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SEASONAL AND SPECIES COMPARISONS OF LEAF CONDUCTANCE
CONTROLS FOR WESTERN MONTANA CONIFERS

by

Jeffrey S. Graham

B. S., University of Montana, 1979

Presented in partial fulfillment of the requirements
for the degree of

Master of Science

University of Montana

1983

Approved by:


Chairman, board of examiners


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Forestry

Seasonal and Species Comparisons of Leaf Conductance Controls in Western Montana Conifers (45 pp.)

Director: Steven W. Running



A central part of forest transpiration modelling is the environmental control of stomatal activity and hence leaf conductance to water vapor. Although field data on leaf conductance control for western conifers has been accumulating, studies to compare species and seasonal differences are needed. The purpose of this study was 1) to contrast spring with summer leaf conductance controls for lodgepole pine, and 2) to compare summertime leaf conductance controls for three conifer species: Douglas-fir, ponderosa pine, and lodgepole pine.

Using a null-balance porometer diurnal measurements of leaf conductance were periodically made from early spring until early fall. Concurrently, several environmental parameters which influence stomatal activity were recorded.

Springtime leaf conductance in lodgepole pine was found to be related to both minimum air temperatures of the previous night and a seasonal degree-day summation. In contrast, summertime leaf conductance was strongly correlated to predawn water potential and absolute humidity deficit.

Comparison of summertime leaf conductance trends found Douglas-fir and ponderosa pine to be more variable and in poorer agreement with prior research than lodgepole pine. Maximum daily leaf conductance in ponderosa pine and lodgepole pine, but not Douglas-fir, was significantly related to predawn water potential. Absolute humidity deficit was significantly correlated to leaf conductance for all sampled species.

ACKNOWLEDGMENTS

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I would like to express my thanks to many people who gave me help and encouragement with this project. First and foremost, Dr. Steve Running for his endless tolerance with my changing directions; the Committee members, Drs. Don Potts and George Briggs, for their advice and comments; Roger Hungerford and Ron Babbit for technical assistance; Daron Duncan for patiently holding the cuvette; and finally, Nan Vance, who offered numerous ideas and suggestions.

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CHAPTER I

CONTRASTING PATTERNS OF SPRING AND SUMMER

LEAF CONDUCTANCE IN LODGEPOLE PINE

INTRODUCTION

The primary environmental factors affecting leaf conductance in conifers are well known. These are shortwave radiation, humidity, air temperature, and leaf water status (Hinckley et al. 1978). Leaf conductance prediction via these parameters has been an integral part of forest transpiration modelling (Running 1983, Tan et al. 1978). However, most functions which relate leaf conductance to controlling environmental factors have been developed using controlled environments or summertime conditions. Hence, it is less certain how or to what degree these parameters influence stomatal activity during non-summer periods. Extrapolation using summertime relationships is especially risky in areas with cold or highly variable winter and spring climates. Many parts of the Rocky Mountain region, for example, may experience freezing temperatures during much of spring. However, decidedly mild conditions are possible through much the year.

During continuous subfreezing conditions stomata generally remain closed (Tranquillini 1982). This may be an effect of both freezing temperatures and morphological or biochemical adjustments induced by cold hardiness. Both Christersson (1972) and Andersson (1980) reported that stomata of hardened conifer seedlings remained closed despite favorable temperatures. However, on mild days following a freeze, Fahey (1979) observed that stomatal activity in Pinus contorta was related to the severity of the frost. Similarly, Tranquillini (1982) describes stomatal opening for Pinus cembra during winter when temperatures rise above 10 C for 24 hours.

Thus, past research has shown that stomatal activity outside the summer in cold winter climates may be influenced by both temperature and dormancy status. The objective of this study was to contrast spring and summer environmental controls of leaf conductance for lodgepole pine in Western Montana.

MATERIALS AND METHODS

This research was conducted at the University of Montana School of Forestry Lubrecht Experimental Forest during the spring and summer of 1982. The Lubrecht forest is located in the Garnet Range approximately 56 km northeast of Missoula, Montana. The study plot was at an elevation of 1250 m and supported an open, mixed conifer stand consisting of Pinus ponderosa, Pseudotsuga menziesii, and Pinus contorta with scattered Juniperis scopulorum, Larix occidentalis, and Populus tremuloides. The habitat type was Pseudotsuga menziesii/ Vaccinium caespitosum (Pfister et al. 1977).

The climate of the Lubrecht forest is characterized by extremes (Steel 1981). The maximum and minimum recorded temperatures at the forest headquarters are 39 C and -43 C respectively. Although frosts have been occasionally recorded throughout the summer, 124 above freezing nights are averaged per year. The typical daily temperature range is 6 C to 28 C in July and -13 C to -3 C in January. The average minimum relative humidity in summer is 30%. Annual precipitation averages 45 cm with 21 cm (47%) falling as rain from May to September. Snow depth typically peaks at 39 cm by late winter and snowmelt is usually complete by May 1.

In addition to weather data collected at the forest headquarters, a meteorological station was maintained on the study site. Air temperatures 1.4 m above the ground and soil temperatures at 5 cm and 50 cm were measured by thermistors. Incoming shortwave radiation was measured by a pyranometer (LI-COR Inc.). Sensors were monitored hourly and recorded by a custom datalogger provided by the U.S. Forest Service. Prior to each measurement set relative humidity was recorded by an aspirated psychrometer (Environmental Electronics Corp.). Precipitation was measured by a standard 20 cm rain gauge at the forest headquarters, approximately 500 meters from the site.

Three sapling size lodgepole pine trees were selected for leaf conductance measurements. Selection was based on healthy outward appearance and close proximity to allow for ease of measurement. The trees were 10.0 cm, 7.3 cm, and 5.0 cm in diameter and 3.6 m, 7.6 m, and 5.5 m in height respectively. On each tree two branches approximately 1.5 m above the ground, one facing north and the other south were chosen. On each branch samples of 15 to 25 healthy needles were prepared by carefully cutting back adjacent needles. During the spring 3 needle age classes were sampled: first, second year, and third year. In the summer only first and second year needles were sampled. The current year's flush was not used. Both north and south branches and multiple

needle age classes were chosen to provide a representation of canopy average leaf conductance. Samples were used on several measurement days before being clipped for needle area determination. Total needle surface area was determined geometrically.

A null balance diffusion porometer (Beardsell et al. 1972) was used for leaf conductance measurements. The previously prepared needle samples were placed in the cuvette. A flow of dry nitrogen was then introduced into the cuvette to balance the transpirational production of water vapor and maintain a constant relative humidity (RH). Leaf resistance was first calculated as:

$$R = (100/RH - 1) * AREA/FLOW$$

where R = leaf resistance in sec/cm

RH = relative humidity in %

AREA = leaf area in the cuvette in cm²

FLOW = dry N₂ flow in cm /sec.

Conductance, (kl), was then calculated as:

$$kl = 1 / R$$

where kl = leaf conductance in cm/sec. Although care was taken to shield the cuvette from direct solar radiation, chamber temperatures up to three degrees C above ambient were occasionally observed.

For each sample tree predawn water potential was measured with a pressure chamber within three days of porometer readings. Evidence exists that errors will result if pressure chamber readings are made on frozen tissue (Evans and Reid 1974). Therefore, on subfreezing spring mornings, clipped twigs were allowed to slowly thaw before measurement. Thawing took place in moistened, sealed plastic bags to maintain water status (Karlic and Richter 1979). Pressure chamber readings were also taken following each porometer data set. Preliminary sampling found within tree water potential ranges to be under 0.2 MPa. For this reason and to conserve twigs only single pressure chamber readings were made on each tree at each measurement set.

The sampling schedule began in late March. At this time nightly freezing was still assured yet day temperatures were mild enough to allow for considerable physiological activity. Since an objective in this study was to evaluate the effects of spring weather on leaf conductance, sampling at first was more intensive. Throughout the study, 3 or occasionally 4 data sets per day each consisting of 12 to 18 porometer readings were taken. During the summer sampling became less frequent. The last measurement day was October 1.

RESULTS

Overall seasonal trends

The seasonal progress in water relations measurements and air temperature extremes for the Lubrecht site are shown in Figure 1. Spring conditions were characterized by freezing nights with mild days. During the summer average air temperature extremes were 6 C and 22 C. Spring soil temperatures at both 5 cm and 50 cm remained at 0 C while covered by snow. Not until April 22 did soil temperatures at 50 cm rise above 5 C. This rise in soil temperature closely followed complete snow melt.

Predawn leaf water potential ($B\psi$), representing soil water status (Hinckley et al. 1978), showed minor fluctuations during spring and early summer. Aside from one day, May 18, pressure chamber readings were between -0.6 and -0.8 MPa. Early summer rains and low evaporative demands apparently aided in maintaining soil water status. By midsummer, predawn water potentials had declined to -1.3 MPa but recovered to -0.9 MPa following a September rain.

Daily maximum leaf conductance was quite low in early spring (0.03 to 0.05 cm/sec) but rose steadily into summer. By June 11 the maximum conductance had increased to 0.21 cm/sec, a more than five fold increase from early April. Leaf conductance then declined steadily to a late summer low

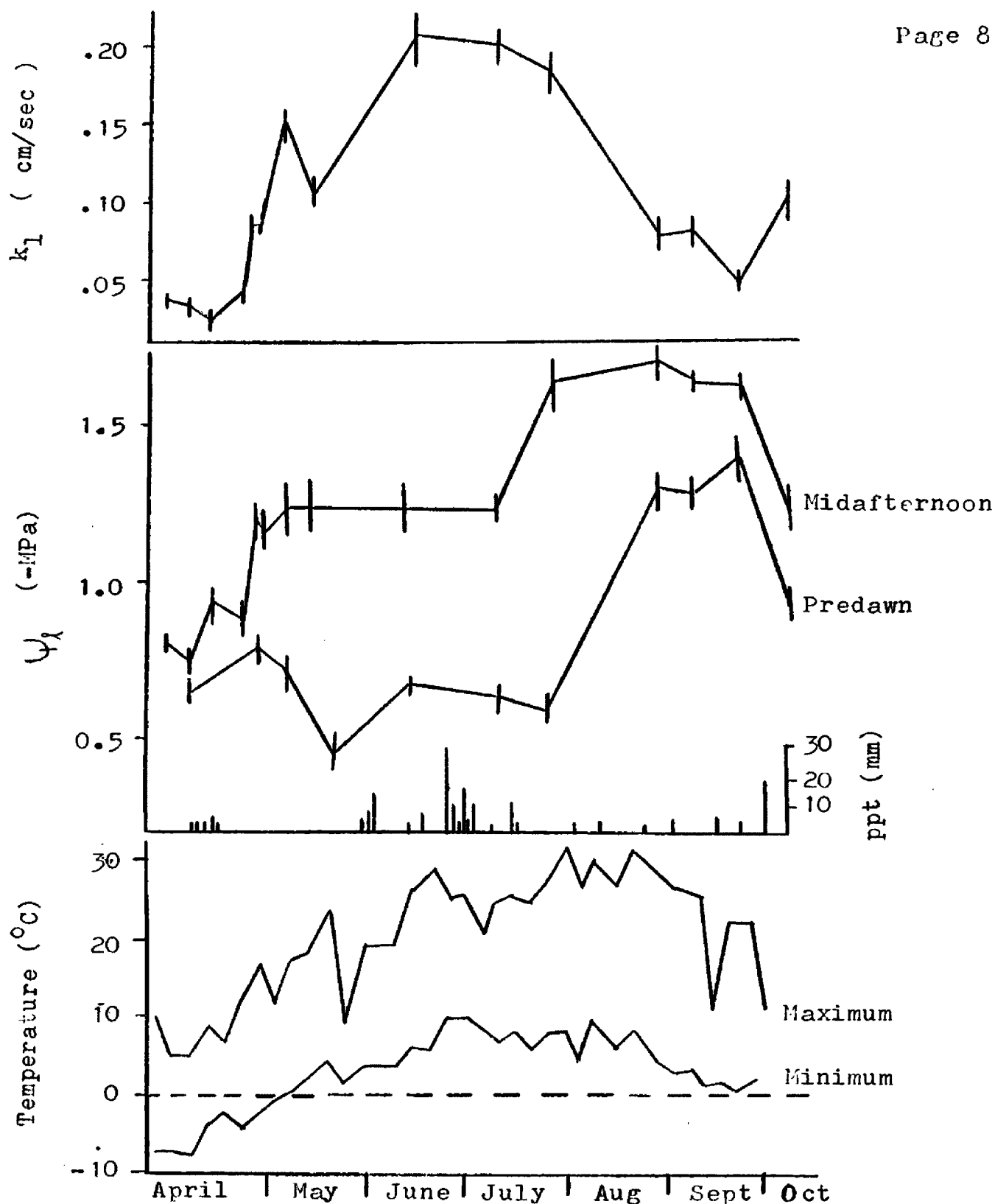


Figure 1. Seasonal trends in daily maximum leaf conductance (k_l), predawn and midafternoon water potential (ψ_x), and minimum and maximum air temperature. Bars are one standard error. Each point is either mean of 12 to 18 k_l measurements, mean of 3 pressure chamber measurements, or a 5-day temperature average.

of 0.05 cm/sec. Similar to predawn water potential, leaf conductance recovered somewhat in October following a wetting rain.

Springtime conditions

Springtime was arbitrarily considered to be the period still experiencing night frosts. Although night minimum temperatures fluctuated markedly as spring progressed (Figure 1), night frosts became milder and less frequent. The last freeze occurred on June 2.

Early season conductances were not only quite low (Figure 1), but they remained fairly constant throughout the day. Diurnal ranges in leaf conductance in spring were usually under 0.03 cm/sec. Moreover, the typical summer pattern of declining leaf conductance throughout the day was not apparent until mid-May. The prominent seasonal rise in leaf conductance (April 21 through 26) closely followed complete snow melt, but did not correspond to a dramatic change in either day or night temperature trends. Night frosts were still frequent. The maximum spring conductance measurement (0.15 cm/sec) occurred on May 4. This was the only sample day during the spring the overnight minimum temperature was above 0 C.

From the May 4 observation it was apparent that spring leaf conductance was related to previous night temperature. Therefore, to develop predictive relationships the average daily leaf conductance was first regressed against the minimum air temperature of the previous night (Figure 2). This is similar to the analysis used by Fahey (1979). Although the linear regression was significant ($p = .002$), some variation remained ($R^2 = .82$). It was observed, however, that 3 days (March 29, April 10 and 23) followed the same minimum temperature (-2 C). Furthermore, on these days markedly different average conductances occurred. Since the later dates were significantly higher, it was suspected that a dehardening or dormancy breaking trend may be influencing leaf conductance. To account for such a phenological event in a regression model, two temperature summations were calculated. These were: (1) the average air temperature for 120 hours (5 days) prior to the morning of measurement, and (2) the summation of degree-days above a threshold of 0 C since February 1. The later summation is similar to those used for bud burst prediction (Thomson and Moncrieff 1982). Coefficients of determination for the regression of each summation against maximum daily leaf conductance were .68 and .74 respectively. The more significant regression is shown in figure 3.

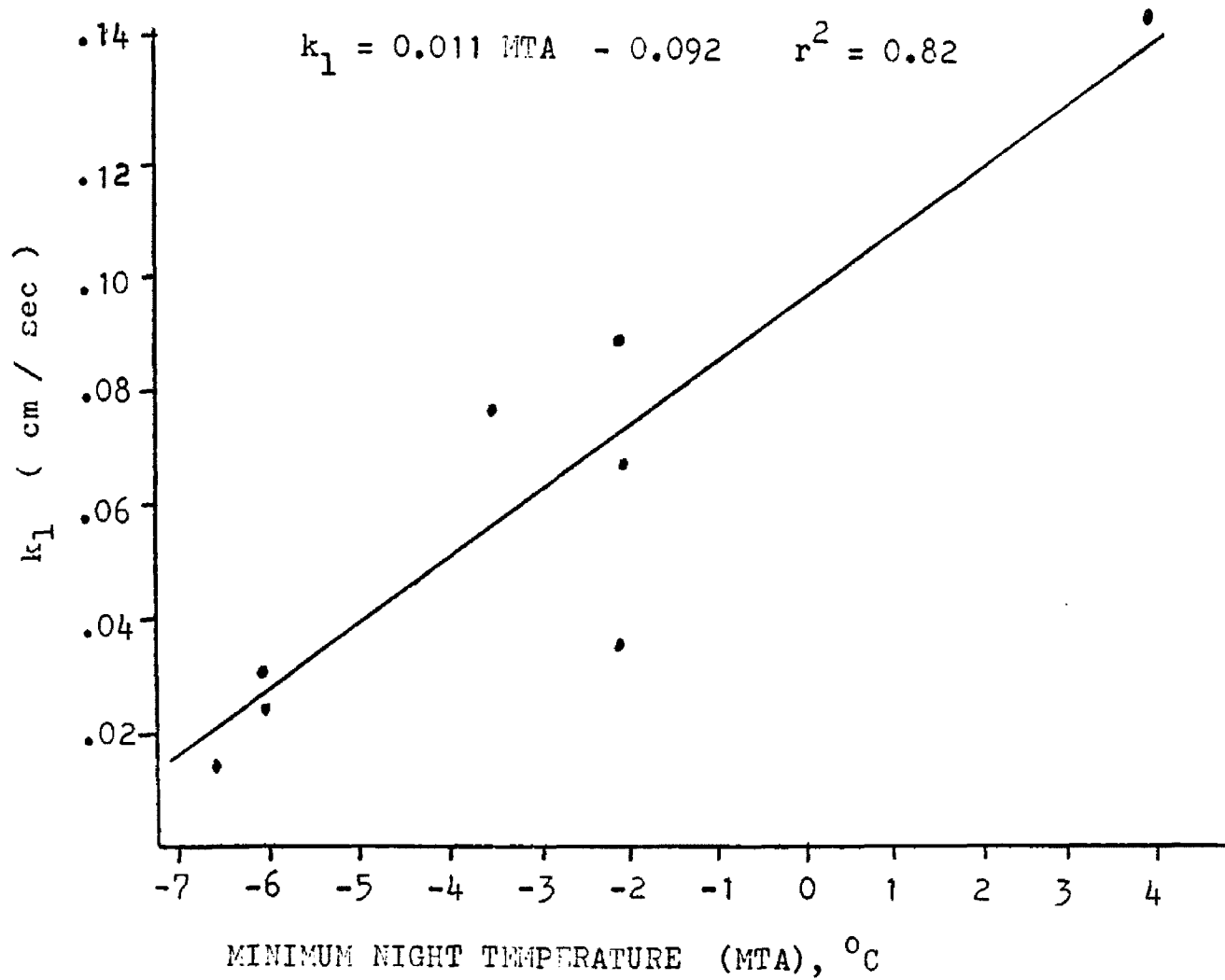


Figure 2. Regression of average daily leaf conductance (k_1) on minimum night air temperature. Each point is the mean of 36 to 48 k_1 measurements.

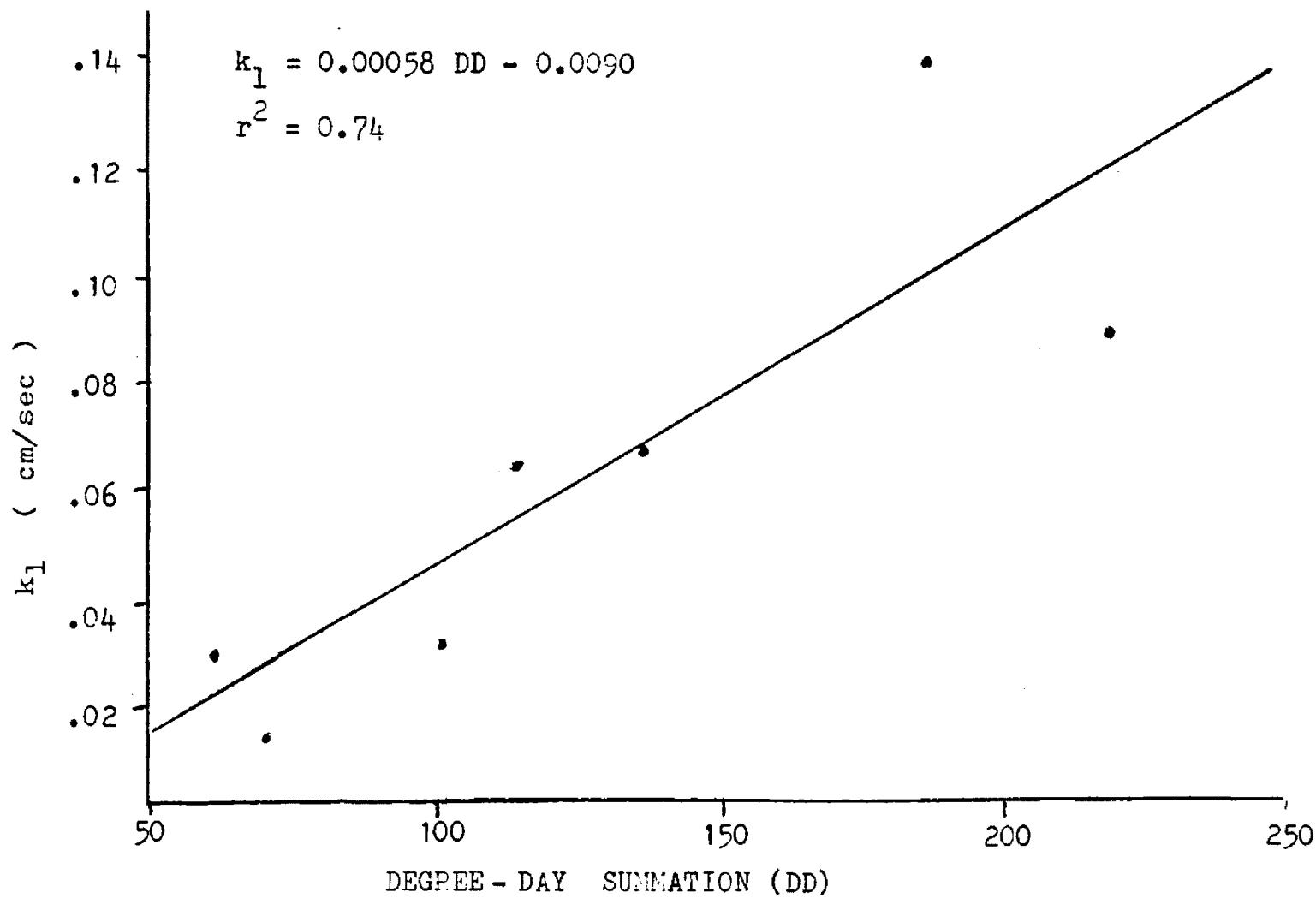


Figure 3. Regression of average daily leaf conductance (k_1) on degree-day summation (see text). Each point is the mean of 36 to 48 k_1 measurements.

The regression using minimum night temperature (MNT) explained more variation in leaf conductance than either temperature summation. However, a plot of the residual conductance from the MNT regression against either corresponding summation produced an apparent correlation. Thus, at low heat sum accumulations the model under predicted conductance and at higher summations the model overpredicted conductance. To adjust for this a multiple regression using both minimum temperature and the summations was performed. The resulting equation was:

$$k1 = 0.0073*MNT + 0.00032*TSUM + 0.043 ; R^2 = .96$$

where TSUM is the degree-day accumulation. The temperature summation based on only the 120 previous hours was not significant ($p < .05$) in the presence of the degree-day summation. The included variables did not show significant statistical interaction.

Because the spring measurements did not show obvious diurnal trends, the above analysis was based solely on average daytime conductance. Therefore, this analysis did not include any factors which varied diurnally. However, both radiation and absolute humidity deficits (ABSHD) have been found to be related to stomatal activity in conifers in natural environments (Kaufmann 1982). Therefore, a stepwise multiple regression including shortwave radiation and

absolute humidity deficit was performed on all spring average leaf conductance measurements. Again night temperature and degree-day summation were the only significant predictors with radiation and ABSHD having no significant contribution.

Summertime conditions

The summertime trends in daily maximum leaf conductance as well as predawn and mid-afternoon water potential are shown in Figure 1. The general trend is a steady decrease in maximum conductance throughout the season. Ultimately, maximum leaf conductance readings were nearly as low as any observed the previous spring (0.05 cm/sec).

The late summer afternoon water potential readings consistently reached a plateau of about -1.65 MPa (Figure 1). Previous research has also shown a water potential plateau in lodgepole pine at about -1.6 MPa (Knapp and Smith 1982, Running 1980). One explanation for this is that a stomatal closure threshold had been reached. Running (1976) observed abrupt reductions in leaf conductance at the water potential plateau with Douglas-fir. However, in the present study leaf conductance showed a gradual diurnal decline. Furthermore, on July 21 an average mid-afternoon leaf conductance of .10 cm/sec was observed when the water potential was -1.6 MPa. Thus, considerable guard cell

turgor could be maintained at the apparent closure threshold. These results suggest that a water potential threshold is not important for lodgepole pine in its natural environment.

Summer trends in maximum leaf conductance mirrored the predawn leaf water potential. The regression of maximum daily conductance on predawn water potential was highly significant ($p < .001$, figure 4). A correlation of similar slope but lower absolute value was found by Running (1980) for lodgepole pine (also included in Figure 4).

Unlike the spring, during the summer a consistent diurnal trend in leaf conductance was observed. Afternoon readings were reduced about 50% from the morning maximum. Past researchers have observed that declining leaf conductance is associated with increasing ABSHD (Kaufmann 1982, Running 1980). To investigate the relationship between leaf conductance and humidity, a simple linear regression was first computed. This regression was only weakly significant due to seasonal changes in maximum daily leaf conductance ($p=.05$, $R^2=.20$). Therefore, a multiple regression using both ABSHD and $B\psi$ was calculated. This time both independent variables were highly significant ($p < .001$). Furthermore, significant statistical interaction was found. Thus, the slope of the relationship between leaf conductance and ABSHD was reduced with increasing $B\psi$. The

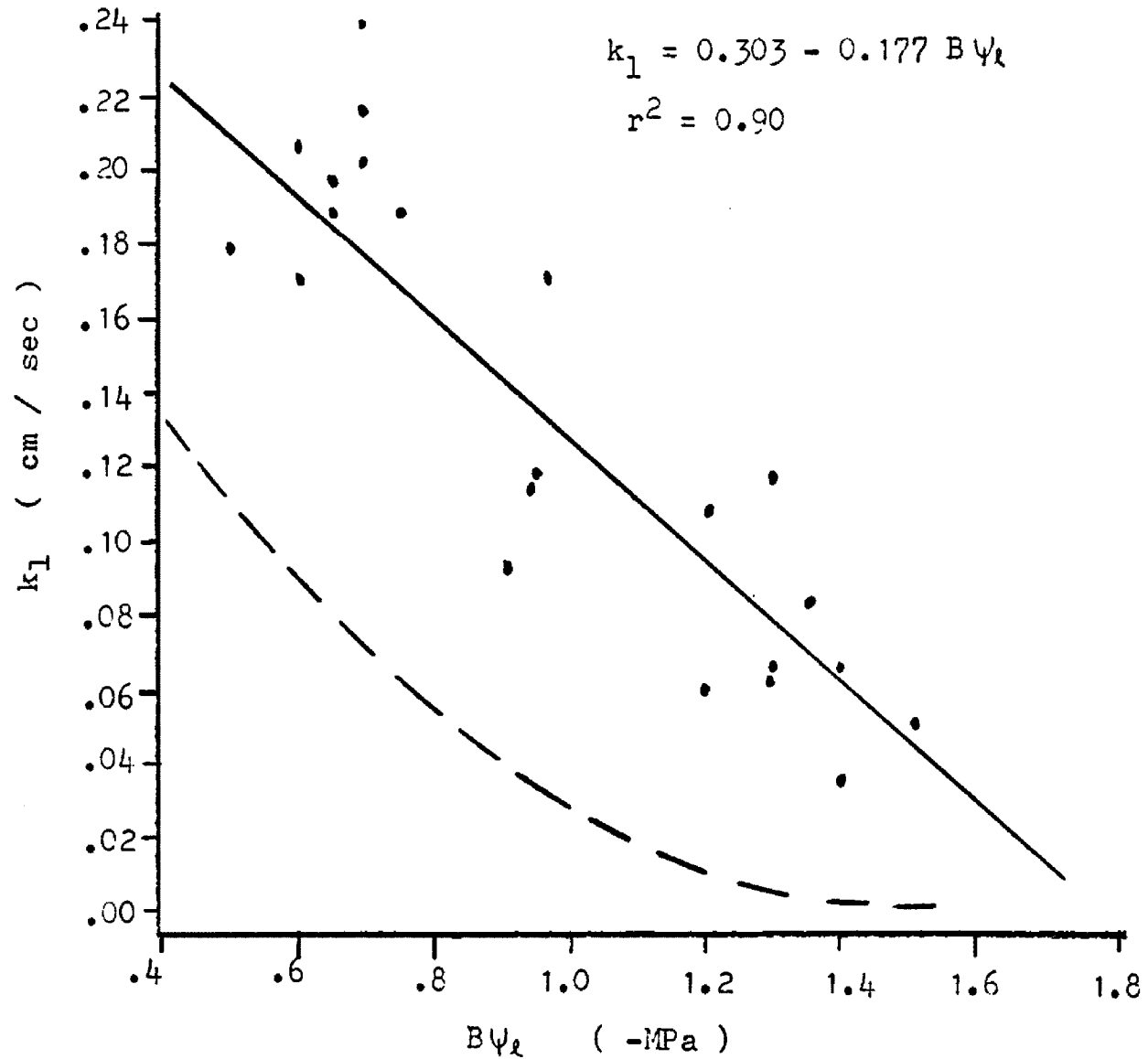


Figure 4. The regression of maximum daily (morning) leaf conductance on predawn water potential ($B\Psi_L$). Each point is the mean of 4 k_L measurements. Dashed line is the same relationship for lodgepole pine from Running (1980).

regression equation including the interaction term was:

$$k1 = .365 - .0079 * ABSHD - .22 * B + .00042 * (B \psi * ABSHD) ; R^2 = .93$$

Figure 5 shows the relationship between leaf conductance and ABSHD. The data were separated into two $B\psi$ levels: < -0.8 MPa and > -0.8 MPa. The mean $B\psi$ for each group ($-.65$ and -1.23 MPa) was then entered into the multiple regression to obtain the two linear equations shown. For comparison, relationships between leaf conductance and ABSHD for lodgepole pine from two other researchers are included in Figure 5.

Within canopy variations

Although the intent of this study was to represent a canopy average leaf conductance, the sampling design allows for comparison between trees, crown aspects, and needle ages. Within each day the average conductance for each tree was similar in both seasons with no individual having consistently higher or lower conductance than the others. Only during late summer did two trees differ by more than 50%. Furthermore, during this period the ranking of trees by mean leaf conductance was consistent throughout the day. This suggests that some factor such as genetic differences or unequal soil water supply was involved. However, there was no apparent relation between this ranking and either predawn or afternoon water potential.

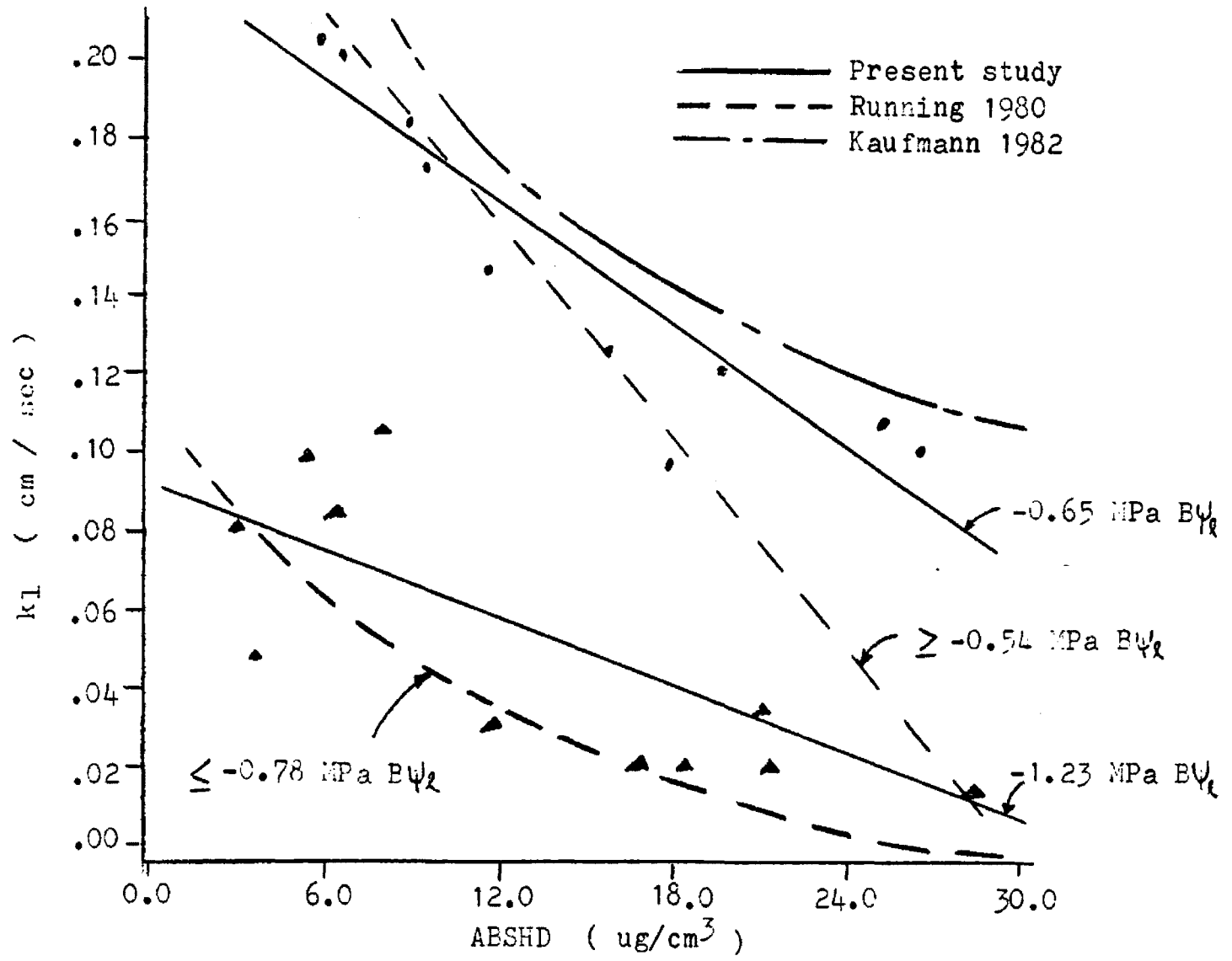


Figure 5. The relationship between leaf conductance (k_l) and absolute humidity deficit (ABSHD). Each point is the mean of 36 k_l measurements. The data are separated into two $B\psi_r$ levels: > -0.8 MPa (\bullet) and < -0.8 MPa (\blacktriangle).

For the spring months there was essentially no difference in leaf conductance between north and south branches. Interestingly, during the summer, conductance of the south branches tended to be slightly higher earlier in the season yet lower once drought developed. Possibly the higher PhAR levels on the south side may have raised conductance when water was adequate. Later, the greater exposure may have produced slightly higher water stress or vapor pressure deficits and induced some degree of stomatal closure.

The difference in leaf conductance between needle ages was consistently small and never significant at the 5% level. However, the ranking of leaf conductance by needle age showed an interesting relationship to night frost. After non-freezing nights the average conductance of first year needles was always highest. In contrast, following a freezing night in the spring the older, third year needles were frequently the highest and first year needles the lowest.

DISCUSSION

In general, the differences in mean leaf conductance between canopy positions or needle ages at any measurement time were small. Between tree differences were larger but rarely significant. Therefore, using a single average leaf conductance for each measurement set appears justified. In contrast, Troeng and Linder (1982) reported consistent differences in stomatal conductance both within a crown and between trees for Scots pine. Conductances were lower on north aspects or positions deep within the canopy suggesting a PhAR effect.

Low leaf conductances following frosts agree with prior research results. Both natural and artificial freezing has produced lower than normal leaf conductances the following day in several conifers (Kaufmann 1982, Neilson and Jarvis 1975). It is understandable, therefore, that the severity of the frost could be related to subsequent stomatal activity. Indeed, Fahey (1979) reported that 89% of the variation in springtime leaf conductance in Pinus contorta could be explained by the frost severity of the previous evening alone. The present study supports the conclusion that minimum night temperatures is an important predictor of leaf conductance during the spring. In fact the rates of reduction of average conductance with night temperature are quite similar: 0.013 cm/sec C for Fahey (1979) and 0.012

cm/sec C for the present study.

The effect of tissue freezing on membrane function provides an explanation for the reduction of stomatal opening after frost. Since convective heat exchange is rapid with finely dissected foliage, it is reasonable to assume that air temperature reflects conifer needle temperature (Jarvis et al. 1976). Furthermore, Christersson and Sandstedt (1978) demonstrated that ice formation will take place in conifer needles when the tissue temperature is between -1 and -2 C. Levitt (1980) contends that freezing, even in cells with some degree of cold tolerance, results in impairment of membrane function.

Dehydration from extracellular freezing may cause a slippage between lipid layers which can dislodge membrane proteins. Although lipid displacement would reverse upon thawing, protein relocation would be slower. Thus, freezing may damage protein mediated ion transport without loss of semipermeability. Since guard cell movements are associated with potassium fluxes, freezing could retard stomatal opening by interfering with potassium uptake.

Despite the correlation with overnight temperature alone, the possible effect of a springtime dehardening cycle must be considered. Cold hardening may render stomata less affected by freezing temperatures (Neilson and Jarvis 1976, Reed 1965). These researchers reported that freezing of

hardened tissue results in rapid stomatal closure followed by nearly full opening upon thawing. This was explained by the enhanced permeability to water of cold-hardy cells. However, these observations have primarily been made for varieties native to regions with mild winters. Work with trees from cold winter climates generally has shown that hardening correlates with stomatal closure (Christersson 1972, Parker 1963, Tranquillini 1982). Parsons (1978) reported that stomata of Cornus stolonifera close when cold tolerance approaches -12 C to -14 C. In areas where soils and stems are usually frozen in winter, stomatal closure associated with hardening would be certainly advantageous in preventing winter dessication.

The strong correlation of leaf conductance with degree-day summation in the present study implies that the dehardening or dormancy breaking process may be influencing conductance for lodgepole pine in Montana. A similar springtime phenological trend was reported by Pelkonen and Hari (1980) for Scots pine in Finland. They observed higher photosynthetic rates later in the spring season. Furthermore, this occurred despite similar environmental conditions. In addition to biochemical changes, phenology of cuticular waxes could also be occurring. Fahey (1979) noted that needle surface waxes were reduced as the season moved from winter into summer. He speculated that winter

transpiration may have been limited by wax build up in the epistomatal chamber.

The relationship between maximum diurnal leaf conductance and predawn water potential is similar to that found with other large conifers (Running 1976, Running 1980, Tan et al. 1977). This pattern has been reported for drying cycles in crop plants as well as conifer seedlings. Evidence exists linking soil water depletion with increased abscisic acid concentrations that cause stomatal closure (Davies et al. 1981, Newville and Ferrell 1980). Murphy and Ferrell (1982) observed a seasonal maximum abscisic acid concentration during the late summer and early fall for Douglas-fir on dry sites. Thus, a plausible explanation for the seasonal decrease in maximum leaf conductances is a rise in abscisic acid levels associated with water stress.

Diurnal leaf conductance measurements in the summer showed a regular downward trend. Total incoming shortwave radiation during the sample periods had no apparent relationship to leaf conductance. Although leaf surface photosynthetically active radiation (PhAR) was not measured, evidence exists that stomatal conductance in conifers approaches PhAR saturation at approximately $300 \text{ } \mu\text{E}/\text{m}^2 \text{ sec}$ (Dykstra 1974, Jarvis 1980). Therefore, limiting measurements to hours when direct sunlight was on the site should have minimized PhAR effects.

The only environmental parameter which was consistently associated with declining leaf conductance was ABSHD. Moreover, the slope of the reduction corresponded quite closely with similar analyses by Running (1980) and Kaufmann (1982) suggesting common stomatal mechanics. The response of stomata to humidity has been known for over ten years (Lange et al. 1971) and has been reported for over 70 species (Losch and Tenhunen 1981). One theoretical explanation for the phenomenon in conifers has been offered by Jarvis and Morison (1981). The presence of a lignified hypodermis, common in conifer needles, provides a sizeable resistance between guard cells and surrounding mesophyll. Guard cells are thus somewhat isolated from bulk leaf water status so that guard cell turgor can be lost independently of whole leaf turgor. This allows stomata to close in response to high evaporative demands and prevents the development of severe water deficits.

Fahaquar (1978) terms such a mechanism a feedforward response. Furthermore, he states that a declining transpiration rate with increasing ABSHD can only occur through a feedforward response. Examination of diurnal transpiration to ABSHD relationships for lodgepole pine did not show consistent trends. However, on three days transpiration peaked at moderate ABSHD and then declined at still higher ABSHD. Thus, although far from conclusive,

evidence exists that a feedforward response may be operating in lodgepole pine. Moreover, a feedforward humidity response may be limiting leaf water loss enough that a water potential plateau is maintained without a stomatal closure threshold.

In conclusion, for lodgepole pine during the spring, leaf conductance is related to both night temperature and seasonal heat accumulation. Absolute humidity deficit or radiation above PhAR saturation has little effect. During the summer, predawn water potential and absolute humidity deficit are the most important predictors of leaf conductance. Diurnally, the influence of humidity overshadows both mid-day water potential or radiation controls.

CHAPTER II

COMPARISON OF LEAF CONDUCTANCE CONTROLS

FOR WESTERN MONTANA CONIFERS

INTRODUCTION

A popular area of tree water relations research has been the comparison of different species in a common environment (Cline and Campbell 1976, Tobiessen and Kang 1974, Roberts et al. 1979, Knapp and Smith 1981). The aim of these investigations has been to provide a physiological explanation for ecological phenomena. Thus, distribution patterns, survival strategy, and successional status have been discussed in terms of water potential maintenance and stomatal activity.

Another topic of water relations research has been the modelling of forest transpiration (Running 1983, Tan et al. 1978). Here the emphasis has been on predicting water consumption and tree water stress as well as understanding fundamental processes. In contrast with ecological studies, most research to develop functions for use in models have used single species and comparison of process functions between species are rare. Prior research

has indicated that environmental control of leaf conductance for a number of western conifers is similar (Running 1980). However, data is fragmentary and there is a need to assess the generality of several fundamental relationships. The purpose of this study was to develop and compare functions relating leaf conductance to environmental variables for three conifer species: Pinus contorta, Pinus ponderosa, and Pseudotsuga mensiezii. Additional comparisons will be made with similar functions from earlier work.

MATERIALS AND METHODS

This study was conducted on the University of Montana Lubrecht Experimental Forest during the summer of 1982. Background information on the study location and plot characteristics was given in chapter 1. Site selection was based on species diversity and outward appearance of xeric conditions. Diversity was needed to provide an adequate selection of the three desired species: ponderosa pine, lodgepole pine, and Douglas-fir. A xeric site was preferred to ensure a range of soil water conditions over the summer season.

Three sapling to pole size trees of each species were chosen. Tree dimensions ranged from 5 cm to 15 cm in diameter and 3.8 m to 9.1 m in height. Selection was based on healthy outward appearance, accessibility of foliage, and proximity to other sample trees. On each tree a north and south facing branch was selected. On each branch one and two year old needles were used for conductance measurement. Needle samples were prepared prior to the sample day. Ponderosa pine was prepared by taping a cluster of fascicles together near their base. Douglas-fir and lodgepole pine were prepared by carefully cutting back adjacent needles. During early summer total needle surface areas ranged from 10 cm² to 30 cm². Due to low transpiration rates by late summer, needle area had to be 70 cm² to 100 cm² for accurate

conductance measurement. Needle samples were used for several measurement days before being clipped for area determination. For Douglas-fir needle area was measured with an optical area meter (Li-Cor Inc.). The factor 1.16 was used to adjust for needle curvature (Drew and Running 1975). Needle area was determined geometrically for ponderosa pine and lodgepole pine.

A null balance diffusion porometer (Beardsell et al. 1972) was used for leaf conductance measurements (Chapter 1). Ponderosa pine needle samples were placed in the cuvette up to the tape. With Douglas-fir and lodgepole pine the entire twig was able to be placed into the cuvette. Prior to each measurement set, air temperature and relative humidity were measured by an aspirated psychrometer (Environmental Tectronica Corp.). Following each measurement set, xylem water potential was measured for each sample tree with a pressure chamber. Water potential was also measured during the predawn hours of each sample day. One twig per tree was used for each pressure chamber reading.

Measurements were made on six days during the summer and one day during the fall. During the summer, three measurements sets were made each day. Sampling times were approximately 9:00am, 1:00pm, and 5:00pm. On October 1 rain prevented a third data set.

RESULTS

Figure 6 shows the seasonal trends in maximum daily leaf conductance (k_l) as well as predawn water potential ($B\psi$) and mid-afternoon water potential (ψ). Early in the season lodgepole pine maximum daily k_l was over twice either Douglas-fir or ponderosa pine. Later in the summer, however, lodgepole pine had decreased to the level of the other two species (.05 to .10 cm/sec). Neither Douglas-fir nor ponderosa pine showed so obvious a seasonal trend. All three species showed k_l increases in late September following a 1.8 cm rain and $B\psi$ recovery.

Within canopy variations in k_l for each species did not show any consistent trends. Significant differences between canopy positions, needle ages, or trees were not sufficiently regular to draw conclusions. It is notable, however, that for the two driest measurement days between tree differences were consistent. It appears that any inherent difference between trees which affects k_l is amplified by low soil water status.

Average $B\psi$ was essentially the same for each species at any given day. In contrast, mid-afternoon water potential showed distinct species differences. Lodgepole pine consistently reached a plateau of about -1.65 MPa during mid and late summer. Ponderosa pine and Douglas-fir

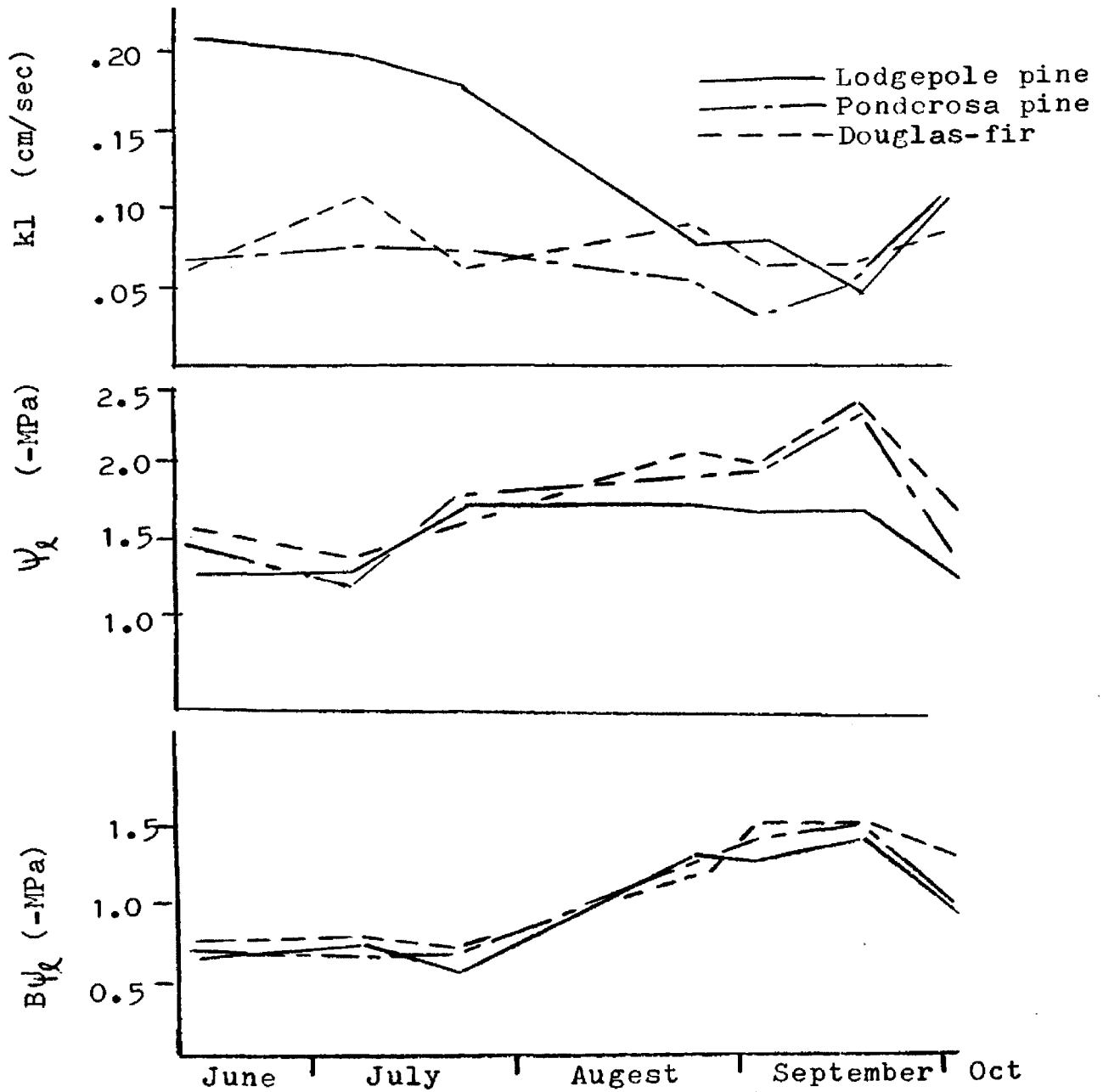


Figure 6. Seasonal comparisons in maximum daily leaf conductance (k_l), average predawn water potential ($B\psi_m$), and average mid-afternoon water potential (ψ_m) for three species.

on the other hand generally reached -1.8 to -2.0 MPa. Prior to fall rain, afternoon readings averaged -1.65, -2.37, and -2.27 MPa for lodgepole pine, Douglas-fir, and ponderosa pine respectively.

Maximum daily leaf conductance has been found to be related to predawn water stress in several conifers (Running 1976, Tan et al. 1977) and this function is useful in transpiration modelling. Comparisons of the regressions of k_l on maximum $B\psi$ are shown in figure 7 and the regression equations are given in table 1. Maximum daily k_l in lodgepole pine was strongly correlated to $B\psi$. For ponderosa pine the correlation was less definitive though still significant. There was no apparent relationship for Douglas-fir. T-tests for slope coefficients showed ponderosa pine and Douglas-fir to not be significantly different at the 5% level. Lodgepole pine, however, was significantly different from both ponderosa pine and Douglas-fir.

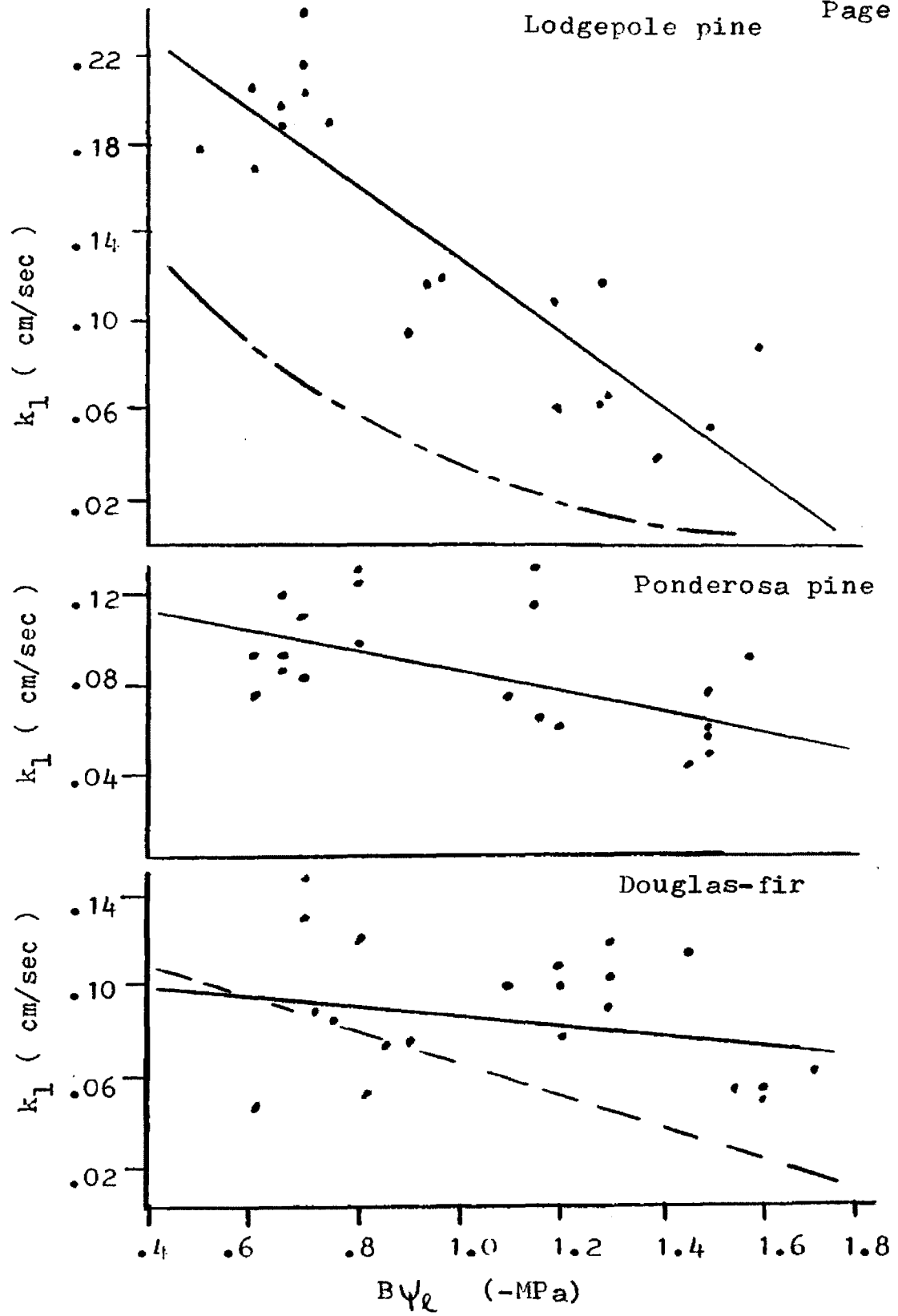


Figure 7. Comparisons of regressions of maximum daily leaf conductance (k_1) on predawn water potential ($B\Psi_e$). Each point is the average of four k_1 measurements of a single tree. Other regressions are — — — — — for lodgepole pine from Running (1980) and - - - - - for Douglas-fir from Running (1976).

Table 1. Comparison of regression equations of maximum daily leaf conductance (k_1) on predawn water potential ($B\psi_e$).

<u>Species</u>	<u>Regression equation</u>	<u>r^2</u>	<u>F prob.</u>
Douglas-fir	$k_1 = 0.109 - 0.0231B\psi_e$.07	.25
Ponderosa pine	$k_1 = 0.132 - 0.00513B\psi_e$.41	.002
Lodgepole pine	$k_1 = 0.303 - 0.0177B\psi_e$.81	.001

Table 2. Summary of stepwise multiple regression to analyze the effect of absolute humidity deficit (ABSHD) on leaf conductance (k_1).

<u>Species</u>		<u>R^2</u>	<u>Sequential F prob</u>
Douglas-fir	$k_1 = 0.92 - 0.0028ABSHD$.57	.0001
	$k_1 = 0.12 - 0.0029ABSHD - 0.020B\psi_e$.64	.11
	$k_1 = 0.10 - 0.0018ABSHD - 0.0066B\psi_e - 0.00095ABSHD*B\psi_e$.65	.56
Ponderosa pine	$k_1 = 0.083 - 0.0019ABSHD$.23	.03
	$k_1 = 0.15 - 0.0019ABSHD - 0.066B\psi_e$.76	.000
	$k_1 = 0.12 + 0.0006ABSHD - 0.035B\psi_e - 0.0023ABSHD*B\psi_e$.80	.11
Lodgepole pine	$k_1 = 0.14 - 0.0036ABSHD$.20	.048
	$k_1 = 0.30 - 0.0038ABSHD - 0.16B\psi_e$.91	.000
	$k_1 = 0.36 - 0.0077ABSHD - 0.22B\psi_e + 0.0039ABSHD*B\psi_e$.93	.022

Additional functions between maximum k_l and $B\psi$ for Douglas-fir (Running 1976) and lodgepole pine (Running 1980) are included in Figure 7. For lodgepole pine the relationship is similar in slope but somewhat lower in magnitude. Despite the large variation, Douglas-fir k_l was comparable in magnitude at low water stress. However, it did not show the previously reported reduction during late summer drought. A similar function for ponderosa pine was not available from the literature.

Another important function in transpiration modelling is the diurnal reduction of k_l by humidity. Figure 8 shows comparisons of the relationship between k_l and absolute humidity deficit (ABS_{HD}). Previous work has shown that the simple correlation between k_l and ABS_{HD} is often poor when $B\psi$ is not accounted for (Running 1980). This was evident for both lodgepole pine and ponderosa pine (table 2). With both these species the addition of $B\psi$ in the regression of k_l with ABS_{HD} was not only significant at the 5% level but also improved the significance of ABS_{HD}. Since Douglas-fir maximum k_l was unrelated to $B\psi$, using this variable in a multiple regression did not significantly contribute to k_l prediction.

Past research has indicated that the rate of reduction of k_1 with ABSHD is not constant (Running 1980, Meinzer 1982). Thus the effect of ABSHD on k_1 tends to decrease with high predawn water stress or needle age. Statistically this would be evident by variable interaction. To test for interaction a multiple regression was computed which included the product of ABSHD and $B\psi$. This interaction term was significant at the 5% level only for lodgepole pine (Table 2).

In summary the three species sampled each showed a different response to the environment. Douglas-fir k_1 was not significantly effected by $B\psi$ and was primarily influenced by ABSHD. Ponderosa pine k_1 was significantly related to both $B\psi$ and ABSHD but the rate of reduction of k_1 by ABSHD was unchanged by $B\psi$. Lodgepole pine k_1 was also significantly related to both ABSHD and $B\psi$. Furthermore, with lodgepole pine the rate of reduction of k_1 by ABSHD was significantly affected by $B\psi$. Figure 8 attempts to show these three different relationships. For Douglas-fir the simple linear regression is graphed. With ponderosa pine and lodgepole pine the average $B\psi$ for two stress levels (<-0.8 MPa and >-0.8 MPa) was entered into the multiple regressions to obtain the two linear equations shown.

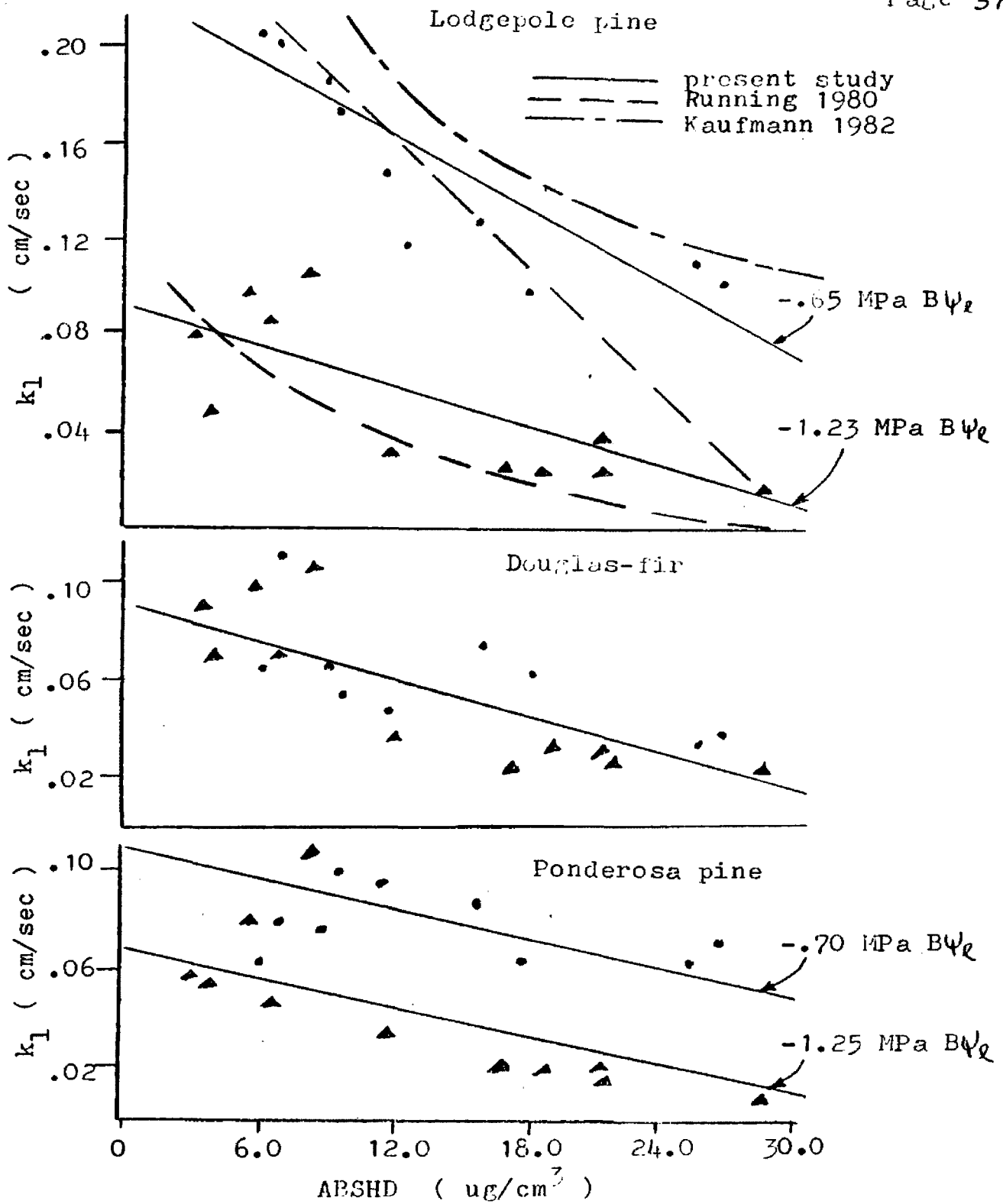


Figure 8. Comparison of the relationship of leaf conductance (k_l) to absolute humidity deficit (ABSHD) for three conifers. Each point is the mean of 12 k_l measurements. The data were grouped into two $B\Psi_e$ levels: > -0.8 MPa (\bullet) and < -0.8 MPa (\blacktriangle). Additional functions for lodgepole pine from other studies are included.

DISCUSSION

Prior to the operational application of transpiration models the evaluation of potential species and site differences of component processes is needed. Running (1980) observed that lodgepole pine and Douglas-fir behaved similarly in their $B\psi$ control of maximum daily k_l . The present study does not support this similarity. Douglas-fir maximum k_l was found to be unrelated to $B\psi$ while lodgepole pine was highly correlated. It should be noted, however, that failure to observe a significant $B\psi$ relationship for Douglas-fir does not demonstrate lack of an effect. Merely this says that the data had such variability that an effect could not be detected. The large variability is dramatically demonstrated by the standard deviations calculated from each sample set. Running (1976) reported standard deviations for Douglas-fir ranging from 0.003 cm/sec to 0.016 cm/sec. Standard deviations for Douglas-fir in the present study ranged from 0.0079 cm/sec to 0.048 cm/sec.

Comparison of the regression for lodgepole pine k_l on $B\psi$ with Running (1980) showed a similar slope yet lower magnitude at all $B\psi$ levels. Thus, Running (1980) reported a seasonal maximum k_l of 0.16 cm/sec whereas .21 cm/sec was observed in the present study. Other research with lodgepole pine supports the higher k_l . Kaufmann (1982)

described k_l for unstressed lodgepole pine as a function of photosynthetically active radiation (PhAR) and ABSHD. At $1750 \mu\text{E}/\text{m}^2\text{-sec}$ and an ABSHD of under $10\mu\text{g}/\text{cm}^3$ k_l was predicted at $0.20 \text{ cm}/\text{sec}$. Similarly, Fetcher (1976) reported early season maximum k_l of $0.2 \text{ cm}/\text{sec}$.

The maximum k_l for unstressed Douglas-fir (about $0.10 \text{ cm}/\text{sec}$) is somewhat lower than previous reports. Typical values are 0.12 to $0.20 \text{ cm}/\text{sec}$ (Leverenz 1981, Running 1976, Tan et al. 1977). However, rather than maximum k_l , the major discrepancy is with the relationship with $B\psi$. Running (1976) reported an average k_l of $0.03 \text{ cm}/\text{sec}$ at the $B\psi$ of -1.4 MPa . In the present study an average k_l of $0.08 \text{ cm}/\text{sec}$ was observed at a $B\psi$ of -1.4 MPa .

It is difficult to make statistical comparisons about humidity effects since all three species behaved differently in relation to $B\psi$. The rate of k_l reduction with increasing ABSHD for Douglas-fir and ponderosa pine were 0.0028 and $0.0019 \text{ cm}/\text{sec}/\mu\text{g}/\text{cm}$ respectively. The value for lodgepole pine ranged from 0.0058 at -0.05 MPa to 0.0029 at -1.2 MPa . Thus, when the maximum k_l for all species was similar the reduction rates were similar. In general, this confirms Running's (1980) conclusion that the rate of k_l reduction by ABSHD is proportional to the maximum diurnal k_l .

For additional comparisons, regressions from prior research were also provided in Figure 8. Although Running (1980) found a somewhat steeper reduction rate at low $B\psi$, the general agreement in both magnitude and slope at both stress levels is apparent. The humidity effect reported by Kaufmann (1982) for unstressed conditions also agrees well. In addition to lodgepole pine, Kaufmann (1982) also reported regressions of k_l on ABSHD for subalpine fir and engelmann spruce. At an ABSHD of 15 ug/cm^3 and PhAR of $1750 \text{ uE/m}^2 \text{ sec}$ reduction rates were 0.0050, 0.0030, and 0.0039 cm/sec/ug/cm^3 for lodgepole pine, subalpine fir, and engelmann spruce respectively. Thus, Kaufmann's (1982) work substantiates several aspects of the present study. Not only was maximum k_l for lodgepole pine about 0.20 cm/sec and often twice its neighboring conifers, but the rates of reduction with ABSHD were as much as 60% greater.

In conclusion, leaf conductance responses to the environment were somewhat different for each sampled species. Douglas-fir k_l was apparently associated only with ABSHD. Ponderosa pine k_l was significantly, although weakly, related to both $B\psi$ and ABSHD. Lodgepole pine k_l was clearly related to both $B\psi$ and ABSHD. Although each species may show apparently different k_l controls, the importance of these differences in the annual carbon budget or transpiration of a stand is less obvious. Clearly this

should be addressed through a modelling context. However, caution must be employed when interpreting a modelling analysis. Appreciable unexplained variability for each process level function would cast uncertainty on model generated predictions.

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