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Title SEASONAL AND DIURNAL VARIATION IN INTERNAL MOISTURE STRESS OF MATURE DOUGLAS-FIR

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The internal moisture stress of Douglas-fir was determined on foliage collected in the Siskiyou Mountains of southwestern Oregon. Internal moisture stress integrates both climatic and edaphic environmental effects as they influence a plant's moisture regime. In this study two laboratory techniques were modified to permit stress measurements to be taken on mature trees in the field. The internal moisture stress was determined directly using vapor equilibrium techniques to measure the diffusion pressure deficit of needle tissue. Relative turgidity, an indirect estimate of stress, was obtained by measuring the relative water content of needle tissue. Tissue was collected from four areas between 2700 and 5500 feet in elevation.

Relative turgidity determinations proved to be of limited value due to seasonal variations not associated with changes in the

internal moisture stress. The technique was, however, of value in providing data concerning diurnal fluctuations and may serve as a measure of the differences in internal moisture stress of trees at the same location.

Using an early morning sampling time, differences between plots were small. By sampling at 1500 hours in late summer, values ranging from 8.5 to 30 atmospheres stress were recorded. Internal moisture stress was not a simple function of either elevation or soil moisture stress. A biologically meaningful classification of tree moisture status was possible based on the maximum seasonal and diurnal internal moisture stress measured during the growing season.

SEASONAL AND DIURNAL VARIATION IN INTERNAL MOISTURE STRESS OF MATURE DOUGLAS-FIR

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TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

SEASONAL AND DIURNAL VARIATION IN INTERNAL MOISTURE STRESS OF MATURE DOUGLAS-FIR

INTRODUCTION

Many ecologists have investigated the moisture regime associated with various plant communities, but few have approached this problem by directly measuring leaf internal moisture stress. By analysis of internal moisture stress it is possible to obtain a biologically significant means of integrating climatic and edaphic environmental effects. In this study, I have undertaken the direct measurement of the internal moisture stress of Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco., over a range of environments.

The advantages of direct moisture stress evaluation led to an attempt to extend measurements to the field, allowing a better evaluation of the stress conditions which actually occur in mature trees. Techniques used primarily on broad-leaves and in the laboratory have been adapted for field use. By employing such techniques one can obtain a greater understanding of the water relations of various forest communities.

This study had the following specific objectives:

1. Measure the internal moisture stress in Douglas-fir at various levels of stress related to different plant

communities in which Douglas-fir is found.

2. Determine the sampling time which best defines the differences in the moisture regime of Douglas-fir.

3. Evaluate the variation in stress within stands and within a given tree.

The attainment of these objectives was felt to be best accomplished by the use of two different methods. One method directly measured the internal moisture stress using the vapor equilibrium technique; the other method indirectly estimated stress by determining the relative water content of needle tissue.

LITERATURE REVIEW

Literature pertaining to the water balance of plants is voluminous and only the most pertinent literature will be reviewed here.

Plant water use and its availability has been studied in plant physiology, soils, and meteorology. Each of these fields has analyzed the water balance from its own viewpoint, often neglecting how these three fields are interrelated. The ecologist, on the other hand, is interested in the plant as it interacts with its total environment, and therefore is required to focus his attention on the salient interdisciplinary relationships. Because each of these disciplines has examined a different aspect of the water balance, the terminology associated with plant water relations contains many overlapping and confusing terms.

Slatyer and Taylor (1960) and Taylor and Slatyer (1962) reviewed past terminology for the expression of a cell's water balance and proposed new terminology based on the laws of thermodynamics. They suggested that the term "water potential" would better describe and unify present usage common to both soils and physiology. The new terminology would revise the system based on pressure to a more correct one which has its foundation in potential energy differences. Slatyer (1962), however, concluded that: "while the newer terminology proposals have merit, it is thought that they, or other proposals, will not be accepted generally until the parameters they describe can be shown to be necessary to a fuller understanding of plant water relationships." I am in accord with this philosophy and therefore have chosen to retain the term "diffusion pressure deficit" (DPD) in pressure units of atmospheres as a specific expression of internal moisture stress. Also used in this study is the term "relative turgidity", referring to a technique for obtaining an index to the internal moisture stress by determining the relative water content of tissue (Weatherley, 1950).

The moisture status of plants has long been interpreted as being very closely related to soil moisture. The availability of moisture to a plant during the growing season has been expressed in different ways. Variables such as depth and stability of the water table, morphological features of the soil profile, and topographic position have been employed to classify sites in relation to a moisture gradient (Hills, 1959; Whittaker, 1960; and Loucks, 1962).

Moisture depletion patterns have been studied by Glatzel (1960) working with four hardwood types in Germany and McMinn (1960) investigating the relation between available soil moisture and the occurrence of western red cedar and Douglas-fir communities. Waring (1964) utilized minimum available soil moisture to derive a moisture gradient in a study of the California redwood region forest types. But, whether the soil moisture is measured directly or indirectly, it must be recognized that soil moisture is only one factor influencing the plants' internal moisture stress.

The water balance in a plant depends on the relative rates of water absorption and water loss. Thus, the internal moisture stress of any given plant is dependent upon three factors: the soil moisture stress, the atmospheric stress, and the ability of the plant to control water losses. The interaction of these three factors determines the internal moisture stress in any given situation.

Recently, the idea that moisture stress should be measured in the plant has been acknowledged and re-emphasized by Slatyer (1957), (1960); Weatherley (1950); and Waring (1965). Kramer and Brix (1965) summarized this point of view: "It is quite clear that we cannot make reliable assumptions concerning the degree of water stress existing in plants from soil moisture data or estimates of evapotranspiration. The only safe procedure is to measure the water stress of the plant by some direct method."

Two methods of determining the internal moisture stress have been adopted in this study. The first involved relative turgidity (RT) determinations as an index to internal moisture stress. Barrs and Weatherley (1962) devised a number of refinements over earlier work by Weatherley (1950). The RT of conifers has been determined by Rutter and Sands (1958) and Clausen and Kozlowski

(1965).

The second procedure involved the determination of diffusion pressure deficit. There are presently two acceptable methods for measuring DPD. One of these, utilizing a thermocouple psychrometer to measure the vapor pressure in a small chamber, has been described by Richards and Ogata (1958), Spanner (1951), and Monteith and Owen (1958). Fry (1965) modified the chamber, allowing smaller amounts of foliage to be used in determining the DPD of laboratory grown seedlings.

The psychrometer method has several disadvantages which led to its rejection in this study. First, it cannot be readily used in field studies because water lost from the tissue during storage and transport to the laboratory cannot be permitted, even when it is retained within an airtight vial. Second, is the high initial cost of equipment needed for this technique.

The vapor equilibrium method, originally described by Arcichovskaja (1931), was considerably modified by Slatyer (1958). This technique involves determining the equivalent stress where no loss or gain in leaf weight occurs in tissue placed above a graded series of osmotic solutions. While requiring a larger tissue sample and more time than the psychrometer method, this procedure is applicable to field collected material.

One other indirect approach to the measurement of leaf internal moisture stress should be discussed here. Scholander, et. al. (1965) measured the negative sap pressure of the xylem in a number of plants using a pressure bomb. He postulated that there is a close relationship between sap pressure and the internal moisture stress in foliage, but this has yet to be documented. This technique is readily adapted for field use and shows promise for future studies in plant water relations.

METHODS

Study Area

This study was conducted in the Siskiyou Mountains of southwestern Oregon with sample plots located on the north and west side of a ridge which runs up Mount Ashland (latitude 42°N, longitude 123°W). The area is characterized by hot dry summers and cool moist winters. Precipitation in the area occurs primarily in the winter and early spring. Summer rains are infrequent and add only limited amounts to the soil moisture supply. Soils of the general area are developed from granitic parent material. Individual plot descriptions are summarized in Table I.

Table 1. Plot Descriptions

Plot Number	Dominant Vegetation	Elevation (Feet)	Aspect
1	P.P.-D.F.-W.F.	5000	W
2	D.F.-W.F.	5500	W
3	P.P.-D.F.-B.O.	2700	N
4	P.P.-D.F.-I.C.	4200	SW

DF - Douglas-fir
IC - Incense-cedar
BO - Black oak
PP - Ponderosa pine
WF - White fir

Field Methods

Foliage samples were collected at two week intervals, beginning the first week in June 1965. At each plot a minimum of three trees were selected for sampling. All of the trees were mature dominants 75 to 125 feet high. A foliage sample was collected from the upper third of the crown using a shotgun. From foliage collected in this manner, a sample of last year's needles was prepared. The needles were trimmed into one centimeter segments and placed into airtight vials. Four replications for each measure of RT were prepared and stored in a refrigerator at 35°F until returned to the laboratory for processing. The number of samples collected for DPD determinations varied depending upon the number of osmotic solutions that were employed. Storage time was kept as short as possible, but normally two to three days elapsed between collection and laboratory processing.

Laboratory Procedures

1. Relative Turgidity (RT)

Upon returning to the laboratory, fresh weight of samples was determined to the nearest tenth of a milligram. Needles were floated in a petri dish on distilled water for 24 hours under a light intensity near their compensation point. Krueger and Ferrell (1965) reported the compensation point to be approximately 100 ft.-c. The needles were transferred, with the aid of a Büchner funnel, blotted, placed in their original vial, and the turgid weight determined. Next, the needles were dried at 70°C for 24 hours to obtain the oven dry weight. Relative turgidity was then calculated from the formula:

$$RT = \frac{\text{Fwt.} - \text{Dwt.}}{\text{Twt.} - \text{Dwt.}} \times 100$$

where:

Fwt. = fresh weight

Twt. = turgid weight

Dwt. = oven dry weight

During this study more than 300 series of relative turgidity determinations were made. Each series consisted of at least four separate samples, with the resulting standard deviation equal to one percent.

In the RT procedure a source of error occurs in the determination of the turgid weight. Water uptake of leaf tissue can be divided into two phases: Phase I, the rapid initial passive uptake; followed by Phase II, a slow steady uptake due to growth and infiltration of the intercellular spaces (Barrs and Weatherley, 1962). Phase II uptake continues as long as the tissue remains floating on water and is healthy. The use of 24 hours as the floating time extends well into Phase II uptake introducing error in the turgid weight, but since the soaking time was of a standard length the RT's obtained should still be reliable indices.

II. Diffusion Pressure Deficit (DPD)

DPD was determined using the vapor equilibrium method of Slatyer (1958), modified for use on coniferous needle tissue. Tests made to determine the minimum sample size, while still maintaining an adequate degree of precision, indicated that a 0.2 gram sample of tissue was required. All tissue was soaked to bring it to the "turgid" condition. This was done to eliminate hysteresis, to shorten equilibrium time, and to allow calculation of the RT of DPD samples. Following the determination of the turgid weight, tissue was placed in a desiccator above a sodium chloride solution.

Each solution was duplicated and the number of concentrations varied. Initially 0.1, 0.3, 0.5, and 1.0 molar concentrations of sodium chloride were used. Later in the study, after verification of the linearity of the DPD curve between 0. 1 M (4. 8 atm) and 0. 5 M (22. 4 atm) on 15 consecutive DPD determinations, only the 0. 1 M and 0. 5 M concentrations were used (Fig. 1). This facilitated the handling of more samples over the range of DPD where all but several samples were recorded. In those few cases where values exceeded 22 atm, the slope of the curve was extrapolated from earlier experiments.

The desiccators were placed in a water bath at 25°C ± .01°C. This temperature control is not as good as that which is recommended by Slatyer (1958) and Barrs and Slatyer (1965). However, a desiccator with a large mass has a long time constant which will damp out any short term fluctuations in temperature. In this study, although temperature control was not to ± .001°C, no lack of precision was encountered which could be attributed to temperature control. Tissue equilibrium time was 72 hours, after which the tissue was removed and the equilibrium weight determined. Needles were oven dried at 70°C for 24 hours to obtain the oven dry weight. Ratios of equilibrium weight to fresh weight were plotted against stress, equivalent to the vapor pressure above the salt solutions (Slatyer and McIlroy 1961). The stress where the equilibrium weight/fresh weight ratio was equal to unity indicated the DPD of the tissue. The curve obtained from a typical DPD

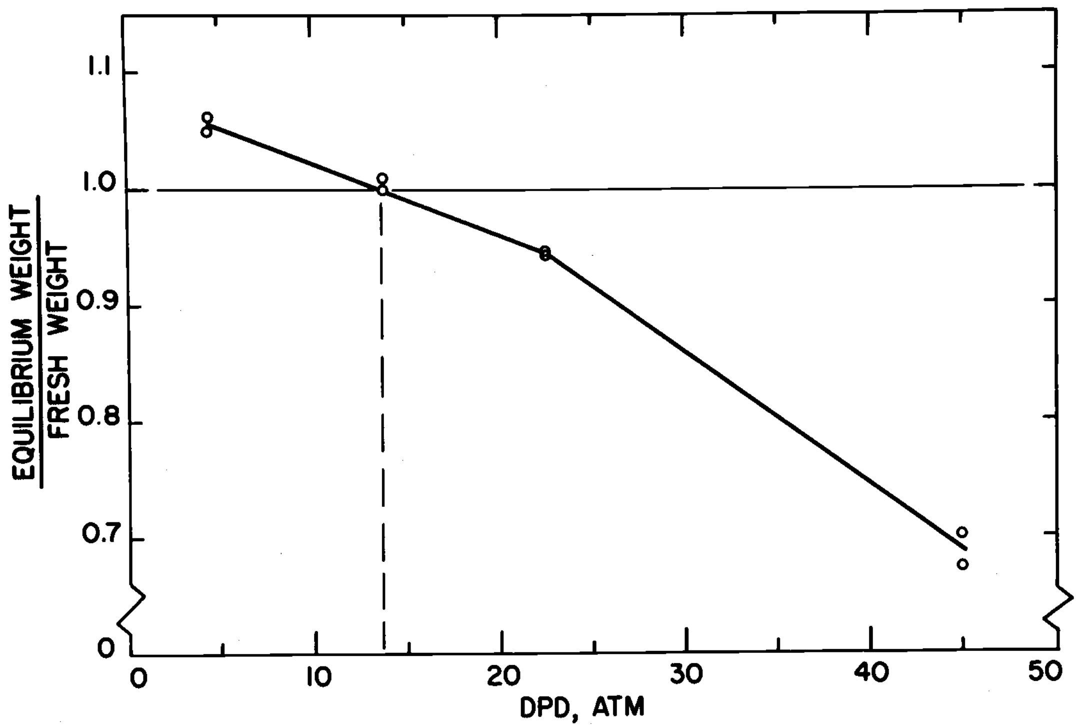

Figure 1. Plot of data for determination of diffusion pressure deficit.

determination is shown in Figure 1. During this study DPD determinations were made on 25 separate sets of samples. The average range in precision using duplicates for each concentration of solution was 2 atm stress. Weight losses due to respiration might be cause for error (Barrs and Slatyer, 1965). However, from the data obtained in this study the effect attributed to respiration appeared to be small. Further study of this problem is being undertaken.

In the past, determination of DPD has been made by finding where neither gains nor losses in the original tissue weight occur (Slatyer, 1958). Ratios are calculated from the equation:

$$\frac{\text{Ewt.}}{\text{Fwt.}} = \frac{\text{Ewt. - Tare}}{\text{Fwt. - Tare}}$$

where:

Ewt. = Weight of the tissue after reaching equilibrium in a desiccator

Fwt = Fresh weight at time of collection

In this study, following an examination of the procedure, the original weight of water rather than tissue was employed as a standard. The change in water status of the tissue was computed by the following formula:

$$\frac{\text{Equil. } H_2O}{\text{Fresh } H_2O} = \frac{\text{Ewt. - Dwt.}}{\text{Fwt. - Dwt.}}$$

where:

Dwt. = Oven dry weight of tissue

This method has several advantages over the former. First, calculations can be done without the determination of tare weight since this value remains constant and cancels out in the computations. Second, it is more meaningful to use a ratio of the weights of H_2O since it is the water relations of cells which are being investigated; the weight of cell material is not important here. Third, by using a ratio based on the weight of H_2O the slope of the resulting curve is greater, thus better defining the point where the ratio equals unity. Removal of the constant (Dwt.) is particularly desirable with only a limited number of replications at each salt concentration. Theoretically, the equilibrium point is identical, regardless of the computation followed; any discrepancy reflects errors in plotting and rounding off.

RESULTS AND DISCUSSION

Beginning early in June, samples were taken from plots 1, 2, and 3. On a portion of the samples only RT was determined, but in most cases the tissue was used to determine both RT and DPD. Because DPD tissue samples were brought to the turgid condition previous to placement above salt solutions, the RT of these samples were readily calculated. In this manner, a curve relating RT and DPD was plotted from each DPD determination (example-Fig. 2). Such a curve permits one to convert RT measurements to absolute values of stress. Curves constructed from my data, unfortunately, are inprecise because of the restricted number of replications possible under the experimental conditions imposed. With some further refinement in the techniques described here, it is likely the utility of these RT-DPD curves can be extended.

Soil moisture was sampled at one and two foot depths, bimonthly, during the summer. The moisture percentage values were converted to stress using soil moisture-stress curves for each of three sampling points located on each plot. On the coarse-textured soils sampled, small variations in moisture content represented a significant variation in stress. Therefore, the 15 atmosphere value was determined on each soil sample. Where discrepancies existed between the 15 atmosphere point on the

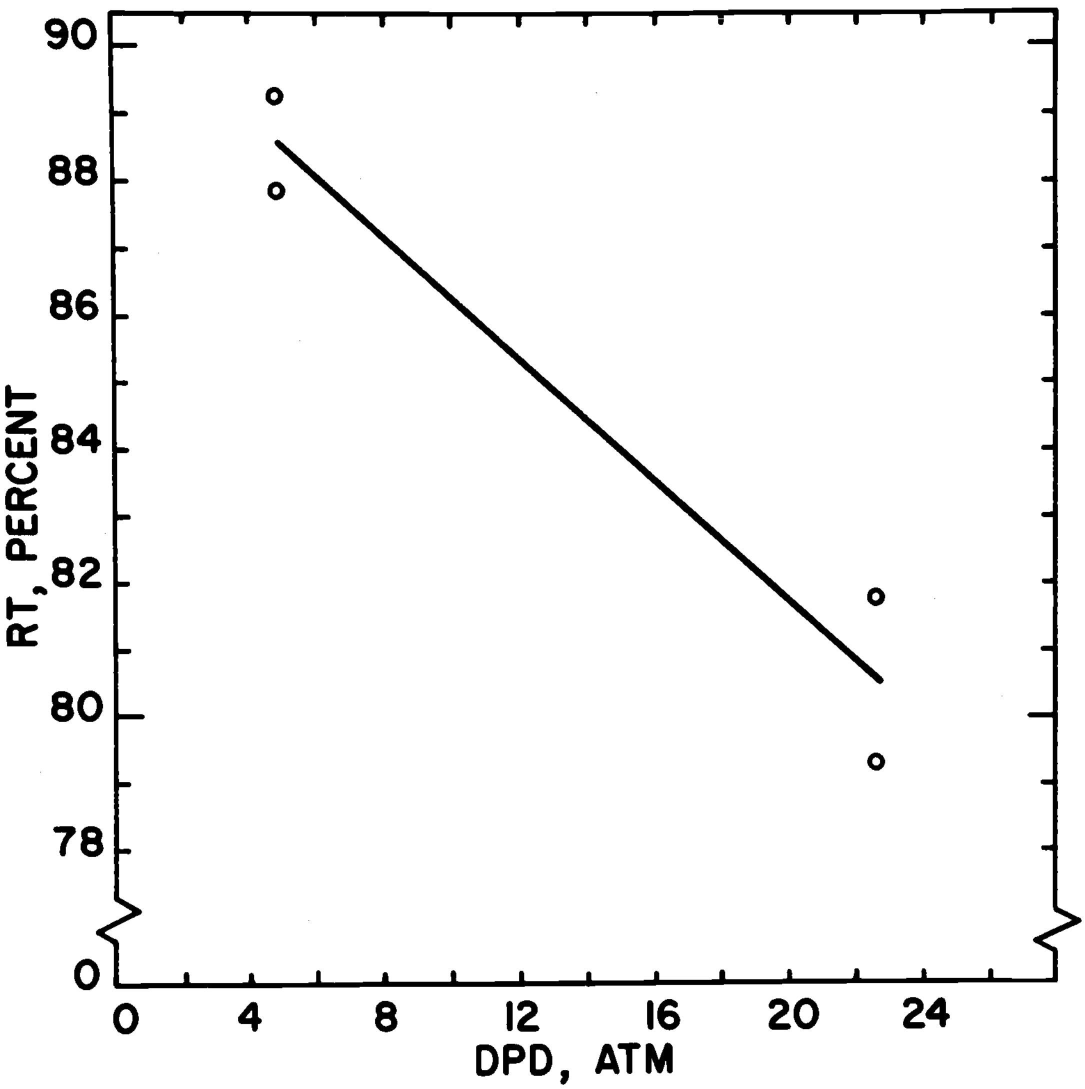

Figure 2. Relative turgidity - diffusion pressure deficit curve obtained from diffusion pressure deficit samples.

master curve and the 15 atmosphere value for individual samples, curves were adjusted up or down accordingly.

The seasonal variation in soil moisture stress on plot 3 at the two foot level is illustrated in Figure 3. The points plotted are averages for three sampling locations. All plots reached a value near 15 atmospheres at the two foot depth by the end of July, and were at or greater than 15 atmospheres except during the brief period following the two rainstorms which occurred in August. This is of significance since over the entire study area soil moisture was in critical supply in the surface two feet by the end of July. Below the two foot zone root distribution was erratic and rock content very high. Soil moisture measurements under such situations are not biologically meaningful and are very difficult to obtain. If any differences in vegetation here can be attributed to soil moisture, they cannot be measured using the most reliable techniques available.

The seasonal variation in RT was followed from the beginning of June. The values presented in Figure 4 are for one tree on plot 3, with the variation among trees on the same plot equal to three percent RT. The three plots investigated throughout the entire summer showed similar trends. According to Slatyer (1960) and Rutter and Sands (1958) sunrise should have been the best sampling time to delineate differences between areas. Under

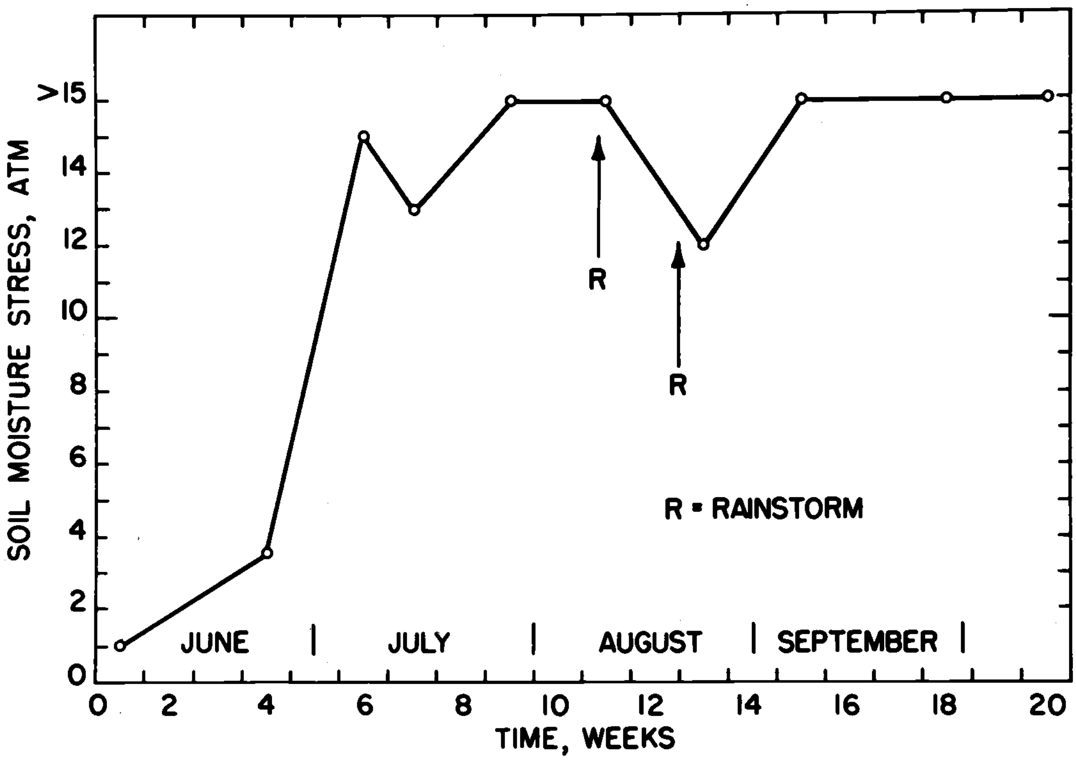

Figure 3. Seasonal variation in soil moisture stress at the two-foot depth. Points plotted are averaged for three sampling locations on plot number three.

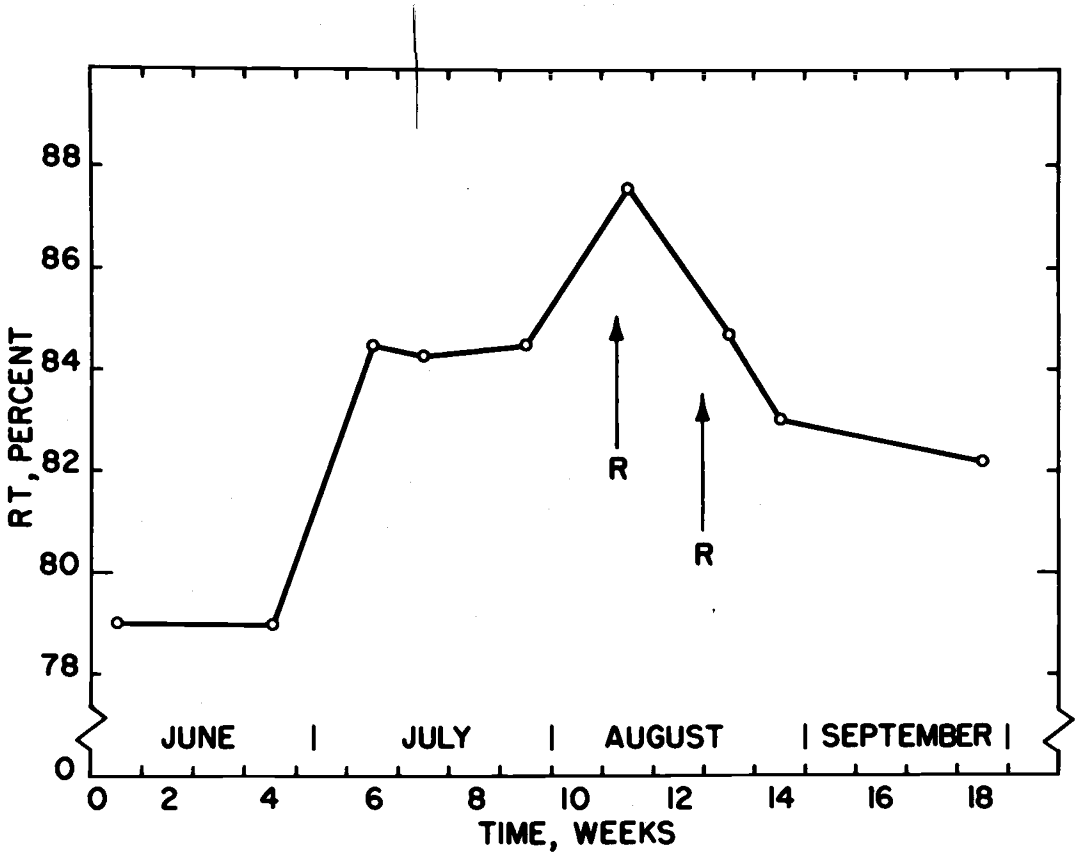

Figure 4. Seasonal variation in relative turgidity on plot number three for foliage collected at 0700 hours.

certain circumstances this is no doubt true, but in this study differences among plots at the early morning sampling time were small. DPD determinations at the end of July indicated that Douglas-fir on all of the plots were under less than 7 atmospheres stress.

To follow the diurnal variation in stress, RT samples were collected at three hour intervals throughout the day on two occasions during the summer. Figure 5 presents the diurnal pattern that occurred on plots 1 and 2 on July 8, 1965, between 0600 and 2000 hours. This range in RT represents approximately 10 atmospheres variation in stress between sunrise and the time of maximum stress, which was recorded at approximately 1500 hours. Thus, RT determinations were able to provide data indicating when to sample diurnally and may serve as a measure of internal moisture stress differences among trees within a given stand.

In themselves, relative turgidity determinations are of limited value unless they can be directly related to internal moisture stress. That this is not a simple procedure is indicated in Figure 4. RT is noted to increase in value in late June and early July, but at this time the soil moisture stress is also increasing. This represents a change in the relationship of RT to DPD, since DPD

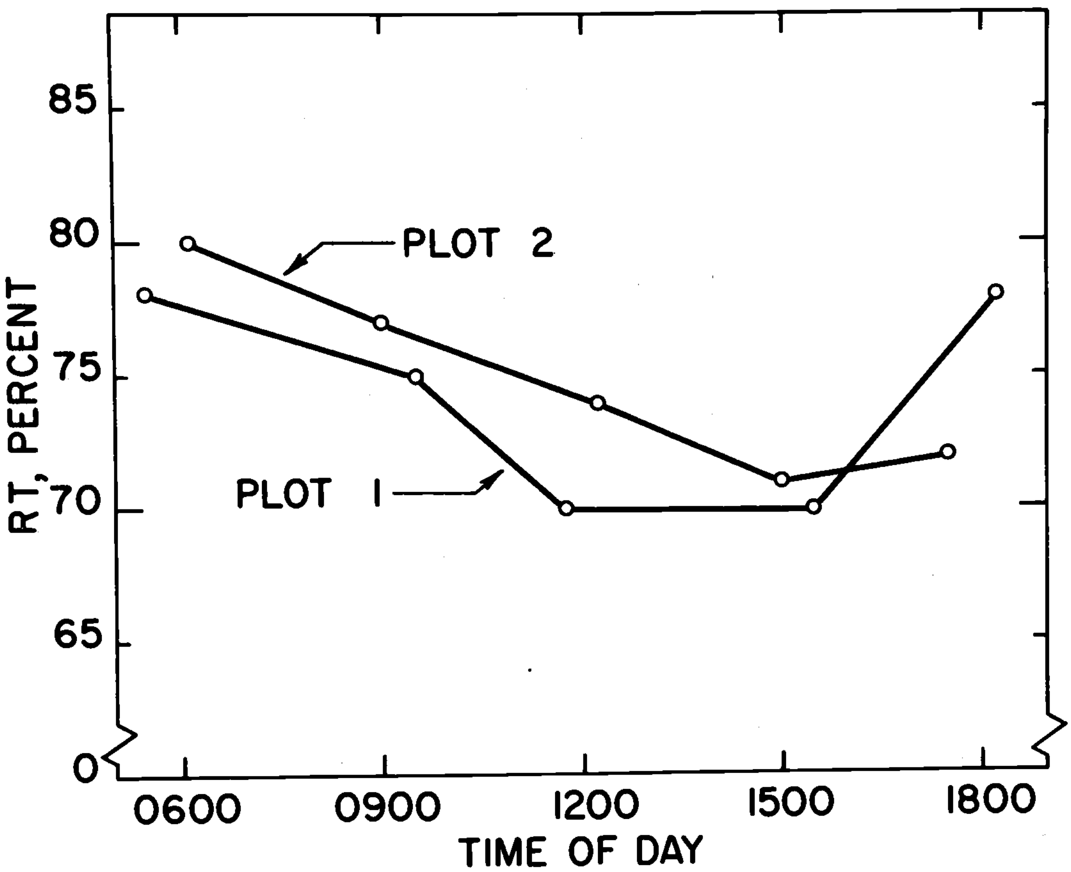

Figure 5. Diurnal variation in relative turgidity on July 12, 1965.

determinations indicated that the internal moisture stress did not increase markedly. The time of this shift corresponds closely with the observation of bud set. The full implication of this shift in RT, heretofore unreported in the literature, remains to be varified by additional tests. Such a shift could be attributed to increases in the osmotic concentration, raising the RT value while maintaining approximately the same DPD value. A reaction such as this is similar to the results reported by Slatyer (1961) where he did experiments with water-culture solutions of varying osmotic concentrations. Gardner and Ehlig (1965) demonstrate another complication in this relationship, that of the changing modulus of elasticity of the leaf. They show that there are two different rates of change of RT with respect to DPD; one rate up to the point where turgor pressure equals zero, and a different rate thereafter.

Although in this study RT values gave a poor estimate of DPD (see Fig. 2), the usefulness of RT-DPD curves has been demonstrated by Slatyer (1960) in his work with Acacia aneura F. Muell. and tomato plants.

In mid-August the moisture stress differences between plots in the early morning were still small. Since plants have differential abilities to maintain their internal water balance as the daily demand increases, it seemed likely that sampling at the time of maximum stress would yield a more finite separation of the environments being examined.

Therefore in mid-August, the sampling time was shifted from 0700 hours to the period of maximum stress — 1500 hours. As values obtained on plots 1, 2, and 3 up to this date were not greatly different, an additional plot, no. 4, was sampled at this time in the hope of extending the range of environments sampled. Plot 4 was dominated by ponderosa pine (Pinus ponderosa Dougl.) with associated understory species and temperature records indicative of an extremely hot and dry situation. Four separate DPD determinations were made on foliage collected on September 8th. Results yielded the following DPD values:

Plot 1	13.3 atm.
Plot 2	8.5 atm.
Plot 3	17.2 atm.
Plot 4	29.7 atm.

Later sampling indicated that the stresses recorded in September approached the maximum for the 1965 growing season, although precipitation did not recharge the soil until November. This anomaly is probably the result of the reduced radiation load associated with changing seasons.

CONCLUSIONS

1. Determination of the internal moisture stress of Douglas-fir has yielded a means of integrating both the climatic and edaphic environmental effects.
2. In this study, the maximum internal moisture stress recorded during the growing season provided a biologically sound index to the moisture regime on different sites.
3. Relative turgidity (RT), an index of relative water balance in the leaves, was not found to be easily correlated to an absolute measure of internal moisture stress due to an abrupt seasonal variation in RT.
4. Soil moisture stress measured to a depth of two feet was not closely related with the internal moisture stress of Douglas-fir trees in the field.

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