Environmental control of leaf water conductance in conifers[1]

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Diurnal measurements of leaf conductance, xylem water potential, temperature, humidity, and radiation were taken on six sites throughout Oregon. Xylem water potential was hypothesized to influence leaf conductance in two ways. First, predawn xylem water potential controlled the early-morning maximum leaf conductance of *Pseudotsuga menziesii* (Mirb.) Franco. Second, irrespective of predawn water potential, a threshold diurnal water potential was found. Whenever water potential of *Pseudotsuga menziesii* dropped below -20 bars (-20×10^5 Pa) during the day, a significant decrease in leaf conductance resulted. If the water potential threshold was not reached during the day, leaf conductance stayed at the morning maximum or decreased slightly in response to decreasing humidity.

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A six stations distribuées à travers l'Orégon, on a effectué des mesures diurnes de conductance foliaire de vapeur d'eau, de potentiel hydrique du xylème, de température, d'humidité et de radiation. On a formulé l'hypothèse que le potentiel hydrique du xylème influençait la conductance foliaire de deux façons. Premièrement, le potentiel hydrique du xylème préalablement submergé a contrôlé la conductance foliaire maximum du matin chez *Pseudotsuga menziesii* (Mirb.) Franco. En second lieu, sans égard au potentiel hydrique suivant submersion, on a observé un seuil de potentiel hydrique diurne. Chaque fois que le potentiel hydrique de *P. menziesii* baissait en bas de -20 bars (-20×10^5 Pa) durant le jour, il en résultait une diminution significative de la conductance foliaire. Lorsque le seuil de potentiel hydrique n'était pas atteint durant le jour, la conductance foliaire demeurait à sa valeur maximum du matin ou décroissait faiblement suite à une chute de l'humidité.

[Traduit par le journal]

Introduction

The ability of different conifers to control water loss is a primary physiological factor affecting their adaptive success in much of the Pacific Northwest, which is characterized by a dry growing season. Consequently, scientists have attempted to quantify the relative abilities of different species to maintain favorable internal water status over a range of environmental conditions.

Lopushinsky (1969) and Lopushinsky and Klock (1974) quantified transpiration control of five species in relation to leaf and soil water potential. Puritch (1973) studied the effect of water stress on photosynthesis, transpiration, and respiration of four *Abies* species. In eastern North America, Tobiessen and Kana (1974) have studied with almost unique methods drought stress avoidance of *Populus* and *Fraxinus*. Other studies of plant water status have dealt primarily with the measurement and interpretation of plant water potential. Sucoff (1972) studied water potential in *Pinus resinosa*. Hinckley and Ritchie (1973) developed a theoretical model for calculation of water potential from climatological variables. Tyree *et al.* (1973) worked with *Tsuga canadensis*, relating pressure-bomb measurements to total water content, turgor, and other aspects of stem water status.

In this study I have attempted to simultaneously measure directly or indirectly important

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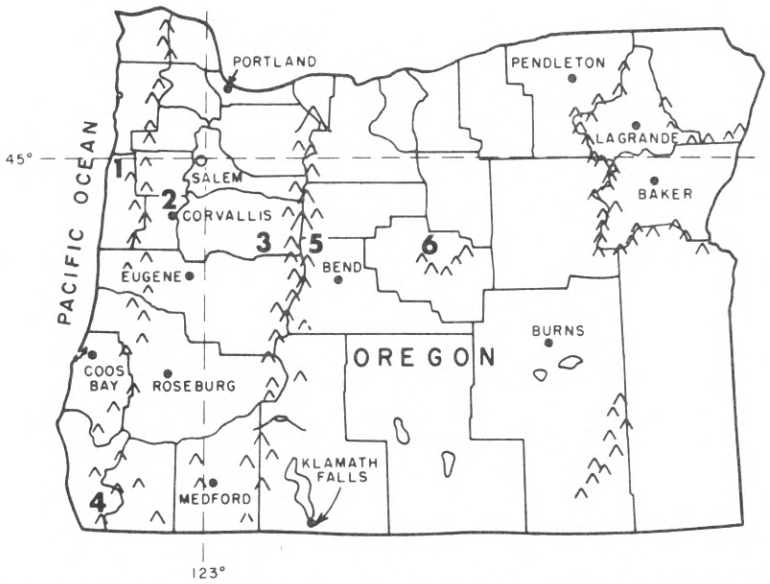

FIG. 1. Map of Oregon showing location of the six study sites: (1) Cascade Head Experimental Forest, (2) MacDonald Forest, (3) H. J. Andrews Experimental Forest, (4) Siskiyou Mts., (5) Metolius River, and (6) Ochoco Mts.

facets of the SPAC (soil–plant–atmosphere continuum) (Philip 1966) in the field on intact naturally growing trees. Plant moisture stress was assumed to represent an integration of soil and internal plant water status. Meteorological variables were measured on site continuously. Leaf conductance is of special importance because it is the tree's major physiological control of water status and directly controls transpiration and often photosynthesis.

My objective was to quantify leaf-conductance responses of various conifers to plant water potential and environmental variables during the growing season. These results were used for inputs into the SPAC model for conifers of Running *et al.* (1975) and Waring and Running (1975).

Methods

Six species of conifers encompassing a range of responses and environmental limits were chosen for study. The two most important and most widely distributed species were Douglas fir (*Pseudotsuga menziesii* (Mirb). Franco) and ponderosa pine (*Pinus ponderosa* Laws.). Because of their wide distribution, at least one of these species was present on every site to provide a reference species for comparisons. Four other primary species were sampled: western hemlock (*Tsuga heterophylla* (Raf) Sarg.), grand fir (*Abies grandis* (Dougl.) Lindl.), noble fir (*Abies procera* Rehd.), and Sitka spruce (*Picea sitchensis* (Bong.) Carr.). During the summers 1972–1974 of data collection, six different study sites were visited (Fig. 1). Table 1 summarizes the study sites, some pertinent long-term climatic averages, and the species sampled on each site.

The physiological measurements of interest to this study were xylem water potential and leaf conductance of water vapor. Xylem water potential was estimated by the Scholander pressure bomb (Scholander *et al.* 1965), using procedures of Waring and Cleary (1967).

Stomatal control was measured by leaf resistance or its reciprocal, leaf conductance. Leaf conductance includes cuticular, boundary-layer, mesophyll, and stomatal resistances to water vapor diffusion. Most short-term variation in leaf conductance of conifers, however, results from rapid changes in stomatal resistance (Slatyer 1967; Waggoner and Turner 1971). Until recently, stomatal response of conifers had been quantified indirectly by the stomatal infiltrometer of Fry and Walker (1967). The advent of the aspirated diffusion porometer of Turner *et al.* (1969), Turner and Parlange (1970), and more recently the null-balance diffusion porometer (Beardsell *et al.* 1972) allowed me to measure leaf conductance directly on intact foliage and the portability to work on various field sites on naturally grown trees. Meteorological data were taken with an M-3 Recording Meteorological Station by Interface Instrument Co. This station continuously records air temperature, dew point, and shortwave radiation.

The calculation of leaf conductance requires measurements of leaf area. At the end of each sampling day, the 10–40 needles in each sample were clipped and taken to the laboratory for determination of total

TABLE 1. A summary of climatic data and species samples for the six study sites in Oregon (from Franklin and Dyrness (1973))

Study site	Site code	Elevation, m	Precipitation yearly, cm	Temp. range, °C		Species sampled*
				Average Jan. minimum	Average July maximum	
Cascade Head	1	200	225	3	20	PSME,PISI,TSHE
MacDonald Forest	2	600	100	0	28	PSME,ABGR
H. J. Andrews	3					
High		1000	240	−5	25	PSME,TSHE,ABGR, ABPR,ABAM
Low		500	200	0	30	PSME,TSHE
Siskiyou Mts.	4	1200	140	−5	30	PSME,ABMA,PIBR PIPO,ABGR
Metolius	5	1100	80	−5	25	PSME,PIPO,ABGR
Ochoco Mts.	6	1200	50	−10	28	PSME,PIPO

**Pseudotsuga menziesii*, PSME; *Picea sitchensis*, PISI; *Abies grandis*, ABGR; *Tsuga heterophylla*, TSHE; *Abies procera*, ABPR; *Abies amabilis*, ABAM; *Abies magnifica* var. *shastensis*, ABMA; *Picea breweriana*, PIBR; *Pinus ponderosa*, PIPO.

surface area. Three different methods were used to measure leaf area. One method was the glass-bead adhesive technique described by Thompson and Leyton (1971), in which needles are coated with an adhesive, weighed, covered with a monolayer of glass beads, and reweighed. A ratio of weight increase to surface area then gives the leaf area estimate. A second technique using optical planimetry also was used. On pine fascicles, surface area was calculated from length–diameter measurement. A comparison of the glass-bead adhesive and optical planimeter techniques has recently been completed (Drew and Running 1975).

Each study site was a recent clear-cutting or open forest with trees from 1 to 3 m tall. At each site, a minimum of two trees per species, each from 1 to 3 m tall and with two branches, was selected for study. All trees were within 40 m of each other so that the meteorological station sensors would be representative of conditions at the study trees. Because radiation was not measured in 1972, sampling was undertaken from 0900 to 1500 on clear days to minimize unquantified fluctuation in radiation. In 1973 and 1974 when radiation was recorded, sampling normally occurred from dawn until dusk. A sampling day began with measuring predawn water potential. As soon as any dew had evaporated, leaf conductance, using both porometers, and plant moisture stress were measured on each tree at about 3-h intervals throughout the day. Meteorological data were recorded continuously.

In 1974, a study of needle age differences in leaf conductance was begun using the null-balance porometer. Three branches on each tree were chosen, and on each branch, needles up to 4 years of age were sampled separately on the same diurnal schedule.

Results

Leaf-conductance Ranges

First, consider instrument and biological variability at high, medium, and low leaf conductances. On a sample of three Douglas-fir twigs measured four times from 0930 to 1500 on a cool day, the mean conductance was 0.122 cm s^{-1}, standard deviation (SD) was 0.012, and coefficient of variation (CV) was 9.8%. At high leaf conductance, when stomata were wide open, biological variability was low, and as shown, instrument precision was excellent. At medium leaf conductance, 11 ponderosa pine samples had a mean value of 0.070 cm s^{-1}, SD was 0.23, and CV was 23%. The increase in variability probably reflects biological variability since stomata are at various stages of closure. At low leaf conductance, 19 Douglas-fir samples had a mean of 0.011 cm s^{-1}, SD was 0.003, and CV was 27%. Biological variability at stomatal closure is insignificant, and most variation is from the null-balance porometer. The Turner porometer can resolve differences in conductance of less than 0.003 cm s^{-1}; however, the range from 0.01 to 0.002 cm s^{-1} leaf conductance is unimportant in terms of water loss by the tree.

Table 2 summarizes the range in leaf-conductance values observed on the eight species of conifers studied over the years 1972–1974. It is difficult to recognize any patterns, but noble fir, Sitka spruce, and western hemlock, the most mesic species, had the lowest maximum conductances. Generally, the species can be divided into two groups based on their minimum conductances. One group, noble fir and Sitka spruce, showed little stomatal control on sites in their range. Group 2, which included all of the other species, showed significant although variable control within its normal habitat.

TABLE 2. Leaf-conductance ranges observed in daylight during growing season

Species	n	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
Sitka spruce	50	0.204	0.047
Noble fir	100	0.267	0.032
Shasta red fir	20	0.476	0.007
Brewer spruce	20	0.278	0.009

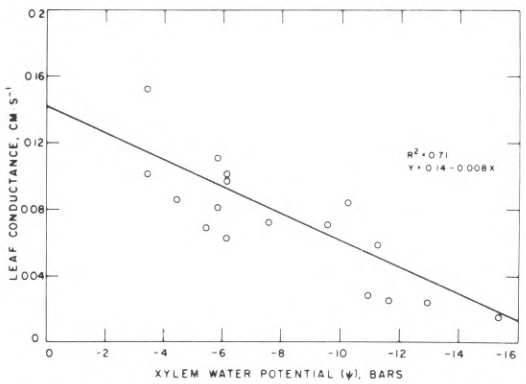

FIG. 2. Regression of maximum morning leaf water conductance as a function of predawn xylem water potential. Each point represents the average of at least nine leaf-conductance measurements taken on four needle ages before 0900 in the canopy of a 1- to 3-m Douglas fir (1 bar = 10^5 Pa).

Leaf-conductance Control

Figure 2 shows maximum morning leaf conductance as a function of predawn water potential for Douglas fir from four sites, with $R^2 = 0.71$. When predawn recovery was complete, to water potentials around -3 bars (-3×10^5 Pa), morning conductance was around 0.14 cm s^{-1} (a canopy average from needle age groups 0 to 4 years). As soil water was depleted throughout the summer and predawn recovery was not complete, the maximum morning leaf conductance dropped. Similar trends were noted in other species but without enough range of predawn water potential for analysis. Data from Zobel (1974) indicate a similar pattern for *Abies grandis*. I have not found Sitka spruce ever to attain predawn water potentials below -5 bars (-5×10^5 Pa), and noble fir, although attaining predawn water potentials of -14.6 bars (-14.6×10^5 Pa), never has shown moisture-stress-triggered control of leaf conductance.

Diurnal Function

The threshold for opening stomata during the growing season in these conifers was less than 0.1 ly min^{-1} (6.98 mW cm^{-2}). During late fall, winter, and early spring, when evaporative demand was low and tree water potential recovered rapidly to maximum levels, stomata of Douglas fir stayed open all night with leaf conductances from 0.12 to 0.08 cm s^{-1}. During daylight hours, once 0.1 ly min^{-1} (6.98 mW cm^{-2}) had been exceeded, I did not find any direct radiation response by leaf conductance, only a response that was more directly related to evaporative demand. When ABSHD (absolute humidity deficit) was low, leaf conductance stayed at its morning maximum all day, as shown in Fig. 3 for a cool December day in Corvallis. Figure 4 shows the course of a clear, mild day in August on the Oregon Coast. At dawn, leaf conductance rose to its daily maximum. Unfortunately, because of dew on the foliage, porometer measurements were not possible until 0900 Pacific Standard Time (PST). As ABSHD increased over the course of the day until the sun went off the site, leaf conductance gradually dropped in Douglas fir from 0.130 to 0.082 cm s^{-1}.

When over the course of a day a tree dropped to its water potential threshold, leaf conductance was reduced to around 0.01–0.02 cm s^{-1} regardless of initial conductance (Figs. 5, 6). This threshold did not depend on predawn water potential, although the threshold was reached more quickly if predawn water potentials began very low. For Douglas fir this threshold was very close to -20 bars (-20×10^5 Pa), and for ponderosa pine, -18 bars (-18×10^5 Pa), values also found by Lopushinsky (1969). A small amount of data on 40-m-tall Douglas fir indicates that they have a lower threshold, at least -25 bars (-25×10^5 Pa). Converse-

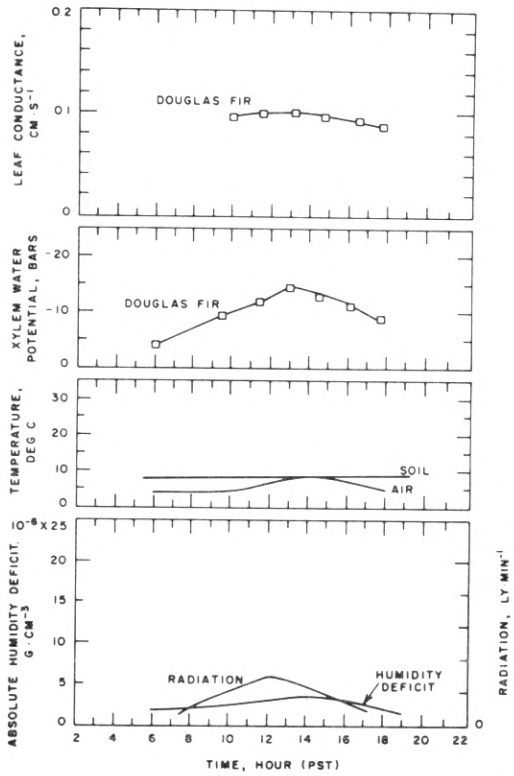

FIG. 3. Environmental and physiological data for Douglas fir taken December 17, 1974, at Corvallis. Each leaf-conductance point represents an average of three 0- to 1-year samples on two 2-m-tall trees (1 bar = 10^5 Pa, 1 ly min^{-1} = 69.8 mW cm^{-2}).

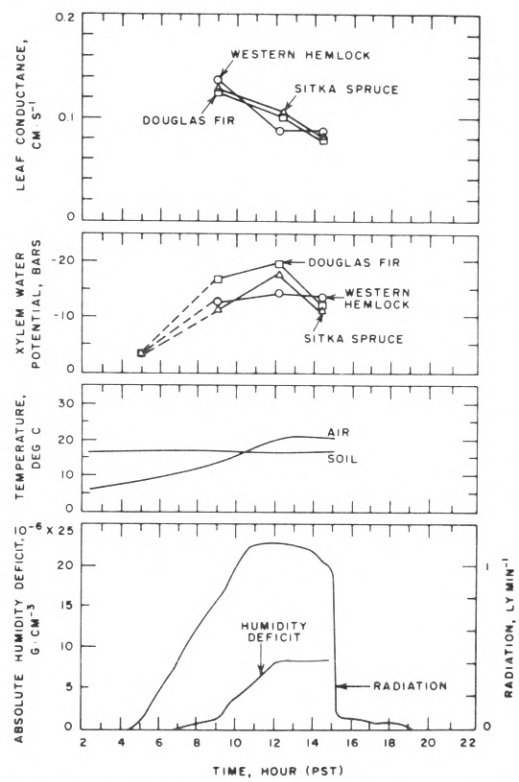

FIG. 4. Environmental and physiological data for Douglas fir, western hemlock, and Sitka spruce, taken August 8, 1974, on the Cascade Head site. Each leaf-conductance point represents a canopy average of at least four measurements on 0- to 1-year needle-age classes on two trees, 1 to 3 m tall (1 bar = 10^5 Pa, 1 ly min^{-1} = 69.8 mW cm^{-2}).

ly, 30-cm seedlings have a higher threshold, around −17 bars (−17 × 10^5 Pa).

Figures 5 and 6 demonstrate some interesting species differences. In Fig. 5, ponderosa pine stomata opened to a much higher morning maximum leaf conductance than Douglas fir would at a similar predawn plant water potential. Ponderosa pine stayed at high leaf conductance through the morning, probably because a humidity threshold was not reached, but then closed at a water potential threshold higher (−18 bars (−18 × 10^5 Pa)) than that for Douglas fir. On a day at the Ochoco site, ponderosa pine did not appear to reach its water potential threshold but reduced leaf conductance from 0.08 to 0.04 cm s^{-1} in response to an ABSHD of 14 × 10^{-6} g cm^{-3}.

Figure 6 shows western hemlock opened to a much higher morning leaf conductance than Douglas fir but then reduced leaf conductance responding to water potential of −21.3 bars (−21.3 × 10^5 Pa). On the coastal site (Fig. 4), all three species acted similarly in respect to leaf conductance, but their diurnal water potential patterns differed. Douglas fir dropped almost to its threshold of −19.9 bars (−19.9 × 10^5 Pa), but Sitka spruce dropped to −17.7 bars (−17.7 × 10^5 Pa), and western hemlock only dropped to −14.6 bars (−14.6 × 10^5 Pa). These differences may be attributed to differing shoot–root ratios and (or) to differing root absorption capabilities, or, as stated by Jarvis (1974) in his analogy of a rigid flow path, to differing internal water flow resistance within the xylem.

Needle-age Effects

The effect of needle age upon leaf conductance varied considerably among species. Two-

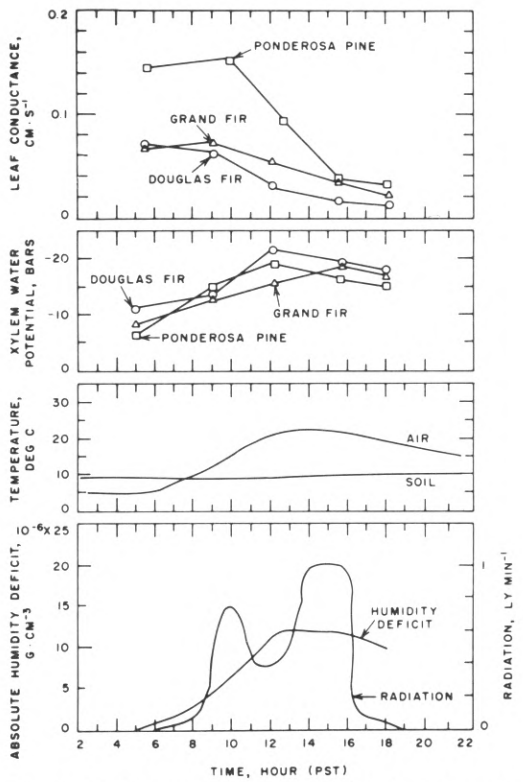

FIG. 5. Environmental and physiological data for Douglas fir, ponderosa pine, and grand fir, taken August 20, 1974, on the Metolius River site. Each leaf-conductance point represents a canopy average of four measurements on 0- to 3-year needle-age classes, three trees, 1 to 3 m tall (1 bar = 10^5 Pa, 1 ly min^{-1} = 69.8 mW cm^{-2}).

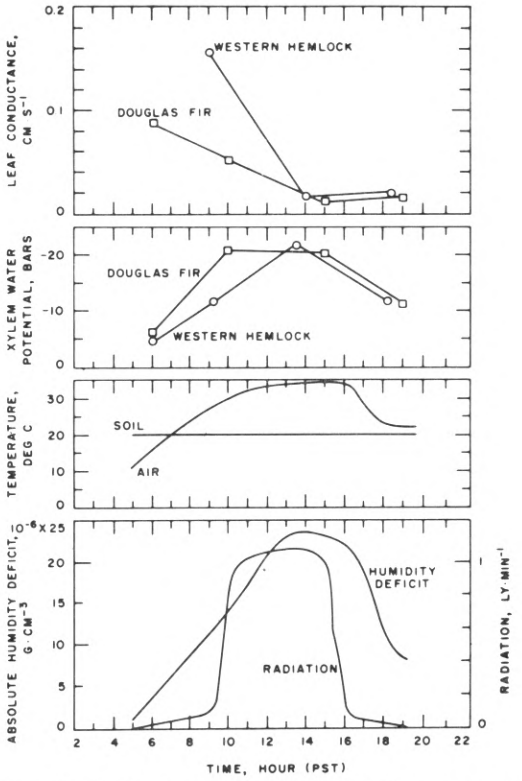

FIG. 6. Environmental and physiological data for Douglas fir and western hemlock taken July 31, 1974, on H. J. Andrews low site. Each leaf-conductance point represents a canopy average of at least nine measurements on 0- to 3-year needle-age classes, three trees, 1 to 3 m tall (1 bar = 10^5 Pa, 1 ly min^{-1} = 69.8 mW cm^{-2}).

m-tall ponderosa pine had needles ranging from current to 3 years old. I detected no differences in leaf conductance by needle-age class at any time of day in mid-August on either the Metolius or Ochoco sites. The age-class structure of western hemlock is not well defined so exact age-class measurements were not possible. It was obvious, though, that samples of predominantly older foliage averaged leaf conductance at least 20% lower than samples of all current foliage. The effect of age class on leaf conductance was most interesting on Douglas fir (Fig. 7). Maximum conductance was higher on older foliage than on current; however, the average leaf conductance throughout the day was equal for all age classes. On other days on the Andrews site and on the Metolius site, average daily leaf conductance was similar for all age classes. On the Ochoco site on a mild day where the water potential theshold was not reached, however, the day leaf-conductance average was 0.078 cm s^{-1} for current foliage, 0.066 cm s^{-1} for 1-year-, 0.051 cm s^{-1} for 2-year-, and 0.041 cm s^{-1} for 3-year-old foliage. From these and other data, it appears that humidity control affects different age stomata differently, but water potential control affects all equally.

Other Controls

Temperature was not treated as a control of leaf conductance because I believe it functions indirectly through ABSHD when air temperatures are above freezing.

On three different occasions with five Douglas fir, extremely low leaf conductances on the order of 0.001 cm s^{-1} were measured on the MacDonald Forest site. In every instance, infiltration pressures of 0.5 to 0.7 bars (0.5 to 0.7 $\times$

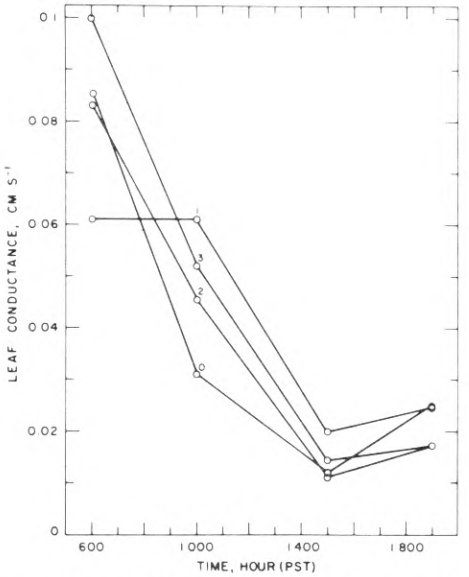

FIG. 7. Diurnal leaf-conductance response of four age classes of Douglas fir needles taken on August 13, 1974, on the H. J. Andrews low site. Each point represents the average of nine leaf-conductance measurements on trees 2 to 3 m tall.

10^5 Pa) indicated stomata at least partly open, and the evaporative demand was very high; ABSHD was 36×10^{-6} g cm^{-3} and VPD was 50 mbars (5×10^3 Pa). Other investigators occasionally have measured resistances seemingly of mesophyll origin (Fry 1965; Lopushinsky 1969; Swank 1972), but it is such a rare occurrence that conclusive data are difficult to obtain.

Discussion

The adaptive significance of stomatal responses of Sitka spruce and noble fir is evident. Sitka spruce is restricted to the foggy coast where evaporative demand is low and precipitation is high. Noble fir and Shasta red fir are considered genetically very close, but noble fir, with little stomatal control, inhabits the northern cooler, wetter part of their combined ranges and Shasta red fir inhabits the drier southern part. Both noble fir and Sitka spruce must ultimately have the ability to close their stomata. In this study, however, little control was evident on days when adjacent Douglas fir were exhibiting significant response.

I hypothesize diurnal leaf conductance to be controlled in two modes on species that exhibit stomatal control within their ranges. One is the control of a maximum-morning leaf conductance contingent on the tree's ability to recharge its sapwood water content during the night, i.e., predawn water potential (Fig. 2). The other mode is the diurnal function after minimum radiation thresholds have been attained and the maximum morning conductance occurs. I see subsequent leaf-conductance changes to be a result of plant water deficits, either external to the plant, low humidity, or internal plant stress, low water potential. The threshold initiating stomatal closure to humidity appears to be about 6×10^{-6} g cm^{-3} absolute humidity deficit or a vapor pressure deficit of 10 mbars (1×10^3 Pa). This threshold has also been identified recently by Black *et al.* (1975). Two factors distinguish the humidity-induced stomatal closure from the water-potential-induced closure. First, the humidity-induced closure does not appear to be species specific (Fig. 4).

Second, the humidity-induced closure is smaller in magnitude, cutting leaf conductance by 50% or less (Fig. 4). Once the water-potential threshold of a species has been reached, leaf conductance may drop by a factor of 10 (Figs. 5 and 6). As evaporative demand increases during the day, plant water potential usually decreases, but this function changes as the rooting zone is depleted and maximum root uptake decreases. A Douglas fir on study site 3 (low) on a hot day in June had a minimum noon water potential of -14 bars (-14×10^5 Pa), but the same tree in August on a day of almost identical evaporative demand had a minimum water potential of -20 bars (-20×10^5 Pa) during the day, with little change (1 bar (1×10^5 Pa)) in its predawn plant water potential.

Notice that water potential has different significance at different times of day. A Douglas fir with a predawn water potential of -16 bars (-16×10^5 Pa) will have a maximum leaf conductance around 0.01 cm s^{-1} (Fig. 2). If the -16-bar (-16×10^5 Pa) measurement represents the minimum noon water potential, leaf conductance may be as high as 0.12 cm s^{-1}. Consequently, studies showing curves of leaf conductance or transpiration as a generalized function of plant water potential are very difficult to interpret. The time of measurement must be included, and preferably both predawn and

minimum noon water potential measurements should be included also.

Several investigators have found transpiration to dip in the early afternoon and rise later in the day. I never observed this pattern but believe it could occur for two reasons. If the drop was induced by low-humidity stomatal response, an increase in absolute humidity would allow recovery. If the drop was induced by a water potential threshold, rapid recovery to a higher water potential could allow stomata to reopen.

My objective was to explain fluctuations in leaf conductance as responses to environmental stimuli. I can now reasonably estimate leaf conductance in Douglas fir and ponderosa pine, given air temperature, radiation, humidity, predawn water potential, and minimum noon water potential. This capability is best organized and most accurately tested in a modeling context. A daily model has been completed (Running *et al.* 1975) that structures these results into a framework allowing further study of the SPAC. Two interesting extrapolations of these data were treated. By coupling biomass data (Grier and Waring 1974) to leaf-conductance data for each species, transpiration could be compared by entire trees, which would be much more useful for interpretation than by unit surface area. Second, a model emphasized the importance of differing root uptake rates and sapwood water storage capacities among different species.

These data also were used for an improved computation of transpiration – potential transpiration (Reed and Waring 1974), used as an environmental ordinate for site classification.

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