

AN ABSTRACT OF THE THESIS OF

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in Forest Science presented on May 17, 1979

Title: DIURNAL AND SEASONAL CHANGES IN XYLEM WATER POTENTIAL,
STOMATAL CONDUCTANCE AND ABSCISIC ACID IN FIVE DIFFERENT HABITAT
TYPES OF DOUGLAS-FIR [*Pseudotsuga menziesii* (Mirb.) Franco]

Abstract approved: Signature redacted for privacy.
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Sapling Douglas-fir trees on five sites in the Coastal and Cascade Mountain ranges of Oregon were measured five times during the year from the summer of 1977 through the spring of 1978 for diurnal patterns of xylem water potential, stomatal conductance and abscisic acid. Vapor pressure deficit and solar radiation were measured as well.

During the summer diurnal patterns of stomatal conductance and xylem water potential were similar to those found by others. High winter and fall stomatal conductances were found and suggest that the potential for photosynthesis exists during these times of the year especially at the coastal site. At some of the sites during the winter an inverted diurnal xylem water potential pattern occurred

which may indicate an adaptation of Douglas-fir to a relatively mild winter climate. During the summer stomatal conductance was most highly correlated with vapor pressure deficit, while during the fall and spring stomatal conductance was correlated with xylem water potential.

Abscissic acid showed large diurnal fluctuations in the summer and fall at some of the sites, and remained relatively constant in the winter and spring. For the most part the diurnal abscissic acid curves showed no clear relationship with the other variables.

Diurnal and Seasonal Changes in Xylem Water Potential,
Stomatal Conductance and Abscisic Acid in Five
Different Habitat Types of Douglas-fir
[Pseudotsuga menziesii (Mirb.) Franco]

by

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A THESIS

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Master of Science

June 1980

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Date thesis is presented May 17, 1979

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ACKNOWLEDGEMENTS

I would like to thank Dr. Robert Claves for his advice and time in developing our gas-liquid chromatography system for ABA detection. I would also like to thank David Hostetler for helping with the field work and graphics, Jon Johnson for his suggestions concerning the data, and Dennis Muscato for computer programming.

This project could not have been completed without the constant support and counsel of Dr. Wm. Ferrell to whom I am very grateful.

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INTRODUCTION

The Pacific Northwest is characterized by mild, wet winters and summer droughts. The ability of Douglas-fir to control water loss has contributed to its adaptive success in this region. Both tree growth and drought survival are related to stomatal conductance (k_s) and xylem water potential (Ψ_x). Consequently several field experiments have been undertaken by others to explain stomatal conductance and xylem water potential in relation to various environmental variables (Hinckley, et al., 1975; Running, 1975; Cline and Campbell, 1976; Hellkvist and Parsby, 1976; and Pereira and Kozlowski, 1978).

Field studies of diurnal behaviour of Ψ_x show that typically after sunrise Ψ_x will fall, reaching the lowest potential at midday, and in the afternoon Ψ_x will rise as the trees start to recharge (Hinckley, et al., 1975; Hellkvist and Parsby, 1976; and Pereira and Kozlowski, 1978). Similarly the stomata open after sunrise with hydroactive stomatal closure beginning as early as 0800 hrs. Normally the stomata do not reopen even though Ψ_x recovers in the late afternoon (Running, 1975; Hinckley, et al., 1975; Tan, et al., 1977; and Pereira and Kozlowski, 1978).

In seasonal studies of Scots pine (Pinus sylvestris) Hellkvist and Parsby (1976) found that the largest daily fluctuations in Ψ_x occurred in May and September, while sustained low values of Ψ_x were

found in the summer and high values in the winter. In a seasonal field study of k_s Cline and Campbell (1976) found that the stomata of western white pine (*Pinus monticola*) were more open in September and April than during the growing season.

Attempts have been made in field studies to explain stomatal regulation in terms of numerous environmental variables. Stomatal conductance may be affected by temperature, vapor pressure deficit (VPD), CO_2 concentration, and irradiance. As Jarvis (1976) points out it is difficult to correlate one environmental variable in particular with k_s because all of these variables are affecting it simultaneously. Investigations have also attempted to explain stomatal regulation in relation to the plant variables Ψ_x and abscisic acid (ABA). In general stomata are insensitive to decreasing Ψ_x until a threshold is reached which varies depending on the species (Lopushinsky, 1969; Puritch, 1973; Running, 1976). Running (1976) found that stomatal closure in Douglas-fir occurred abruptly when the trees reached a threshold of -2.0 MPa. Studies have shown that water stress causes an increase in endogenous levels of ABA in a variety of plants (Wright and Hiron, 1969; Loveys and Kriedemann, 1973; Zabadal, 1974; Beardsell and Cohen, 1975) and that ABA may be related to stomatal regulation (Horton, 1971; Little, 1975; and Blake and Ferrell, 1977). Blake and Ferrell (1977), using Douglas-fir seedlings, noted that ABA increased as soil moisture and Ψ_x decreased, and when ABA reached a threshold level, the stomata

rapidly closed. The relationship of ABA to diurnal and seasonal patterns of Ψ_x and k_s has not been investigated.

The objectives of this study were to determine: 1) the seasonal and diurnal patterns of k_s and Ψ_x of Douglas-fir in five contrasting habitats, and 2) to what degree the k_s and Ψ_x may be related to ABA levels.

MATERIALS AND METHODS

Experimental Design

Five sites in the Coastal and Cascade Mountain ranges of Oregon were selected for the study. The five sites, coastal (Cascade Head), foothill (MacDonald Forest), low Cascade (Trout Creek), high Cascade (Deer Creek), and dry Cascade (Metolius River), vary over a wide temperature, elevation, and moisture range (Table 1). At each site two representative Douglas-fir trees, 10-15 cm in diameter and 5-6 m high, were measured five times during the year from the summer of 1977 through the spring of 1978. Measurements were taken at: 1) July, before the onset of the summer drought; 2) August, during the drought; 3) October, after the first fall rains; 4) January-February, during dormancy; and 5) May, after dormancy had broken. At each of the five time periods Ψ_x , k_s , air temperature, solar radiation, and vapor pressure deficit (VPD) were measured six times in one day beginning at predawn and continuing after sunset. At each sampling time needles were removed from the trees for ABA analysis.

Field Techniques

k_s was measured directly on intact foliage using a Null-Balance porometer (Beardsell, et al., 1972). The previous season's foliage was used for both conductance and ABA measurements. When k_s was high (above $0.3 \text{ cm}\cdot\text{sec}^{-1}$) or low (below $0.07 \text{ cm}\cdot\text{sec}^{-1}$) variability in measurements between the trees at each site was minimal

($0.002 \text{ cm}\cdot\text{sec}^{-1}$). When k_s was in the medium range ($0.3\text{--}0.07 \text{ cm}\cdot\text{sec}^{-1}$) variability between the trees was higher ($0.08 \text{ cm}\cdot\text{sec}^{-1}$). Ψ_x was measured with a Scholander pressure chamber (Scholander et al., 1965). Ψ_x rarely varied by more than 0.1 MPa between the trees at individual sites with the exception of the foothill site. During July and August Ψ_x often varied by 0.3 MPa between the two trees there. At the other times of the year the variation of Ψ_x at the foothill site was consistent with the other sites. All measurements were taken on the south side of the tree on branches 1–1.5 m above ground. The same needles were used for the stomatal conductance readings throughout the day, while needles and shoots for ABA and Ψ_x readings were sampled nearby on the same main branch. The needles collected for ABA analysis were stored on ice in a methanol-acetic acid (50:1, v/v) mixture to which 20 mg/l butylated hydroxytoluene was added as an antioxidant. Dew temperature was measured using a heated lithium chloride sensor (Interface Instruments, Corvallis, OR). Solar radiation was measured with a Weston Illuminometer. Needle surface area measurements were made with a Licor portable surface area meter (Lambda Instrument Corp., Lincoln, Neb.) and used in the calculation of stomatal conductance by converting the planar surface area to total surface area by multiplying by a factor of 2.36 (Gholz, et al., 1976).

Laboratory Techniques

The ABA samples were stored in the methanol extracting solution (methanol, acetic acid, BHT) at -10°C in the dark. ABA was assayed using a procedure described by Zabadal (1974) with the following modifications. The methanol extracting solution was poured off the needles and saved. The needles were then ground to a fine powder with liquid nitrogen in a mortar and pestle. The powder was placed in a preweighed vial and freeze-dried. The samples were dried in approximately four hours and the dry weight was determined. The powdered needles were suspended in 100 mls of the methanol extracting solution for 24 hours at 5°C in the dark. The sample was then filtered, the filtrate saved, and reextracted. 10,000 cpm DL-cis, trans-(2- ^{14}C) ABA (specific activity 11.1 mCi/mmol, Amersham Corp., Arlington Heights, Ill.) was added to the combined filtrate as an internal standard. The samples were partitioned against dichloromethane and water as in Zabadal's procedure. Whatman 1PS phase separating paper was used in the partitioning procedure and the aqueous phase was acidified to pH 2.5 instead of 3.0 as in Zabadal's procedure.

The samples were methylated with diazomethane and chromatographed on 0.5 mm preparative thin layer plates of Silica Gel GF-254 using hexane and ethylacetate (1:1) as the solvent. Thin layer chromatography was repeated using 0.25 mm Silica Gel plates.

A gas-liquid chromatograph equipped with a ^{63}Ni electron capture detector was used to determine the ABA content of the samples.

Best results were obtained with a 1.16 m by 3 mm glass column packed with Ultrabond 100/120 mesh (Supelco, Inc., Bellefonte, PA). The column temperature was 190°C, injection port temperature 205°C, and detector temperature 290°C. 10% methane in argon was used as the carrier gas. Column flow rate was 22 cc·min⁻¹ and purge flow 30 cc·min⁻¹. ABA was confirmed in this system using mass spectrometry. The ¹⁴C ABA was counted on a Packard Tri-Carb Scintillation counter. ABA usually varied by 200 ng/g dry wt between the trees at individual sites.

RESULTS

Seasonal Trends

The average k_s in July for the five sites were around $0.1 \text{ cm}\cdot\text{sec}^{-1}$ (Table 2). In general during the height of the summer drought in August the stomata were partially closed most of the day (below $0.1 \text{ cm}\cdot\text{sec}^{-1}$). After September rains the stomata opened to a greater degree (around $0.2 \text{ cm}\cdot\text{sec}^{-1}$) in October. In the winter it was not unusual to have averages of $0.4 \text{ cm}\cdot\text{sec}^{-1}$. In May k_s had fallen to between 0.1 and $0.2 \text{ cm}\cdot\text{sec}^{-1}$.

The average daily Ψ_x decreased between July and August in all except the coastal site. In October Ψ_x recovered except at the dry Cascade site where fall rains had not occurred. Winter Ψ_x was much lower than expected at the coastal, low Cascade and high Cascade sites. May again showed lower Ψ_x readings than expected in all of the areas except the foothill site.

ABA content rose between July and August and reached the highest average value in October. The ABA content then dropped markedly during the winter and began to rise again in May. The exception to this seasonal pattern occurred at the coastal site where the ABA content was high in July followed by a decrease in August, October and May. The highest average ABA value for the coast occurred during the winter.

Diurnal Trends

In July the diurnal trend of k_s started high in the morning at the foothill, low Cascade and high Cascade sites (Figure 2). k_s decreased after early morning readings and fell below $0.1 \text{ cm}\cdot\text{sec}^{-1}$ at midday. The stomata remained partially closed (below $0.1 \text{ cm}\cdot\text{sec}^{-1}$) for the rest of the day except at the high Cascade site. The coastal site had relatively low k_s in July. The stomata did not open significantly at the dry Cascade site the entire day. The trend of k_s in August was similar to that in July except the values were much lower (Figure 3).

In October, after September rains, the diurnal k_s pattern generally remained between 0.1 and $0.3 \text{ cm}\cdot\text{sec}^{-1}$ for all of the sites (Figure 4). k_s peaked at 0800 or 1000 hrs and then gradually decreased. The foothill and dry Cascade sites displayed the lowest k_s values and least diurnal change.

The winter diurnal k_s values started very high in the morning, decreased to a low point in the late afternoon, and at two sites (coastal and low Cascade), k_s started to increase again in the evening (Figure 5). The diurnal curves were relatively flat for the coastal, high Cascade and dry Cascade sites.

In May the foothill and high Cascade sites had high early morning k_s values which decreased rapidly and leveled off for the rest of the day (Figure 6). The coastal and dry Cascade sites had low diurnal k_s curves similar to the previous July values.

The predawn Ψ_x values in July were around -0.5 MPa except for the dry Cascade site which was much lower (Figure 2). Ψ_x decreased after 0700 hrs reaching its lowest point at 1000 hrs (foothill and low, high and dry Cascade sites) or 1400 hrs (coastal site). Ψ_x gradually increased throughout the afternoon.

The diurnal Ψ_x trend in August was generally similar to that in July (Figure 3).

The predawn Ψ_x values were higher than before for all of the sites in October (Figure 4). Ψ_x decreased to a low midafternoon value which was similar to the August midday Ψ_x values, and then increased sharply in the late afternoon.

The predawn Ψ_x values during the winter were extremely low at the coastal, low Cascade and high Cascade sites (Figure 5). The coastal and low Cascade sites showed an increase in Ψ_x during midday followed by a sharp decrease in the late afternoon and evening. The foothill and dry Cascade sites had relatively constant and high Ψ_x values throughout the day.

The May diurnal Ψ_x curves were similar to August at the foothill, low Cascade and high Cascade sites (Figure 6). The coastal and dry Cascade sites had extremely low predawn Ψ_x values, -3.3 and -4.1 MPa respectively. Ψ_x increased rapidly until 1000 hrs at the dry Cascade site and gradually increased the rest of the day.

In July the ABA values remained relatively constant until 1400 hrs except at the coastal site (Figure 2). The ABA diurnal trends in

August were less consistent than in July (Figure 3). The ABA values did not show any consistent diurnal patterns in October (Figure 4).

Except for the coastal site the ABA values were low and constant throughout the day during the winter (Figure 5). At the coastal site the ABA started very high, decreased during midday and increased again in the late afternoon. The May ABA values again showed no consistent diurnal pattern (Figure 6).

Regression Analysis

A regression analysis was used to determine if there were significant relationships between k_s , Ψ_x , ABA and a few environmental variables (Table 3). A multiple linear regression was used with k_s as the dependent variable and Ψ_x , ABA and $1/VPD$ as the independent variables. The transformation $1/VPD$ was used because of the apparent hyperbolic relationship between k_s and VPD . Only the 1000, 1400 and 1700 hrs readings of the combined July values were regressed to eliminate variation due to light. $1/VPD$ showed the highest correlation with k_s ($r^2 = 0.28$) in July followed by ABA ($r^2 = 0.14$) and Ψ_x was not significant. In August $1/VPD$ showed a strong correlation with k_s ($r^2 = 0.76$) and it was the only significant variable. Due to shorter days only the 1000 and 1400 hrs readings were used in the October, winter, and May multiple regressions. In October Ψ_x was strongly related to k_s ($r^2 = 0.78$). ABA ($r^2 = 0.01$) and $1/VPD$ ($r^2 = 0.01$) did not significantly contribute to the model. In the winter radiation was inconsistent from site to site and no variables

significantly contributed to the model. Ψ_x was an important variable ($r^2 = 0.53$) again in May, followed by $1/VPD$ ($r^2 = 0.17$).

DISCUSSION

Seasonal Trends

The summer average k_s values are similar to those found by others (Fetcher, 1976; Cline and Campbell, 1976; Running, 1976; Pereira and Kozlowski, 1978) for conifers (Table 2). The high winter k_s values are unusual, but not an artifact. Care was taken throughout the year to only measure dry needles. This was done by covering the needles with cellophane the night before the measurements were made. This technique did not restrict air flow, but did prevent dew formation on the needles. The cellophane was removed after sunrise.

In laboratory studies Reed (1968) found that the stomata of Douglas-fir closed at or below -2°C . Lassoie et al. (1977) found that diurnal net assimilation was enhanced in eastern red cedar during the winter at low leaf temperatures. However, when freezing temperatures were reached gas exchange rates were negligible. In our study the high winter and fall k_s values suggest that the potential for photosynthesis exists at these times of the year especially at the coastal site where mild temperatures occur throughout the winter (Figures 4 and 5). A modeling effort by Emmingham and Waring (1977) indicates that Douglas-fir may accumulate from 30 to 55% of their total annual assimilate during the period between October and May in the Pacific Northwest.

The low winter and spring average Ψ_x values may be due to cold soil temperatures. Kaufmann (1975) found that cold soil temperatures reduced Ψ_x in Engelmann spruce (*Picea engelmannii*) and he suggested that increased root resistance results from changes in root membrane permeability which is both species and preconditioning specific (Kuiper, 1972; Anderson and McNaughton, 1973). It is possible then that different ecotypes of Douglas-fir respond differently to cold soil temperatures.

Changes in the osmotic potential (Ψ_π) could also account for the lower average Ψ_x values in the winter and spring. Seasonal adjustments in Ψ_π have been observed in irrigated apple trees (Goode and Higgs, 1973) and sorghum (Fereris et al., 1976). Ericsson (1979) found that the starch content in Scots pine peaked in the summer and was low in the winter. This trend was contrasted with seasonal changes in soluble carbohydrates which were high during the winter and low during the summer. Soluble carbohydrates (myo-inositol, fructose, glucose, pinitol and sucrose) would have the tendency to lower Ψ_π while starch would have the opposite effect.

Seasonal trends of ABA in conifers has been previously studied in relation to dormancy. Webber (1974) found that the ABA level in Douglas-fir was low in winter and high in July and October. The seasonal trends that Webber described for Douglas-fir buds are similar to what we found in the needles at all of the areas except the coastal site. At the coastal site ABA levels peaked in the winter. A combination of mild temperatures and adequate moisture

could increase the growing season at the coast. If ABA level is an indicator of moisture-stress-induced dormancy then high ABA levels would be expected to occur later in the season in trees growing in moist habitats, which is supported by the longer growing season of western hemlock and coastal Douglas-fir.

Diurnal Trends

The July and August k_s diurnal trends are similar to patterns found by others (Hinckley et al., 1975; Running, 1975; Tan et al., 1977; and Pereire and Kozlowski, 1978) (Figures 2-6). The stomata were usually open during the predawn measurements as has been previously noted for Douglas-fir (Running, 1976; Blake and Ferrell, 1977). In August the brief stomatal opening in the morning is highly correlated with $1/VPD$ ($r^2 = 0.72$) when the morning values are used in a multiple linear regression with k_s as the dependent variable and $1/VPD$ and radiation as the independent variables.

In October and January there is a definite upward trend in k_s in the late afternoon at the coastal and low Cascade sites (Figures 4 and 5). In October this trend is probably associated with the water status of the tree. Both the coastal and low Cascade sites are under the least amount of moisture stress in October. The k_s in the fall is highly correlated with Ψ_x ($r^2 = 0.78$) and in the winter somewhat associated with radiation ($r^2 = 0.42$). Running (1976) found that during late fall, winter and early spring stomata of Douglas-fir

opened at night and attributed this to low evaporative demand and rapid recovery of Ψ_x .

In May the diurnal k_s curves are for the most part lower than expected, similar to July trends. Moisture is usually abundant in the spring so the low values may be due to cold soil temperatures and high evaporative demand. Together Ψ_x and $1/VPD$ contribute significantly to the variation in k_s ($r^2 = 0.70$) (Table 3).

The Ψ_x diurnal trends in July, August and October are analogous to patterns found by others (Hellkvist and Parsby, 1976; Hinckley *et al.*, 1975; Pereira and Kozlowski, 1978). The flattest diurnal curves (little morning or evening recovery) occurred when the trees were under the most stress (Figure 3). The low diurnal Ψ_x in October at the dry Cascade site may be explained by lack of fall rains, however, this Ψ_x pattern is contrasted with a relatively high k_s pattern. A decrease in Ψ_{π} may allow the maintenance of substantial turgor despite low Ψ_x which could account for high k_s patterns.

The Ψ_x diurnal inversions that occurred during the winter and spring have been noted before in Scots pine (Hellkvist and Parsby, 1977). The inversions they found were not as dramatic as those found in this study. The diurnal Ψ_x curves in the winter and spring for the coastal site are perhaps the most interesting. Freezing temperatures seldom occur at the coast and were not recorded during our diurnal measurements. In the winter the air temperatures at the coastal site were 1°C at predawn, 9°C at 1400 hrs, and 6°C after sunset. Clearly the low morning and evening Ψ_x are not due to frozen

stems. In addition diurnal VPD remained low and relatively constant throughout the day. The winter Ψ_x patterns are similar to diurnal radiation and to a lesser degree to air temperature patterns. It is impossible to establish a cause and effect relationship with our limited data, however, it is interesting to speculate on the physiological processes that may be contributing to these low water potentials. Three explanations may account for the inverted Ψ_x patterns: 1) diurnal changes in the solute potential (Ψ_π), 2) changes in membrane permeability with respect to solute transport, and 3) temperature-related changes in the viscosity of water.

It has been demonstrated that increases in soluble carbohydrates occurs during the winter and may be a mechanism to avoid freezing damage (Levitt, 1956; Sakai, 1961; Yoshida and Sakai, 1967; Ericsson, 1979). Diurnal fluctuations in Ψ_π have been noted in western white pine (*Pinus monticola*), sitka alder (*Alnus sinuata*), and Rocky mountain maple (*Acer glabrum*) (Cline and Campbell, 1976) and in white oak (*Quercus alba*), red oak (*Q. rubra*), black oak (*Q. velutina*) and sugar maple (*Acer saccharum*) (Hinckley et al., 1978) in the summer. It is often hard to determine whether an actual increase in solutes has occurred because of the effects of dehydration. Ψ_π has been shown to oscillate diurnally in maize and cannot be attributed to changes in the relative water content, i.e. an actual increase in solutes did occur (Acevedo, 1977).

Changes in solute levels could occur through changes in starch-glucose ratios. In various tree species it has been reported that

increases in free sugar levels occurs at the expense of starch during low temperature while at higher temperatures (above 10°C) free sugars are reconverted back into starch (Parker, 1959; Siminovitch et al., 1968; Precht, 1973). Investigations of changes in enzymes which could control starch-glucose ratios have often been contradictory and inconclusive.

A decrease in Ψ_{π} could also occur if translocation of photosynthate is inhibited in response to decreasing temperatures. Swanson and Whitney (1953) found that translocation out of the leaves of beans was decreased by low temperatures. Effects on the loading step of translocation could occur through changes in membrane permeability. Giaquinta and Geiger (1973) noted that sieve-tube permeability of beans was altered by temperatures below 10°C.

Waring and Running (1978) recently suggested that sapwood water storage may contribute to transpiration in Douglas-fir. They reasoned that if the resistances between storage tissue and xylem are lower than between xylem and soil, water may be withdrawn from tissues to meet transpirational demand. Air temperatures between 1°C and 9°C significantly increase the viscosity of water which in turn would decrease the flux of water if it was being drawn from the sapwood. However, since the average winter soil temperature at the coast is 4°C it is doubtful that the resistances are higher between the xylem and soil than between storage tissue and xylem. Also this would not explain the low afternoon Ψ_x values.

In spite of the fact that we don't definitely know why the winter diurnal Ψ_x is inverted at the coast, it is interesting to note the possible ecological significance. The trees at the coastal site may be actively photosynthesizing during the warm parts of the day, while decreasing Ψ_x in the evening to avoid damage from freezing. This adaptation would be less pronounced or non-existent at higher elevations where low temperatures are common.

ABA has received much attention for its role in stomatal regulation. Several investigators have found that water stress could bring about large increases in the amounts of ABA in leaves (Wright and Hiron, 1969; Beardsell and Cohen, 1975; Zeevaart, 1971; Zabadal, 1974; Blake and Ferrell, 1977). Most of the work has been done with herbaceous species and has not involved short term changes of stomatal aperture and ABA associated with diurnal patterns of transpiration.

For the most part the diurnal ABA curves show no clear relationship with the other variables. In July an increase is noted in the late afternoon at three of the sites which may have been triggered by low Ψ_x . The stomatal closure began earlier in the day. In August the two sites that were under the most stress (foothill and dry Cascade), as measured by low Ψ_x , low k_s and high VPD, showed dramatic increases in ABA during midday. Again the increased ABA followed the initiation of stomatal closure. The October diurnal ABA curves are even more erratic, showing only a general relationship to k_s . The ABA values in the winter were relatively low,

corresponding with high k_s levels. Late afternoon decreases in k_s were not clearly related to the ABA values. Finally in May, the ABA diurnal curves were again erratic, low, and showed no clear relationship with the other variables.

It is evident from these data that there is no clear relationship between ABA, k_s and Ψ_x . In many cases total ABA levels in the needles fluctuate throughout the day. In the winter and spring total ABA levels are more constant throughout the day. It is possible that ABA is "compartmentalized" in the cells and that its redistribution triggers stomatal closure (Cummins, 1973; Raschke, 1975). The relatively constant ABA levels that occurred during this study while k_s fluctuated support this hypothesis. On the other hand under prolonged moisture stress the sensitivity of guard cells to ABA may change as proposed by Kriedemann et al. (1972). During summer drought conditions continued low Ψ_x may initiate increased levels of ABA. At other times of the year changes in ABA promoting stomatal functioning may be too small to detect accurately.

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TABLE 1. GENERAL DESCRIPTION OF THE STUDY SITES. TEMPERATURE AND PRECIPITATION BASED ON TEN-YEAR AVERAGES.

Location	Elevation	Temperature (C)			Precipitation (mm)		
		Avg. Annual	Jan. avg. Minimum	July avg. Minimum	Avg. Annual	June-Aug.	Avg. annual Snowfall
Coastal site	200 m	10.3	3	15	2500	163	---
Foothill site	450 m	10.3	1	28	1000	55	200
Low Cascade site	500 m	9.2	-1	25	2350	117	200
High Cascade site	1300 m	7.2	-4	16	3200	127	2500
Dry Cascade site	850 m	6.0	-10	26	600	40	60

TABLE 2. DAILY AVERAGES FROM EACH SITE.

	July	August	October	January- February	May
Coastal site					
k_s (cm·sec ⁻¹)	0.09	0.13	0.28	0.42	0.10
ψ_x (MPa)	-1.03	-0.96	-0.55	-2.89	-2.50
VPD (mbs)	9.3	5.1	2.3	3.1	8.0
ABA (ng/g dry wt)	733	380	403	835	475
Foothill site					
k_s	0.10	0.00	0.12	0.26	0.28
ψ_x	-1.33	-1.66	-1.34	-1.07	-1.08
VPD	15.6	34.2	8.9	3.2	6.0
ABA	712	778	1290	217	513
Low Cascade site					
k_s	0.14	0.08	0.22	0.41	0.15
ψ_x	-0.98	-1.3	-0.79	-2.11	-1.59
VPD	14.0	17.8	4.6	2.2	2.0
ABA	222	336	716	196	521
High Cascade site					
k_s	0.19	0.05	0.24	0.44	0.21
ψ_x	-0.97	-1.2	-1.05	-1.44	-1.47
VPD	15.3	15.7	3.3	0.97	9.7
ABA	182	578	858	399	226
Dry Cascade site					
k_s	0.03	0.01	0.15	0.39	0.06
ψ_x	-1.46	-1.64	-1.84	-1.02	-2.42
VPD	18.6	27.6	4.1	1.5	11.3
ABA	459	711	786	142	286

TABLE 3. CORRELATIONS FOR MULTIPLE LINEAR REGRESSION ANALYSIS WHERE k_s IS THE DEPENDENT VARIABLE. SEPARATE MULTIPLE REGRESSIONS WERE PERFORMED FOR EACH TIME OF THE YEAR. IN JULY AND AUGUST THE 1000, 1400 AND 1700 HRS VALUES WERE USED. AT OTHER TIMES ONLY THE 1000 AND 1400 HRS VALUES WERE USED IN THE REGRESSION.

	Independent Variables			
	Ψ_x	1/VPD	ABA	Radiation
July values	0.06	0.28*	0.14*	---
August values	0.01	0.76*	0.04	---
October values	0.78*	0.01	0.01	---
January-February values	---	---	0.05	0.42*
May values	0.53*	0.17	0.06	---

*Significant at the 0.05 level.

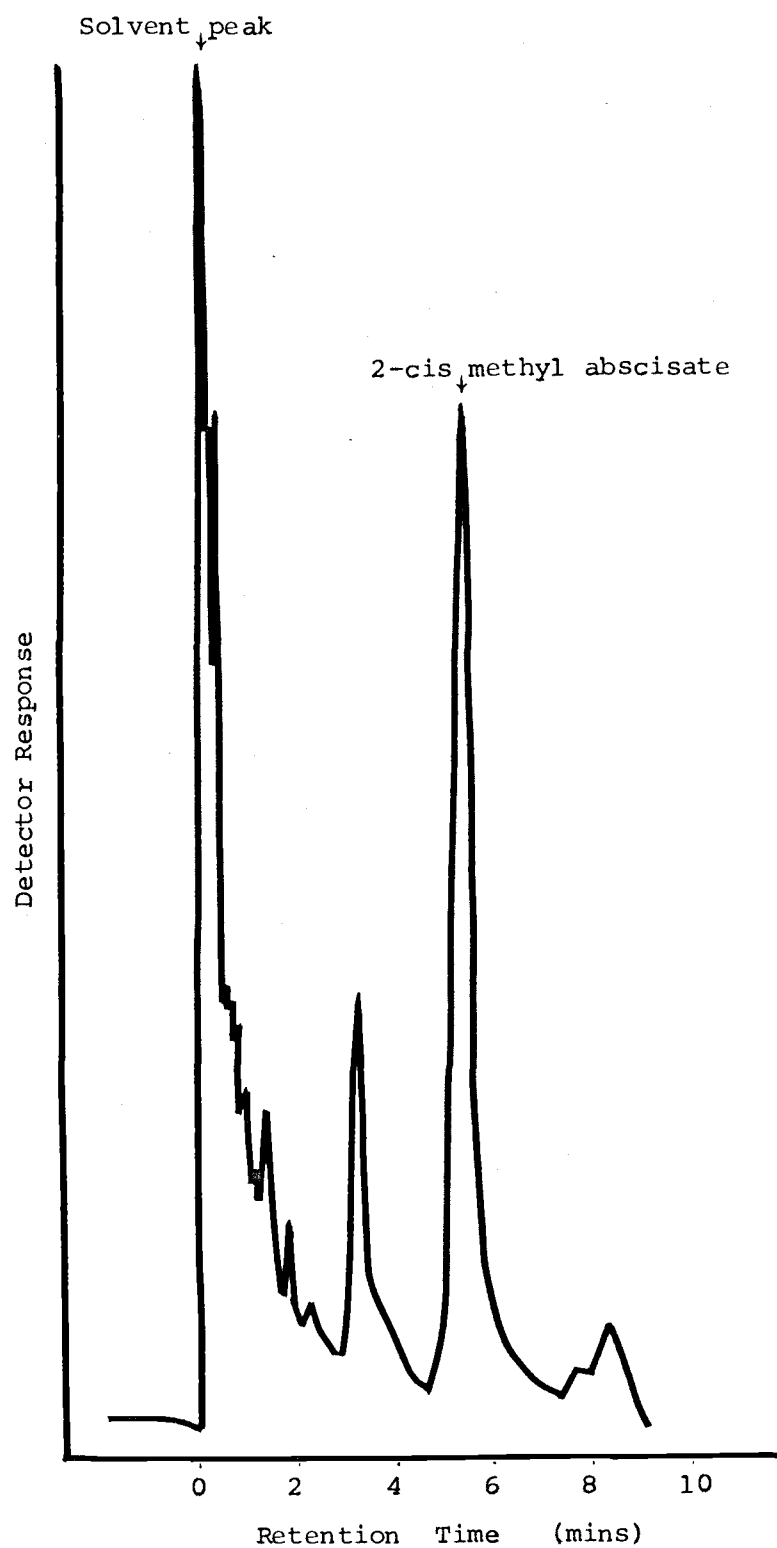


Figure 1. Gas-liquid chromatography analysis of methylated plant extract. Chromatography conditions as noted in text.

Figure 2. July diurnal patterns of k_s , Ψ_x , ABA and VPD for the five study sites. Coastal site, ●—●; foothill site, o-----o; low Cascade site, □-----□; high Cascade site, ●-----●; and dry Cascade site, ○-----○. Some ABA data are missing.

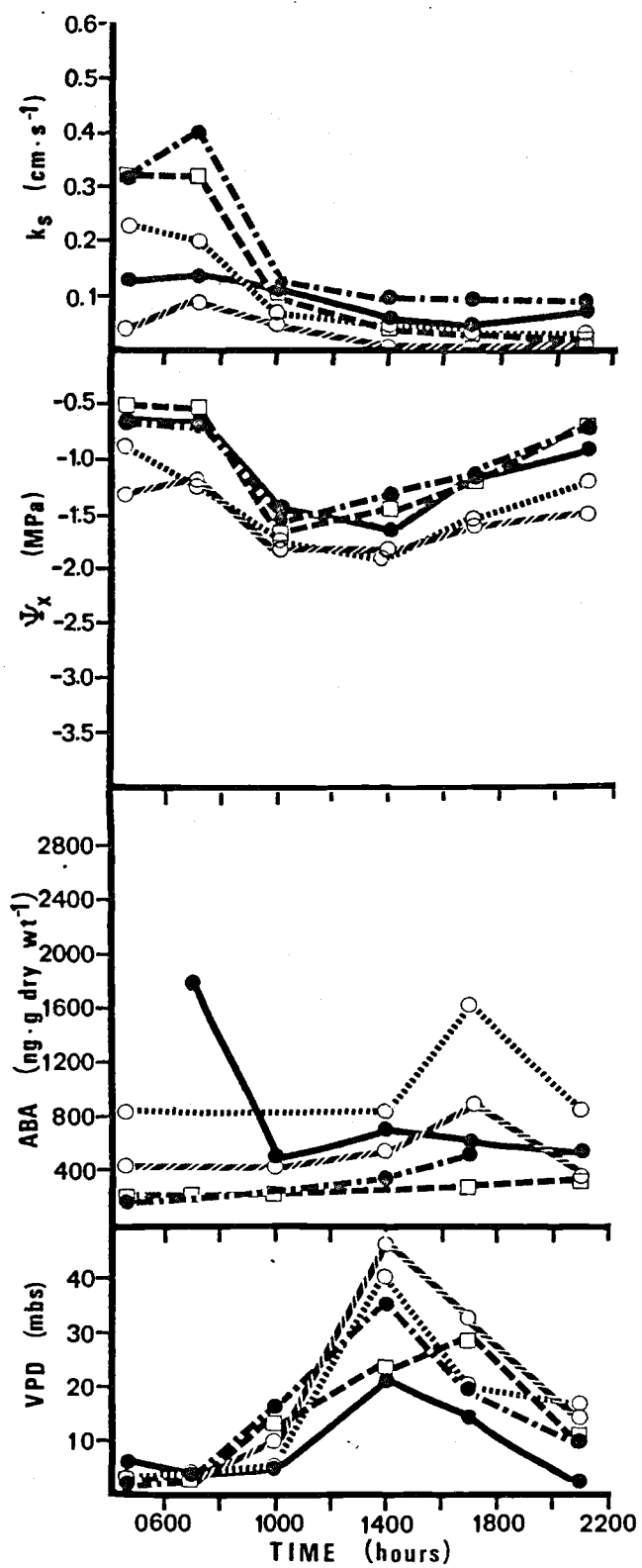


Figure 2.

Figure 3. August diurnal patterns of k_s , Ψ_x , ABA and VPD for the five study sites. Coastal site, ●—●; foothill site, ○-----○; low Cascade site, □-----□; high Cascade site, ●----●; and dry Cascade site, ○-----○. Some ABA data are missing.

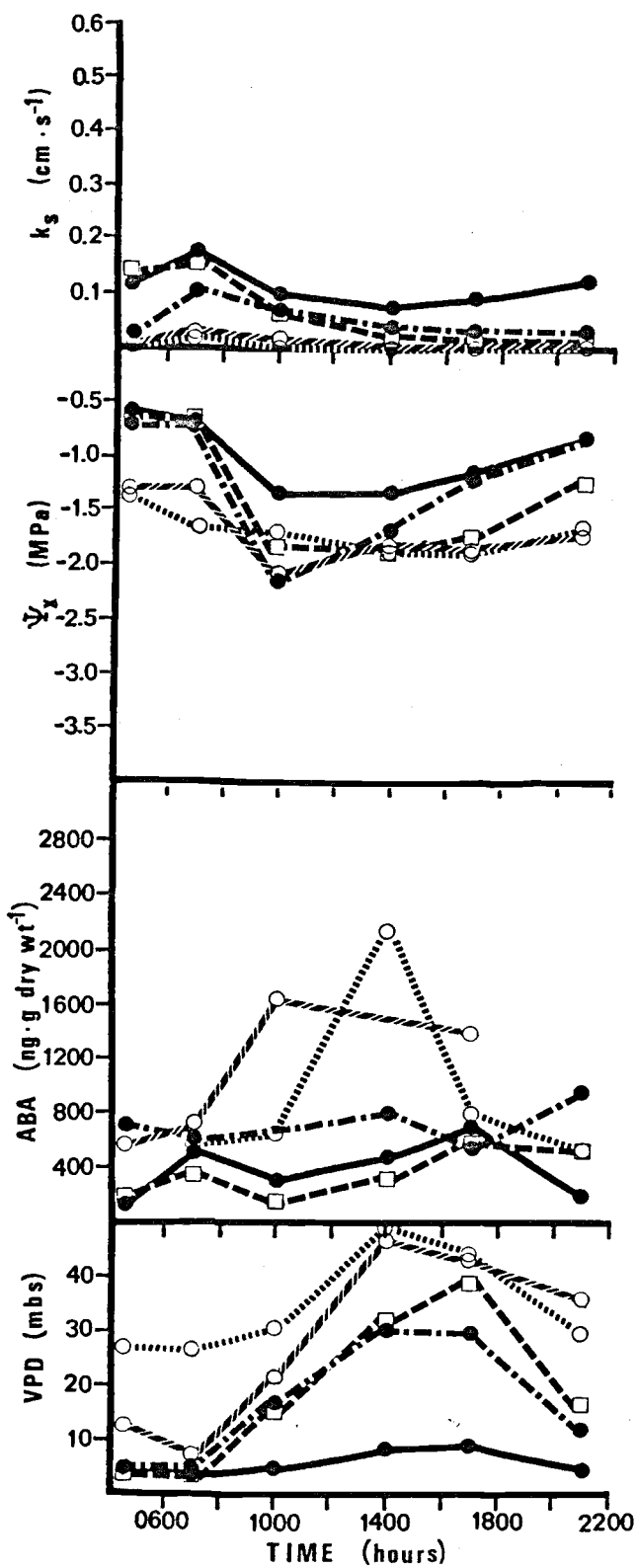


Figure 3.

Figure 4. October diurnal patterns of k_s , Ψ_x , ABA and VPD for the five study sites. Coastal site, ●—●; foothill site, ○-----○; low Cascade site, □----□; high Cascade site, ●-.-.-●; and dry Cascade site, ○-/-/-○. Some ABA data are missing.

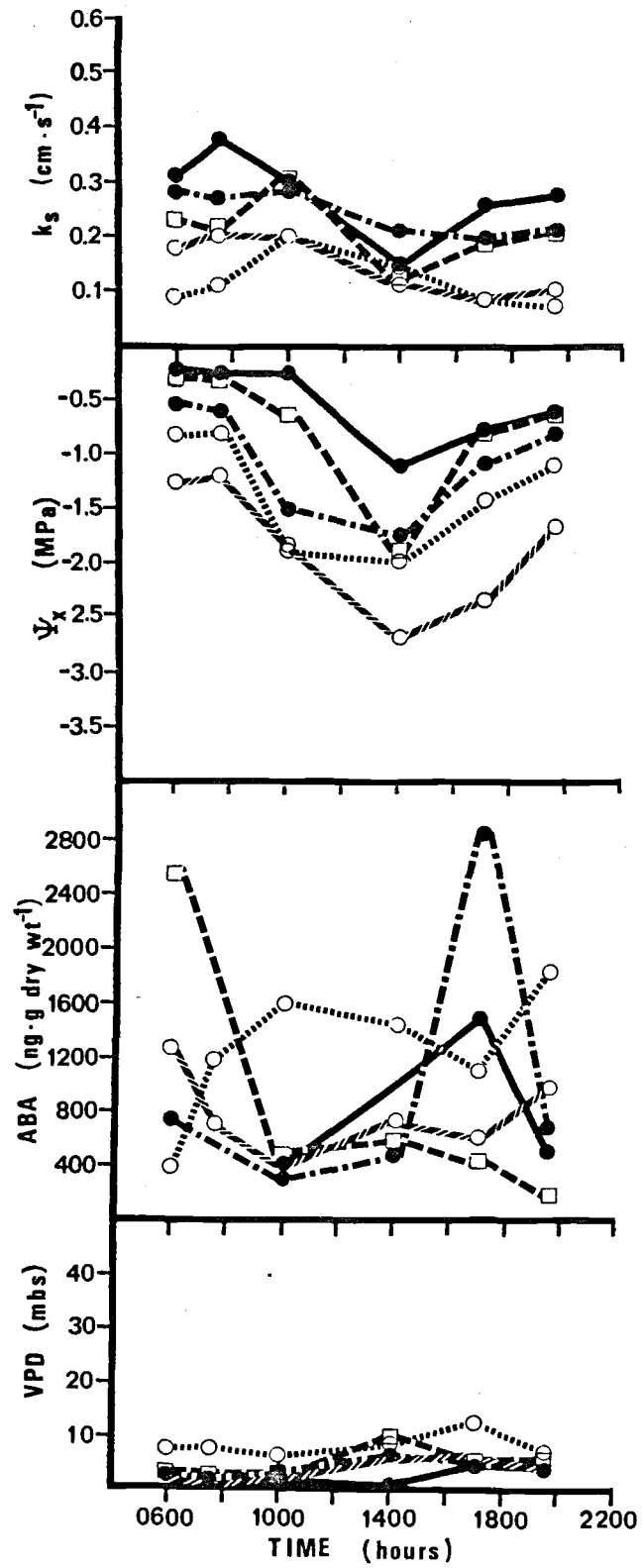


Figure 4.

Figure 5. January-February diurnal patterns of k_s , ψ_x , ABA and VPD for the five study sites. Coastal site, ●—●; foothill site, ○-----○; low Cascade site, □---□; high Cascade site, ●-·-·-●; and dry Cascade site, ○-----○.

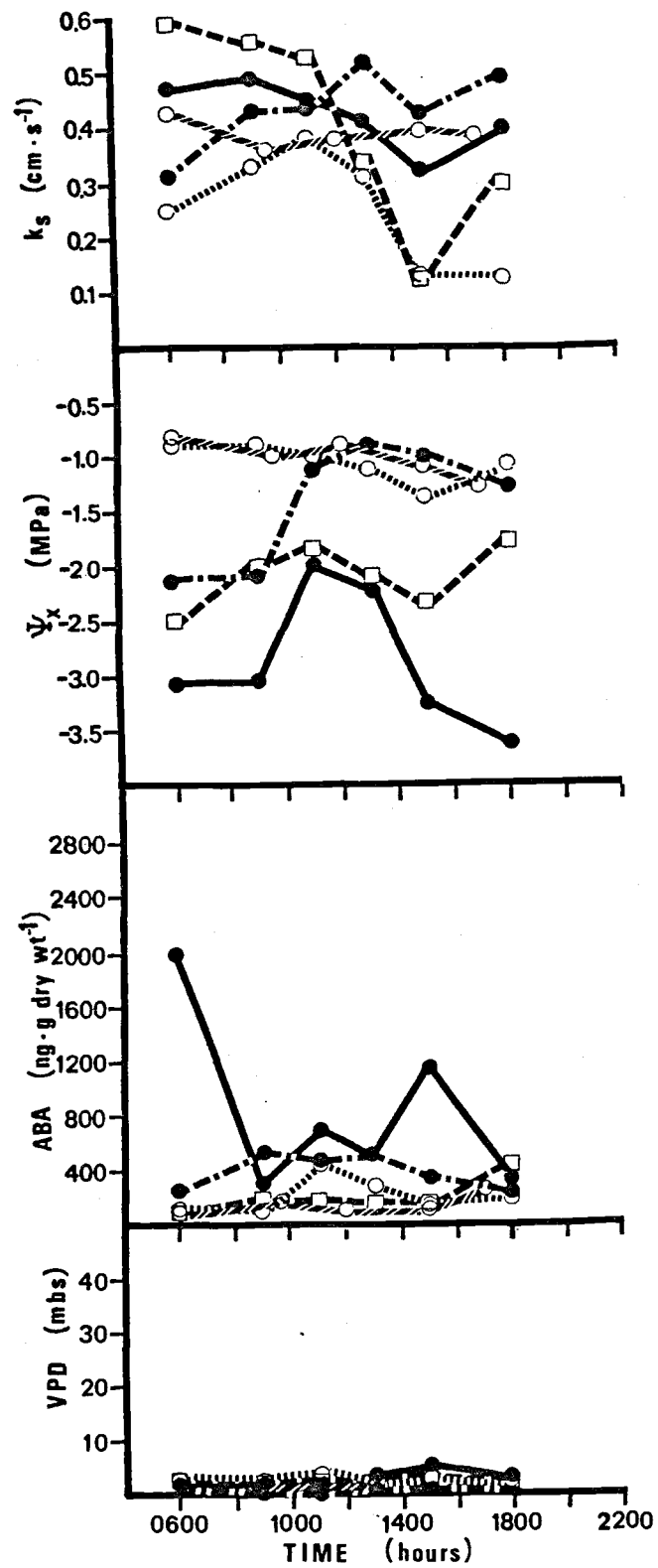


Figure 5.

Figure 6. May diurnal patterns of k_s , Ψ_x , ABA and VPD for the five study sites. Coastal site, ●—●; foothill site, ○-----○; low Cascade site, □----□; high Cascade site, ●-----●; and dry Cascade site, ○-----○. Some ABA data are missing.

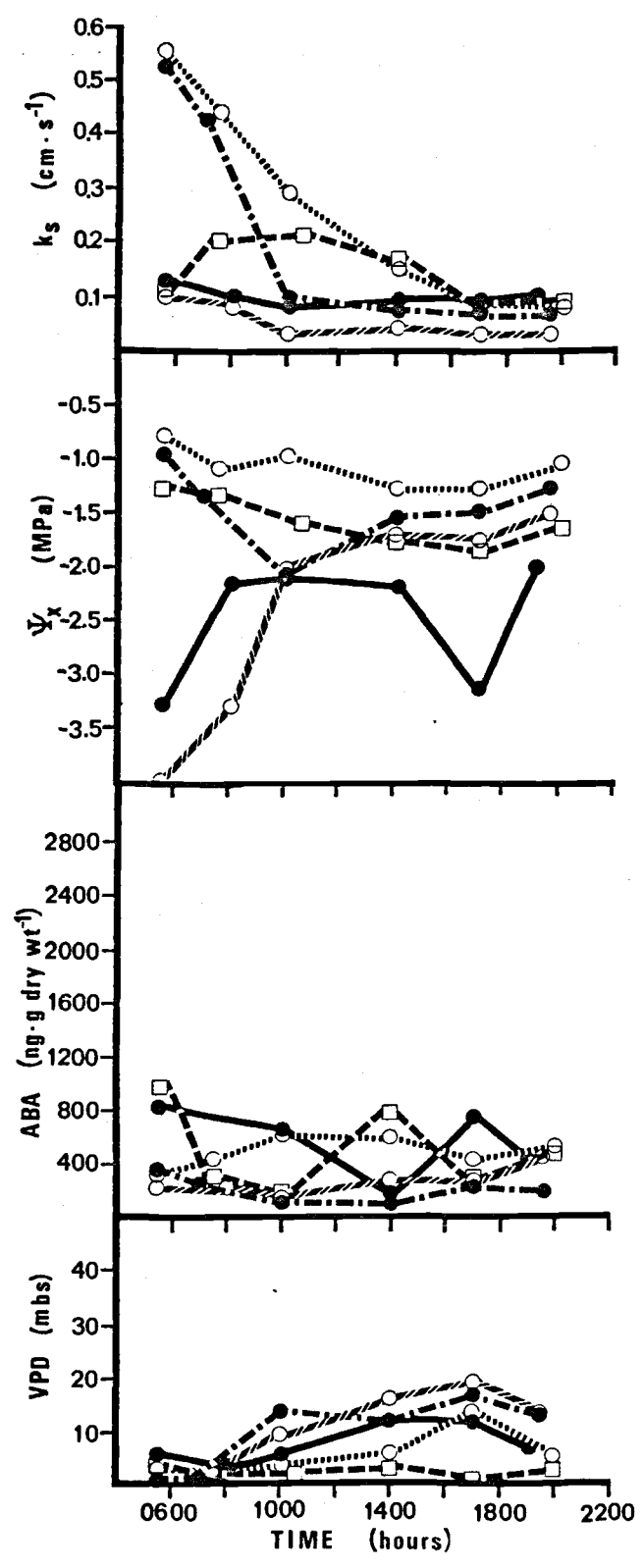


Figure 6.