INTERNAL REPORT 4

DIURNAL DIMENSIONAL FLUCTUATIONS IN DOUGLAS-FIR STEMS IN RESPONSE TO PLANT INTERNAL MOISTURE STATUS AND ENVIRONMENT

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ABSTRACT

Preliminary results of a comprehensive study of hydraulic fluctuations in Douglas-fir (Pseudotsuga menziesii) stems in response to plant water status and environment are presented. Diurnal changes in stem circumference near DBH of a dominant Douglas-fir were monitored using automated band dendrometers. Measurements of transpiration rate, internal moisture stress and stomata aperture were used to characterize the water status of the tree. Environmental monitoring involved the measurement of net radiation, air temperature and atmospheric vapor pressure above the forest canopy. The results from three typical days during the summer of 1971 are examined and discussed.

INTRODUCTION

Transpiration resulting from an evaporative demand at a tree's foliage produces an energy gradient causing water to move throughout the entire plant system. During periods of high transpiration it is possible for water loss to exceed the amount absorbed through the roots. When this occurs, certain tissues in a tree will dehydrate before stomatal closure limits water loss. As transpiration lessens, continued water absorption will rehydrate these tissues in response to a water potential gradient. A primary result of this phenomenon is diurnal dimensional fluctuations in the tissues involved. Such patterns have been shown for stem diameters of Pinus canariensis (MacDougal, 1924; Holmes and Shim, 1968), Prunus serotina (Kozlowski, 1968) and Pseudotsuga menziesii (Dobbs, 1966). These patterns are, of course, very dependent upon and interrelated with atmospheric and soil moisture conditions as well as physiological features of the trees involved.

Understanding physical changes in stem dimensions caused by internal hydraulic fluctuations is becoming increasingly important in tree physiology. Because environmental variables may interact to affect cell division and tissue hydration differentially, measurement of actual stem diameter growth (i.e. cell addition) using band dendrometers may be greatly confounded. Therefore, problems quickly arise when daily growth rates are to be correlated with environmental factors. Also, as the pattern of stem change is so closely related to the water status of the plant, monitoring diurnal fluctuations might prove to be a technique for continuously monitoring plant internal moisture stress. Such a relationship has been recently

shown for cotton (Namken, et. al., 1969) and red pine (Waggoner and Turner, 1971).

The phenomenon associated with hydraulic changes in stem dimensions is also closely tied with the concept of water storage in plants. Ritchie (1971) has used a compartment model to replace the catenary model of water transport (van den Honert, 1948). Ritchie's model depicts various plant-organ systems as acting either as sources or sinks for water. This model contains a storage compartment which represents any tissue or organ within the tree that will store and release water in response to water potential gradients. It is thought that tree stems act as storage areas for water, dehydrating to meet transpirational demands when the need arises. The probable seat for these hydraulic fluctuations has been suggested by Dobbs (1966) to be located at the cambium zone or possibly the bark.

This paper presents the preliminary results of a comprehensive examination of hydraulic fluctuations in Douglas-fir stems in response to internal water status and environment. This study is being conducted in conjunction with the IBP Coniferous Biome studies of plant water relations and carbon dioxide assimilation in forest ecosystems.

METHODS

This study was conducted at the Allen E. Thompson Research Center located about 35 miles southeast of Seattle in the foothills of the Washington Cascade Mountains. The Research Center, containing about 60 acres, is located on the western portion of the Cedar River watershed. The climate is typical of lower elevations in western Washington; the average temperature in July is 16°C, in January, 3°C. The average annual precipitation is 144 cm, with the majority falling during the winter months, as less than 20% falls during June through September. The soil is an Everett series, gravelly sandy loam, a brown podzolic soil derived from Pleistocene glacial outwash. The most prominent forest cover found on the area is a 40-year-old Douglas-fir plantation. The dominant trees are about 80 feet in height, the principal subordinate species being salal, Gaultheria shallon (Pursh.); Oregon grape, Berberis nervosa (Pursh.) (Nutt); bracken fern, Pteridium aquilinum (L.) (Kuhn) var. pubescens (Underw.); sword fern, Polystichum munitum (Kaulf.) (Pres1.); vine maple; and various species of moss. The climate, geology, soils, and vegetation of the area have been more completely described by Cole and Gessel (1968).

Diurnal changes in stem circumference of a dominant 70-foot-high Douglas-fir were monitored near DBH using an automated band dendrometer. With the exception of a slightly modified mounting bracket, these were constructed, calibrated, and installed according to procedures outlined by Dobbs (1966). Resolution of these dendrometers was better than 0.001 of an inch in circumference.

Internal moisture stress (P_S) and stomata infiltration pressure (SIP) of the study tree were monitored in conjunction with a study of carbon dioxide assimilation by R. B. Walker and D. Salo. Water stress was evaluated using a Scholander pressure chamber, described by Scholander, et. al, (1965), and techniques of Waring and Cleary (1967). Three samples were taken from about 60 feet for each sample period and averaged for that period. Six SIP measurements were taken periodically and averaged to characterize relative stomata apertures. Pressure infiltration apparatus, theory, and measurement techniques have been described by Fry and Walker (1967).

The transpiration rates of the study tree were estimated using the heat-pulse-velocity (HPV) technique (Swanson 1967, Hinckley 1971). The heat-pulse-velocity meter used in this study enabled multipoint simultaneous sampling of up to six points every hour. Two measurements were taken, one from the north side and one from the south side, near the DBH of the study tree. These hourly measurements were averaged for each sample period.

Standard meteorological data were collected and processed by Peter Machno in conjunction with hydrological studies being conducted at the Research Center. These data included net radiation (\mathbf{R}_n) and atmospheric vapor pressure measured above the canopy and air temperature (T_a) measured at 60 and 100 feet above the ground. The net radiometer used was constructed and calibrated according to Fritschen (1960 and 1965). Atmospheric vapor pressures were monitored using a lithium chloride dewprobe similar to those described by Tanner and Suomi (1956). The bobbin cavity temperature as well as \mathbf{T}_a were measured using temperature diodes constructed and calibrated according to Hinshaw and Fritschen (1970). These data were used to calculate the vapor pressure deficits (VPD) of the atmosphere.

RESULTS

The results presented in this paper represent typical data collected during the summer and autumn of 1971. The actual days to be discussed are July 23 and 27 and August 3. During these days, among others, Dr. Richard Walker and Mr. David Salo of the Botany Department, University of Washington, were monitoring carbon dioxide assimilation of the study tree. Results presented here are primarily for the daylight hours, approximately 0500 to 1700 Pacific Standard Time (PST).

Figure 1 shows water status and environmental data for July 23. This day was overcast, which resulted in low T_a , R_n and VPD values throughout the day. Transpiration rates (HPV) were quite low during the day, but P_s increased slowly. Stomata opened in the morning and closed in the afternoon, probably as a result of light levels rather than P_s . No major shrinkage occurred in the stem during this day, though a twin peak did occur.

Figure 2 shows similar data for July 27, which was clear and sunny. Air temperature and VPD rose steadily throughout the day and reached peaks in the late afternoon. Net radiation, except for a slight depression in the morning, rose steadily to a peak at about 1200 PST, at which time it began to decline. Internal

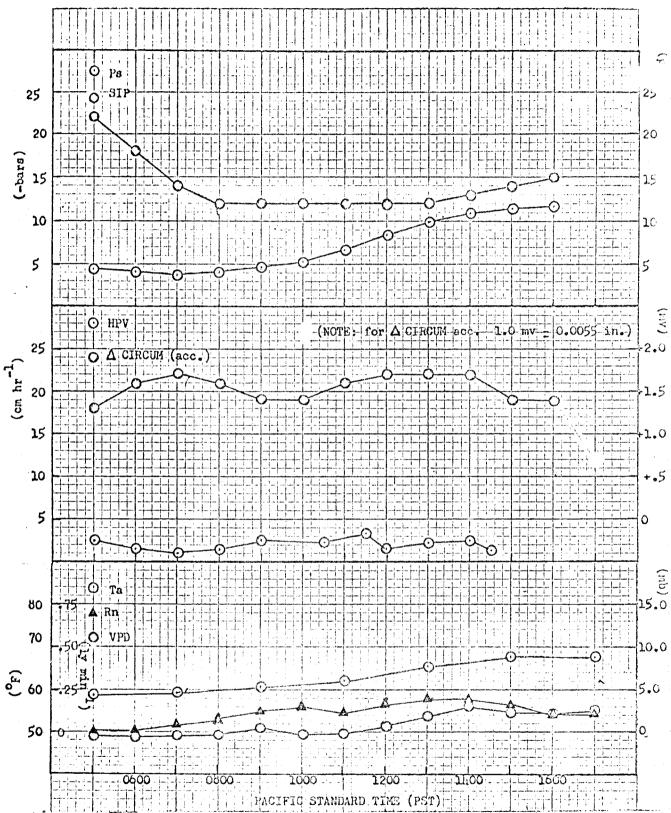


FIGURE 1. Patterns of daylight fluctuations in branch moisture stress (Ps), stomata infiltration pressure (SIP), heat pulse velocity (HPV), accumulative change in circumference (ACIRCUM(acc.), air temperature (Ta), net radiation (Rn), and vapor pressure deficit (VPD) for Douglas-fir on July 23,1971 at A.E. Thompson Research Center,

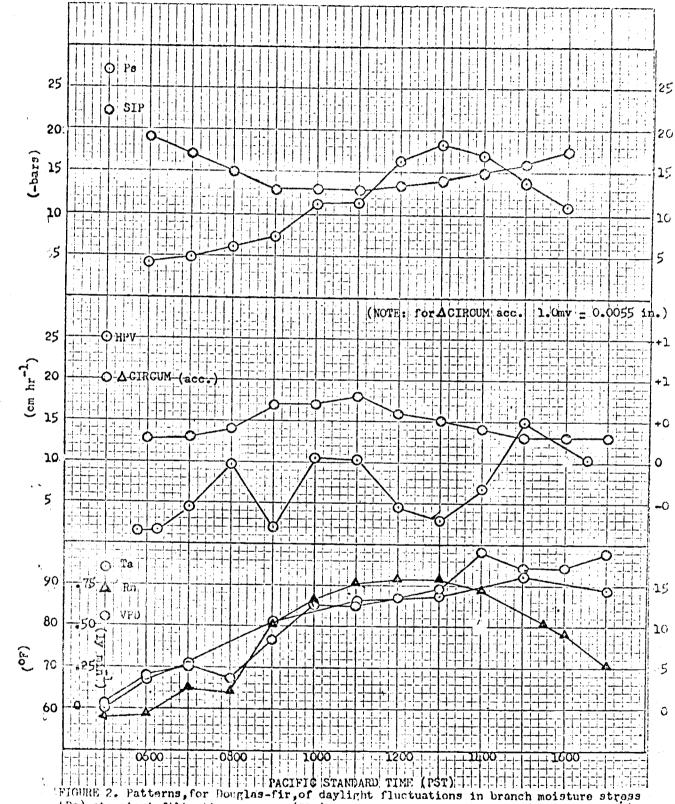


FIGURE 2. Patterns, for Bouglas-fir, of daylight fluctuations in branch moisture stress (Ps), stomata infiltration pressure (SIP), heat pulse velocity (HPV), accumulative change in circumference (\Delta CIRCUM (acc.), air temperature (Ta), net radiation (Rn), and vapor pressure deficit (VPD) for July 27, 1971 at A.E. Thompson Research Center.

moisture stress rose throughout the morning, and peaked at 1300 PST. Transpiration rates (HPV) oscillated during the day. A drastic decrease in HPV occurred at 0900, probably the result of a lower VPD brought on by a temporary decrease in $R_{\rm n}$. Heat-pulse-velocity measurements dropped again in the late morning, but increased in the afternoon. Stomata opened in the morning as on July 23, but began closing 2 hours earlier. Opening was probably the result of increased light levels, but closure was prompted by high $P_{\rm S}$ levels. The tree stem increased in circumference until about 1100, after which it decreased to a minimum at 1500 PST.

August 3 (Figure 3) was marked by an early morning fog that cleared by 0900 PST. Air temperature, VPD and $\rm R_{\rm R}$ values increased steadily throughout the morning, as did $\rm P_{\rm S}$, apparently not greatly influenced by the foggy period. Stomata, though, closed during the morning and remained fairly constant until about 1300 PST, after which they continued to close. Transpiration rates (HPV) were very low until after 1200 PST, at which time they increased sharply. No marked increase in stem circumference occurred on this day, as they did on July 23 and 27. In fact, shrinkage began by 0800 PST, three hours earlier than on July 27. Circumference shrinkage continued throughout the sample period.

Table 1 shows average daily values for water status and environmental data for the three days examined. Averages of $P_{\rm S}$, HPV and SIP were calculated from values taken from the figures between 0600 and 1600 PST. Air temperature, VPD, and $R_{\rm R}$ averages also were calculated from values on the figures, but between 0500 and 1700 PST. The maximum changes in stem circumference ($\Delta \text{CIRCUM max})$ were calculated by subtracting the smallest daily circumference from the largest.

These averages illustrate the major differences between the days examined. July 23 was marked by low $\rm R_{n}$, VPD and $\rm T_{a}$ averages. As a result $\rm P_{S}$ and HPV averages were low, stomata were open, and little stem shrinkage occurred. July 27 was very sunny and clear, which resulted in high $\rm T_{a}$, $\rm R_{n}$ and HPV averages. The results were high $\rm P_{S}$ and HPV averages, more closed stomata, and greater stem shrinkage. Averages of $\rm R_{n}$, VPD and $\rm T_{a}$ for August 3 were lower than for July 27; however, $\rm P_{S}$ was higher and a greater shrinkage in the stem occurred. Stomata were somewhat more closed and the HPV average was lower.

DISCUSSION

The results of this study indicate the effects and interrelationships of environment and internal moisture stress on the patterns of diurnal fluctuation in stem circumference. During the day, as the atmospheric evaporative demand increased and stomata opened, increases in transpiration rates and internal moisture stresses occurred. As absorption became less able to match transpiration losses, stem tissue dehydrated because of transpirational demands. This resulted in a measurable decrease in stem circumference.

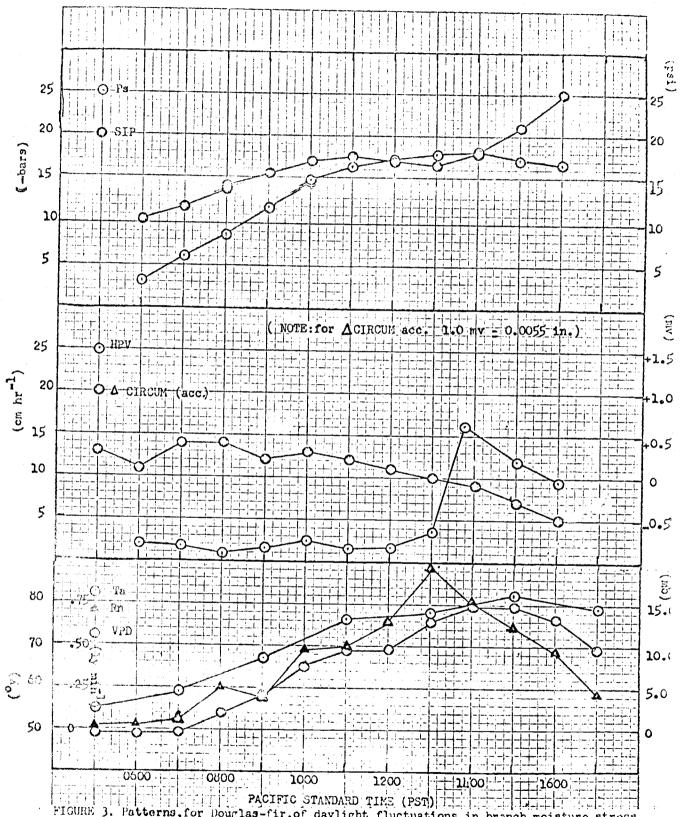


FIGURE 3. Patterns, for Douglas-fir, of daylight fluctuations in branch moisture stress (Ps), stomats infiltration pressure (SIP), heat pulse velocity (HPV), accumulative change in circumference (\Delta GIRCUM(acc.), air temperature (Ta), net radiation (Rn), and vapor pressure deficit (VPD) for August 3, 1971 at A.E. Thompson Research Center.

DATE	Ps	SIP	НЪЛ	△ CIRCUM(max)	Rn	V PD	Ta
1971	-bars	psi	cm hr	in.	ly min-1	mb	\mathbf{o}_{F}
July 23	7.4	13	2.0	0.0016	0.102	1.055	63
27	11.3	15	7.6	0.0028	0.478	11.298	81
Aug. 3	13.5	17	4.9	0.0050	0.396	7.448	71

TABLE 1. Daylight averages of Douglas-fir water status; branch moisture stress (Ps), stomata infiltration pressure (SIP), heat pulse velocity (HPV), and maximum change in stem circumference (\(\Delta \text{CIRCUM max.} \); and environment; net radiation (Rn), vapor pressure deficit (VPD), and air temperature (Ta); at A.E.THOMPSON RESEARCH CENTER.

Between the different days, the amount of shrinkage seemed to depend greatly upon the amount of water lost during the day. Increases in internal moisture stress resulted in greater shrinkage of the stem. August 3 was marked by the greatest stress and shrinkage, though environmental data suggested a lower atmospheric demand and infiltration pressures suggested more closed stomata. These results possibly suggest the influence of progressive soil drying on the magnitude of internal moisture stress and stem shrinkage. As no recorded precipitation occurred during this period, the soil presumably had dried and become less able to supply water to meet transpirational demands. Therefore, a lower demand on August 3 resulted in higher stresses and greater dehydration of internal stem tissue.

Transpiration rates did not prove indicative of increased stress and shrinkage. The highest HPV average was associated with the highest atmospheric moisture demand of July 27. This could be the result of soil moisture being more able to supply water to the transpirational stream on July 27 than on August 3. This seemed possible, because less shrinkage and lower stresses occurred on July 27. It should also be pointed out the HPV gives only the rate of water movement through the stem section and not the volume moved. Swanson, in 1967, reported that actual volume flow is dependent upon not only the velocity but also the conducting area and its moisture content. Both these factors are shown to vary greatly during the same season in lodgepole pine (Pinus contorta) and Engelmann spruce (Picea engelmanni). Therefore, it is possible that a different volume of water was transpired on August 3 and on July 27, even though the average HPV's were lower on August 3.

CONCLUSION

The preliminary results and discussion presented in this paper allow only a few tentative statements concerning diurnal fluctuations in stem circumference in response to plant water status and environment. For the days examined it may be stated that:

- 1) internal moisture stress seemed to be a good indicator of the magnitude of shrinkage in stem circumference.
- 2) increasing internal moisture stresses, in response to changing environmental conditions, tended to produce progressive shrinkages in tree stems.
- 3) the magnitude of the daily transpiration-absorption lag may be important in determining the total amount of diurnal shrinkage.

This report presented only preliminary results of a comprehensive examination of hydraulic fluctuations in Douglas-fir stems in response to plant water status and environment. The complete study is primarily three-fold. First is a field examination of daily $\Delta CIRCUM$ associated with average daily environmental conditions. Next, field and laboratory work will examine diurnal $\Delta CIRCUM$ in response to internal moisture conditions. Finally, a laboratory study will assess the influence of bark hydration on diurnal $\Delta CIRCUM$. Field work will be conducted

at or near the A. E. Thompson Research Center on the Cedar River watershed, and laboratory work will be done on campus. These studies will be conducted during 1971 and 1972 in conjunction with the IBP Coniferous Biome studies of water relations and primary productivity.

An examination of seasonal trends in daily maximum ΔCIRCUM is being conducted at the A. E. Thompson Research Center. It is hoped that this study will demonstrate that the amount of dimension decrease during the day is very dependent upon the daily environmental conditions. Automated band dendrometers were installed in June near DBH on six Douglas-fir trees. Heat-pulse-velocity probes were installed in four of these trees. Standard meteorological data, sampled atop a 100-foot tower, are being collected and processed by Peter Machno in conjunction with hydrologic and fertilization studies being conducted at the Center. These data will include solar and net radiation, wind speed and direction, dew point, and air temperature. Soil temperatures at various depths and precipitation data are also being collected. Soil moisture will be calculated using the Thornthwaite method as outlined by Machno (1964). Dendrometer band data will be used to calculate the maximum ACIRCUM, as explained earlier in this paper, for each 24-hour period. Environmental data and heat-pulse velocities will be averaged for each day. Multiple regression analysis will be used to examine the relationship between daily maximum ACIRCUM and environment. The results from the six sample trees will be compared and contrasted.

The second phase of this study will be a field and laboratory examination of $\Delta CIRCUM$ in response to internal moisture conditions. The field study will involve the use of the weighing lysimeter installed by L. J. Fritschen during the summer of 1971. Six to ten automated band dendrometers will be installed along the stem of the dominant Douglas-fir in the lysimeter. The water status of this tree will be monitored on a diurnal basis. Data will include transpiration rates (using the heat-pulse-velocity technique and the lysimeter), internal moisture stresses (using the Scholander pressure-chamber technique), and stomata apertures (using the Fry-Walker infiltration technique). Environmental data, similar to those collected during 1971, will be collected with a system installed by L. J. Fritschen. Again, multiple regression analysis will be used to deliniate the influence of environment and water status on the diurnal $\Delta CIRCUM$ of various internodes.

The laboratory examination of changes in stem dimension in response to internal moisture conditions will utilize a temperature and humidity-controlled environment chamber and small potted Douglas-fir seedlings. A small radial dendrometer sensitive enough to monitor changes in seedling stem dimension will be constructed. Fluctuations in radial dimension will be monitored under various regimes of humidity, temperature, light and soil moisture. The actual chamber environment will be monitored using thermocouples, a LiCl dew probe, a net radiometer and a solarimeter. Soil moisture

will be measured gravimetrically. The assessment of water status and data analysis will be similar to that used in the previous field study. The results will be compared and contrasted with those found for large forest-grown trees.

The final phase of this study will involve a controlledenvironment examination of the effects of bark dehydration and hydration on the diurnal patterns of ACIRCUM. Dobbs (1966) indicated that hydraulic fluctuations occurred either in the bark or cambium. Therefore, diurnal ACIRCUM possibly are associated with the hygroscopic characteristics of the outer bark, and respond to changes in atmospheric moisture content. It is hoped that this study will indicate the majority of diurnal ΔCIRCUM is not attributable to water exchange between the bark and the atmosphere, therefore implying primarily internal water exchange. A dominant Douglas-fir will be felled at the A. E. Thompson Research Center. Four internodes, two below and two within the live crown, will be sectioned from the stem. The cut ends will be sealed to prevent water exchange through these cut surfaces. Automated band dendrometers will be installed on each section. The sections will be placed in a controlled-environment chamber and ACIRCUM monitored under various temperature and humidity regimes. Actual chamber environment will be monitored as in the seedling study.

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