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Environmental and physiological control of water flux through *Pinus contorta*[1]

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This study reports measurements of leaf conductance, leaf water potential, temperature, humidity, and radiation collected on a stand of *Pinus contorta* Dougl. ex Loud. lodgepole pine throughout a growing season at the Fraser Experimental Forest in central Colorado, U.S.A. The daily range of leaf conductances decreased 10-fold from June through August. A high correlation ($R^2 = 0.75$) was found between predawn leaf water potential and morning maximum leaf conductance. Low atmospheric humidity significantly decreased midday leaf conductance. A comparison with humidity responses published for other conifers showed good agreement with this study. Seasonal change in total soil-plant resistance to water flux was nonlinearly correlated ($R^2 = 0.99$) with change in predawn leaf water potential, an indirect measure of soil water potential.

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Cette étude rapporte des mesures de la conductance et du potentiel hydrique foliaires, de la température, de l'humidité et du rayonnement reçu par un peuplement de *Pinus contorta* Dougl. ex Loud., pins à feuilles tordues, tout au long d'une saison de croissance à la Forest Expérimentale Fraser dans le centre du Colorado, U.S.A. De juin à août, une diminution d'un facteur de 10 a été mesurée pour le spectre quotidien des conductances foliaires. Une forte corrélation ($R^2 = 0.75$) s'établit entre le potentiel hydrique foliaire noté peu avant l'aurore et la conductance foliaire maximale en matinée. Une faible humidité atmosphérique diminue significativement la conductance foliaire à la mi-journée. Les résultats publiés de travaux relatifs aux réponses des conifères à l'humidité sont comparables à ceux de cette étude. La variation saisonnière de la résistance totale du système plante-sol, en regard du flux hydrique, est corrélée non linéairement ($R^2 = 0.99$) avec le potentiel hydrique foliaire mesuré peu avant l'aurore, le tout constituant une mesure indirecte du potentiel hydrique du sol.

[Traduit par le journal]

Introduction

The central importance of stomatal control of water transport through the soil-plant-atmosphere continuum (SPAC) has been recognized for some time. However, until the last 10 years instrumentation for measuring stomatal response and the variables controlling it were sufficiently bulky and expensive that field studies on coniferous trees were rare. The advent of diffusion porometers (Turner and Parlange 1970; Beardsell *et al.* 1972; Kaufmann and Eckard 1977) and the pressure chamber (Scholander *et al.* 1965; Ritchie and Hinckley 1975) have resulted in a portable and efficient instrument package for field study of leaf water relations. When combined with meteorological data, a relatively complete representation of the environmental factors controlling stomatal response can be obtained. The popularity of this instrumentation package is attested to by the dozens of papers referenced in a recent review of forest water relations work (Hinckley *et al.* 1978).

Stomatal activity responds to four primary environmental variables. These are air temperature, humidity, radiation, and soil water supply as transmitted by internal plant water status. The purpose of this paper is to present leaf conductance data collected on lodgepole pine, *Pinus contorta* Dougl. ex Loud., and quantitatively relate diurnal and seasonal changes in leaf conductance to some of the controlling factors mentioned above. Secondarily, these data will be compared with those of other western conifers. It is important as predictive models of tree stomatal control and forest transpiration are developed that it is determined how generalized these process controls are, both within species and among species that share similar habitats. Do western conifers have generally similar magnitudes and ranges of leaf conductance? More importantly, do they respond similarly to environmental factors?

Methods

The field data were collected during the summer of 1978 in an uneven-aged *Pinus contorta* stand with occasional *Populus tremuloides* at the U.S. Forest Service Fraser Experimental Forest in the Central Colorado Rocky Mountains. The stand was at 2700 m elevation on a level glacial outwash. Because of incomplete canopy closure, tree ages ranged from 10 years to 60-year-old canopy dominants which averaged 12 m in height. Stand basal area was 30.7 m^2 ha^{-1}, and stand density was 2742 trees/ha. with a site index of 22.6 m at 100 years.

Information on the specific trees used in this study is presented in Table 1. Needle weight and total (aboveground) tree

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TABLE 1. Biomass data for lodgepole pine trees at Fraser Experimental Forest, Colorado

Tree No.	DBH, cm	Age, years	Height, m	Mean annual[a] increment, mm/year	Total needle weight, kg	Total tree[b] weight, kg	Needle area,[c] cm^2
PC-1	10.0	30	6.5	—	3.84	18.12	280 680
PC-2	9.3	30	6.2	—	2.75	13.71	201 010
PC-3	9.4	40	7.9	1.6	3.88	20.73	283 600
PC-4	4.8	12	2.7	—	1.52	3.71	111 100
PC-6	8.9	41	7.6	1.8	2.87	16.44	209 780
PC-7	4.4	28	5.3	1.2	0.79	4.29	57 740
PC-9	7.9	30	7.3	1.7	1.88	10.27	137 420
PC-10	11.9	37	8.0	2.2	5.66	32.37	413 710
PC-11	7.6	37	7.0	1.7	1.99	11.29	145 460
PC-12	5.3	14	4.5	2.5	1.28	4.67	93 560
PC-13	7.1	37	6.7	0.9	1.08	6.92	78 940
PC-14	11.9	33	7.0	2.8	9.91	37.89	724 350

[a] Mean annual radial increment during last 10 years.

[b] Not including cone and root weight.

[c] Calculated based on the ratio 73.1 cm^2/g dry weight of needles a ratio determined for a stand in the Medicine Bow Mountains, Wyoming.

weight were obtained by felling and weighing the entire tree after sampling. Total needle area was obtained by subsampling the foliage, oven drying, and measuring lengths and diameters of each fascicle, then calculating the total fascicle surface area geometrically. A ratio of 73.1 $cm^2\ g^{-1}$ dry weight of foliage was found.

The climate of this area is cool and dry for coniferous forests. Temperature extremes of −40°C to 32°C have been recorded. Frost is possible on any night during the growing season, with minimum temperatures on site during summer 1978 always below 4°C. Maximum daily air temperatures during the summer of 1978 were 20°C to 23°C with a high of 26°C. Midday relative humidity typically ranged from 15 to 25% except during thundershowers.

Precipitation averages 58.4 cm/year with nearly two-thirds falling as snow between October and May (Alexander and Watkins 1977). Snowmelt was complete at the study site by mid-May in 1978 and provided the only effective soil water recharge for the growing season. Summer thundershowers did not contribute significantly to soil water supply. Monthly neutron probe readings were taken with four access tubes at 15 cm depth intervals down to 1.8 m by Forest Service technicians on a similar stand about 200 m from this study site. An average of the four readings at each depth for each month calibrated to percentage soil moisture was calculated. Hydrologic estimates place evapotranspiration at 50 to 60% of yearly precipitation in this area (Alexander and Watkins 1977). Obviously, forest transpiration is a major component of the hydrologic balance in these watersheds.

Although the Forest Service maintains a permanent weather station at Fraser Experimental Forest headquarters 5 km from the study site, some climatic data were recorded on site during the study period (June 1 to September 1, 1978). Air temperature measured by a thermistor was continuously recorded on a strip-chart recorder. Dew point temperature was measured with a heated lithium chloride dew point sensor, also recorded continuously on the strip chart. These instruments were mounted in a standard vented weather station box located 1.5 m above the ground. Backup data were available from both a sling psychrometer and the diffusion porometer sensors. Onsite soil temperature at 18 cm depth was taken with a dial temperature probe at noon each day. A quantum sensor mounted on the porometer cuvette measured photosynthetically active radiation (PAR). Extensive vertical profiles through the canopy of temperature, wind speed, and vapor pressure were measured in a concurrent study on this site. Preliminary results are reported in Miller *et al.* (1979). Because summer precipitation normally does not provide any effective input to the soil it was not measured on site, but was recorded at the Fraser Experimental Forest headquarters.

A null balance diffusion porometer (Beardsell *et al.* 1972) was used for the leaf conductance (k_l) measurements. With this instrument, dry air is introduced into the cuvette at a rate just sufficient to balance the water vapor transpired by the enclosed needles. At a given null balance humidity the flow rate of dry air is proportional to the k_l of the enclosed needle sample. On each study tree, three branches were chosen for sampling. Vertically the branches were approximately midcrown. One branch was chosen at each of north, southeast, and southwest aspects of the crown. On each branch, needle samples were prepared representing each of the previous 3 years, and by midsummer, the current-year's foliage ages. Each tree was sampled between 4 and 6 days during a 2- to 3-week period and these twigs were used for all measurements on that tree. At the end of sampling period for a given tree, the twigs were clipped to assess leaf surface area for the leaf conductance calculation. Each fascicle was picked, diameter and length measured, and total surface area calculated geometrically. Total leaf surface area enclosed in the porometer cuvette was typically 75 to 125 cm^2, and composed of 30 to 40 fascicles.

Xylem pressure potential measurements were taken on individual fascicles using a pressure chamber and dissecting microscope. At any given sampling period three fascicles were measured, one off each sample branch, and the average recorded. Between branch variability was rarely greater than 0.033 MPa.

A study day began with predawn measurement of base xylem pressure potential ($B\Psi_l$) taken around 0400 mountain standard time (MST). Because of limitations of porometer response, leaf conductance data could not be taken until air temperature reached 5°C and any dew or frost had evaporated. Consequently, the first sampling period was typically completed between 0700 and 0800 MST. Sampling was repeated at 2- to 3-h intervals until direct sunlight left the site, except when thunderstorms temporarily interrupted the schedule. Normally, five sample sets were collected per day. Each sample set consisted of porometer measurements on the 9 to 12 samples per tree, three fascicle pressure chamber measure-

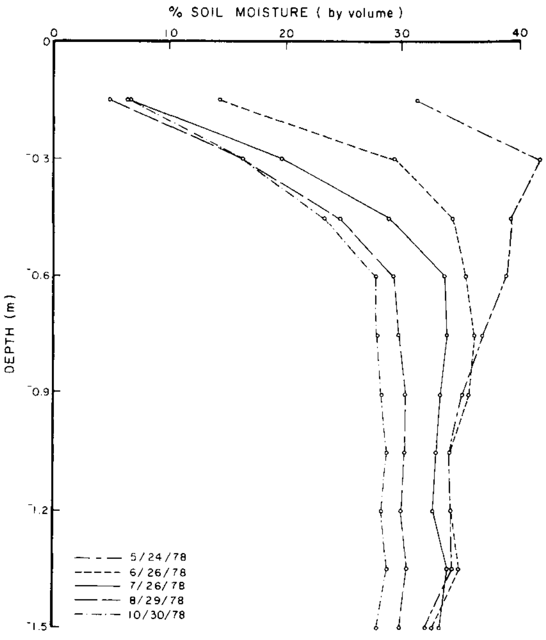

FIG. 1. The seasonal depletion of soil water by depth on the Fraser site. Data taken with a neutron probe.

ments per tree, and recording of air temperature, dew point, and PAR both at leaf level and in an unshaded open spot. Because each age of needles represented a roughly equal proportion of the crown, estimates of whole crown transpiration rates were obtained by averaging the 9-12 leaf conductance measurements per tree at each sample period. An analysis of stomatal response by the different leaf age-classes was done separately.

Evaporative demand was calculated from air temperature and dew point data in mass units as an absolute humidity deficit (ABSHD) in units of micrograms H_2O per centimetre cubed. When multiplied by leaf conductance (k_l) in centimetres per second a simple equation for transpiration flux density (TFD) results,

$$[1] \quad \mathrm{TFD} = \mathrm{ABSHD} \times k_l$$

with TFD units of micrograms per square centimetre per second (Elfving *et al.* 1972).

Much use has been made of various analogies of Ohm's law equations for SPAC water flow. In a form adapted to this data analysis:

$$[2] \quad \mathrm{TFD} = \frac{\Psi_{\mathrm{soil}} - \Psi_l}{R_{\mathrm{SPAC}}}$$

where Ψ_l is total water potential of the leaf, $B\Psi_l$ is used to estimate Ψ_{soil} in MPa, and R_{SPAC} is a cumulative total water flux resistance from the soil to the atmosphere (Kaufmann and Hall 1974; Hinckley *et al.* 1978). Because TFD was computed in this study, Eq. 2 was rearranged to analyze R_{SPAC}.

Results

The seasonal depletion of soil water is shown in Fig. 1. Note that until the July 26 measurement the majority of transpired water came from the upper 0.6 m of the soil profile. After July 26 less water was taken from this upper profile and the primary location of water uptake was the 0.6 to 1.5 m of soil depth.

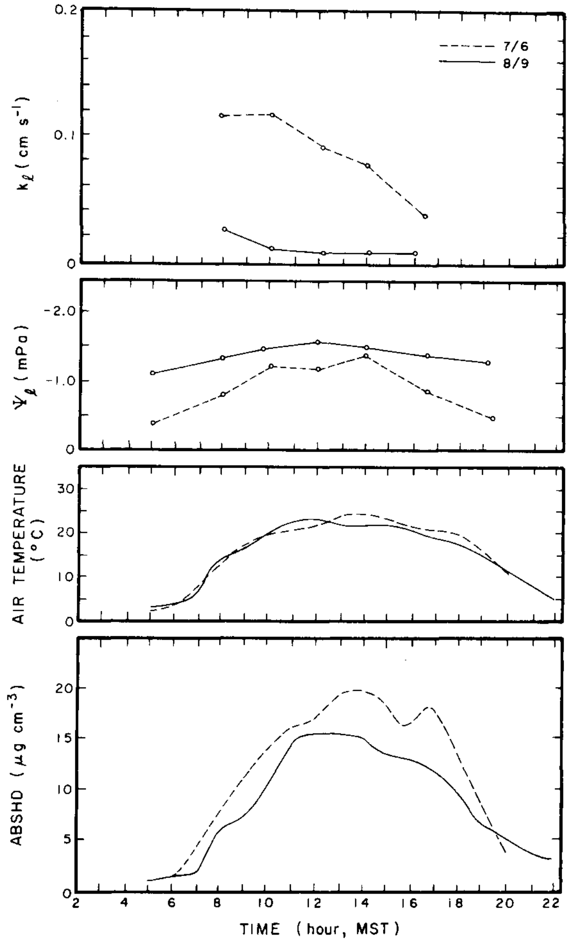

FIG. 2. Diurnal patterns of leaf conductance (k_l) and leaf water potential (Ψ_l) for lodgepole pine representing the seasonal extremes at the Fraser site, with accompanying climatic data.

Patterns of k_l and Ψ_l illustrating seasonal ranges are shown in Fig. 2. Note that although temperatures were similar and the evaporative demand on August 9 was actually somewhat lower, the average k_l was 80% lower than for July 6. This reduction was a result primarily of depletion of available soil water causing a decrease in predawn Ψ_l, ($B\Psi_l$), from -0.4 MPa on July 6 to -1.02 MPa on August 9. In June and early July, canopy average k_l in the morning was typically 0.12-0.16 cm s^{-1} with individual k_l readings as high as 0.4 cm s^{-1}. By mid-August, k_l was always below 0.03 cm s^{-1} and not uncommonly below 0.01 cm s^{-1} during the afternoon.

The age of a needle has been found to affect stomatal response in some species. Running (1976) found older

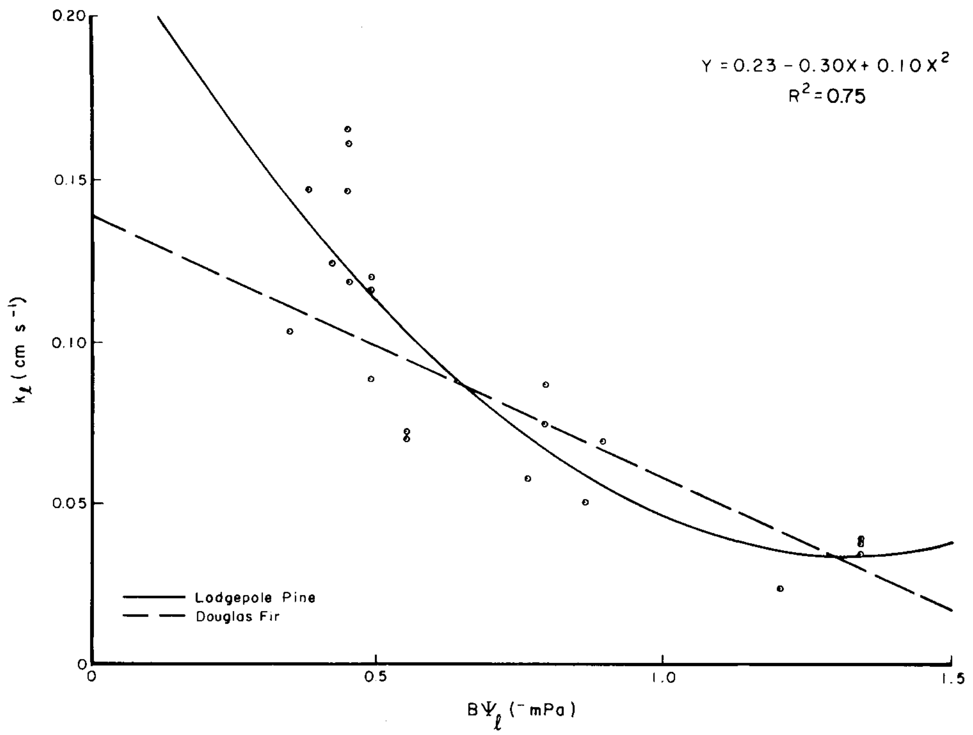

FIG. 3. A second degree regression from a least squares curve fit of maximum morning k_l on predawn Ψ_l ($B\Psi_l$). The solid line represents the equation fitting data points for lodgepole pine. The dashed line is for Douglas-fir from a previous study (Running 1976).

needles to have an average daily k_l one-half that of current foliage in *Pseudotsuga menziesii*. However, no difference was found between age-classes in *Pinus ponderosa*. In this study, lodgepole pine showed no age-related response sufficiently predictable for formal analysis. It did appear that stomatal control was more erratic as needles aged. In the oldest needles, maximum k_l seemed lower than the current needles. Also, under water stress or low light, older needles appeared unable to close their stomata quite as tightly as newer needles, resulting in higher minimum k_l. This factor could contribute to needle turnover if older needles could not maintain adequate internal water under severe stress and became irreversibly desiccated.

The effect of air temperature on k_l of conifers is weak between 0 and 40°C, with k_l increasing slightly with increasing temperature (Hinckley *et al.* 1978). At some temperature below 0°C xylem water freezes, and stomata are closed. However, when a warm spring day is preceded by an overnight frost, k_l is greatly reduced even after air temperatures have recovered. Limited data from Fraser and a site in central Oregon show morning k_l to be less than one-half of expected values after -3 to -4°C nights at an air temperature of 10°C (S. W. Running, unpublished data). I have found this frost response in Douglas-fir, ponderosa pine, and lodgepole pine, but do not yet have sufficient replication to analyze statistically. Data from any day having a previous night minimum below -1°C were excluded from the following analysis.

Incoming radiation was also measured, as PAR directly affects stomatal activity. A wide variety of species have a threshold of about 10% of full sun or 70-80 $\mathrm{Wm^{-2}}$ for full stomatal opening (Hinckley *et al.* 1978). Consequently, when leaf level PAR readings were below 70 $\mathrm{Wm^{-2}}$, those data were removed from the following analysis in an attempt to analyze only water stress related responses.

A direct correlation was found between predawn Ψ_l and morning maximum k_l in Douglas-fir by Running (1976). This same correlation was developed for the lodgepole pine studied and is shown in Fig. 3 with the relation for Douglas-fir superimposed. Note the good agreement in both magnitude and slope. It was difficult to get a true morning maximum k_l after sufficient radiation was received but before humidity-related k_l reduction began. Consequently, the correlation may be higher if optimal conditions could be sampled.

Midday Ψ_l minimums are also known to abruptly close stomata when a certain threshold is reached

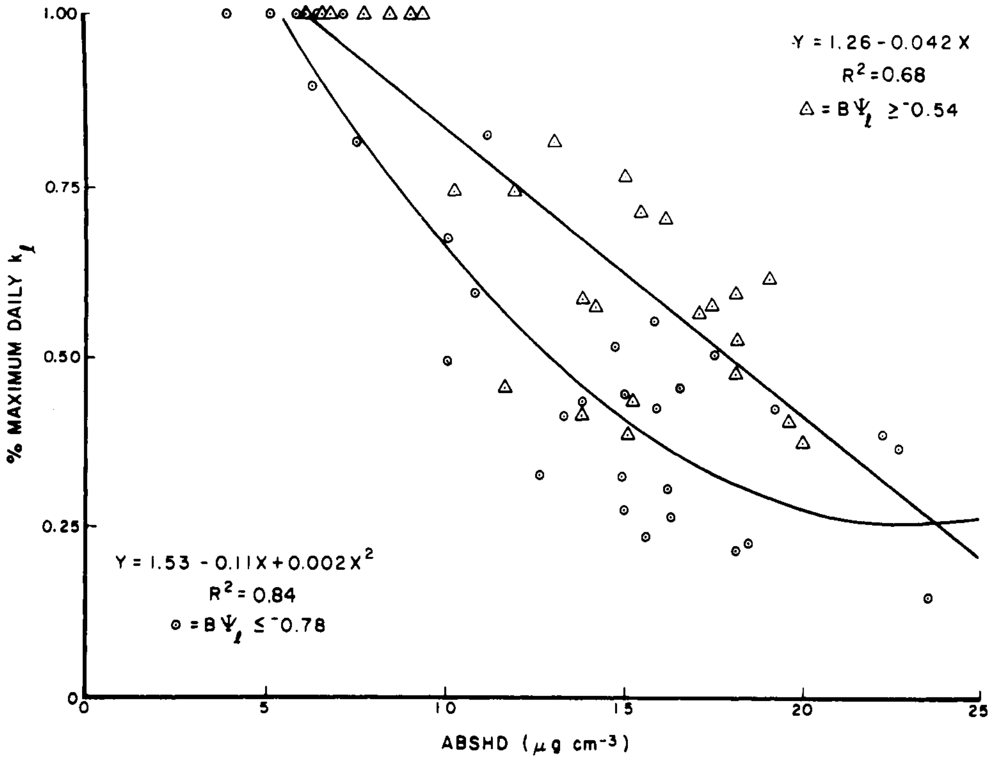

FIG. 4. The influence of absolute humidity deficit (ABSHD) on k_1 for lodgepole pine at the Fraser site. Reduction in k_1 is plotted as a fraction of the measured morning maximum k_1 for that tree on that date. The lower curve shows the shift in k_1 response as $B\Psi_1$ declines below -0.78 MPa.

(Hinckley *et al.* 1978). This threshold has been found to be -2.0 MPa in Douglas-fir and -1.8 MPa in ponderosa pine (Running 1976). Under induced stress conditions reported in Running (1979*b*), these lodgepole pine showed a similar minimum Ψ_1 threshold of -1.8 to -2.0 MPa, duplicating greenhouse results for lodgepole pine by Lopushinsky and Klock (1974). However, under natural conditions, despite $B\Psi_1$ levels below -1.3 MPa, midday Ψ_1 never was below -1.6 MPa.

Direct response of stomata to low humidity was first demonstrated by Lange *et al.* (1971). Before that time, observed k_1 versus humidity response was thought to be caused predominantly by Ψ_1. Analysis of the k_1 versus humidity response is made difficult in that it must be separated from $B\Psi_1$ control such as in Fig. 3. Two methods of analysis were attempted. First, a direct regression of k_1 on ABSHD was done with data separated into categories of $B\Psi_1 > -0.54$ MPa and $B\Psi_1 < -0.78$ MPa, there being no data points in between. The regression of k_1 on ABSHD above -0.54 MPa showed an $R^2 = 0.60$, while below -0.78 MPa the $R^2 = 0.38$.

Second, the diurnal humidity related k_1 reduction was normalized to the measured morning maximum k_1 for a particular tree on that day. The result of this analysis is shown in Fig. 4. Data pooled for the entire season showed an $R^2 = 0.68$ for k_1 versus ABSHD. When these data were separated above 0.54 MPa and below -0.78 MPa, correlations were $R^2 = 0.68$ and $R^2 = 0.84$, respectively.

Note that the slope is steeper and the reduction of k_1 is sharper in the less than -0.78 MPa group than in the lower stress group (Fig. 4). It appears that some portion of the leaf water storage must be depleted before humidity response predominates. In Fig. 2, k_1 stayed unchanged from 0800 to 1000 on July 6 despite an ABSHD of 13 μg cm^{-3} which should, according to Fig. 4, cause a 30% reduction. However, the August 9 data showed the expected k_1 reduction from 0800 to 1000 even with only a 10 μg cm^{-3} ABSHD. For all trees measured with $B\Psi_1 > -0.78$ MPa, morning k_1 stayed constant until around 1000, similar to July 6 in Fig. 2. After 1000 the humidity-induced control shown in Fig. 4 appeared to predominate. This suggests a small reservoir of leaf water that postpones humidity-induced guard cell turgor loss. As seasonal water stress increases, this reservoir may not be refilled each night, causing more rapid humidity sensitivity later in the growing season. This hypothesis is supported by recent work that shows guard

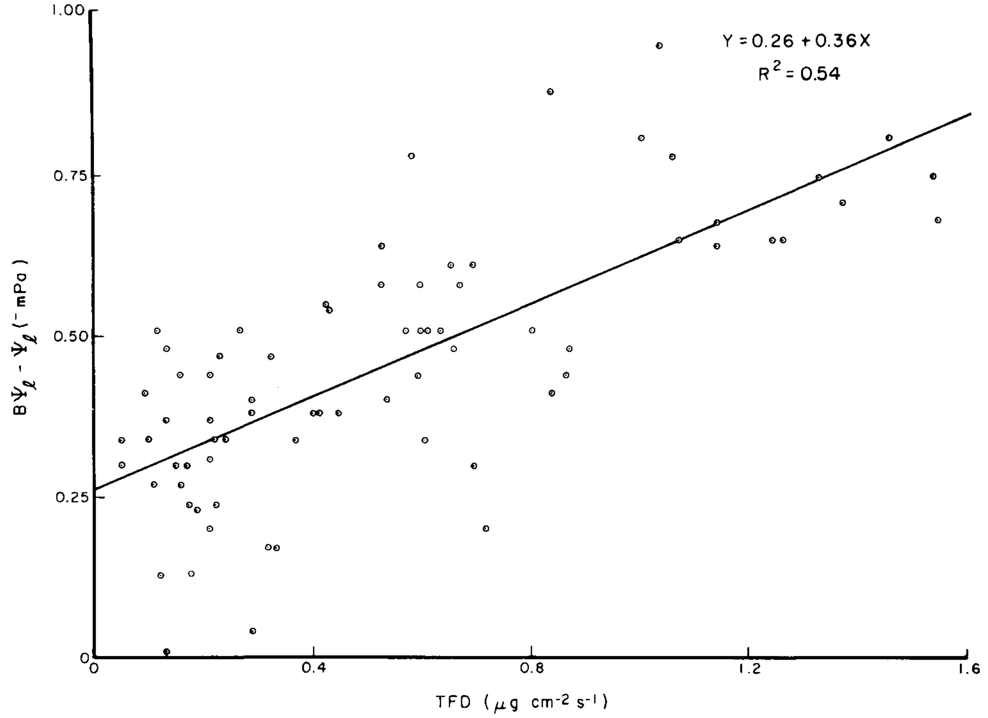

FIG. 5. A regression of the $B\Psi_l - \Psi_l$ gradient developed with increasing transpiration flux density (TFD) for lodgepole pine.

cell turgor loss at low humidity to be the result of direct evaporative water loss by the guard cells and immediate mesophyll cells (Edwards and Meidner 1978; Losch and Schenk 1978).

Equation 2 predicts a linear relationship between the gradient of Ψ_{soil} (or $B\Psi_l$) to Ψ_l, and crown transpiration or TFD. This is occasionally found in crops of deciduous trees (Jarvis 1975; Landsberg *et al.* 1975; Hinckley and Bruckerhoff 1975). However, when this relation was attempted on these data from lodgepole pine the result was poor, as seen in Fig. 5. Two factors, plant capacitance (internal water storage) and variable R_{SPAC}, caused this poor correlation. A more careful analysis of the Ψ_l versus TFD relationship is presented for four lodgepole pine under progressively higher soil water stress (Fig. 6).

On each day a significant hysteresis occurred. In the morning a given Ψ_l produced a much higher rate of TFD than later in the afternoon. This is best explained by diurnal depletion and recovery at night of storage tissue within the tree and water recharge of soil near the roots. Waring and Running (1978) showed that sapwood can be drawn down to 20% of saturation by a -1.0 MPa xylem water potential. They also calculated significant storage capacity in the foliage and sapwood of coniferous trees and rapid exchange rates. Running (1979c) demonstrated that Ψ_l is very sensitive to small changes in needle water content. Equation 2 cannot cope with this additional component of SPAC water flow. A modified Eq. 2 can predict the average slope of the $\Delta\Psi$/TFD curves in Fig. 6 if R_{SPAC} is changed as soil water is depleted. R_{SPAC} was calculated for each day at the point of minimum Ψ_l as shown by the dotted lines, by dividing Ψ_l by TFD. When this R_{SPAC} value was correlated with $B\Psi_l$ a very strong relation was generated ($R^2 = 0.99$) (Fig. 7). A pooled analysis of all 12 trees in Table 1 showed an R_{SPAC} versus $B\Psi_l$ relation only slightly weaker, with an $R^2 = 0.89$.

A prime reason for this success is that R_{SPAC} was calculated solely from Ψ_l, not ($\Psi_{soil} - \Psi_l$) or ($B\Psi_l - \Psi_l$) as is usually done (Hinckley *et al.* 1978). Midday Ψ_l has both a static ($B\Psi_l$) and dynamic ($B\Psi_l - \Psi_l$) component. However, total Ψ_l is the necessary force being generated for moving water in the SPAC at that time. $B\Psi_l - \Psi_l$ only contributes to the flux component, and in particular neglects the static soil water availability which is contributed by the $B\Psi_l$ measurement. This analysis suggests that the decrease in soil water potential and hydraulic conductivity represented by the $B\Psi_l$ measurement provides a major component of the overall SPAC water flow resistance in these trees.

In order to determine if the functions developed from this data on the Fraser site are generally representative of lodgepole pine responses, I compared these results

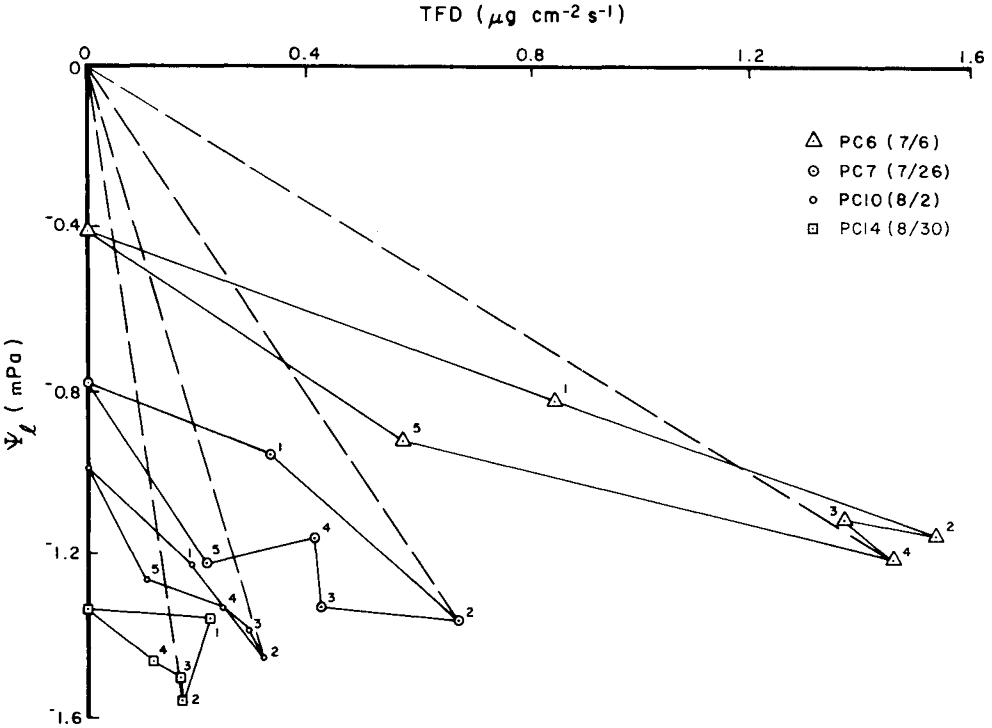

FIG. 6. Plots of Ψ_l versus TFD for four lodgepole pine showing diurnal hysteresis. Numerically labeled points indicate sampling time: 1, 0800; 2, 1030; 3, 1300; 4, 1530; 5, 1730 all in MST. Points on the ordinate are $B\Psi_l$. Dashed lines show the slopes used for SPAC flow resistance (R_{SPAC}) calculations in Fig. 7.

with those from an earlier study I had done on lodgepole pine. During the summer of 1975, 5 days of data were taken on a stand of 2-3 m tall lodgepole and ponderosa pine in central Oregon. Instrumentation included a null balance porometer, a pressure chamber, and a portable climatic station, all identical to the equipment used in the Fraser study. The sampling scheme was also identical.

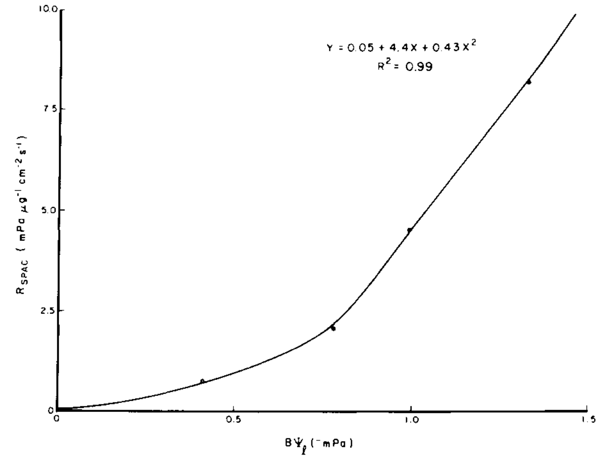

FIG. 7. The influence of $B\Psi_l$ on the seasonal increase in R_{SPAC} for the four lodgepole pine in Fig. 6.

Diurnal courses of k_l and Ψ_l for the lodgepole pine are shown in Fig. 8. The general ranges of k_l, 0.167-0.023 cm s^{-1} and Ψ_l, -0.65-1.8 MPa were similar to the Fraser results. However, a few differences were evident. The $B\Psi_l$ readings on May 15 and June 18 of -0.65 to -0.75 MPa would suggest a morning k_l around 0.08 cm s^{-1} according to Fig. 3, while in fact they were double that. But the data for July 23, August 12, and September 9 were more in agreement. Weather on the May 15 and June 18 study days was abnormally cool, with high temperatures of only 14 to 15°C, and ABSHD not exceeding 7 μg cm^{-3} during the afternoons. However, the k_l levels were normal for that time of year. The real discrepancy was the $B\Psi_l$ of -0.6 to -0.75 MPa rather than the -0.4 to -0.5 MPa that might have been predicted under the presumed high soil water conditions shortly after snowmelt. Soil temperature was 9°C so should not have been a factor. Fetcher (1976) also found $B\Psi_l$ of -0.9 to -1.1 MPa in lodgepole pine in Wyoming during and shortly after snowmelt when soil water could not have been limiting. In his study, the accompanying k_l data were also high, 0.2 cm s^{-1}, indicating that the trees were not under the stress predicted by Fig. 4 for $B\Psi_l$ of that magnitude.

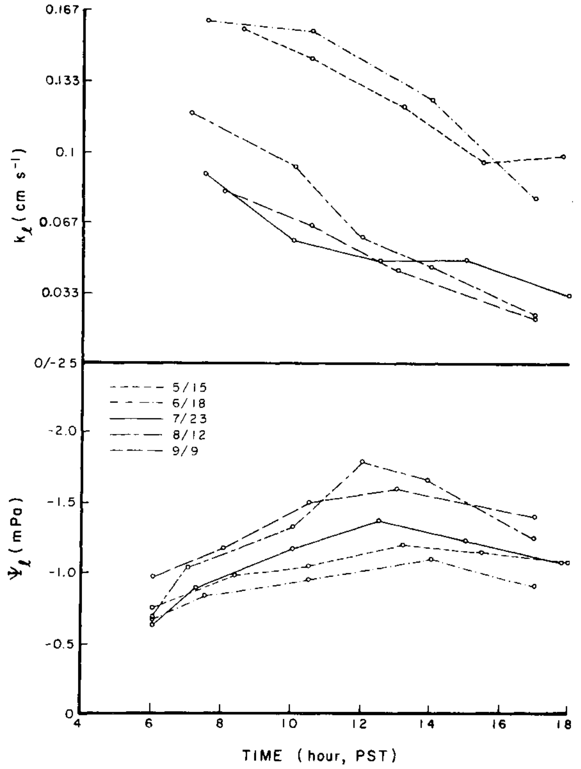

FIG. 8. Diurnal patterns of k_l and Ψ_l for lodgepole pine from a study site in central Oregon, taken on the indicated dates in 1975.

Discussion

Before using the functions developed in this paper for general transpiration models (Waring and Running 1976; Running 1979*a*), it is crucial to determine if these functions (Figs. 3, 4, and 7) are representative of responses of other western conifers to environmental stresses. In this regard, I feel the similarity of responses of morning k_l to $B\Psi_l$ in two different conifer species on sites 1700 km apart to be significant. In addition, correlating k_l and Ψ_l is not a simple task. As graphically illustrated in Fig. 3 of Running (1976), Ψ_l can change diurnally from −0.3 to −1.5 MPa while k_l stays constant. Conversely, in Fig. 2 on July 6, Ψ_l was constant from 1000 to 1200 while k_l decreased 20%. At a Ψ_l of around −1.3 MPa, k_l was 0.08 cm s^{-1} on July 6, but only 0.01 on August 9 (Fig. 2). This variability also makes it difficult to separate Ψ_l from ABSHD control of k_l. However, k_l correlates much better with ABSHD than Ψ_l during the day. I conclude, beyond the $B\Psi_l$ reading, that Ψ_l only controls k_l at the threshold of leaf Ψ_π which is normally between −1.8 and −2.0 MPa in these conifers (Hinckley *et al.* 1978; Running 1979*c*). I have only found a strong seasonal correlation between k_l and Ψ_l using the analysis of Fig. 3 with $B\Psi_l$.

It is physiologically reasonable that $B\Psi_l$ and morning k_l be related. Barring rainfall, predawn Ψ_l ($B\Psi_l$) usually represents the maximum water stress recovery the plant attains during that day. This water stress is measured by $B\Psi_l$ at the leaf under zero or the lowest flux conditions of the day not confounded by subsequent flow related Ψ gradient development. Other data from this study, published in another paper, found Ψ_l directly related to needle water content when measured under low flux conditions (Running 1979*c*). One would expect maximum k_l under these conditions as soon as the radiation threshold was satisfied. Then as leaf water reservoirs are depleted and humidity reduction occurs, k_l declines during the remainder of the day (Fig. 2).

Another critical function compared among other conifers was the k_l response to humidity. Comparison was best with other studies by relating k_l to ABSHD segregated into different categories of $B\Psi_l$ or Ψ_{soil}. A comparison of k_l versus ABSHD was done for the lodgepole pine from the central Oregon study. The regression of k_l on ABSHD had an $R^2 = 0.79$ because the seasonal range in $B\Psi_l$ was rather small compared to the Fraser lodgepole pine.

TABLE 2. Comparison of the reduction rate in leaf conductance to humidity deficit for some western conifers

$B\Psi_l$ or Ψ_{soil}	Douglas-fir	Sitka spruce	Western hemlock	Engelmann spruce	Lodgepole pine	Ponderosa pine
−0.0 to −0.4	0.007[a]	0.019[c]	0.006[b]	—	—	—
	0.006[b]	0.006[b]	—	—	—	—
−0.4 to −0.8	0.005[a]	—	—	0.008[f]	0.008[d]	0.003–0.005[b]
	0.007[b]	—	—	—	0.004[e]	0.004[e]
−0.8 to −1.5	0.003[a]	—	—	—	0.002[d]	—
	0.004[b]	—	—	—	—	—

NOTE: Slopes are given in centimetres per second per microgram per centimetre cubed.

[a] Tan *et al.* 1977.

[b] Running 1976.

[c] Watts *et al.* 1976.

[d] This study.

[e] Running, unpublished data from central Oregon.

[f] Kaufmann 1976.

Of greater importance is the slope of the k_l versus ABSHD function. These slopes were compared for data from six western conifers from four different authors (Table 2). Note that with one exception the range for all species under all conditions was 0.002-0.008 cm $s^{-1}/\mu g\ cm^3$. The one exception, from Watts *et al.* (1976), was for Sitka spruce (*Picea sitchensis*) in Scotland. Their k_l data only ranged from 0.25 to 0.13 cm s^{-1} because these trees were never subjected to soil water limitation. If these trees could be analyzed for the k_l range of 0.3-0.01 cm s^{-1} that the other studies covered, the results might have been more comparable. Also, the slope decreased as Ψ_{soil} decreased, as best shown for Douglas-fir. This was expected since $B\Psi_l$ dropped the total possible range of k_l as limited by the Fig. 3-type response. From a modeling perspective, the comparability of slopes in Table 2 for six separate species is encouraging.

Use of Eq. 2 in various forms to calculate a total R_{SPAC} has been attempted before (Hellkvist *et al.* 1974; Landsberg *et al.* 1976; Roberts and Knoerr 1978). However, the experimental conditions and units of measurement were so different that comparison was difficult. Observations of the seasonal slope change in Fig. 6 have also been published (Hinckley and Bruckerhoff 1975; Kaufmann 1975). However, the overall slope change has never been related to $B\Psi_l$ or Ψ_{soil} before, as illustrated in Fig. 7. Consequently, it is difficult to determine if the function in Fig. 6 will be of a general nature until that analysis is performed on other data. In larger trees, the diurnal capacitance change will probably erode the overwhelming soil-root resistance control suggested by Fig. 6 (Waring and Running 1978). The role of plant capacitance in the water relations of these lodgepole pine was reported in other papers (Running 1979*b*, 1979*c*).

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