracheid diameter depend upon seasonal fluctuations in the growth rate during the enlargement phase, while the final cell wall thickness is determined by the duration of the maturation phase (Wodzicki 1971). The duration of the latter phase is in turn controlled by the delay in the onset of autolysis of the cytoplasm, which marks its termination. All these processes seem to be greatly influenced by the water relations of the vascular cambium (see review by Zahner 1968); however, the controlling influence of hormonal action should not be neglected (Pharis 1976; Wodzicki and Wodzicki 1980).

The phloem of conifers is composed of conducting tissue, consisting of living, mature sieve cells that lack nuclei and tonoplasts, various types of parenchyma cells, and dead, nonconducting tissue. Typically, sieve cell production and differentiation begin in the spring and continue until fall

(Srivastava 1963). In Douglas-fir, callose plugs form on sieve areas during the middle of July but then dissolve the following year; therefore sieve cells remain alive and functional for most of two growing seasons (Grillos and Smith 1959).

In Douglas-fir phloem, parenchyma cells typically accumulate substances such as resins, tannins, and starches (Grillos and Smith 1959). Fusiform ray initials and resin canals are also common in older individuals. Ray parenchyma and ray cells act as channels for moving materials between the phloem and the xylem. The radial transport of water along these channels has been suggested to be an important aspect of stem water storage (Stewart 1967) and stem dimensional fluctuations (Dobbs and Scott 1971).

Auxin, the traditional cambial stimulus, is generated in the needle primordia contained in the buds and is propagated basipetally in forest trees, affecting cambial activity in a gradient extending downward and inward from the shoot tips. No doubt such activity also involves the balance of several growth regulators (for example, auxin, gibberellins, and cytokinins) and various synergistic effects between them (Kozlowski 1971b, Pharis 1976; Berlyn 1979). In addition, internal gradients of various growth components (for example, water, nutrients, and photosynthates) as well as the various environmental factors that control them are also involved, and all result in longitudinal variations in cambial growth rates along Douglas-fir stems (Dobbs 1966). Thus those factors discussed earlier that affect net photosynthesis also, at least indirectly, affect cambial growth rates (Berlyn 1979); however, the relation is probably confounded in Douglas-fir by the existence and utilization by the cambium of stored photosynthates (Ross 1972).

Tree water balance and internal water deficits seem to have direct influence on cambial cell activity and growth potential. Both division and elongation usually occur only under conditions of relatively high cell turgor (Vaadia et al. 1961). Lassoie (1975, 1979) has reported that positive cambial growth increments in various crown classes of Douglas-fir abruptly terminated at both breast height (1.3 m) and near midcrown when base xylem pressure potentials decreased below about -0.5 MPa. Thus summertime irrigation has been shown to enhance seasonal diameter growth in field-grown Douglas-fir by extending the growing season into late summer (Woodman 1971a). In contrast, Ross (1972) reported that irrigation in midsummer following an extended and severe drought did not influence cambial growth, presumably because of cambial dormancy initiated during the drought period.

Growth Interdependency

The foliage, stems, and roots of forest trees seem to be so hydraulically and biochemically interrelated that their growth dynamics are mutually interdependent (Reich et al. 1980; Hinckley and Lassoie 1981). In Douglas-fir, water flux through a stem is closely related to its sapwood cross-sectional area (Figure

6.11; Huber 1956; Kline et al. 1976), which is in turn linearly related to leaf biomass (Figure 6.12; Grier and Waring 1974) and to leaf area (Chapter 5; Grier and Running 1977). A similar relation between sapwood area and foliar area has been reported for other conifers (Grier and Waring 1974; Running 1980) and for various hardwood trees (Waring et al. 1977; Rogers and Hinckley 1979). Recent results by Long et al. (1981) have extended this relationship to include any point along the stem of a large Douglas-fir. In addition, Santantonio et al. (1977) have found a significant correlation between diameter at 1.3 m and root biomass in mature Douglas-fir trees. Thus it seems that the entire root-sapwood-leaf water transport system maintains a dynamic equilibrium that assures adequate water uptake and transport to foliar surfaces in order to meet transpirational demands (Hinckley et al. 1978).

TEMPORAL AND SPATIAL VARIATIONS IN PHYSIOLOGICAL ACTIVITY

Forest trees are long-lived, three-dimensional organisms that must interface with highly variable soil and atmospheric environments. Hence their physiological activity depends not only on diurnal and seasonal fluctuations in controlling environmental variables but also upon spatial and age-related factors. In this section, temporal variations in certain physiological processes are first discussed, followed by a consideration of within-tree variations, specifically those related to height, aspect, and age.

Temporal Variations

Growing Season Activity

The spring and summer comprise the major portion of the growing season for Douglas-fir. The period is characterized by aboveground meristematic activity and is defined by a seasonally fluctuating set of interrelated environmental variables. These factors are also geographically variable and the timing, trend, and magnitude of various physiological processes in Douglas-fir are different throughout the coniferous forest biome (Campbell and Sugano 1979). For example, the initiation, rate, duration, and total increment of cambial and apical growth in Douglas-fir varies throughout Oregon depending primarily upon the elevation (Table 6.3). The influence of elevation includes such controlling factors as water, temperature, and light, which are generally more favorable for net photosynthesis and growth at lower elevations; thus growing season lengths typically decrease with altitude (Larcher 1975). Work by Emmingham (1977) with Douglas-fir also has shown that growth rate may be

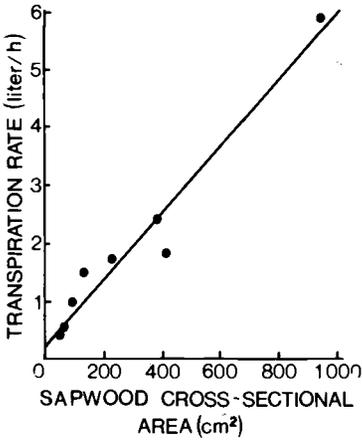


FIGURE 6.11 The relation between sapwood cross-sectional area and transpiration rate in various Douglas-fir trees (after Kline et al. 1976).

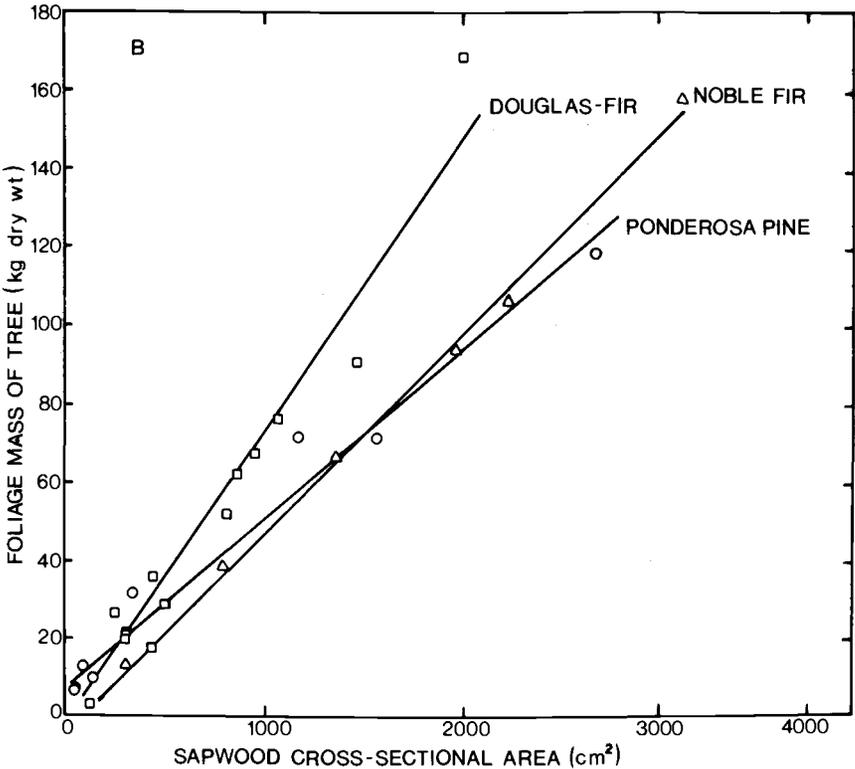


FIGURE 6.12 The relation between sapwood cross-sectional area at 1.3 m and total foliage mass for Douglas-fir (coefficient of determination [r^2] = 0.97), noble fir (r^2 = 0.98) and ponderosa pine (r^2 = 0.97) (after Grier and Waring 1974).

TABLE 6.3 *Phenology and growth for cambiums and leaders of sapling Douglas-fir (coastal range—Corvallis, Oregon, seed source) in three western Oregon plantations.^a*

Location ^b	Leader growth and phenology (1971)						Cambial growth and phenology (1971)						
	Bud swell	Bud break	Extension growth		Rate ^c	Duration ^d	Total	Start of divisions	Start of latewood	Growth (90%)	Rate ^e	Duration ^f	Total
			90%	100%	(cm/d)	(d)	(cm)				(mm/d)	(d)	(mm)
CAS	June 1	June 22	Aug. 9	Sept. 8	0.66	135	33	June 4	Aug 9	Aug 20	0.032	77	2.56
COA	Apr 18	May 10	July 26	Aug 18	1.14	100	73	Apr 18	Aug 3	Sept 3	0.047	139	6.45
WIL	Apr 20	May 10	July 4	Sept 3	2.00	87	120	Apr 19	Aug 4	Sept 2	0.071	139	10.38

^aFrom Emmingham (1977).

^bCAS = Cascade Mountains near Molalla, Oreg., at 1050 m; COA = Coast Range Near Corvallis, Oreg., at 570 m; WIL = Willamette Valley near Salem, Oreg., at 70 m.

^cGrowth rates taken from slope of leader and cambium growth curves.

^dLeader growth duration is time from budbreak to growth cessation.

^eCambial growth duration is time from initiation of cell divisions to completion of 90 percent of growth.

equally as important as duration, especially when considering the terminal leader (Table 6.3).

In general, Douglas-fir phenology and growth at low to medium elevations in western Washington varies within the extremes defined by data from the Coast Range and Willamette Valley in Table 6.3 (Dobbs 1966; Woodman 1968; Ross 1972; Lassoie 1975). It seems that the greatest discrepancies between the Washington site and the Oregon sites involve the specific timing of the termination of both cambial and apical meristematic activity. Such differences probably indicate geographic variability in controlling environmental factors as well as possible genetic differences.

Genetic differences within the species Douglas-fir can have an effect on an individual's physiological activity. For example, two distinct varieties are commonly recognized, a coastal form (var. *menziesii*) and a Rocky Mountain or inland form (var. *glauca*), with intergradations occurring in size and phenological traits within their transition zone (Sorensen 1979). Provenance trials have illustrated differences between these two varieties with respect to the timing of budbreak and onset of dormancy and to apical and cambial growth rates (Irgens-Moller 1968; Rehfeldt 1977). In general, adaptation to a maritime environment has genetically fixed the coastal variety with growth potentials superior to the Rocky Mountain variety. In addition, it seems that coastal Douglas-fir seedlings, when compared with those from inland sources, have relatively higher net photosynthesis rates at all light intensities below saturation (Krueger and Ferrell 1965). This superiority is realized only in relatively mild climates, however, as the coastal form typically does not survive the severities of continental climates (Rehfeldt 1977).

There also seem to be marked genetic differences within each of the two Douglas-fir varieties. Hermann and Lavender (1968) and Campbell (1979) have demonstrated altitudinal and topographical differentiations within the coastal form. In general, seedling growth potential decreased with the altitude of the seed source regardless of the testing environment. There was also a shorter growth period and a larger root-to-shoot ratio for the progeny of trees from south-facing slopes compared with those from north-facing locations. These differences were viewed as survival adaptations to the environmental extremes associated with southern exposures. A similar study has examined genetic variations within the inland variety (Rehfeldt 1974, 1979a,b).

Temporal fluctuations in Douglas-fir physiological processes during the growing season can often be separated into three intergrading phases that depend on tree water status: the predrought, drought, and recovery or postdrought periods. In most of the coniferous forest biome, precipitation is normally sparse during July, August, and early September when atmospheric evaporative demand is relatively high; decreasing soil moisture levels throughout this period characterize the summer drought phase (Figure 6.13).

Typically, the predrought period is marked by low evaporative demands, high soil and tree moisture levels, and intense cambial activity (Figure 6.13).

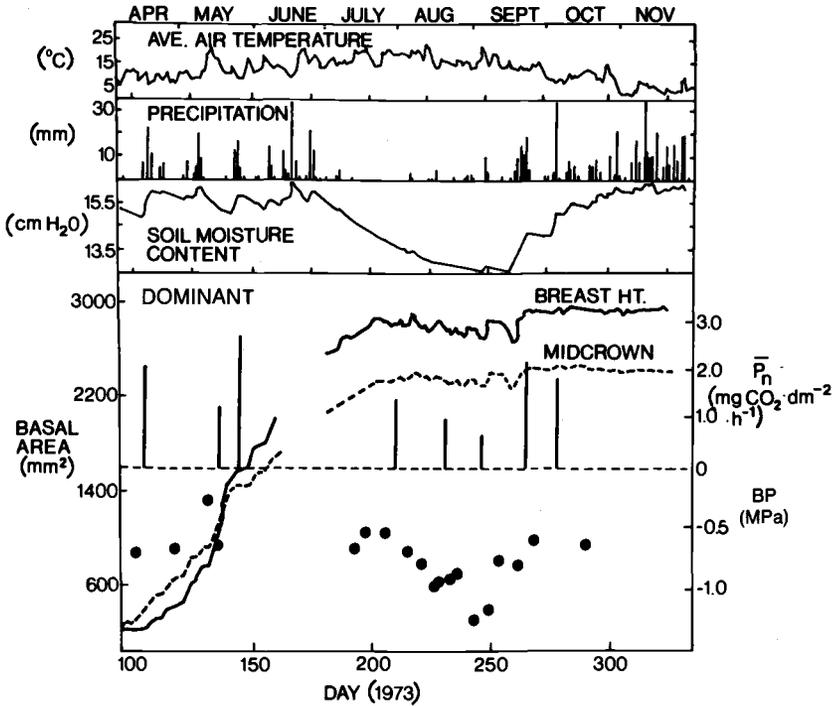


FIGURE 6.13 Seasonal trends in average daily air temperature, total daily precipitation, soil moisture content in the top meter of soil, basal area increment at breast height (1.3 m) and midcrown (20 m), daylight mean net photosynthesis rate (\bar{P}_n), and base (predawn) xylem pressure potential (BP) for a dominant Douglas-fir (after Salo 1974; Lassoie 1975, 1979).

Surprisingly, the seasonally greatest stem respiration rates (indicative of cambial activity) are not typically associated with this period, as the formation of springwood uses less carbon per unit increment of radius than summerwood formation (Linder and Troeng 1977). In the early spring, stem growth commences earlier and progresses more rapidly near midcrown than at lower levels, because of the differential initiation of cambial activity starting from the top downward. Interestingly, much of this early growth may not involve actual cell division. Dobbs (1966) has noted that increases in stem circumference in Douglas-fir occur about three to five weeks prior to actual growth because of the rehydration and swelling of the cambial zone before meristematic activity is initiated. The cambial zone can exchange water internally and undergo minor diurnal contractions in size during this period; however, the predrought growth phase is characterized by the continuous increase in stem size arising from nighttime recoveries surpassing daytime shrinkages (Figure 6.14a). In fact, mitotic activity by the cambium during the spring may not seem to be greatly affected by the diurnal contractions of the bole (Wilson 1966); however the expansion phase is most definitely terminated during such shrinkage periods.

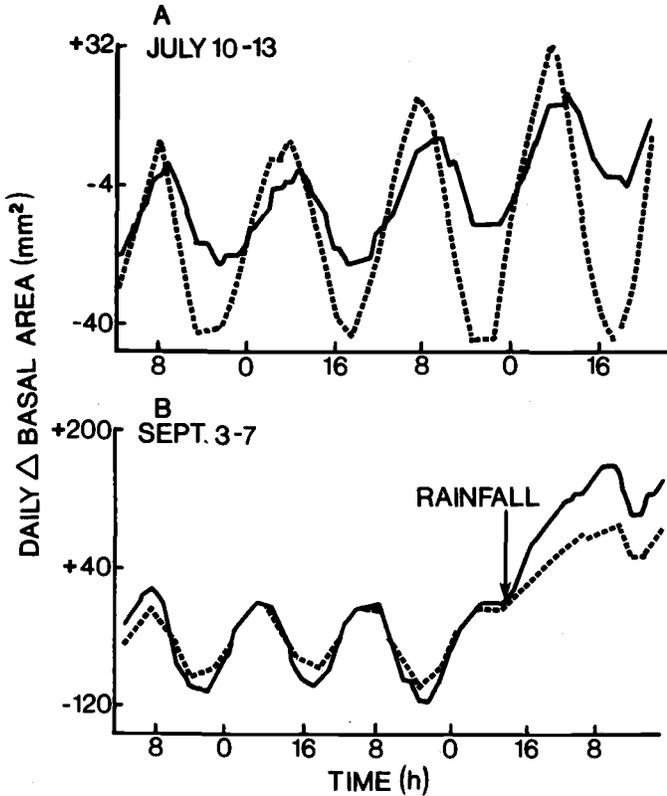


FIGURE 6.14 Diurnal fluctuations in basal areas at breast height (1.3 m; solid line) and near midcrown (20 m; dotted line) in a forty-year-old, twenty-nine-meter, dominant Douglas-fir during the: (A) predrought, late-growth phase and (B) peak of the summer drought period (after Lassoie 1975, 1979).

Since water does not seem to be greatly limiting during this period, cambial growth responds primarily to warm, rainless periods (especially in May; Figure 6.13). This fact suggests that light and temperature are probably regulating the growth process (Doley and Leyton 1968).

By midsummer, soil moisture reserves become depleted, thereby causing a comparable decrease in base xylem pressure potentials (Sucoff 1972; Lassoie 1975). At this time, afternoon and evening rehydration (swelling) of cambial tissue fails to completely account for daytime dehydration (shrinking) (Figure 6.14b) and net stem contractions occur (Figure 6.13). The progressive contraction of the stem is periodically interrupted by temporary increases during periods of relatively low evaporative demand, and some actual cell growth may occur (Shepherd 1964; Green 1969). However, such major diurnal shrinkages represent a time of cambial cell dehydration and loss of turgor (Hopkins

1968), and thus cell divisions and expansions during that phase are greatly limited (Wilson 1966; Doley and Leyton 1968). In support, Linder and Troeng (1977) have reported that, with twenty-year-old Scotch pine late in the growing season, the diurnal minimum in stem respiration rates occurred simultaneously with the diurnal minimum in stem radius. These authors cautioned, however, that precise correlations between stem respiration and cambial growth activity are not possible without careful consideration of the stem shrinkage phenomenon and the seasonal changes occurring in growth ring densities. Additional work is warranted.

Stem shrinkage in the morning and recovery in late afternoon commence up to four hours earlier at a midcrown position compared with breast height (Figure 6.14a,b; Dobbs and Scott 1971; Lassoie 1973, 1979). Such a lag probably results because water reserves nearest the transpiring crown are relatively more sensitive to fluctuating tree water deficits developed at the foliage than those elsewhere along the stem.

Rehydration of the stem during the late afternoon and evening occurs in two recognizable phases (Figure 6.14a,b). First there is a rapid expansion phase that has been attributed to hydraulic recharge (Hinckley et al. 1974), followed by a slower rate of increase that continues until the commencement of shrinkage the next morning and implies actual cell growth (Namken et al. 1969). Similar two-phase increases in leader length have been reported for Douglas-fir seedlings by Zaerr and Holbo (1976).

Daily trends in net photosynthesis vary depending on the progression of various environmental factors that control its functioning. Under adequate light conditions (clear, sunny summer days), net photosynthesis rates depend primarily on the stomatal mechanism and its control by changing soil moisture levels and internal tree water deficits (Figure 6.15; Lassoie and Salo 1981). Under well-watered conditions, net photosynthesis varies with early morning increases and late afternoon decreases in light (Figure 6.15, curve 1). As the soil progressively dries, stomata tend to be less responsive to early morning increases in light (Running 1976) and initiate closure earlier in the day (Figure 6.15, curves 2 to 5) until no opening occurs and net photosynthesis remains negative most of the day (Figure 6.15, curve 6). On cloudy, overcast days when light levels are fluctuating and are often below those saturating the photosynthetic machinery (Figures 6.3 and 6.4a), net photosynthesis rates closely reflect the fluctuations in light (Salo 1974). Leaf temperatures can also modify these general diurnal trends in net photosynthesis but normally only as they approach freezing or exceed about 25°C (Figures 6.3 and 6.4b).

Seasonal trends in net photosynthesis are commonly reported by computing either the total daily net carbon dioxide exchanged or by averaging that value over the daylight period. Since day length varies appreciably over the year, the latter approach is often preferred if comparisons are to be interpreted in relation to other limiting factors. In the spring, average daily net photosynthesis rates are the highest on cool, cloudy days when internal water deficits

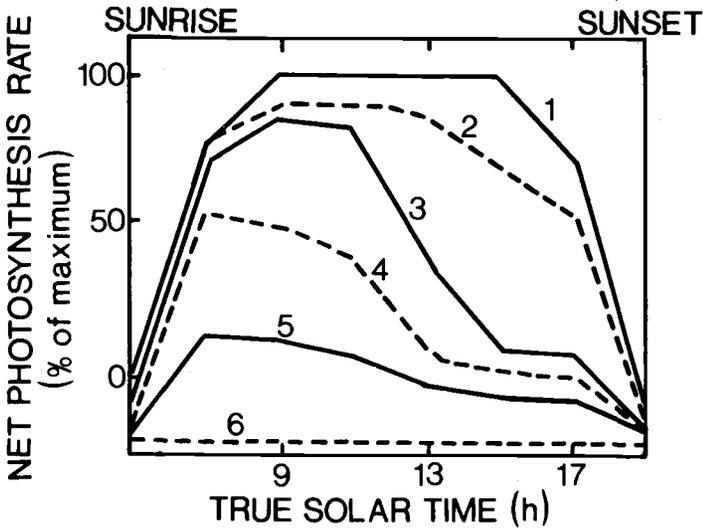


FIGURE 6.15 Hypothetical diurnal trends in net photosynthesis rates showing the effect of increased soil water deficits (for example, curve 1, base xylem pressure potential equal to about -0.2 MPa; curve 6, about -2.0 MPa) for various sunny spring and summer days (based on data for Douglas-fir; Leverenz 1974, Salo 1974, and selected literature).

remain low (for example, May 24, Figure 6.13). In contrast, sunny, hot days are marked by reduced assimilation activity (for example, May 15, Figure 6.13) because of either supraoptimal leaf temperatures (Figure 6.3) or hydroactive stomatal closure during the afternoon (Running 1976; Lassoie et al. 1977c; Lassoie and Salo 1981). As soil and tree moisture levels decrease during the summer drought, stomata remain open for progressively shorter times, thereby confining active carbon dioxide uptake to the early morning hours (August and early September, Figure 6.13).

Similar midday depressions in net photosynthesis rates have been reported by others for Douglas-fir (Gentle 1963; Helms 1965; Woodman 1968; Leverenz 1981). In addition, modeling efforts by Emmingham and Waring (1977) have illustrated the impact of such midday stomatal closure on seasonal net photosynthetic trends in Douglas-fir at various locations throughout western Oregon. They found a summertime reduction in potential net photosynthesis due to drought that ranged from 25 percent at a moist coastal site to 65 percent at a dry interior range site (see Chapter 3).

The fall is normally characterized by cool temperatures and frequent rainfall leading to the recharge of soil and tree moisture levels and the rapid enlargement of Douglas-fir stems (Figures 6.13 and 6.14b). Since temperature and tree water deficits are generally moderate, assimilatory activity can be

substantial (Figure 6.13). By late October, however, the relatively short day length limits total daily net photosynthesis (Salo 1974).

From the preceding discussion the question remains as to whether Douglas-fir foliage retains the same photosynthetic potential throughout the year. It is well known that different-aged needles have different assimilatory capabilities and that expanding new needles have relatively low net photosynthesis rates because of their growth activity. Such features will be discussed when spatial variabilities are considered; however, does the assimilatory capacity change in a given age class of needles during the year? If so, the change could greatly affect the interpretation of field measurements of net photosynthesis.

Brix (1971) has examined this possibility by measuring net photosynthesis rates under optimal light and temperature conditions in shoots periodically excised from a twenty-four-year-old Douglas-fir. Results indicated that net photosynthesis rates in new needles increased from negative values (that is, net respiration) in the early stages of shoot expansion to a high of about $8.3 \text{ mg CO}_2 \cdot \text{dm}^{-2} \cdot \text{h}^{-1}$ by the end of August (Figure 6.16). During the winter the rate decreased to a low (about 25 percent of maximum) in early February and then increased steadily throughout the next spring. Such data indicate that certain endogenous factors, probably related to biochemical, hormonal, or enzymatic

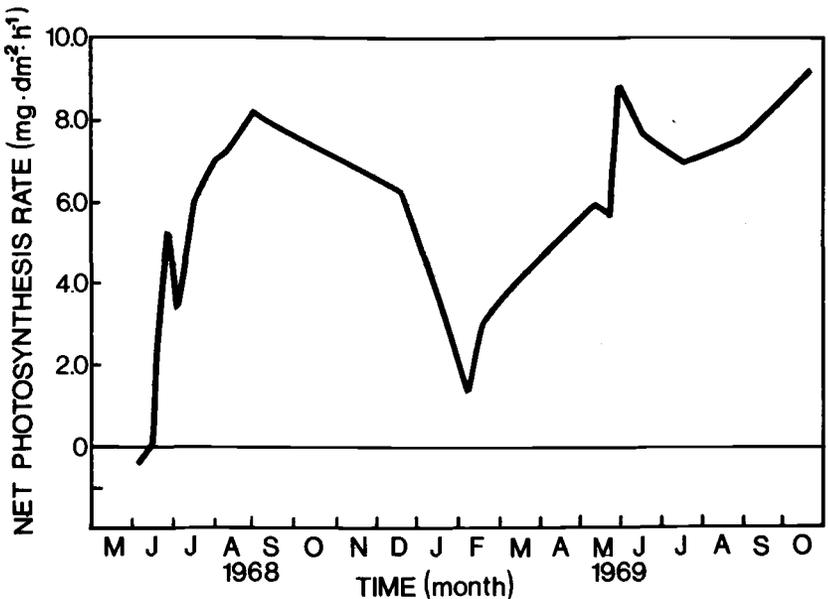


FIGURE 6.16 Seasonal trend of maximum potential net photosynthesis rate for current-year shoots in 1968 and one-year-old shoots in 1969 excised from twenty-four-year-old Douglas-fir trees and measured under 2500 ft-c and 20°C conditions (after Brix 1971).

reactions, or all three, or possibly to seasonal changes in the source-sink strength for photosynthates in the needles (Chung and Barnes 1980a,b), may affect net photosynthesis rates. In addition to these rhythms, temperature adjustments over the year in both net photosynthesis and leaf conductance have been noted in Douglas-fir (D. J. Salo, R. G. Amundson, and R. B. Walker, pers. comm.) as well as in Sitka spruce (Watts et al. 1976). Thus a portion of the seasonal variability illustrated in Figure 6.16 may have resulted from maintaining experimental temperatures at an optimal 20°C (Brix 1971) while actual temperature optima in the field changed to reflect changes in ambient temperatures. The adaptive significance of such an occurrence is obvious but has yet to be fully examined for Douglas-fir.

Being able to quantify and interpret temporal fluctuations in net photosynthesis rate and stem growth, based on their controlling biotic and abiotic factors, unfortunately lends little to an understanding of how cells eventually arise from carbon dioxide exchanged at the needles. Quite generally, the translocation and incorporation of carbon once it enters the stomata involve the relative strengths of various sources (primarily the needles) and sinks (primarily meristematic tissues). Simply stated, source-strength is related to needle age and sink-strength is dependent on the growth activity of meristematic tissues (for example, root, stem, and branch cambiums and apical meristems, and new needles); translocation between the sources and the sinks is a function of their proximity to each other and the time of year.

Ross (1972) has examined the source-sink relationship in ten-year-old, field-grown Douglas-fir using the carbon-14 technique. He observed that diurnal assimilation rates were similar to those discussed earlier where light controlled net photosynthesis rates during the morning and late afternoon and increasing tree water deficits became limiting throughout the daylight period (Figure 6.15). There was also a 75 percent reduction in the rate of photosynthate efflux from one-year-old needles toward new shoots during the day, presumably because of a drop in the availability of photophosphorylation energy for vein loading (Plaut and Reinhold 1969), and possibly decreases in respiratory activity associated with cool nighttime temperatures (Hartt and Kortschak 1967).

The observed diurnal differences in the fate of currently assimilated carbon must be interpreted in terms of the changing environmental conditions associated with the light/dark cycle as well as the tree's developmental stage and physiological status on the specific days examined. Environmental conditions that promote high internal tree-water deficits also limit meristematic activity throughout the tree, thereby confining positive increases in shoot length and diameter to evening periods when conditions for growth are more favorable (Figure 6.14; Ross 1972; Lassoie 1975; Zaerr and Holbo 1976). The findings of Ross (1972) indicate that both photosynthesis and the export of photosynthetic products are less affected by high internal water deficits during the day than are cell growth processes. Similar conclusions have been presented by

Boyer (1970) for several herbaceous plants and by Brix (1972) and Leverenz (1981a) for Douglas-fir. Thus, under drought conditions, nocturnal shoot growth in Douglas-fir utilizes current photosynthates accumulated during the day in storage tissues of the old internodes (Ross 1972).

Diurnal and seasonal trends in foliar transpiration can closely resemble those illustrated for net photosynthesis because of the common influence of the stomata (Figure 6.15). The transpiration process is also dependent on the vapor pressure gradient between the leaf mesophyll cells and the atmosphere. Examinations of diurnal transpiration rates in Douglas-fir based on measurements at the foliage (Leverenz 1974, 1981a; Salo 1974) and on estimates for entire trees (Fritschen et al. 1977; Lassoie et al. 1977c) have exemplified the relationship between stomatal activity and evaporative demand in determining water loss rates. In general, such control changes temporally, with transpiration mimicking evaporative demand as long as stomata remain open. Hydroactive stomatal closure during the afternoon reduces water loss rates even though evaporative demands may be high.

Seasonal transpiration patterns have also been examined by modeling both potential and actual transpiration for one- to two-year-old Douglas-fir growing in various environments in southwestern Oregon (Reed and Waring 1974). Striking differences were noted between the predictions of potential and actual water losses depending on the particular location. The ratio of these two factors varied from 1.0, indicating that no measurable stomatal closure was occurring and soil water levels were adequately meeting the transpirational demand, to about 0.3 at drier sites. At such locations hydroactive stomatal closure was exercising a major influence on tree water losses. Similar results have been noted by Hinckley and Ritchie (1973) in noble fir (*Abies procera*) and Pacific silver fir.

More recent studies have indicated that the preceding view that hydroactive stomatal closure and soil moisture are simply and directly related may need to be reevaluated. That is, there now seems to be ample evidence that internal sources of water may be called upon during periods of reduced soil water availability and might postpone hydroactive stomatal closure, thereby maintaining carbon dioxide uptake into the afternoon (Hinckley et al. 1978; Running 1980; Hinckley and Lassoie 1981). Two primary water storage areas exist in tree stems, the living tissues at and near the cambium and the water-conducting sapwood.

The formation of internal tree-water deficits occurs as water content at a particular location decreases due to transpirational losses exceeding supplies and/or water between cells or specific parts of the tree being redistributed (Richter 1973; Jarvis 1976). As water moves from nearby tissues, hydrostatic tensions are transmitted throughout the tree. As tensions increase within elastic tree tissues, their deformation occurs; with the release of internal tensions they recover in size. In tree stems, roots, and branches such dimensional fluctuations occur principally in the living phloem, cambium, and newly derived

xylem cells (Dobbs and Scott 1971; Jarvis 1975). These fluctuations are directly related to changes in tissue water content, thereby providing an internal storage area (that is, a source-sink) for water (Oertli 1971). It appears that inelastic stem tissues, the sapwood and heartwood, are also involved as internal water storage areas in large forest trees (Running et al. 1975; Roberts 1976; Waring and Running 1976, 1978). The subject of stem tissue water storage has been reviewed by Jarvis (1975), Hinckley et al. (1978) and Hinckley and Lassoie (1981).

Dimensional contractions are generally equivalent in magnitude to the amount of water lost to the transpiration stream (Jarvis 1975). Thus calculations of volumetric contractions along tree stems (both diurnal and seasonal) would provide estimates of the amount of water exchanged internally between extensible tissues and the conducting xylem. Such calculations indicate that the maximum amount of water stored seasonally in elastic stem tissues of a dominant Douglas-fir between breast height and midcrown is about 2.5 liters (Lassoie 1979). On a seasonal basis, this net amount of water seems insignificant considering the quantity that moves through the tree from the soil reserve (Jarvis 1975; Roberts 1976; Fritschen et al. 1977). Therefore such seasonal water losses are probably more important in that they indicate the gradual depletion of internal water reserves available for daily exchange (Lassoie 1979).

When similar calculations are made based on the maximum diurnal shrinkage and recovery noted during a summer period, it appears that a potential maximum of 1.8 liters of water is available per day (Lassoie 1979). It is presently unknown whether this water is lost daily through transpiration or merely exchanged between elastic and inelastic stem tissues. The value is relatively high considering the amount available seasonally and represents about 5 percent of the maximum total daily water loss from a large Douglas-fir (Fritschen and Doraiswamy 1973; Kline et al. 1976; Fritschen et al. 1977). Obviously the elastic stem tissues near the cambium between breast height and midcrown represent only a small part of the total living tissues capable of undergoing internal water exchange (Jarvis 1975). In addition, R. H. Waring (pers. comm.) has estimated that about 4 percent of the xylem in Douglas-fir stems constitutes living parenchyma cells that are capable of exchanging water with the transpiration stream but that do not contribute to stem dimensional fluctuations (Dobbs and Scott 1971). The impact of such storage in living tissues on net photosynthesis and growth may be significant if the stomatal mechanism is favorably affected but such a phenomenon has yet to be adequately considered.

The contribution of water from nonelastic, sapwood tissues to total tree-water balance has also been examined (Running et al. 1975; Waring and Running 1976, 1978). Initially a water-flux model was developed that included a sapwood compartment from which water was withdrawn daily to meet transpirational demand (Running et al. 1975). For an 80-m Douglas-fir, the model

predicted an average transpiration rate of 390 liters/day over a summer marked by seventeen days when water loss was reduced because of hydroactive stomatal closure. The maximum change in volume of water in the sapwood was estimated to represent more than a ten-day supply for transpiration. Whether this water was immediately available for transpiration was not verified, but work by Kline et al. (1976) has shown a daily water loss of 530 liters in a 76-m Douglas-fir, a value close to that of Running et al. (1975) when one considers that their lower average included low transpiration periods. The model indicated that a 2-m sapling lost an average of 4.3 liters of water per day during the summer with actual transpiration falling short of potential for 54 days. Because of its size, this tree had a relatively small sapwood water storage capacity.

In an examination of a 50- to 60-m, old-growth Douglas-fir stand, Waring and Running (1978) have reported that sapwood water represented a storage reservoir of about 268×10^3 liters/ha (26.8 mm) with 75 percent of this residing in the stemwood. The depletion of sapwood storage areas reached 1.25 to 1.70 mm/d on clear days following cloudy or rainy weather.

The internal redistribution of water discussed above is exemplified when foliar transpiration rates are compared with the rates of water movement through the stem (Lassoie et al. 1977c; Waring et al. 1980). Simplistically, they should be equal, but because of internal sources and sinks for water within the tree the relation is often more complex. Though Lassoie et al. (1977c) reported a good correlation between sap velocity at breast height and actual foliar transpiration, time lags often exist between these two phenomena (Waring et al. 1980). For example, during the morning, water loss from Douglas-fir foliage depleted internal reserves and sap velocities lagged behind transpiration (Lassoie et al. 1977c). In the late afternoon, or when evaporative demands otherwise decreased, the reverse was observed, indicating the recharge of those tissues dehydrated during the transpiration period. As tree-water deficits increased due to drying of soil and/or high rates of tree water loss these lags become exaggerated, suggesting a temporary lack of significant water uptake by the roots. The transpirational demand evidently was supplied by water stored in internal reservoirs (Swanson 1972).

Wintertime Activity

During the late fall and winter conifers are often considered to be dormant throughout the coniferous forest biome. This idea arises from the fact that net photosynthesis rates are often limited by light, temperature, water transport, or all three (Gentle 1963; Helms 1965; Salo 1974). Aboveground meristematic activity is negligible. However, recent modeling efforts indicate that Douglas-fir trees may accumulate more than 50 percent of their total annual assimilate between October and May (Chapter 3; Emmingham and Waring 1977). In support, gas exchange studies with Douglas-fir in the Pacific Northwest (Salo

1974; D: J. Salo, R. G. Amundson, and R. B. Walker, pers. comm.) and with eastern red cedar (*Juniperus virginiana*) in mid-Missouri (Lassoie et al. 1977a) have shown that appreciable net photosynthesis rates are possible during periods of the year other than the aboveground growing season. Furthermore, Bradbury and Malcolm (1978) have reported doubling of dry weights of Sitka spruce seedlings between late September and mid-April, an indication of appreciable photosynthetic activity.

Diurnal stem contractions during cold periods (Figure 6.17) are atypical compared with those occurring in the summer (Figure 6.14a) and primarily reflect the freeze/thaw cycle of the foliage (Turner and DeRoo 1974). When temperatures drop below -2°C , the sapwood water freezes (thereby disrupting the water conduction system; Hammel 1967), eventually promoting extremely low xylem pressure potentials, continuously closed stomata, and net respiration rates in the foliage (Figure 6.17). Often there is a reversal of the normal

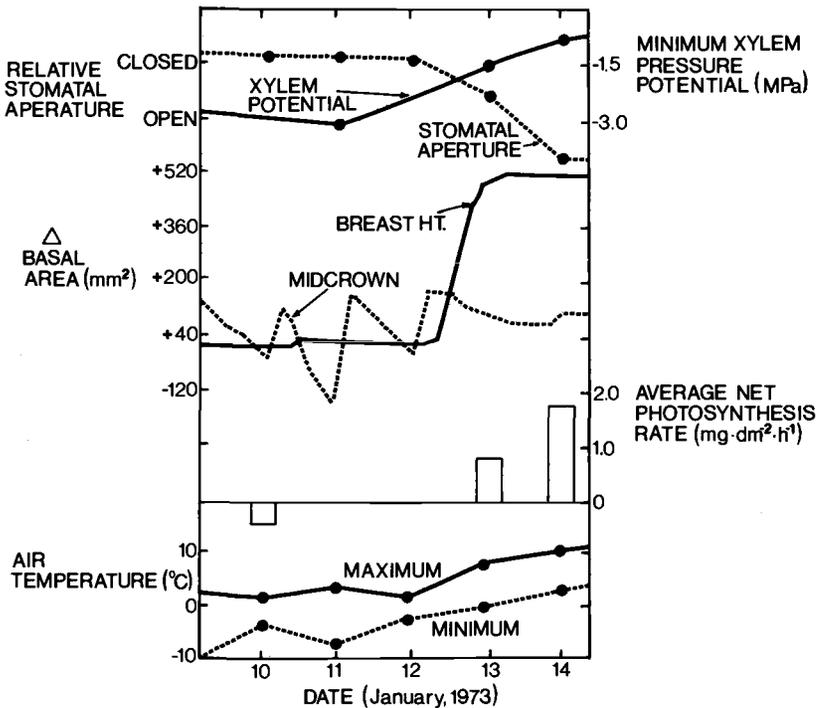


FIGURE 6.17 The diurnal progress of stem basal area, daylight average net photosynthesis rates, minimum daily xylem pressure potentials, and relative stomatal aperture openings (based on pressure infiltration measurements; Fry and Walker 1967) for a dominant Douglas-fir during a cold winter period. Maximum and minimum daily air temperatures are also shown (after Salo 1974; Lassoie 1975).

(summertime) pattern of tree-water deficits, with xylem pressure potentials actually increasing during the daylight period after a predawn minimum (Evans 1973; Salo 1974).

Following an increase in temperature and a thawing of the sapwood water, the hydraulic conducting system is re-established, internal tensions relax, and internal water levels increase. This causes an abrupt rehydration and expansion of tree stems, stomatal opening, and subsequent increases in net photosynthesis rates (Figure 6.17). Once again, light becomes a controlling factor, after having been superseded by hydroactive stomatal closure during freezing periods.

Potentially, conifers are physiologically active throughout most of the year. In addition, positive net photosynthesis rates during the winter may have a significant impact on Douglas-fir throughout the coniferous forest biome (Chapter 3; Helms 1964; Salo 1974; Emmingham and Waring 1977). This general subject has yet to be examined in detail, however, especially with respect to photosynthate translocation, storage, and subsequent utilization.

Within-Tree Spatial Variations

Forest trees, whether standing alone or as part of a community, are subject to a temporally fluctuating gradient of different environmental variables including temperature, light, wind, and relative humidity. Vertical gradients of environmental variables have been examined within Douglas-fir communities in relation to canopy carbon dioxide exchange and water vapor loss (Kinerson 1973, 1974; Kinerson and Fritschen 1973; Doraiswamy 1977). Such gradients in environment, in association with biological factors related to tree-tissue age, result in striking physiological heterogeneity within and between trees occupying a forest stand. A tree's three-dimensional nature further complicates the picture (Hinckley and Ritchie 1970; Woodman 1971b; Hinckley et al. 1978; Hinckley and Lassoie 1981). Thus point sampling within a tree canopy in order to characterize physiological activity is difficult since obvious microclimatic variations, differences in tissue age and morphology, internal redistribution of water, nutrients, and photosynthates, and differences in internal resistances to transport all contribute to considerable physiological variability (Richter 1973, 1974).

Height Above the Water Table

Under conditions of no flow (zero transpiration), the water potential at any point in a tree should merely be a function of the density of water, gravity, and the height above the water table (Richter 1973). Theoretically, a negative hydrostatic gradient, approximately equal to 0.01 MPa/m, should then exist

from the roots upward. Under conditions of transpirational flux, however, a more negative hydrostatic gradient (0.12 MPa/m in Douglas-fir; Tan et al. 1977) would be expected due to frictional shear forces between the xylem sap and the conduit walls as well as between the torus and the xylem sap in conifer pits (Richter 1973).

The hydrostatic water potential gradient combines with radiation attenuation through the canopy to cause variations in leaf conductance with height. On sunny days, Tan et al. (1977) found stomatal conductance to be highest at the top of a 7- to 9-m Douglas-fir canopy and lowest at the bottom, a trend also found in Sitka spruce (Beardsell et al. 1972; Watts et al. 1976); however, a number of factors may change the pattern. For example, on cloudy days, when diffuse light penetrates the lower canopy, differences in stomatal conductance between the upper and lower canopy are usually much reduced (Beardsell et al. 1972). In addition, Waring and Running (1978) have found that the hydrostatic gradient in a 80-m Douglas-fir may alone cause lower conductances than expected in the upper canopy. Osmotic potentials also change with tree height and season, which can affect stomatal reponse (Hellkvist et al. 1974).

Obviously, vertical gradients in light, water potential, and leaf conductance all potentially affect net photosynthesis. In 1975, D. J. Salo, R. L. Amundson, and R. B. Walker (pers. comm.) investigated spatial variability in net photosynthesis rates with respect to height in large Douglas-fir. Light response curves for net photosynthesis were generated under controlled greenhouse conditions using branches excised in the field from various heights. Results indicated that foliage obtained from the lower part of the canopy (15 m) had a 15 percent lower potential for assimilation than foliage from more sunlit locations in the upper canopy (at twenty-three meters). These data were used to generate simple predictive equations relating net photosynthesis to light intensity at various temperatures. The model was then used to estimate net photosynthesis rates at various canopy heights following field measurements of light and temperature. The estimate indicated that, under a wide variety of climatic conditions, total daily net photosynthesis decreases considerably at canopy levels below 21 m as do total daily light levels (Figure 6.18). Field measurements by Woodman (1968, 1971b), using a multiple cuvette system in a forty-nine-year-old, dominant Douglas-fir crown, support these findings. Kinerson (1973), using the aerodynamic approach to investigate the flux of water vapor and carbon dioxide through a forty-year-old Douglas-fir stand, concluded that leaf area and the attenuation of light were the chief factors controlling the variations in net photosynthesis with canopy height. Therefore it appears that differences between samples, especially with respect to branch water status, light, and leaf temperature, are probably more important in determining maximum assimilatory activity than merely height in the crown. As discussed later, however, foliage age can also be an important consideration when examining photosynthetic differences between branch samples.

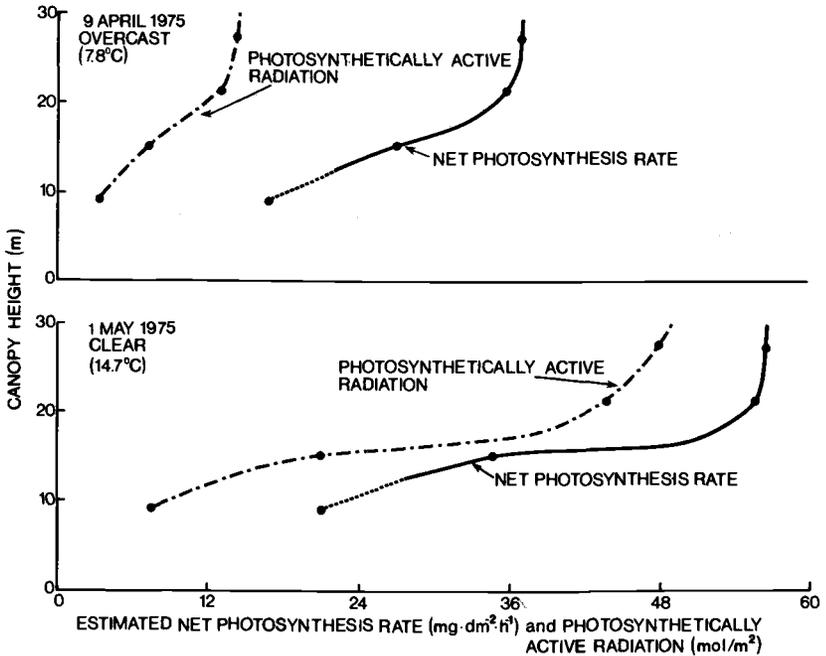


FIGURE 6.18 Daily totals for estimated net photosynthesis rates and measured photosynthetically active radiation at various heights in the crown of a dominant Douglas-fir on two spring days (overcast versus clear); average air temperature above the canopy is also shown for each day (after D. J. Salo, R. G. Amundson, and R. B. Walker, pers. comm.).

Crown Aspect

A conifer crown has differential radiation loads impinging upon it, which cause different microclimates and variations in physiological activity with aspect. This seems to be especially true with respect to leaf conductance (Hinckley et al. 1978; Leverenz and Jarvis 1979). Fetcher (1976) found that with large, field-grown lodgepole pine (*Pinus contorta*), sunlit needles had a mean conductance of water vapor of 0.24 cm/s while shade needles averaged 0.06 cm/s. In contrast, Hinckley and Ritchie (1970), working with Pacific silver fir, have reported more closed stomata (hence lower conductances) on southerly exposed needles compared with more shaded needles, presumably due to induced hydroactive closure arising from high transpiration rates. Though Douglas-fir has a different range of needle conductances (Running 1976), these data indicate the controlling importance of local microclimatic differences in determining the degree of stomatal opening (Leverenz 1981a).

Considerable variation in branch xylem pressure potentials is possible within the crowns of large Douglas-fir, because various plant and environmen-

tal factors combine to influence internal water supply and demand at particular locations (Hinckley et al. 1978). Variations one might expect in conifers are summarized in Table 6.4. In general, the greatest variation is associated with days marked by high evaporative demand and moderate soil water deficits. At lower soil water levels, hydroactive stomatal closure reduces water losses throughout the crown and variability in xylem pressure potentials decreases. Furthermore, the greatest variability can be expected to occur within the crown, as such measurements reflect both the variation due to differential radiation loads as well as hydrostatic pressure differences due to height.

When considering net photosynthesis rates in large Douglas-fir, light appears to be the primary factor controlling variability throughout the crown (Salo 1974). For example, Woodman (1971b) has reported that maxima in daily total net photosynthesis occur on the south side of a dominant Douglas-fir crown while minima occur on the north; the east and west sides have similar rates. When these findings are viewed with vertical variations in net photosynthesis rates, the crown can be divided into distinct, three-dimensional zones depending on the maximum daily mean net photosynthesis possible: Zone I is the highest (about $3.0 \text{ mg CO}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$) and is located near midcrown at the boundary between continuous sun and shade conditions; while zone III is the lowest (about $0.5 \text{ mg CO}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$) and is located at the very bottom of the crown. Zone II has maximum daily mean photosynthesis rates of about 1 to 3 $\text{mg CO}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$. It is located at the top of the crown under full sun conditions and in the bottom half of the crown between zones I and III.

Varying microclimates would also be expected to affect transpiration rates

TABLE 6.4 *Expected variation in xylem pressure potential within a branch, between sun- and shade-exposed branches, and within a conifer tree.^a*

Environmental conditions ^b		Location within conifer (\pm MPa) ^c		
Atmospheric evaporative demand	Soil water potential	Within branch	Sun vs. shade	Within tree
Very low	Very high	0.01	0.03	0.04
Low	High	0.04	0.06	0.07
Moderate	Low	0.06	0.11	0.16
High	High	0.06	0.11	0.16
High	Low-medium	0.10	0.19	0.27
High	Medium	0.14	0.20	0.31

^aFrom Hinckley et al. 1978.

^bAtmospheric evaporative demand ranges from less than 0.5 kPa to greater than 3.5 kPa while soil water potential ranges from greater than or equal to -0.03 MPa to less than -1.5 MPa.

^cData combined for various conifers under field conditions (Waring and Cleary 1967; Hinckley and Ritchie 1970; Hinckley and Scott 1971; Kotar 1972; Lassoie 1973).

from various portions of a Douglas-fir crown; the controlling factors are primarily those affecting the evaporative gradient between the leaf and the air. Differences in foliar water loss between eastern and western crown sections of a 15-m Pacific silver fir have been noted by Hinckley and Ritchie (1970). In addition, when soil moisture was relatively low, transpiration in Norway spruce (*Picea excelsa*) was found to be greater in the lower portion of the crown than in the upper (Pisek and Tranquillini 1951). When soil moisture was high, the trend was reversed. Similar results have been observed by Beardsell et al. (1972) in Sitka spruce. Furthermore, indirect evidence has been provided by the investigations of Lassoie et al. (1977c), who examined sap velocities in a twenty-year-old, dominant Douglas-fir stem. They found that the highest velocities occurred on the south side of the stem and the lowest on the north. An interrelation between stem aspect and time of day was observed, as the east side had the greatest rates in the morning and the west side had the greatest rates in the late afternoon. It is tempting to suggest that these data indicate the daily progression of differential radiation loads on the crown. This conclusion must be viewed carefully, however, as the sap-ascend pattern in Douglas-fir is actually much more complicated due to the anatomical complexity of the xylem system (Rudinsky and Vité 1959).

Conifers retain their needles for a number of years depending upon species, tree vigor, and environment (see Chapter 5); hence their crowns are composites of needles that differ morphologically and physiologically. Needles throughout a Douglas-fir crown are morphologically different depending on the light conditions occurring during their growth and development (Phillips 1967). In a forty-year-old dominant Douglas-fir, the largest needles are those growing in the full sun. Shade needles in the lower canopy are shorter, narrower, and thinner, and have a greater leaf surface area per unit dry weight than needles growing in the sun. A similar needle condition has been observed in one-year-old Douglas-fir seedlings grown under low light intensities (Drew and Ferrell 1977). Furthermore, the number of stomatal rows and the depth of the stomatal tubes increase with height in the crown but the number of stomata per unit length of a row does not. Stomatal densities per unit needle length (lower epidermis) are about 20,000 for sun and 16,000 for shade needles. The influence of these morphological characteristics on observed spatial differences in gas exchange rates and leaf conductances needs to be examined.

Shade-adapted foliage should be characterized by greater assimilatory efficiencies at relatively lower light levels than sun needles, which are in turn capable of utilizing high light intensities producing a much greater total quantity of photosynthate. Shade needles also have a lower light compensation point (net photosynthesis = 0) than sun needles (Larcher 1969). Leverenz (1974) has observed higher net photosynthesis rates in sun-adapted foliage than in needles growing elsewhere, but the difference seemed readily attributable to differences in leaf conductance, dry weight, and radiation intensity.

Leverenz (1974; 1981b) has also suggested that shoot hierarchy may influence net photosynthesis rates. He observed that net photosynthesis and transpiration rates in current-year terminal and lateral shoots had similar patterns of response, however, on warm and sunny days the absolute rates were generally lower in the laterals. Lateral shoots also had larger specific leaf ratios (that is, the area divided by oven-dry weight) than terminal shoots, a characteristic of shade-adapted Douglas-fir needles (Phillips 1967). Differences in gas exchange rates were not directly attributable to differences in microclimate, water status, or carbon dioxide concentration. Leverenz (1974) hypothesized that the controlling factor might involve differences in hormone concentrations. In partial support, Ross (1972) has found that current-year needles are a strong sink for photosynthates that export little carbon until the following year, thereby suggesting a degree of hormonal control. In addition, terminal shoots are a considerably stronger sink than are lateral shoots, based both on the amount of photosynthate exchanged and on actual growth rates. Terminal shoots typically elongate more than laterals and have higher dry weight to leaf area ratios (Leverenz 1981b).

There is a strong physiological relation between shoot growth and cambial activity along the stem owing to the regulatory influence of foliar-derived auxins and photosynthates (Pharis 1976). Since the physiological activity of the foliage varies throughout the crown, the distribution of cambial growth varies at different heights along the stem (Hinckley and Lassoie 1981). For example, the stem basal area increment added annually to a large Douglas-fir is greater at breast height than near midcrown (Lassoie 1975; see Figure 6.13). Though cambial activity, as exemplified by ring width, is generally greater at midcrown heights in large trees, greater basal area increments commonly occur at bole locations below the live crown (Heger 1965; Dobbs 1966; Hinckley and Lassoie 1981). This is primarily the result of the interaction between cambial growth rates and the size of the initial stem in determining the magnitude of basal area increments.

Studies by Dobbs (1966) have supplied a complete picture of the intra-seasonal development of longitudinal growth in field-grown Douglas-fir. He observed that ring width increased from the apex to a point in the crown in the vicinity of the most physiologically active foliage, below which ring width decreased (Figure 6.19). This longitudinal pattern is quite typical of coniferous trees in general (Duff and Nolan 1953; Walters and Soos 1962). Dobbs (1966), however, found the mass increment pattern to increase basipetally (Figure 6.19). Mass increment is the product of volume increment and annual ring density or specific gravity. Hence its distribution along a stem is an estimate of the longitudinal distribution of the metabolite consumption and is the result of the interrelation between patterns of photosynthate production, translocation, storage, and utilization. From such data, Dobbs concluded that the distribution of mass increment along the stem was not significantly influenced by patterns

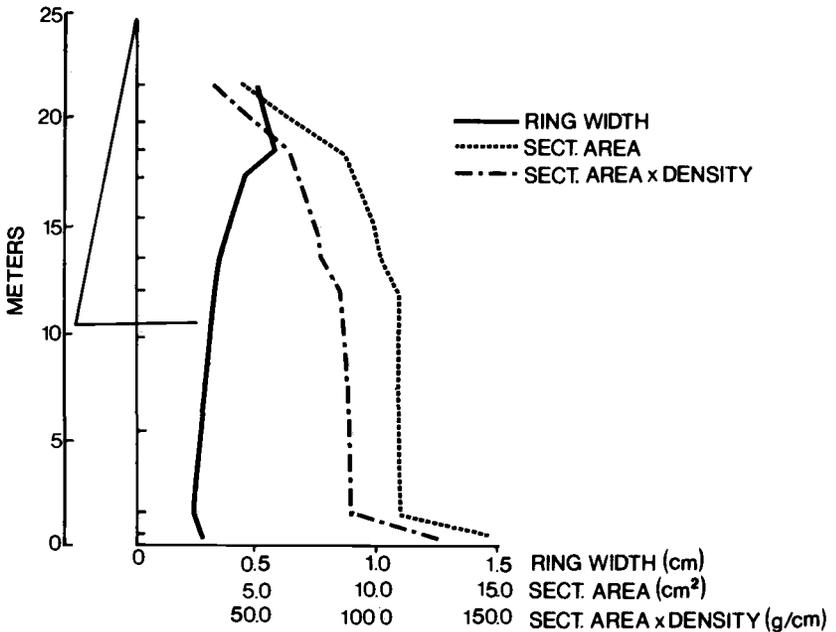


FIGURE 6.19 Longitudinal distribution of the current-year width, volume increment, and mass increment for a dominant Douglas-fir (after Dobbs 1966).

of carbohydrates export within the crown. The mass increment distribution is obviously affected by the longitudinal distribution of earlywood and latewood. In Douglas-fir, the maximum width of earlywood generally occurs a short distance from the apex while the maximum latewood occurs below this point, often on the lower bole (Heger 1965). Such patterns indicate the interaction between internal auxin levels and photosynthate production (Kozlowski 1971b).

Tissue Age

Douglas-fir in the humid transition zone usually retain their needles for five to seven years depending on the site and on tree vigor (see Chapter 5). Since the physiological activity of these needles progressively changes as they age, total branch net photosynthesis becomes a component of varying assimilatory rates that depend on needle age as well as local microclimatic factors. Work by Salo (1974), however, suggests that net photosynthesis rates are not affected until the needles are three years old. For example, it appears that the portion of each age class (current-year, one-, and two-years-old) contributing to total branch net photosynthesis closely approximates the fraction contributed to the total branch leaf area (D. J. Salo, pers. comm.). In support, R. G.

Amundson, R. B. Walker, and D. J. Salo (pers. comm.), using excised branches under controlled environmental conditions, have observed that the photosynthetic capacities of second- and third-year needles were, respectively, only 5 percent and 25 percent lower than fully expanded first-year needles. These data are in contrast to those reported for Douglas-fir by other investigators (Woodman 1968; Brix and Ebell 1969; Brix 1971). All these authors noted appreciable decreases in net photosynthesis rates with increasing foliage age (for example, about a 22 percent decrease in maximum net photosynthesis per year of needle age for at least four years).

The impact of foliage age also affects the fate of carbon once it is fixed and involves the relative source-sink strengths of various tree tissues. Ross (1972) has examined the internal dynamics of carbon-14 photoassimilated by different age classes of needles. His results indicated that the relative magnitudes of net photosynthesis measured in foliage of different ages cannot be used as a reliable index for the amount of photosynthate available for growth elsewhere in the tree. The proportion of photosynthate exported from needles was found to be a function of age, with one-year-old needles exporting more than two-year-old needles. Rapidly elongating new needles were observed to be the strongest photosynthetic sinks even after the completion of growth extension, and they exported very little to the rest of the tree compared with older needles. Thus their contribution to stem and branch growth was relatively small. Preferential transport between the sources and sinks depended on the distances and the relative growth rates involved. Both primary and secondary one-year-old needles preferentially translocated photosynthates toward new shoots (acropetally) while two-year-old needles exported more to the stem (basipetally). An exception occurred during periods of active shoot elongation, when two-year-old needles also translocated the bulk of their photosynthates acropetally. It seemed that only the older, less productive, two-year-old needles near the branch base made any significant photosynthate contribution to the stem during its period of rapid diameter growth. Little photosynthate was available from older needles until branch extension growth was near completion. Thus Ross suggested that stored photosynthates possibly play a more important role in cambial growth in Douglas-fir than has been previously recognized.

Age-related effects on net photosynthesis rates seem to be closely tied to the progressive loss of stomatal reactivity to light, which occurs as a leaf ages (Turner 1974). A variety of suggestions have been proposed for this loss of reactivity but the exact causative agent or agents have yet to be clearly identified (Hinckley et al. 1978).

Conductances in western white pine (*Pinus monticola*) needles appear to increase during the first year following emergence (Cline and Campbell 1976). Waggoner and Turner (1971) cited maximum daily leaf conductances for red pine (*Pinus resinosa*) of 0.091, 0.059, 0.045, 0.043, and 0.036 cm/s for newly emerged to four-year-old needles. With Sitka spruce, Watts et al. (1976) reported that recently emerged needles had lower conductances than one-year-

old needles, but following complete shoot expansion conductances were similar in both age classes. Contrary to these findings, Running (1976) has detected no differences in leaf conductances of current to three-year-old ponderosa pine (*Pinus ponderosa*) needles. In Douglas-fir saplings he observed a complex relationship between conductance, needle age, and the local environment. Maximum conductances were often higher in older foliage than in current-year foliage but daily averages were usually comparable for all age classes. On a mild day, however, when hydroactive stomatal closure did not occur, average daily leaf conductances were 0.078, 0.066, 0.051, and 0.041 cm/s for current-year to four-year-old foliage. From these and other data, Running suggests that atmospheric humidity has a differential impact depending on needle age while midday xylem pressure potential affects all needle ages equally. Such data might help explain the variable effects that different needle ages seem to have on net photosynthesis in Douglas-fir compared with other species.

SUMMARY

The coastal variety of Douglas-fir (var. *menziesii*) is well adapted physiologically to the mesic, maritime climate (that is, relatively wet, warm winters and dry summers) that characterizes the coniferous forest biome. Douglas-fir abounds throughout the biome, surviving on a variety of sites, living for centuries; and accumulating a tremendous amount of biomass (see Chapter 5). Its longevity is no doubt genetically based but also reflects the relatively low occurrence of major windstorms within the biome (Waring and Franklin 1979).

Douglas-fir is considered intermediate with respect to shade tolerance but is a hearty pioneer species thriving in openings created by glaciation, fires, and logging operations (Fowells 1965). General physiological responses in Douglas-fir to certain environmental factors are not extremely different from those exhibited by other western conifers or even by deciduous trees in other biomes. Net photosynthesis is controlled by such limiting factors as temperature, light, carbon dioxide, and water, which are often mediated through their influence on the stomatal mechanism. In addition, stomatal activity is regulated by the vapor pressure gradient between the leaf and the air and probably by the hormone abscisic acid. These specific responses in combination give Douglas-fir a unique set of physiological characteristics that accounts for its ecological success.

Douglas-fir stomata open very rapidly with increasing light levels and typically reach their maximum aperture at less than 10 percent of full sunlight. Furthermore, the photosynthetic process light-saturates near 25 percent of full sunlight and exhibits a broad temperature optimum between about 2° and 25°C. Therefore, high net photosynthesis rates can occur in Douglas-fir during springs typically marked by relatively cool, overcast climatic conditions. Such relatively high rates occur during the time when photosynthates are needed for

the production of new foliage and assure large photosynthetic areas in the future.

Summers in the coniferous forest biome are characterized by limited amounts of water (Waring and Franklin 1979). Throughout much of July, August, and early September precipitation is infrequent and soil moisture levels rapidly decrease while atmospheric evaporative demands remain high. Douglas-fir stomata respond to such conditions and reduce excessive water loss via hydroactive closure. A number of interrelated reactions seem to be involved.

First, maximum stomatal opening during the day is closely regulated by the amount of water in the rhizosphere such that maximum daily needle conductances decrease with decreasing base (predawn) xylem pressure potentials. Second, a threshold xylem pressure potential initiates stomatal closure during the day. This threshold varies between different species and also seems to depend on tree size. For example, Douglas-fir seedlings initiate closure at higher xylem pressure potentials (-1.7 MPa) than saplings (-2.0 MPa) or very large, old-growth trees (-2.2 MPa). These differences may reflect variations in the extent of root development (hence the ability to utilize larger and deeper soil masses), osmotic potential differences, and/or differences in evaporative severities within the respective crowns. In addition, the hydrostatic gradient (0.01 MPa per meter of height) alone can regulate the extent of stomatal opening in very large trees, thereby possibly placing some limit on maximum tree height and water loss from tall, exposed crowns. Third, if threshold water deficits are not reached, needle conductances can be controlled by the atmospheric evaporative demand occurring at the leaf-air interface. Thus high vapor pressure gradients (which include the influence of leaf temperature) can override either base or threshold xylem pressure potentials and the photoactive stomatal response, in order to promote closure or limit aperture size. Therefore Douglas-fir stomata seem capable of fine-tuning their activity to atmospheric conditions, thereby preventing excessive rates of water loss during those times when soil and internal water levels might otherwise promote stomatal opening. Such conditions in the coniferous forest biome would probably exist during the late spring or early summer before a major amount of soil drying had occurred.

It seems definite that low soil moisture levels and high evaporative demands promote hydroactive stomatal closure and reduced carbon dioxide uptake throughout much of the summer in Douglas-fir (see Chapter 3). This species, however, as well as other conifers within the coniferous forest biome and elsewhere, is capable of active net photosynthesis during those periods of the year when its meristems are dormant. Specifically, Douglas-fir can fix a major amount of carbon between October and May owing to its active assimilation at temperatures near freezing and the fact that wintertime environmental conditions are relatively mild throughout the coniferous forest biome (Waring and Franklin 1979).

Douglas-fir needles may be held for five or more years and seem to be a photosynthetic asset for at least three years. During their first year, however, most of their photosynthates go directly into their own growth and development. Once the needles are fully developed, photosynthates are then supplied to other growth centers (for example, buds, cambial and apical meristems, and fruits) and to storage areas, which are utilized at a later date. A large foliar area (that is, small root-to-shoot ratio) can be a liability when water becomes limiting, as it represents the major site for tree water loss. Thus an important tradeoff is necessary between maximizing photosynthate production and maintaining an adequate internal water balance. Such a tradeoff also involves root production and maintenance but these important aspects of tree-water relations were not directly addressed in this chapter.

There are also other features associated with holding multiple age classes of needles that are important to a tree's water balance. Not only are old needles less efficient at fixing carbon dioxide, they also lose relatively less water because of the reduced photoactivity of their stomata. Thus needles progressively become less of a liability as they age. Furthermore, a large amount of foliar biomass promotes selfshading in and between separate branches throughout the crown. This lowers needle temperatures, which in turn reduces vapor pressure gradients and water loss rates. Even though shaded, the needles probably maintain open stomata and high net photosynthesis rates owing to the relatively low light requirements necessary for these processes.

While maintaining a large amount of foliage, Douglas-fir similarly amasses a great quantity of conducting tissue, as the two seem to be hydraulically interrelated. Undoubtedly, the amount of root surface area maintained is similarly interrelated in order to supply the transpiring surfaces adequately. The living tissues and the conducting sapwood in large trees act as internal reservoirs for water and probably nutrients and carbohydrates. Such internal storage of water could be critical to large trees if this source is used to retard hydroactive stomatal closure and to allow for more carbon dioxide uptake than would be possible based only on water supplied by the soil.

Though a qualitative picture of the control of net photosynthesis and tree growth has yielded an understanding of the distribution and abundance of Douglas-fir within the coniferous forest biome, there remain areas of uncertainty and voids in our quantitative understanding of certain physiological processes. Additional effort is needed before a precise interpretation of the abiotic and biotic control of the stomatal mechanism emerges. This is especially true concerning the possibility of synergistic interactions between such factors as vapor pressure gradient, water, temperature, carbon dioxide, and endogenous abscisic acid. The photosynthate translocation process and the biochemical conversion to specific biomass constituents remains vague. This is especially true concerning the carbon dioxide fixed during the growth dormancy period. The intriguing question of storage during this period and mobilization and utilization at a later time needs quantification. In addition, the impact of internal water storage and the possibility of concurrent nutrient

storage in portions of large tree stems needs to be tied more closely to stomatal activity, photosynthesis, and tree growth. Furthermore, the water storage phenomenon associated with living tissues near, and including, the cambial zone needs to be more closely related to cambial meristematic activity (both division and elongation), diurnal and seasonal contractions in size, and translocation processes in the phloem (Hinckley et al. 1978). Finally, though not directly addressed in this chapter, there is a need to incorporate root physiological activity into the aboveground phenomena discussed herein.

Faced with the temporal and spatial complexities and variabilities typical of tree physiological processes under field conditions, it is not surprising that many areas remain vague even after years of intense investigation. Such unknowns encourage continued and refined research activities. The research accomplished within the coniferous forest biome under the auspices of the International Biological Program has sharpened our understanding of many physiological processes and has revealed specific voids in our understanding. Perhaps a major value of such studies is not so much what was discovered but what was not. Such identification is, and will remain, the basis on which scientific discipline evolve in order to continually address questions of increasing complexity and importance, thereby enhancing our understanding and appreciation of the ecosystems of the world.

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