

WATER RELATIONS OF INTERIOR DOUGLAS-FIR

W. Lopushinsky

ABSTRACT

Water relations of interior Douglas-fir are important because plant water status greatly affects physiological processes controlling growth and survival. Data on water relations, based mainly on studies with seedlings, show that interior Douglas-fir has the following characteristics: (1) moderate rate of transpiration, similar to that for ponderosa pine and less than that for lodgepole pine, (2) smaller decrease in transpiration in response to a moderate soil moisture stress than that for ponderosa and lodgepole pine, (3) relatively low leaf water potential threshold for stomatal closure, -1.9 MPa for Douglas-fir compared to -1.6 MPa for ponderosa pine and -1.4 MPa for lodgepole pine, (4) incomplete closure of stomata at night; nighttime transpiration rate in seedlings was 26% of daytime rates, (5) relatively small sapwood water storage capacity, and (6) moderate drought resistance, less than that of ponderosa pine. Transpiration rate of seedlings with roots in cold soil (1.3°C) was 18.8% of the rate at 20°C, xylem pressure potential decreased to -2.0 MPa, and stomatal conductance was reduced 50% or more. In large field-grown trees, seasonal and diurnal transpiration behavior in Douglas-fir was similar to that for ponderosa pine.

INTRODUCTION

Water relations of interior Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco) are important because plant water status strongly affects most of the physiological processes that directly control growth and survival. The growth of interior Douglas-fir probably is reduced more often by water deficits than by any other factor. Moderate water deficits can result in stomatal closure, and reduced photosynthesis. More severe deficits can damage the photosynthetic apparatus, affect respiratory and translocation processes, disrupt carbohydrate and protein metabolism, damage membrane structures, and cause changes in enzyme activity. Water deficits often increase susceptibility to attacks by pathogens and insects, and in the arid west, desiccation, as a result of inadequate soil moisture, is a major cause of mortality in seedlings. Thus, the occurrence and distribution of interior Douglas-fir depends, to a large degree, on its ability to maintain favorable water relations. Consequently, information on the water relations of Douglas-fir, particularly its response to water deficits and its water use behavior, is helpful in understanding its growth responses to environmental factors, and its ecological and hydrological relationships compared to other species with which it is commonly associated.

Relatively little information is available specifically on the water relations of interior Douglas-fir compared to that available for coastal Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco), and other species such as lodgepole pine (*Pinus contorta* Dougl. ex. Loud.). Much of the information that is available for interior Douglas-fir has been obtained in studies with seedlings. Such results may not reflect the actual behavior of large forest trees, but they are valuable in pointing out differences between species during the seedling stage. The survival of seedlings often is the most critical stage in the development of a stand, since it is at this stage that the trees are most vulnerable to environmental stresses.

The water relations of interior Douglas-fir are most interesting when they are compared with other species, and that approach will be followed in this paper. The objective of this paper is to summarize several aspects of the water relations of interior Douglas-fir, including transpiration, internal water storage, water absorption, stomatal behavior, internal water stress, and drought resistance. Data shown in tables and figures in this paper are for interior Douglas-fir unless otherwise indicated. Where information is lacking for interior Douglas-fir, data for coastal Douglas-fir is included to provide general water relations parameters for the species. Additional information on the water relations of coastal Douglas-fir is available in several theses and dissertations (Fry 1965; Phillips 1967; Reed 1968; Daniels 1978; Menzies 1980; Meinzer 1981).

TRANSPIRATION

Few data are available for water use by individual trees, but Black *et al.* (1980) reported that with adequate soil moisture, the transpiration rate of 22-year-old coastal Douglas-fir trees in a thinned stand in July was 23.6 L·tree⁻¹·day⁻¹. Fritschen *et al.* (1977) found that average evapotranspiration during the summer and fall by a 28-m coastal Douglas-fir in the weighing lysimeter near Seattle, Washington, was 55.8 L or 14.7 gallons·day⁻¹. Kline *et al.* (1976), using tritiated water as a tracer for water movement in individual trees of coastal Douglas-fir, reported that transpiration rates ranged from 8.4 L·day⁻¹ in a small tree to 530 L·day⁻¹ in a large old-growth tree.

Some of the earliest data on transpiration of interior Douglas-fir seedlings are those of Bates (1923) and Roeser (1932). Bates (1923) reported that the transpiration rate of Douglas-fir seedlings, per unit of leaf area, was less than that of lodgepole pine and ponderosa pine. Roeser (1932) also found that the transpiration rate of Douglas-fir seedlings, per unit of seedling dry weight, was less than that for lodgepole pine, and it was slightly less or equal to that for ponderosa pine. Direct comparison of results is difficult in these early studies because of differences in experimental conditions, ages of seedlings, and methods of expressing water loss. In tests conducted under controlled conditions with 3-year-old seedlings (Lopushinsky 1981), Douglas-fir had a moderate rate of transpiration, similar to that for

ponderosa pine and less than that for lodgepole pine, grand fir (*Abies grandis* (Dougl. ex. D. Don) Lindl.), and white fir (*Abies concolor* (Gord. and Glend.) Lindl. ex. Hidrbr.) (Table 1).

Table 1. — Transpiration rates¹ of western conifer seedlings (Lopushinsky 1981).

Species	Water Loss (mg/g dry wgt needles/h)
Lodgepole pine	610
Grand fir	542
White fir	427
Douglas-fir	393
Ponderosa pine	364
Engelmann spruce	263

¹Transpiration was determined by weighing potted 3-year-old seedlings. Soil was at field capacity, and seedlings were kept in a growth chamber at 20°C, humidity 60% and radiation 0.2 ly/min.

In the interior west, lack of soil moisture is a major factor which often limits transpiration in conifers. Lopushinsky and Klock (1974), in an experiment with 4-year-old potted seedlings, found that the transpiration rate of Douglas-fir and grand fir seedlings was reduced to a lesser extent, in response to decreasing soil water potential, than was transpiration in ponderosa pine and lodgepole pine (Table 2). At a soil water potential of -1.0 MPa, the transpiration rate of Douglas-fir seedlings was 37% of their maximum rate (at zero water potential), similar to that for grand fir, while rates for the pines and Engelmann spruce (*Picea engelmannii* Parry), were 12-13% and 21% respectively. At -2.0 MPa, the transpiration rate of Douglas-fir still was 18% of maximum, while rates for the pines and spruce were only 2 to 5% of maximum. The relatively high transpiration rate in Douglas-fir and grand fir compared with the pines probably reflects the ability of the firs to maintain open stomata at lower leaf water potentials than the pines (Lopushinsky 1969). Also, the seed source of seedlings can affect the transpiration rate (Table 3). Douglas-fir seedlings from a xeric seed source exhibited a lower transpiration rate at all levels of soil moisture stress than seedlings from a mesic source. At a soil water potential of -1.5 MPa, the transpiration rate of seedlings from the xeric source was reduced to 2.7% of the rate for well watered conditions, while the rate for seedlings from a mesic source was only reduced to 7.6%.

Table 2. — Reduction in transpiration of five conifer species with respect to decreased soil water potential (Lopushinsky and Klock 1974).

Species	Transpiration (% of maximum)		
	-0.5 MPa	-1.0 MPa	-2.0 MPa
Ponderosa pine	36	12	2
Lodgepole pine	48	13	2
Engelmann spruce	51	21	5
Douglas-fir	59	37	18
Grand fir	63	37	17

Table 3. — Comparison of transpiration rates of Douglas-fir seedlings from mesic (Stevens Pass, WA) and xeric (eastern Oregon) environments at various soil moisture stresses (Zavitkovski and Ferrell 1970).

Soil Water Potential (MPa)	Transpiration Rate (g/g dry needles/day)	
	mesic	xeric
< -0.01	23.7	18.7
-0.01	10.5	6.4
-0.20	4.4	2.3
-1.50	1.8	0.5

Seasonal and diurnal trends of transpiration in 55-year-old Douglas-fir and ponderosa pine were monitored by Lopushinsky (1986) using the heat pulse method to estimate rates of sap flow in tree trunks. Heat pulse velocity (HPV) in both fir and pine increased rapidly in April, reached maximum levels during June and July, and then decreased as soil moisture levels declined during late summer and fall (Figure 1). During spring and early summer, variations in rates of HPV of both the fir and pine were directly related to changes in solar radiation, air temperature and vapor pressure deficit. During the summer and fall, however, increases in temperature and vapor pressure deficit had little effect on HPV because of increasing stomatal control of transpiration as soil moisture declined. Sap flow rates then exhibited a relatively nonfluctuating decline similar to transpiration declines observed in water-stressed conifer seedlings (Lopushinsky 1969). A similar lack of correlation between transpiration and environmental factors during dry periods has been reported for coastal Douglas-fir by Hinckley and Scott (1971) and Lassoie *et al.* (1977). If rainfall during this period increased soil moisture, as in August 1975, then HPV again increased in response to increases in air temperature and vapor pressure deficit. Transpiration responses to rainfall usually were

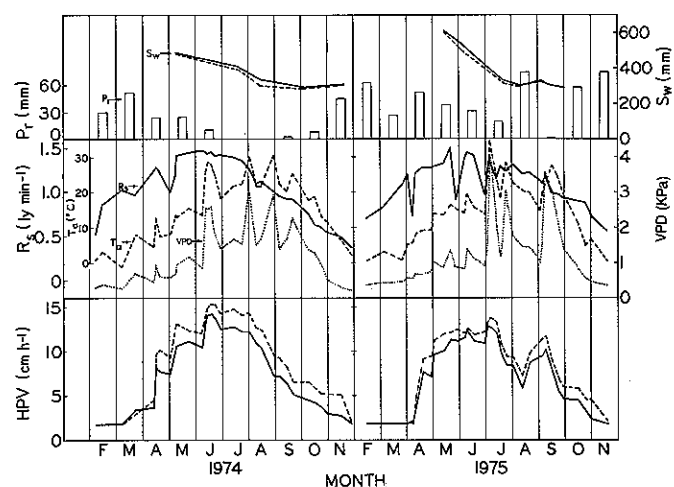


Figure 1. — Seasonal variation in heat pulse velocity (HPV) and environmental factors including solar radiation (R_s), air temperature (T_a), vapor pressure deficit (VPD), monthly precipitation (P_r), and total water content (S_w) in the soil profile for Douglas-fir (○) and ponderosa pine (◊). Measurements were made between 1100 and 1300 Pacific standard time on cloud-free days, or on days with few clouds (Lopushinsky 1986).

greater in Douglas-fir than in ponderosa pine, probably because of the shallower, more finely divided root system of Douglas-fir. Seasonal rates of HPV generally were higher in Douglas-fir than in the pine, suggesting a higher sap flux in the fir, but the difference could simply be the result of a smaller sapwood area for water conduction in the fir. Consequently, equal volumetric water transport in the two species would be expected to result in higher HPV in the fir. In addition, Douglas-fir is known to have a larger foliage mass per unit of sapwood than ponderosa pine (Grier and Waring 1974). Diurnal patterns of transpiration also changed as soil moisture declined. As summer progressed, daytime levels of sap velocity for both Douglas-fir and ponderosa pine decreased, and sap flow began later in the day and stopped sooner (Figure 2). In June and July, maximum sap flow occurred near midday, while in late summer and fall, maximum sap flow occurred earlier in the day, followed by a gradual decline the remainder of the day. Also, sap movement observed during early morning and late evening in June and July did not occur in August and September.

is evidence that the effect of vapor pressure deficit on transpiration is not constant during the summer, but varies with soil water stress. For example, Tan *et al.* (1977) found that as the soil dries, stomatal resistance in coastal Douglas-fir rises more quickly in response to increasing vapor pressure deficit.

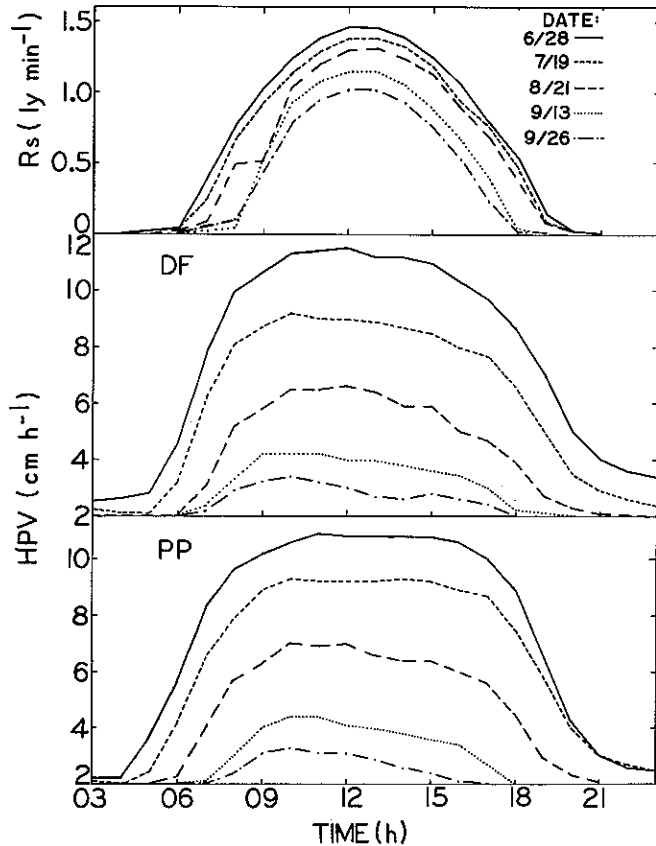


Figure 2. — Seasonal variation in diurnal trends of heat pulse velocity (HPV) in Douglas-fir (DF) and ponderosa pine (PP), and solar radiation (Rs) during clear days in the summer and fall (Lopushinsky 1986).

Heat pulse velocities exhibited generally similar curvilinear relationships with solar radiation, air temperature and vapor pressure deficit (Figure 3). The relatively large increases in sap flow associated with small increases in vapor pressure deficit indicate that vapor pressure deficit had a larger effect on transpiration than did air temperature or solar radiation. There

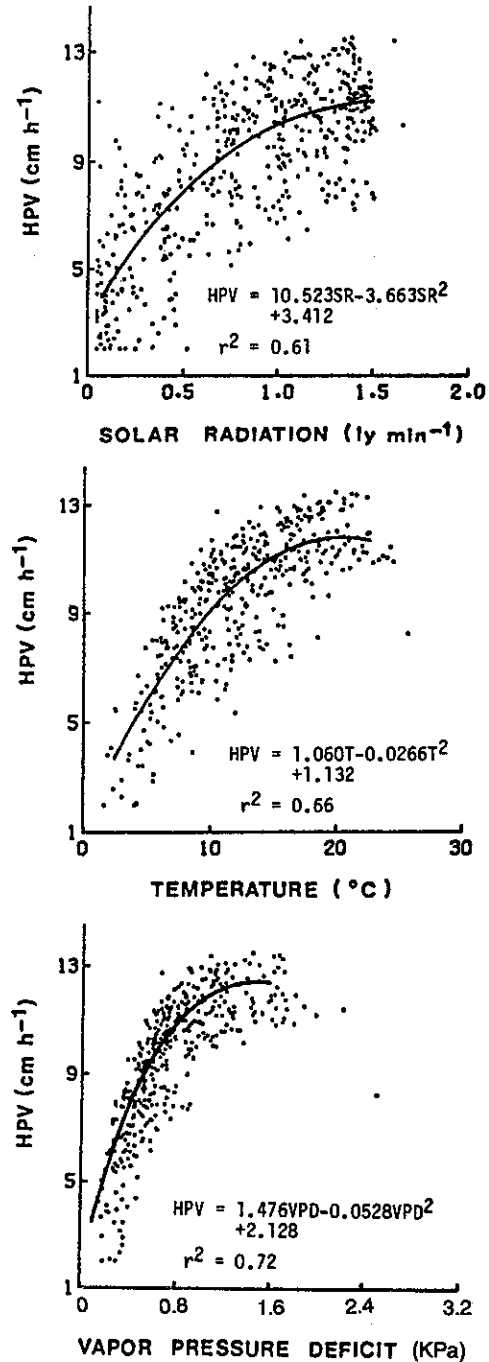


Figure 3. — Relationship of HPV to solar radiation (Rs), air temperature (Ta), and vapor pressure deficit (VPD) in Douglas-fir. Data points are based on measurements taken hourly (dawn to 1300) during days without precipitation from April to July, when HPV was not limited by low soil moisture (Lopushinsky 1986).

The similarity of seasonal and diurnal trends of sap flow, and sap flow responses to variation in climatic factors and soil moisture for Douglas-fir and ponderosa pine, suggest that the

transpiration behavior of large field-grown Douglas-fir and ponderosa pine trees generally is similar. This contrasts with results found for potted seedlings (Table 2), however, transpiration responses of large field-grown trees is more complex in that their transpiration reflects the influence of unrestricted root systems and significant sapwood water storage capacities, factors not found in potted seedlings. Such disparities emphasize the need for caution when attempting to extrapolate results obtained with seedlings to large field-grown trees.

INTERNAL WATER STORAGE

The sapwood of trees contains considerable amounts of water which can act as a reservoir for transpiration. In a study with field-grown Douglas-fir and ponderosa pine, Lopushinsky (1986) found that appreciable sap movement occurred at night during periods when daytime transpiration was high (Figure 4), suggesting that the nighttime sap movement was largely a result of stem recharge. No nighttime sap movement was observed

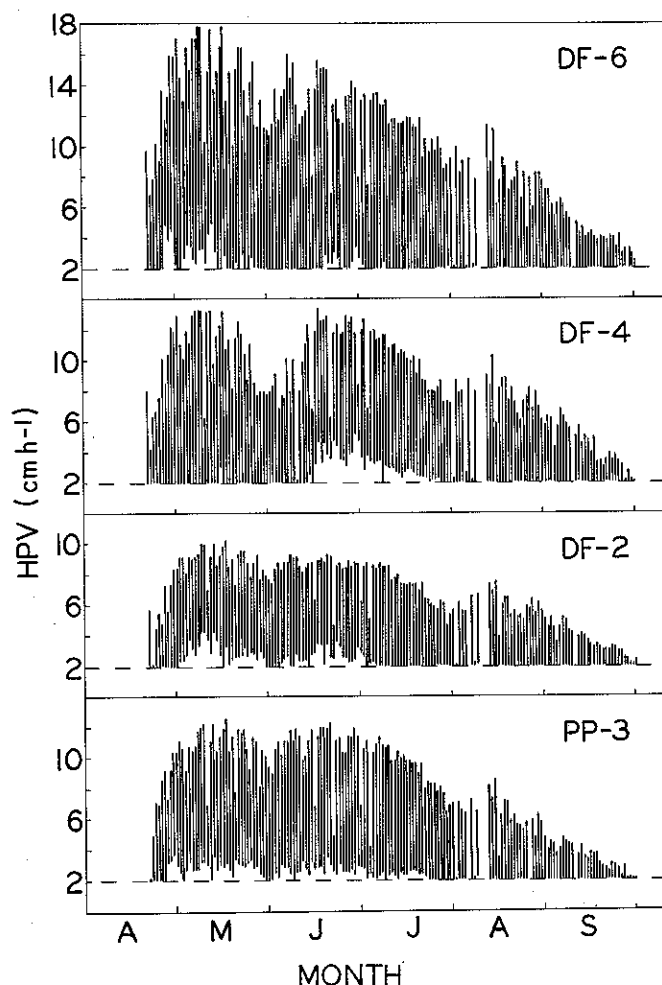


Figure 4. — Seasonal trend of nighttime and midday HPV values in individual Douglas-fir (DF) and ponderosa pine (PP) trees. Vertical lines connect values at 0300 and 1300 each day (Lopushinsky 1986).

during late summer or fall. While not significant in the case of seedlings, sapwood water storage in large trees may provide

an appreciable fraction of the water lost by transpiration, but estimates vary widely. Waring and Running (1978) estimated that $270 \text{ m}^3 \text{ ha}^{-1}$ of water could be stored in a stand of 50- to 60-m-tall old-growth coastal Douglas-fir, equivalent to 16 days' transpiration. Seventy-five percent of the storage was in the sapwood. By contrast, Nnyamah and Black (1977) estimated that water withdrawal from trunk storage in a 20-year-old stand of coastal Douglas-fir accounted for only 2% of total evapotranspiration during a four-week period, or 12 hours of transpiration at a rate of 27 liters day^{-1} . In lodgepole pine, water from internal storage was calculated to be capable of providing only 0.6 h of maximum transpiration, or 4.7 h of minimum transpiration (Running 1980). The contribution of needle water storage in these estimates is small, 0.1% in old-growth coastal Douglas-fir, and 4% in lodgepole pine. Although the contribution of leaf water to total tree storage is minor in mature trees, leaf water storage is important because leaf water content determines leaf water potential which greatly affects stomatal conductance and thereby transpiration. Thus, an important function of stem water storage may be to act as a temporary diurnal reservoir for refilling leaf storage. Sapwood water content can also affect water conductivity in the xylem. Waring and Running (1978) found that as sapwood water content in coastal Douglas-fir falls throughout the season, water conductivity also decreases. Edwards and Jarvis (1982) reported that a reduction of relative water content from 100% to 90% in stem sections of lodgepole pine caused permeability to water to fall to 10% of the saturated value.

While similar data on sapwood water storage are lacking for interior Douglas-fir, it is known that interior Douglas-fir has a relatively small amount of sapwood compared with other species in the interior west (Lassen and Okkonen 1969) (Figure 5). Lopushinsky (1986) found that when water-conducting pathways in stem segments of Douglas-fir and ponderosa pine were delineated with acid fuchsin dye solutions, sapwood in Douglas-fir occupied only 51% of the cross-sectional area compared with 88% in ponderosa pine. Parker (1954), who followed seasonal trends in trunk water content in Douglas-fir and ponderosa pine in Idaho, found that sapwood water content increased during the fall and winter following rainfall, and decreased gradually during spring and summer months. Douglas-fir contained little water in heartwood, compared to ponderosa pine which contained almost equal amounts of water in heartwood and sapwood. This would appear to confer a water storage advantage to ponderosa pine which might partially explain its relatively high drought resistance, but variation in stem water storage cannot wholly explain differences in drought resistance. Lassen and Okkonen (1969), for example, found for trees of equal inside bark diameter, that coastal Douglas-fir had a greater sapwood thickness than interior Douglas-fir, although the coastal form is known to be less drought resistant (Pharis and Ferrell 1966; Ferrell and Woodard 1966). The reason for the larger volume of sapwood in the coastal type is that it generally grows more rapidly than interior Douglas-fir, and rapidly growing trees have the widest sapwood bands. In any case, the relatively small volume of sapwood in interior Douglas-fir suggests that internal water storage plays less of a role in its water relations compared to a species like ponderosa pine with a large sapwood volume.

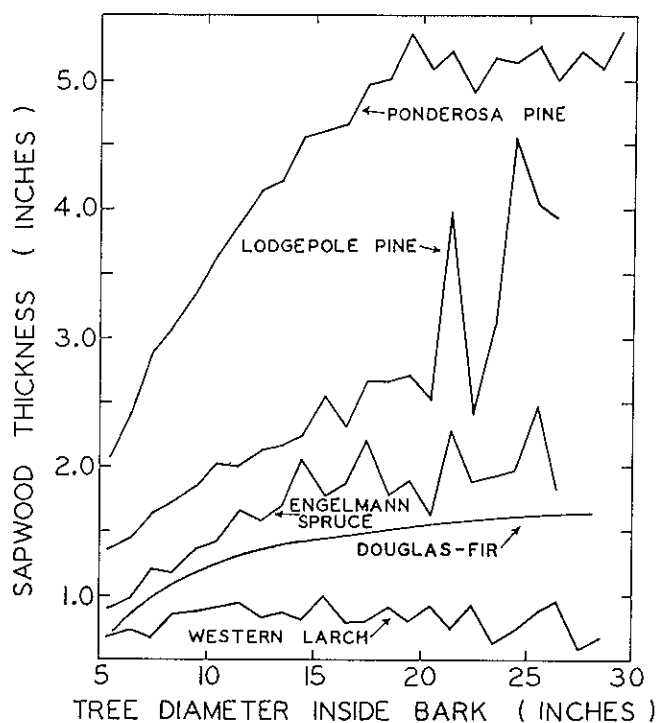


Figure 5.—Relationship of sapwood thickness to tree diameter in western conifers (Lassen and Okkonen 1969; the curve for interior Douglas-fir is redrawn from Figure 1 of Lassen and Okkonen 1969).

Another way in which the amount of sapwood influences the water relations of a tree is through its relationship to the amount of transpiring crown. There is a strong correlation between the amount of leaf area of an individual tree and the cross-sectional area of conducting sapwood, the so-called "pipe model" theory (Shinozaki *et al.* 1964; Waring *et al.* 1982). "Pipe model" theory suggests that for a given species there is an optimal amount of leaf area that can be supported by the water conducting column. The exact relationship varies with species. For coastal Douglas-fir, the ratio of leaf area to sapwood cross-sectional area is 0.54, compared with 0.25 for ponderosa pine, and 0.16 for lodgepole pine (Waring *et al.* 1982).

Water Absorption

Soil drought and low soil temperature probably are the two major factors limiting water absorption by interior Douglas-fir and other inland conifers. Lopushinsky and Klock (1974), in a study with interior Douglas-fir seedlings, found that transpiration began to decline at a soil water potential of -0.1 to -0.2 MPa, indicating that reduction of water absorption began at a relatively high water potential. Ballard and Dosskey (1985) working with coastal Douglas-fir seedlings, found that the water uptake rate declined sharply with decreasing soil water potential and dropped to zero when soil water potential reached -3.0 MPa. Water uptake by trees in a forest stand is more complex because of unrestricted rooting. Nnyamah and Black (1977) found a gradual downward shift of the soil zone of maximum root water uptake by a stand of coastal Douglas-fir as the soil dried.

Low soil temperature also can severely limit water uptake in Douglas-fir. At low soil temperatures, the viscosity of water

increases, and the permeability of root cell membranes decreases (Kramer 1940). Lopushinsky (1978) found that the rate of water movement through detopped root systems of Douglas-fir seedlings at 0.2°C under a pressure gradient of 0.3 MPa was 12% of the rate at 20°C (Figure 6). In a subsequent study (Lopushinsky and Kaufmann 1984), the transpiration rate of Douglas-fir seedlings, taken as a measure of water uptake, declined linearly with decreasing soil temperature, and at a soil temperature of 1.3°C was 19% of the rate at 20°C (Figure 7). As a result of reduced water uptake, seedling water potential (xylem pressure potential) and stomatal conductance declined. Water potential of seedlings maintained under a high evaporative demand for 10 days in soil at 1.3°C averaged -2.0 MPa, compared to a water potential of -1.3 MPa for seedlings in soil at 26°C (Figure 8). Stomatal conductance of seedlings in cold soil was 50% or less of the rate for seedlings in warm soil.

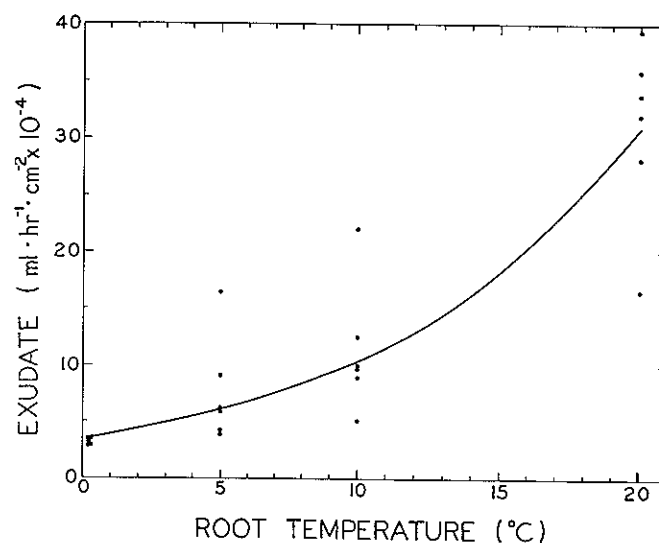


Figure 6.—Rate of water movement through detopped roots of Douglas-fir seedlings at various root temperatures. Stumps of detopped root systems were sealed into the lid of a pressure chamber in such a way that the roots could be immersed in tap water maintained at various temperatures and subjected to hydrostatic pressure while the stumps projected through the lid of the chamber. Water collected at the stump (exudate) is expressed on a per-unit of root surface basis. Each point represents a separate root system (Lopushinsky 1978).

The data shown in Figures 5, 6 and 7 were obtained with bare-root interior Douglas-fir transplants which had not yet produced any new root growth, thus all water uptake occurred through the old suberized root system. Although water absorption and shoot water potential decreased in response to low soil temperature, concurrent decreases in stomatal conductance and transpiration, coupled with nighttime recovery, prevented daytime seedling moisture stresses from approaching known lethal limits (Cleary 1971). In addition to effects on water relations, low soil temperature severely restricts root growth in interior Douglas-fir seedlings (Lopushinsky and Max 1990). Little or no root growth occurs at soil temperatures less than 5°C (Figure 9). New root growth begins when soil temperature exceeds 5°C, increases rapidly above 10°C, and maximum root growth occurs at 20°C. These results suggest that the primary

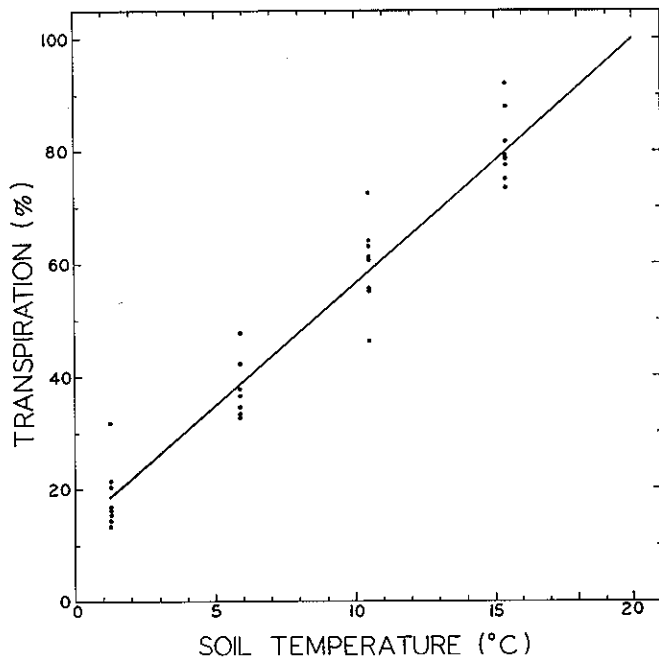


Figure 7. — Effect of soil temperature on transpiration of Douglas-fir seedlings. Transpirational water loss was taken as an index of water absorption. Transpiration rates are expressed as a percent of rates at 20°C (Lopushinsky and Kaufmann 1984).

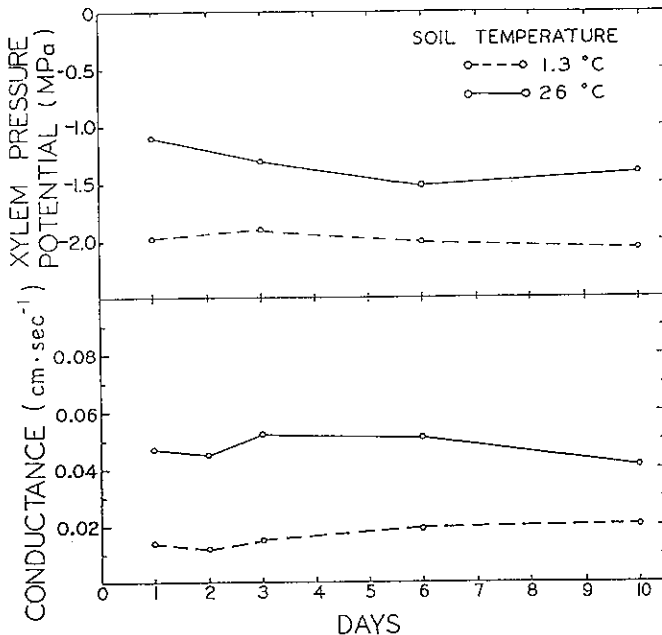


Figure 8. — Effect of soil temperature on xylem pressure potential and stomatal conductance of Douglas-fir seedlings. Environmental conditions in a growth chamber were: air temperature 25°C, radiant energy 356 Wm⁻², and vapor pressure deficit 19 mbar (Lopushinsky and Kaufmann 1984).

cause of poor field survival of seedlings outplanted in cold soil is not immediate desiccation of seedlings as a result of reduced water uptake in cold soil. More likely, it is the result of insufficient water uptake later through root systems in which new root growth was suppressed by low soil temperature.

Water movement through conifer roots occurs mainly by mass flow in response to transpiration. Osmotically induced flow, in response to a differential in solute concentration from the soil solution to the root xylem, rarely is observed in conifers, but Lopushinsky (1980) found root pressure exudation from detopped root systems of interior Douglas-fir and several other species of conifers (Figure 10). This shows that an osmotic component of water movement can occur in the roots of these species. Analysis of the xylem exudate from interior Douglas-fir (Ketchie and Lopushinsky 1981) showed that it was low in sugar content and high in nitrogen compared to other species. Stark *et al.* (1985) proposed that xylem sap of interior Douglas-fir extracted from branches with a pressure chamber could be used to determine the nutritional status of trees.

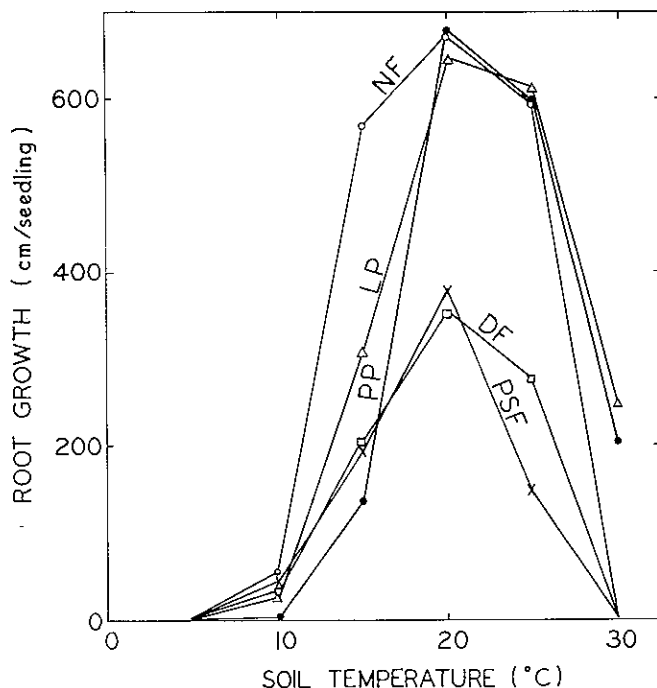


Figure 9. — Effect of soil temperature on total length of new roots (> 1 cm) per seedling produced in 5-1/2 weeks by Douglas-fir (DF), noble fir (NF), Pacific silver fir (PSF), ponderosa pine (PP), and lodgepole pine (LP) seedlings. Seed sources were eastern Washington and Oregon, except NF (western Washington) and PSF (western Oregon). Seed source elevation was 1372 m for all species except lodgepole pine, 1542m (Lopushinsky and Max 1990).

Stomatal Behavior

An understanding of stomatal behavior is particularly important because of the direct control of stomata over transpiration and exchange of carbon dioxide. Consequently, numerous studies of stomatal physiology in conifers have been conducted, particularly since the development of the null balance diffusion porometer which provides direct measurements of stomatal conductance. Relatively little work, however, has been done with interior Douglas-fir. Ranges of stomatal conductances for Douglas-fir (coastal and interior combined) and some associated species are given in Table 4. Maximum conductances for Douglas-fir are similar to those for ponderosa pine and higher than those for western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) and grand fir.

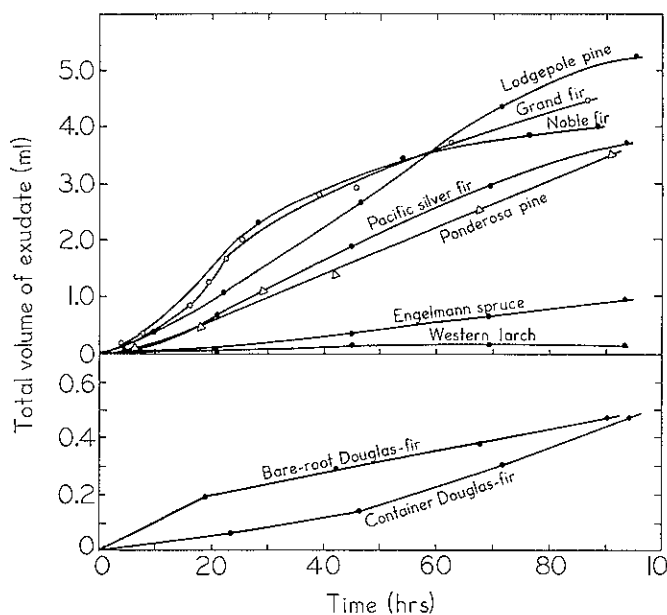


Figure 10. — Total volume of exudate from detopped conifer seedlings. Volume of exudate is expressed as milliliters per seedling (Lopushinsky 1980).

Table 4. — Leaf-conductance ranges in daylight during growing season (Running 1976).

Species	Sample Size	Maximum (cm s ⁻¹)	Minimum (cm s ⁻¹)
Douglas-fir	400	0.333	0.003
Western Hemlock	200	0.227	0.007
Ponderosa pine	200	0.323	0.005
Grand fir	200	0.192	0.003

Stomatal functioning is affected by many environmental factors including air and soil temperature, light, humidity, and leaf water status. During summer in the interior west, soil moisture frequently is limiting, thus a major factor influencing stomatal behavior is leaf moisture stress. In an experiment with potted three-year-old seedlings of Douglas-fir, grand fir, ponderosa pine, lodgepole pine and Engelmann spruce, Lopushinsky (1969) found that the stomata of Douglas-fir closed at a shoot water potential of -1.90 MPa, while stomatal closure in the pines and spruce occurred at higher water potentials ranging from -1.46 to -1.65 MPa (Table 5). Stomatal closure in grand fir occurred at a water potential of -2.51 MPa. The value for Douglas-fir in Table 5 is similar to that by Running (1976) who found that stomatal closure in 1- to 3-m-tall Douglas-fir trees in Oregon occurred at a leaf water potential of -2.0 MPa. There are indications that the water potential threshold for stomatal closure in Douglas-fir is lower in large forest trees than in seedlings, and that it becomes lower as trees acclimate to water stress. Running (1976), for example, reported a threshold for stomatal closure of -2.5 MPa in 40-m-tall coastal Douglas-fir. A similar shift in stomatal sensitivity to leaf water stress has been observed in ponderosa pine. Lopushinsky (1986) noted that sap velocity and stomatal conductance in large ponderosa pine trees remained relatively high during midday in the summer despite the fact

that needle water potential decreased to values lower than -2.0 MPa, a stress level known to close stomates in seedlings and saplings (Lopushinsky 1969; Running 1976).

Table 5. — Shoot water potential at stomatal closure for conifer seedlings (Lopushinsky 1969).

Species	Xylem Pressure Potential (MPa)
Ponderosa pine	-1.65
Lodgepole pine	-1.46
Grand fir	-2.51
Douglas-fir	-1.90
Engelmann spruce	-1.60

Tan *et al.* (1977), working with 7- to 10-m-tall coastal Douglas-fir on Vancouver Island, found that the threshold value for closure during an initial drying period was -1.95 MPa, but it decreased to -2.35 MPa during a second drying period. Also, there is a direct correlation between predawn leaf water potential and maximum morning leaf water conductance in Douglas-fir (Running 1976). Thus, as soil water becomes depleted during the summer and nighttime tree moisture recovery is not complete, the maximum morning leaf conductance drops in spite of environmental conditions conducive to a high transpiration rate.

Moisture stress causes endogenous levels of abscisic acid to increase rapidly in plants, and it has been reported that abscisic acid precipitates the stomatal closing response to the leaf water potential threshold in coastal Douglas-fir (Blake and Ferrell 1977). Subsequently, Newville and Ferrell (1980) monitored abscisic acid levels and stomatal responses in coastal and inland Douglas-fir seedlings during several drying periods. They found that although exposure to successive droughts did trigger sharp increases in abscisic acid, stomatal behavior was not always directly related to abscisic acid concentration, particularly in seedlings from the interior seed source.

The stomata of well hydrated interior Douglas-fir seedlings remain open at night and show little change from dark to light (Figure 11). In contrast, the stomata of ponderosa pine and lodgepole pine seedlings are closed in the dark and open rapidly in response to light. Engelmann spruce is intermediate in behavior. As a result of these differences in stomatal behavior, nighttime transpiration as a percent of the daytime rate was 26% for Douglas-fir compared to only 0.8, 4.8 and 7.6%, respectively, for lodgepole pine, ponderosa pine and Engelmann spruce. Open stomates at night also have been reported for coastal Douglas-fir under well water conditions (Reed and Waring 1974; Running 1976).

The stomata of Douglas-fir also respond to changes in atmospheric humidity, with the result that high vapor pressure deficits may override predawn or threshold leaf water potentials and photoactive stomatal responses. The vapor pressure deficit threshold initiating stomatal closure in coastal Douglas-fir is about 1.0 KPa (Running 1976; Livingston and Black 1987), and complete closure occurs at 3 to 4 KPa (Figure 12). Stomatal responses to changes in vapor pressure deficit within this range also have been noted for other coniferous species (Sandford and Jarvis 1986).

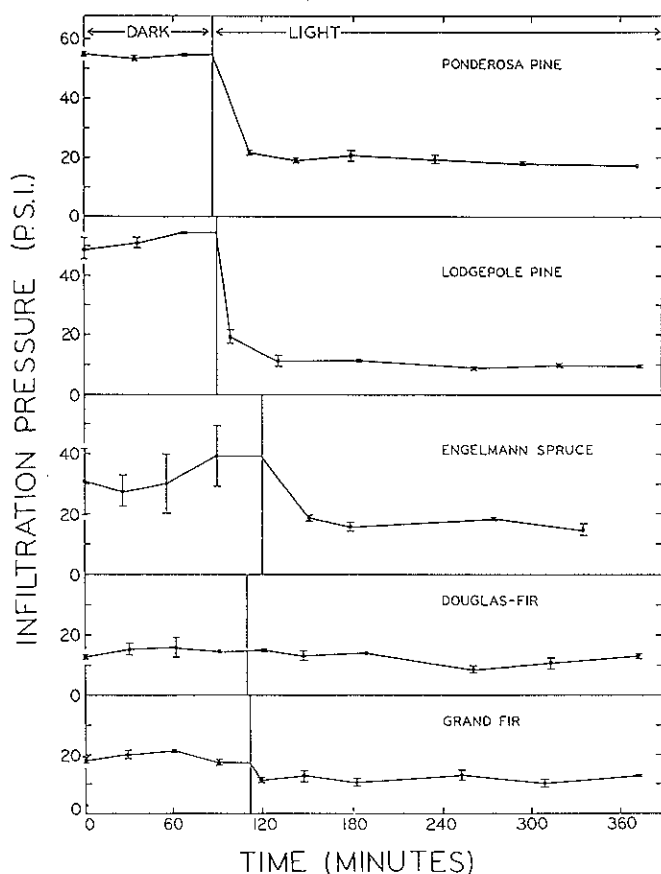


Figure 11.—Relative stomatal opening in darkness and light for ponderosa pine, lodgepole pine, Engelmann spruce, Douglas-fir and grand fir. Seedlings were 3 years old and potted in soil. Soil moisture was at field capacity during the test. Stomatal opening was determined with a pressure infiltration method. High pressures indicate closed or nearly closed stomata, and low pressures open stomata (Lopushinsky 1975).

The interaction of various environmental factors to control stomatal conductance under field conditions can be complex. Livingston and Black (1987), who monitored stomatal responses of coastal Douglas-fir seedlings planted on a high-elevation clearcut, found that a multiplicative boundary-line model that related stomatal conductance to hourly average solar irradiance, air temperature, vapor pressure deficit and average root zone water potential, accounted for over 70% of the variability in stomatal conductance. Several investigators also have reported that Douglas-fir stomata are sensitive to low air temperature. Reed (1968) found that the stomata of large seedlings of coastal Douglas-fir responded to sub-zero temperature by closing to various extents. Smith *et al.* (1984), working with interior Douglas-fir trees (<5 m tall) in the field, reported that subsequent to the beginning of seasonal stomatal closure, stomatal conductance declined sharply following the onset of freezing air temperatures at night. Decreases in maximum conductance during the day were highly correlated with decreases in minimum nighttime air temperatures the preceding night. Douglas-fir stomata also respond to low soil temperature. Lopushinsky and Kaufmann (1984) found that the stomatal conductance of interior Douglas-fir seedlings with roots in cold

(1.3°C) soil was 50% or less of the rate for seedlings in warm (26°C) soil.

One area of stomatal physiology that has received little attention in interior Douglas-fir is the stomatal behavior of seedlings following outplanting. The only study appears to be one by Childs (1980) who found that stomatal conductances of seedlings planted on a clearcut in northeastern Washington were high immediately after planting but dropped significantly during a six-week period after planting even though vapor pressure deficit remained unchanged.

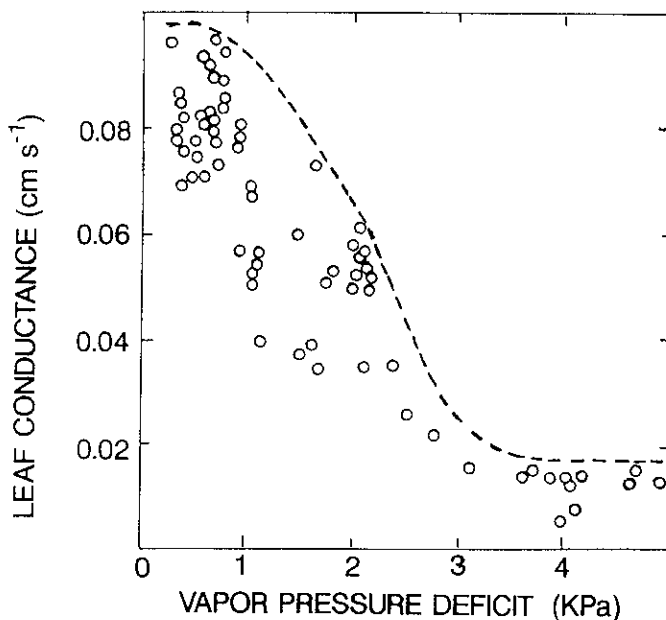


Figure 12.—Leaf conductance as a function of vapor pressure deficit in coastal Douglas-fir (redrawn from Lassoie 1982).

INTERNAL WATER STRESS AND DROUGHT RESISTANCE

Internal water stress in Douglas-fir can vary widely, depending on environmental and site conditions. In field-grown trees, plant water potentials vary both diurnally and seasonally. With adequate soil moisture, predawn potentials normally are quite high. Kelliher *et al.* (1984), for example, cited predawn values for seedlings and small trees of coastal Douglas-fir that range from -0.12 to -0.5 MPa. Jones (1972), who measured water stresses in 1- to 1.7-m-tall trees of interior Douglas-fir trees in Arizona, reported that water potentials at dawn in mid-June averaged -0.6 MPa, compared to -1.2 MPa at midday. Eissenstat and Mitchell (1983) found that summertime predawn water potentials in container-grown Douglas-fir seedlings planted on a clearcut in Idaho were above -0.5 MPa during a wet year, and rarely lower than -1.0 MPa during a dry year. As soil moisture decreases, predawn and midday water potentials can decrease considerably. Lindquist (1977), in a study with 1- to 3-m-tall coastal Douglas-fir on a south-facing clearcut in northwestern California, found that predawn water potential in June was -0.77 MPa, and the midday potential was -1.68 MPa. By September the predawn potential had decreased to -2.1 MPa, and the midday value to -2.42 MPa. Water potentials also can

vary with stock types. Hobbs and Wearstler (1983), who measured water potentials in three Douglas-fir (coastal) stock types planted on southwestern Oregon, found that predawn xylem pressure potential was highest in 1-0 plug seedlings, intermediate in plug-1 bare-root seedlings, and lowest in 2-0 bare-root seedlings.

Few data are available on trends of water potential in large trees of interior Douglas-fir. Lopushinsky (1986) found that predawn water potential in large field-grown Douglas-fir decreased from -0.9 MPa in June to a low of -1.58 MPa in September and then increased following rainfall in late September and early October to the level recorded in June (Figure 13). Midday water potential declined from -1.65 MPa in June to -2.10 MPa in late July, and then increased to -1.85 MPa in September. The low midday water potentials in late August and mid-September were associated with midday stomatal conductance near zero. Midday water potential in October remained low despite adequate soil moisture and low evaporative demand. From late July to mid-September, values for predawn and midday water potentials tended to converge, as would be expected during a drying period with minimal rainfall. Diurnal trends of water potential changed as the season progressed (Figure 14). On June 24, predawn water potential was -0.9 MPa. It decreased to -2.1 MPa just before noon, and then increased during the remainder of the day to the predawn value. On August 5, predawn and evening water potentials were lower than comparable values on June 24, and there was less variation during the day. On both days, minimum water

potential occurred during periods of rapid transpiration indicated by high values of heat pulse velocity, but minimum water potentials were not associated with peak values of air temperature or vapor pressure deficit.

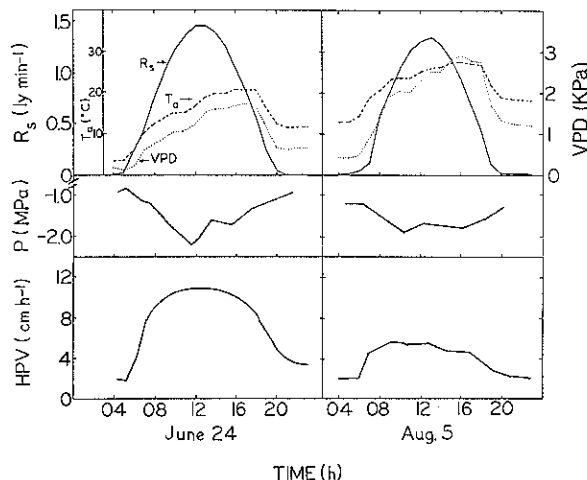


Figure 14. — Diurnal variation in solar radiation (R_s), air temperature (T_a), vapor pressure deficit (VPD), heat pulse velocity (HPV) and xylem pressure potential (P) for a codominant Douglas-fir during a sunny day in June and August (Lopushinsky 1986).

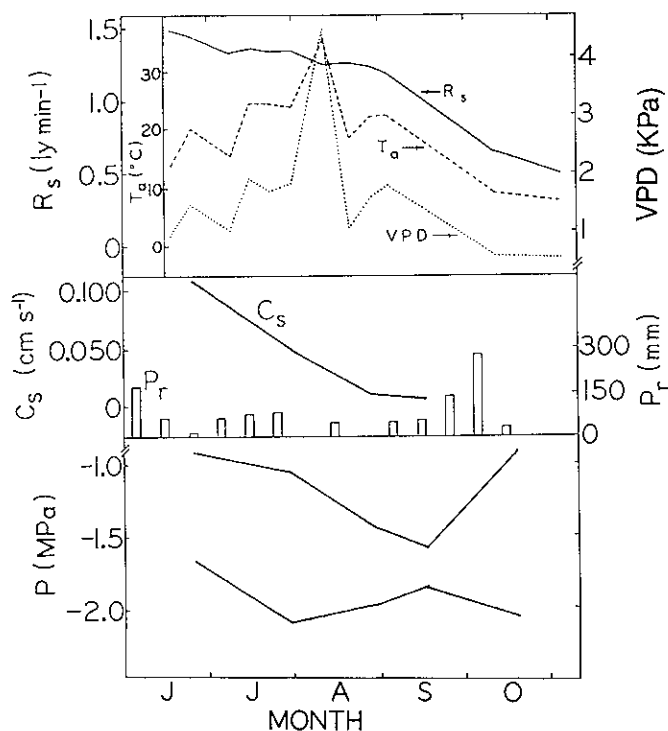


Figure 13. — Seasonal variation in predawn (○) and midday (---) xylem pressure potential (P), stomatal conductance (C_s), 10-day precipitation (P_r), solar radiation (R_s), air temperature (T_a), and vapor pressure deficit (VPD) during the summer and fall. Values for P and C_s are averages for four codominant Douglas-fir (Lopushinsky 1986).

Water potentials in interior Douglas-fir also are influenced by the presence of competing vegetation. Eissenstat and Mitchell (1983) found that both predawn and midday water potentials in planted container-grown seedlings in Idaho were reduced by grass competition, especially during a dry year. Barber (1984), who compared several methods of treating planting spots in eastern Washington, reported a predawn water potential of -0.91 MPa for Douglas-fir seedlings planted in spots previously sprayed with atrazine herbicide to eliminate grasses, compared to -4.1 MPa for seedlings in nontreated spots. Reducing stocking by thinning also reduces tree water stress. Aussenac and Granier (1988) found that when half of the trees in a stand of coastal Douglas-fir were removed, predawn water potentials of thinned trees were higher than those in a control stand, especially during the first three years after thinning.

Douglas-fir generally is considered to be more drought resistant than Engelmann spruce, western hemlock and the true firs, but less drought resistant than ponderosa pine and lodgepole pine (Minore 1979). Also, it has been shown that Douglas-fir seedlings from inland seed sources are more drought resistant than those from coastal sources (Ferrell and Woodard 1966; Pharis and Ferrell 1966). Differences in drought resistance related to seed sources may be due in part to inherent growth patterns which affect internal plant water balance. Joly *et al.* (1989), for example, found that inland populations of Douglas-fir seedlings are characterized by early budset, slower rate of shoot extension and a higher root-shoot ratio, morphological responses that are advantageous in avoiding drought. Also, drought resistance in many tree species is related to root depth

(Parker 1969). This is particularly important during the establishment of seedlings. Stein (1978) found that tap roots of 2-year-old coastal Douglas-fir seedlings grown outdoors in three different soils were considerably shorter than those of ponderosa pine and several other conifers.

Low water potentials are known to adversely affect physiological processes in Douglas-fir that directly influence growth. Cleary (1971) found that photosynthesis in coastal Douglas-fir seedlings declined when leaf water potential dropped below -1.0 MPa, and became zero at a water potential of -5.4 MPa. Lethal limits of moisture stress are not precisely known for either coastal or interior Douglas-fir, but Cleary (1971) found that a majority of coastal Douglas-fir seedlings died when shoot water potential dropped below -5.0 MPa. Brix (1979), on the other hand, found no mortality in coastal Douglas-fir seedlings until seedling water potential fell below -11.0 MPa. The lethal threshold probably varies seasonally because it has been shown that coastal Douglas-fir seedlings are at their highest level of resistance to water stress during winter and early spring (Hermann 1967; Ritchie 1984; Lavender 1985).

SUMMARY

Information on the water relations of interior Douglas-fir has been obtained mainly from studies with seedlings. The transpiration rate of seedlings of interior Douglas-fir is similar to that for ponderosa pine, but less than that for lodgepole pine, grand fir and white fir. Transpiration in Douglas-fir seedlings is less sensitive to decreasing soil water potential than is transpiration in ponderosa and lodgepole pine, indicating poorer stomatal control of water loss. The transpiration behavior of large Douglas-fir trees in the field, however, generally is similar to that of ponderosa pine, probably because the water relations of large trees reflect factors not found in seedlings, such as an unrestricted root system and water storage in the sapwood. Interior Douglas-fir trees have a relatively small amount of sapwood, compared to other inland conifers, and thus possess a relatively small capacity for internal water storage. Water absorption through roots of Douglas-fir seedlings is greatly reduced by low soil temperature, resulting in a decrease in shoot water potential and stomatal conductance. When soil moisture is adequate, stomates in Douglas-fir seedlings remain open in the dark, whereas stomates in ponderosa pine and lodgepole pine close in the dark. The stomata of interior Douglas-fir seedlings are less sensitive to leaf water stress, and close at a lower leaf water potential than stomata in ponderosa pine and lodgepole pine. Lethal limits of leaf water potential are not precisely known for interior Douglas-fir, but mortality in seedlings from coastal seed sources occurs in the range -5.0 to -11.0 MPa. The moderate stomatal control of water loss, small internal water storage capacity and relatively shallow root system help to explain why interior Douglas-fir is restricted to more mesic sites than ponderosa pine.

LITERATURE CITED

- Aussenac, G. and A. Granier. 1988. Effects of thinning on water stress and growth in Douglas-fir. *Can. J. For. Res.* 18:100-105.
- Ballard, T. M. and M. G. Dosskey. 1985. Needle water potential and soil-to-foilage flow resistance during soil drying: a comparison of Douglas-fir, western hemlock, and mountain hemlock. *Can. J. For. Res.* 15:185-188.
- Barber, H. W., Jr. 1984. Effects of site preparation on survival and moisture stress of interior Douglas-fir seedlings planted in grass. *Tree Planters Notes* 35:7-10.
- Bates, C. G. 1923. Physiological requirements of Rocky Mountain trees. *J. Agric. Res.* 24:97-164.
- Black, T. A., C. S. Tan, and J. U. Nnyamah. 1980. Transpiration rate of Douglas-fir trees in thinned and unthinned stands. *Can. J. Soil Sci.* 60:625-631.
- Blake, J. and W. K. Ferrell. 1977. The association between soil and xylem water potential, leaf resistance, and abscissic acid content in droughted seedlings of Douglas-fir (*Pseudotsuga menziesii*). *Physiol. Plant.* 39:106-109.
- Brix, H. 1979. Effects of plant water stress on photosynthesis and survival of four conifers. *Can. J. For. Res.* 9:160-165.
- Childs, S. W. 1980. Water relations of newly planted Douglas-fir seedlings. Ph.D. Dissertation, Washington State Univ., Pullman.
- Cleary, B. D. 1971. The effect of plant moisture stress on physiology and establishment of planted Douglas-fir and ponderosa pine seedlings. Ph.D. Dissertation, Oregon State Univ., Corvallis.
- Daniels, T. G. 1978. The effects of winter plant moisture stress on survival and growth of 2 + 0 Douglas-fir seedlings. M.S. Thesis, Oregon State Univ., Corvallis.
- Edwards, W. R. N. and P. G. Jarvis. 1982. Relations between water content, potential and permeability in stems of conifers. *Plant, Cell and Environment* 5:271-277.
- Eissenstat, D. M. and J. E. Mitchell. 1983. Effects of seedling grass and clover on growth and water potential of Douglas-fir seedlings. *For. Sci.* 29:166-179.
- Ferrell, W. K. and E. S. Woodard. 1966. Effects of seed origin on drought resistance of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco). *Ecology* 47:499-503.
- Fritschen, L. J., J. Hsia, and P. Doraiswamy. 1977. Evapotranspiration of a Douglas-fir determined with a weighing lysimeter. *Water Resources Res.* 13:145-148.
- Fry, K. E. 1965. A study of transpiration and photosynthesis in relation to the stomatal resistance and internal water potential in Douglas-fir. Ph.D. Dissertation, Univ. Washington, Seattle.
- Grier, C. C. and R. H. Waring. 1974. Conifer foliage mass related to sapwood area. *For. Sci.* 20:205-206.
- Hermann, R. K. 1967. Seasonal variation in sensitivity of Douglas-fir seedlings to exposure of roots. *For. Sci.* 13:140-149.
- Hinckley, T. M. and D. R. M. Scott. 1971. Estimates of water loss and its relation to environmental parameters in Douglas-fir saplings. *Ecology* 52:520-524.
- Hobbs, S. D. and K. A. Wearstler, Jr. 1983. Performance of three Douglas-fir stocktypes on a skeletal soil. *Tree Planters Notes* 34:11-14.

- Joly, R. J., W. T. Adams, and S. G. Stafford. 1989. Phenological and morphological responses of mesic and dry site sources of coastal Douglas-fir to water deficit. *For. Sci.* 35:987-1005.
- Jones, J. R. 1972. Moisture stresses in Arizona mixed conifer seedlings. USDA For. Serv. Res. Pap. RM-86. 8 pp. Rocky Mountain Forest and Range Exp. Sta., Ft. Collins, CO.
- Kelliher, F. M., T. A. Black, and A. G. Barr. 1984. Estimation of twig xylem water potential in young Douglas-fir trees. *Can. J. For. Res.* 14:481-487.
- Ketchie, D. O. and W. Lopushinsky. 1981. Composition of root pressure exudate from conifers. USDA For. Serv. Res. Note PNW-395. 6 pp. Pacific Northwest Forest and Range Exp. Sta., Portland, OR.
- Kline, J. R., K. L. Reed, R. H. Waring, and M. L. Stewart. 1976. Field measurement of transpiration Douglas-fir. *J. Appl. Ecol.* 13:272-283.
- Kramer, P. J. 1940. Root resistance as a cause of decreased water absorption by plants at low temperatures. *Plant Physiol.* 15:63-79.
- Lassen, L. E. and E. A. Okkonen. 1969. Sapwood thickness of Douglas-fir and five other western softwoods. USDA For. Serv. Res. Pap. FPL-124. 16 pp. Madison, WI.
- Lassoie, J. P. 1982. Physiological activity in Douglas-fir. Pp. 126-185 in *Analysis of coniferous forest ecosystems in the western United States*. U.S./IBP Synthesis Series No. 14. (R. L. Edmonds, ed.). Hutchison Ross Pub. Co., Stroudsburg, PA.
- Lassoie, J. P., D. R. M. Scott, and L. J. Fritschen. 1977. Transpiration studies in Douglas-fir using the heat pulse technique. *For. Sci.* 23:377-390.
- Lavender, D. P. 1985. Bud dormancy. Pp. 7-15 *In Evaluating seedling quality: principles, procedures, and predictive abilities of major tests* (M. A. Duryea, ed.). Forest Research Laboratory, Oregon State Univ., Corvallis.
- Lindquist, J. L. 1977. Plant moisture stress patterns in planted Douglas-fir: a preliminary study of the effects of crown and aspect. USDA For. Serv. Res. Note PSW-325. 5 pp. Pacific Southwest Forest and Range Exp. Sta., Berkeley, CA.
- Livingston, N. J. and T. A. Black. 1987. Stomatal characteristics and transpiration of three species of conifer seedlings planted on a high elevation south-facing clearcut. *Can. J. For. Res.* 17:1273-1282.
- Lopushinsky, W. 1969. Stomatal closure in conifer seedlings in response to leaf moisture stress. *Bot. Gaz.* 130:258-263.
- Lopushinsky, W. 1975. Water relations and photosynthesis in lodgepole pine. Pp. 135-153 *In Proc. Management of lodgepole pine ecosystems* (D. Baumgartner, ed.). Washington State Univ. Coop. Ext. 823 pp.
- Lopushinsky, W. 1978. Effects of low soil temperature on water relations of Douglas-fir seedlings. Pp. 416 *In Proc. Fifth North American Forest Biology Workshop*, (C.A. Hollis and A. E. Squillace, eds.). School of Forest Resources and Conservation, Univ. Florida.
- Lopushinsky, W. 1980. Occurrence of root pressure exudation in Pacific northwest conifer seedlings. *For. Sci.* 26:275-279.
- Lopushinsky, W. 1981. Plant-water relationships in interior west watersheds. Pp. 99-106 *In Proc. Interior West Watershed Management* (D. Baumgartner, ed.). Washington State Univ. Coop. Ext. 288 pp.
- Lopushinsky, W. 1986. Seasonal and diurnal trends of heat pulse velocity in Douglas-fir and ponderosa pine. *Can. J. For. Res.* 16:814-821.
- Lopushinsky, W. and G. O. Klock. 1974. Transpiration of conifer seedlings in relation to soil water potential. *For. Sci.* 20:181-186.
- Lopushinsky, W. and M. R. Kaufmann. 1984. Effects of cold soil on water relations and spring growth of Douglas-fir seedlings. *For. Sci.* 30:628-634.
- Lopushinsky, W. and T. A. Max. 1990. Effect of soil temperature on root growth and on budburst timing in conifer seedling transplants. *New Forests* 4:9-26.
- Meinzer, F. C. 1981. Water use efficiency in Douglas-fir; the nature of plant response to selected environmental variables. Ph.D. Dissertation, Univ. Washington, Seattle.
- Menzies, M. I. 1980. Effect of nursery conditioning on the water relations of two-year-old Douglas-fir seedlings after lifting and outplanting. Ph.D. Dissertation, Univ. Washington, Seattle.
- Minore, D. 1979. Comparative autecological characteristics of northwestern tree species. USDA For. Serv. General Technical Report PNW-87. 72 pp. Northwest Forest and Range Exp. Sta., Portland, OR.
- Newville, E. G. and W. K. Ferrell. 1980. Abscissic acid levels and stomatal behavior during drought and recovery in Douglas-fir (*Pseudotsuga menziesii*). *Can. J. Bot.* 58:1370-1375.
- Nnyamah, J. U. and T. A. Black. 1977. Rates and patterns of water uptake in a Douglas-fir forest. *Soil Sci. Soc. Am. J.* 41:972-979.
- Parker, J. 1954. Available water in stems of some Rocky Mountain conifers. *Bot. Gaz.* 115:380-385.
- Parker, J. 1969. Further studies of drought resistance in woody plants. *Bot. Rev.* 35:318-371.
- Pharis, R. P. and W. K. Ferrell. 1966. Differences in drought resistance between coastal and inland sources of Douglas-fir. *Can. J. Bot.* 44:1651-1659.
- Phillips, R. A. 1967. Stomatal characteristics throughout a tree crown. M. F. Thesis, Univ. Washington, Seattle.
- Reed, K. L. 1968. The effects of sub-zero temperatures on the stomata of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco). M.S. Thesis, Univ. Washington, Seattle.
- Reed, K. L. and R. H. Waring. 1974. Coupling of environment to plant response: a simulation model of transpiration. *Ecology* 55:62-72.

- Ritchie, G. A. 1984. Assessing seedling quality. Pp. 243-259
In Forest nursery manual: production of bareroot seedlings
(M. A. Duryea and T. D. Landis, eds.). Martinus Nijhoff/Dr. W. Junk Publishers. The Hague/Boston/Lancaster,
for Forest Research Laboratory, Oregon State Univ.,
Corvallis.
- Roeser, J., Jr. 1932. Transpiration capacity of coniferous seedlings and the problem of heat injury. *J. For.* 30:381-385.
- Running, S. W. 1976. Environmental control of leaf water conductance in conifers. *Can. J. For. Res.* 6:104-112.
- Running, S. W. 1980. Relating plant capacitance to the water relations of *Pinus contorta*. *Forest Ecology and Management* 2:237-252.
- Sandford, A. P. and P. G. Jarvis. 1986. Stomatal responses to humidity in selected conifers. *Tree Physiol.* 2:89-103.
- Shinozaki, K., K. Yoda, K. Hozumi, and T. Kira. 1964. A quantitative analysis of plant form—the pipe model theory. I. Basic analyses. *Jpn. J. Ecol.* 14:97-105.
- Smith, W. K., D. R. Young, G. A. Carter, J. L. Hadley, and G. M. McNaughton. 1984. Autumn stomatal closure in six conifer species of the central Rocky Mountains. *Oecologia* 63:237-242.
- Stark, N., C. Spitzner, and D. Essig. 1985. Xylem sap analysis for determining nutritional status of trees: *Pseudotsuga menziesii*. *Can. J. For. Res.* 15:429-437.
- Stein, W. I. 1978. Naturally developed seedling roots of five western conifers. Pp. 28-35 *In* Proc. Root Form of Planted Trees, (E. Van Eerden and J. M. Kinghorn, eds.). British Columbia Ministry of Forests/Canadian Forestry Service, Victoria, B.C.
- Tan, C. S., T. A. Black, and J. U. Nnyamah. 1977. Characteristics of stomatal diffusion resistance in a Douglas-fir forest exposed to soil water deficits. *Can. J. For. Res.* 7:595-604.
- Waring, R. H. and S. W. Running. 1978. Sapwood water storage: its contribution to transpiration and effect upon water conductance through the stems of old-growth Douglas-fir. *Plant, Cell and Environment* 1:131-140.
- Waring, R. H., P. E. Schroeder, and R. Oren. 1982. Application of the pipe model theory to predict canopy leaf area. *Can. J. For. Res.* 12:556-560.
- Zavitkovski, J. and W. K. Ferrell. 1970. Effect of drought upon rates of photosynthesis, respiration, and transpiration of seedlings of two ecotypes of Douglas-fir. *Photosynthetica* 4:58-67.

Author

W. Lopushinsky
Forestry Sciences Laboratory
1133 N Western Avenue
Wenatchee, WA 98801