VARIATIONS IN WATER STRESS
OF PONDEROSA PINE

by

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SIGNED: Gary L. Cunningham

APPROVAL BY THESIS DIRECTOR

This thesis has been approved on the date shown below:

Harold C. Fritts — September 7, 1965

Harold C. Fritts
Associate Professor of Dendrochronology

Date

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TABLE OF CONTENTS

LIST OF ILLUSTRATIONS

LIST OF ILLUSTRATIONS--Continued

ABSTRACT

Seasonal and diurnal variations in water stress of the one year old needles in ponderosa pine were followed using the Schardakow method of estimating diffusion pressure deficit and the relative turgidity method of estimating moisture deficit. Soil moisture, vapor pressure deficit of the atmosphere and changes in trunk radius were measured to ascertain their relationship to needle water stress.

Diffusion pressure deficit increased with decreasing soil moisture until growth was initiated. At that time diffusion pressure deficit values were markedly reduced and this is attributed to changes in solute content resulting from high carbohydrate metabolism and translocation.

Diurnal variations in diffusion pressure deficit followed closely the diurnal variations in vapor pressure deficit, but the measured changes in relative turgidity did not follow closely the changes in diffusion pressure deficit. Measurements of changes in trunk radius appear useable for estimating needle tissue water status except during periods of terminal and cambial activity.

INTRODUCTION

The water status of plant tissues is not only one of the most important factors which influence plant growth and development but also one of the most difficult to measure. Kramer and Kozlowski (1960) cite water as the factor which is most often limiting to plant growth. Kozlowski (1964) further maintains that water availability probably exerts more control over tree growth than any other environmental factor.

Water probably influences plant growth to some extent during cell expansion. This expansion cannot take place unless the cell wall is in a plastic state and the turgor pressure (the pressure exerted by the protoplast upon the cell wall) exceeds the wall pressure (the pressure exerted by the cell wall upon the protoplast). This turgor pressure cannot be developed unless an adequate water supply is available to the growing cell (Broyer, 1950).

The water status of plant tissue influences the rate of enzymatic reactions. The magnitude and direction of this influence cannot always be predicted, and the mechanisms involved are not understood completely. It is clear however, that much of the effect of water stress on respiration, photosynthesis, and other physiological processes is brought about by a change in rate of enzymatic reactions (Crafts, Currier, and Stocking, 1949).

In addition to these direct effects, water stress can limit growth through its influence on stomatal aperture. Water stress causes guard cells to become flaccid and stomatal closure to occur (Zucker, 1963). This closure decreases the diffusion rate of carbon dioxide into the leaf and thus inhibits photosynthesis (Brix, 1962). The resulting decrease in available carbohydrates has a detrimental effect on growth and development of the plant. Closed stomata and lack of water also decrease the transpiration rate. Such a decrease in transpiration may result in decreased cooling which, if coupled with a heat load imposed by solar radiation, may lead to heating of the leaf tissue (Mellor, Salisbury and Raschke, 1964). If, concomitant with heating, an increase in respiration occurs, energy reserves needed for plant growth may approach depletion.

Although the above relationships are generally accepted, some of the experimental evidence is conflicting. Kozlowski (1964) points out that much of the conflict can be attributed to difficulty in measuring the water status of plant tissues. Water status of plant tissues is under the influence of water absorption, water loss, solute production, and cell wall condition. It is, therefore, a complex variable dependent on many factors and cannot be properly estimated from a measurement of any one of the contributing factors.

Most studies of the effects of water stress have used measurements of soil moisture to infer the water status of the plant tissues. Kramer (1962) discusses why this type of inference is not valid. The chief reason soil moisture has been used as a measure of water stress in many of the studies conducted to date may be that more direct methods are either too difficult to use or are not properly standardized to make evaluations which are consistent and meaningful. An overview of some of the direct methods used to ascertain the water status of plant tissues will give some idea why so many workers have elected to use the soil moisture methods, particularly for field work.

Probably the most obvious indication of water stress is wilting in the plant. The lack of a quantitative measure of wilting makes this a poor method for all but the most superficial studies. The measurement of stomatal aperture, while it can be quantified more easily, has certain disadvantages. It is difficult to calibrate stomatal aperture, so that a given amount of closure can be attributed to a given amount of water stress. Also, factors other than water status, such as light intensity and carbon dioxide concentration, can affect stomatal aperture.

Trunk diameter changes have been used as an indication of water stress in trees (Fritts, 1958; Kozlowski, Winget, and Torrie, 1962). Although diameter changes give an accurate measure of volume changes in the stem resulting from the difference between water absorption and water loss, they may not give an indication of the water status in other organs which are involved in carrying on important physiological processes which determine the growth and development of the plant. Oleoresin exudation pressure also has been used to evaluate water stress in trees (Vité, 1961). Since resin pressure is the result of pressure being exerted on the resin ducts by the xylem, it is an indicator of the water content of the conductive tissue (Bourdeau and Schopmeyer, 1958). Resin pressure changes, therefore, have the same disadvantages as diameter changes in that they provide a measure of the water status only in the stem.

The osmotic pressure of the vacuolar sap has been used as an indicator of the water status of individual plant tissues. Osmotic pressure is more difficult to ascertain than are most other measures of water stress. In addition, most methods for finding osmotic pressure require that the vacuolar sap be extracted, a practice which can lead to a considerable amount of error due to contamination by material from the protoplasm (Bennet-Clark, 1959). For a review of methods which have been used see: Bennet-Clark (1959), Kozlowski (1964), and Crafts et al. (1949).

During the past few years relative turgidity (Weatherley, 1950) and saturation deficit (Stocker, 1929) have become popular due, in part, to the ease with which these measurements can be made. In general, the methods involve comparing the weight of water in fresh tissue to the weight of water in the tissue after it has been allowed to equilibrate with pure water.

The most valuable measure of the water status of a plant tissue is one which indicates the free energy deficit of water in the tissue. A measure of this type indicates the tendency of the tissue to absorb water. This can be compared to similar measures of free energy deficit of water in the soil and in the air, so that a complete picture of the soil-plant-air water complex can be obtained (Kramer, 1962). Diffusion pressure deficit or DPD is the most widely used measure of free energy deficit of water (Meyer, 1945). Other terms such as water potential, suction pressure, and suction potential have been applied to the same concept (Taylor and Slatyer, 1961). In order to avoid confusion DPD will be used in this paper to indicate the free energy deficit of water.

Reports of the seasonal and diurnal changes in transpiration and soil moisture and their relationship to plant physiological processes are abundant in the literature (Kramer and Kozlowski, 1960; Kramer, 1962). However studies which provide information on the seasonal and diurnal variations in tissue water status are much less numerous.

Sands and Rutter (1958) have used the relative turgidity method to measure the diurnal variations in needle water status of two to three year old *Pinus sylvestris* grown in pots with varying soil moisture levels.

Most of the studies dealing with seasonal or diurnal variations in water stress under natural conditions which have not used soil moisture or transpiration exclusively have used trunk diameter changes (Haasis, 1934; Fritts, 1958; Kozlowski *et al*., 1962) or resin pressure variations (Vite, 1961; Bourdeau and Schopmeyer, 1958) as indicators of water status. Little has been done, however, in ascertaining the seasonal and diurnal changes in the water status of leaf tissue under natural conditions.

Therefore, the primary purpose of the present investigation was to ascertain what diurnal and seasonal variations in needle water stress occur in ponderosa pine (*Pinus ponderosa* Lawson) under natural conditions and to associate these variations with possible causal factors due to conditions within the tree or resulting from changes in the environment. Since DPD measurements over extended periods of time are rather difficult and time consuming, it also was of interest to see how closely the more easily obtained measures of water stress, such as relative turgidity and trunk diameter changes, corresponded to the DPD values.

METHODS

Site and Tree Description

The site selected for this study is a south facing slope at an elevation of 8,500 feet above mean sea level on Mount Bigelow, a peak in the Santa Catalina Mountains of Southern Arizona. This slope is marked by numerous granite outcrops, and the soil is rocky. The vegetation around the study site is dominated by ponderosa pine. Other species such as southwestern white pine (*Pinus reflexa* Engelm.), Douglas fir (*Pseudotsuga mensisii* Hutt.), and Palmer oak (*Quercus palmeri* Engelm.) also occur as minor components of the stand.

A single ponderosa pine with a diameter at breast height of 14 inches and a height of 23 feet was selected for study. This tree was thought suitable because, in dendrochronological terms, its ring chronology is "sensitive" (mean sensitivity of 0.36 and a moderate serial correlation of 0.44) which indicates that moisture frequently limits growth of this tree (Fritts, Smith, Budelsky, and Cardis, 1965).

DPD Estimation

Many methods have been developed and employed for the measurement of DPD (Crafts *et al.*, 1949; Kozlowski, 1964).

All but a few of these, however, are unsuitable for field use because elaborate equipment is required. The methods which are practical in the field employ a series of solutions with varying osmotic pressures which cover the expected range of the tissue DPD. Samples of the tissue to be tested are placed in each of the solutions in the series. After an appropriate length of time has elapsed for water exchange to take place, the direction of water movement in each of the solution-tissue systems is ascertained. When a solution is found in which no net water exchange has taken place with the tissue, the osmotic pressure of the solution is inferred to be equal to the DPD of the tissue. In practice, since only a finite number of solutions can be used, the DPD usually can be ascertained to lie within a particular range and cannot be assigned an absolute value.

These field methods differ from each other in the manner in which the direction of water movement is discerned. Most employ some technique which measures a change in the tissue to ascertain whether water diffuses into or out of the tissue. This has been done by measuring changes in length, thickness, weight, and tension of the tissue (Crafts et al., 1949). Changes in the concentration of the surrounding solution also have been used to detect the direction of water movement. Lemee and Laisne (1951) have used the refractive index of a solution to observe this change in concentration.

More recently Schardakow (1953) has developed a technique which utilizes measurement of slight changes in specific gravity to detect changes in the concentrations of the solutions.

Because of the shape of pine needles and the heavily cutinized epidermal layer, it was thought that changes in tissue size could not be used easily to detect water movement. Weight changes have not proven satisfactory for this purpose because the filling of intercellular spaces with solution gives results which are in error (Kozlowski, 1964). It was decided, therefore, that one of the methods utilizing measurement of changes in solution concentration would be the best indicator of water movement between the pine needles and the surrounding solution. The Schardakow method was selected for use in this study because it requires less equipment and can be more easily adapted for field use than the refractometer method. In addition the Schardakow method has been found to correlate well with the more elaborate and precise vapor pressure method of measuring DPD (Brix and Kramer, 1962).

The Schardakow method employs, as do the other field methods of measuring DPD, a series of solutions of varying osmotic pressures. Samples of the tissue to be tested are placed in each of the solutions in the series. The tissue need not remain in the solution until an equilibrium is reached, but only until enough exchange has occured for the difference in the solution concentration to be detected. After this time (which must be established for the kind and amount of tissue being used) has elapsed, the tissue is removed from the solution. The solution then is tested for a change in specific gravity by placing a drop of solution with the same osmotic pressure as the original solution into the solution to be tested. The test drop is dyed with methylene blue so that it can be seen easily. If the test drop sinks to the bottom it is an indication that the solution being tested has decreased in specific gravity, that is, water has diffused out of the tissue. When this occurs the DPD of the tissue is less than the osmotic pressure of the solution. If, on the other hand, the test drop rises to the top of the solution, the DPD of the tissue is greater than the osmotic pressure of the solution. A test drop which remains in the center of the solution and then slowly diffuses in all directions indicates a tissue DPD which exactly matches the osmotic pressure of the solution. Solutions of varying osmotic pressures were prepared with sucrose according to the values given by Molz (1926).

Since the amount of tissue in pine needles is rather small, some modifications of the original method were necessary. Most workers recommend that the tissue to solution ratio be kept as high as possible for best results (Kozlowski, 1964). Extensive sampling from a single tree was anticipated so it was necessary to keep the size of each tissue sample as small as possible. It was found that when using a tissue sample equivalent to one whole needle not more than 0.4 ml of solution was desirable. With this small amount of tissue it was necessary to leave the tissue in the solution for at least 18 hours before a detectable amount of water exchange took place. Tests using varying intervals for water exchange showed that the tissue could be left in the solution for as long as 60 hours without affecting the DPD value obtained. In practice the tissue was left in the solution at least 24 hours, but not more than 48 hours.

It was noticed during early attempts to measure DPD by this method that the location of the drop in the solution often affected its direction of movement. This was attributed to the formation of concentration gradients in the solution. To avoid any errors which might be introduced by this occurence, solutions were gently mixed with the end of a pipette before the test drops were introduced. In all tests three drops were placed in the solution at different levels, and no decision was made as to direction of movement unless all three drops behaved in the same manner.

DPD measurements were made during nine sample periods, each 24 hours in length, at approximately weekly intervals from April 17 - June 27, 1965. For each of the sample periods, three branches on the study tree were selected. At each sample time nine needles were removed from each of the three branches. The needles were cut so that each branch provided 30 needle pieces. A needle piece from each of the three branches was placed in each vial of solution, so that each solution-tissue system was a composite of the three branches. Three vials of each of the ten solution concentrations were used giving three replications for each of the sample times. The three branches used for each sample period were selected to give as accurate a picture as possible of the DPD of the entire tree. This was done by selecting one branch from the north and one from the south side of the top of the crown and one branch from the south side in the lower part of the crown. No branches were located on the lower north side of the tree. Only the needles produced in 1964 were used for measurement, to minimize differences which might arise from differing age.

Due to the limited number of solutions used to test each sample, exact DPD values seldom were found, and it could only be shown that the DPD lay between two values. In order to facilitate statistical analysis of the data the DPD was arbitrarily assigned the midpoint value of this range. The values which appear on the graphs (Figs. 1-14) are the means of the three midpoint values at the given time.

An analysis of variance was used to determine whether or not a significant difference existed between the mean values for the different samples during the 24 hour sample periods. If a significant difference was found, Duncan's multiple range test was used to determine which means differed significantly from the others (Freund, Livermore and Miller, 1960).

Relative Turgidity

Relative turgidity measurements were made using the method developed by Harms and McGregor (1962). The same three sample branches selected for DPD measurements were used to obtain needles for relative turgidity determinations. Again only needles produced during 1964 were used. Nine needles were taken from each of the three branches. Three needles from each of the branches were placed together giving nine needles for each of three samples. This made each relative turgidity sample, as nearly as possible, a composite of the entire tree.

As with the DPD values, the relative turgidity values on the graphs (Figs. 2-14) represent an average of the three values obtained at the indicated time. The same types of statistical analysis were used to determine significant differences between mean relative turgidity values as were used for DPD values.

Trunk Diameter Changes

Changes in trunk diameter were measured with a continuously recording dendrograph (Fritts and Fritts, 1955). Several dendrographs had been placed on the tree, and some showed diameter changes with differing amplitudes of variation dependent upon location. The dendrograph located 12 feet above the base of the tree was selected for use in this study because it was in the crown of the tree and, therefore, nearest the sample branches. Each unit on the dendrograph scale corresponds to a trunk radius change of 0.0001 inches.

Vapor Pressure Deficit of the Atmosphere

Temperature and relative humidity measurements were made with a hygrothermograph employing a human hair hygrometer. The hygrothermograph was located in a small white lacquered shelter mounted on the north side of the trunk and in the crown of a nearby tree about 15 feet above the ground. The recorded temperature and relative humidity values were used to calculate vapor pressure deficit.

Soil Moisture

Colman fiberglass resistance blocks were used to measure soil moisture (Colman, 1946). The soil moisture meter readings in microamps were corrected for temperature using the correction graph of Horton (1955). No direct calibrations of microamps with soil moisture have been made at this time so all values presented here are only relative indicators of soil moisture. The resistance blocks were located at depths of from 4 to 24 inches and were scattered throughout the study site. Each value reported here is an average of values obtained from all functional blocks which at any one time were 15 or more in number.

RESULTS

Diurnal Variations in DPD

The diurnal variations in DPD are plotted along with other parameters in Figures 1-9. During some of the 24 hour sample periods there were large and easily detectable variations throughout the period (Fig. 5) while during others significant variations were nonexistent (Fig.1). On days which showed large and significant diurnal variations the highest DPD usually came sometime in the early afternoon and the lowest just after sunrise.

The first sample period which showed a significant variation in DPD occured on May 1 and 2 (Fig. 2; Appendix Table 2). The DPD rose to a high of 1.82 atm. at 6:30 P.M. which was the only significantly different value for that period. On May 8 - 9 the DPD of 2.45 atm. at 11:00 A.M. was the only significantly different value (Fig. 3; Appendix Table 3).

The values on May 15 and 16 showed a pronounced pattern or trend (Fig. 4). The first sample was taken at 11:00 A.M. on May 15. The DPD at that time exceeded 9.00 atm. A gradual decrease occured until about 10:30 P.M. The next sample was taken at 7:30 A.M. the next morning, at which time the DPD was approximately the same value as it had been at 10:30 P.M.

Fig. 1.--DPD and Radial Measurements for the Study Tree From Noon April 17 to 7:00 A.M. April 18, 1965.

DPD (Atm)........................... ●
Radius............................... ○

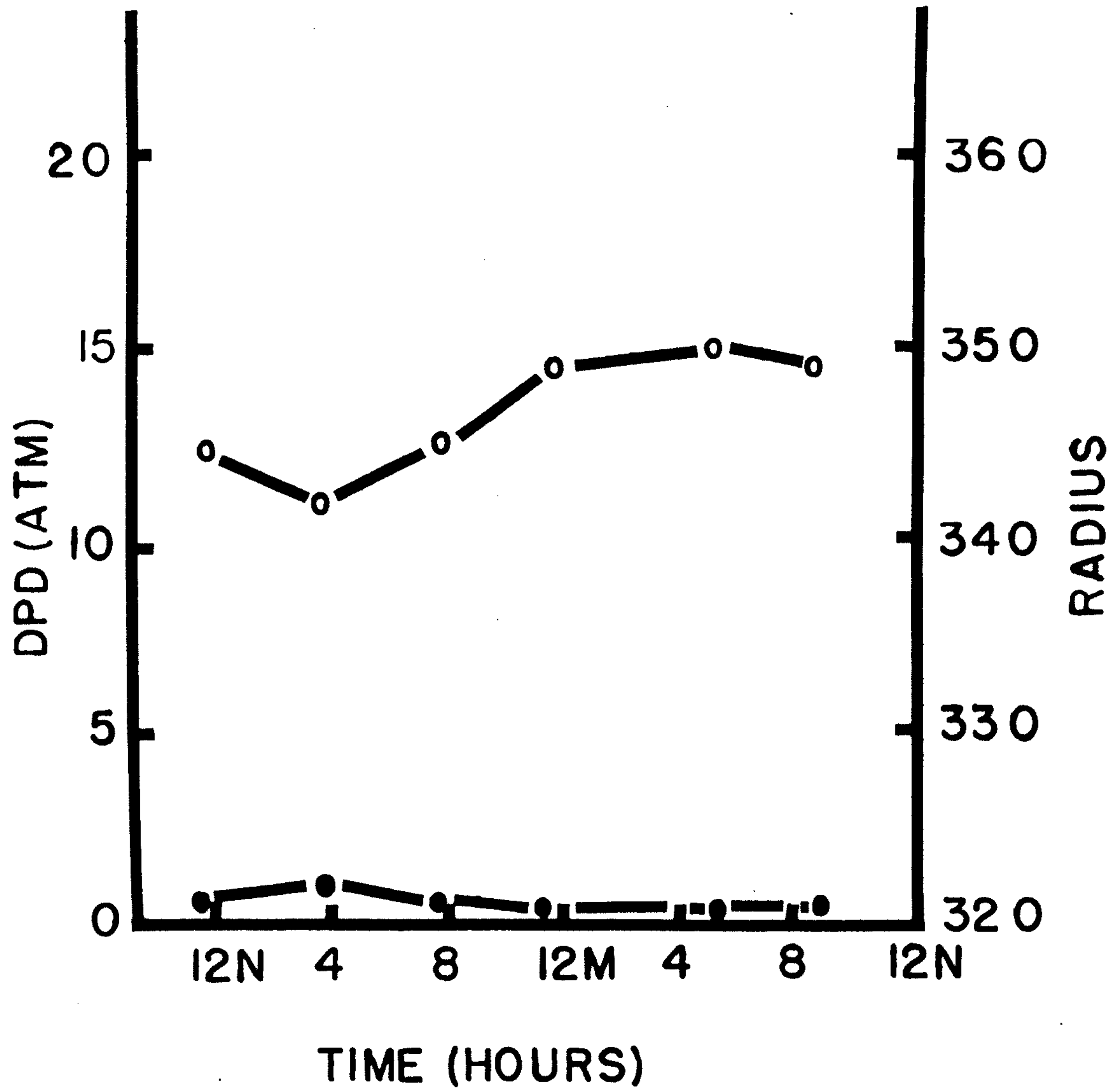
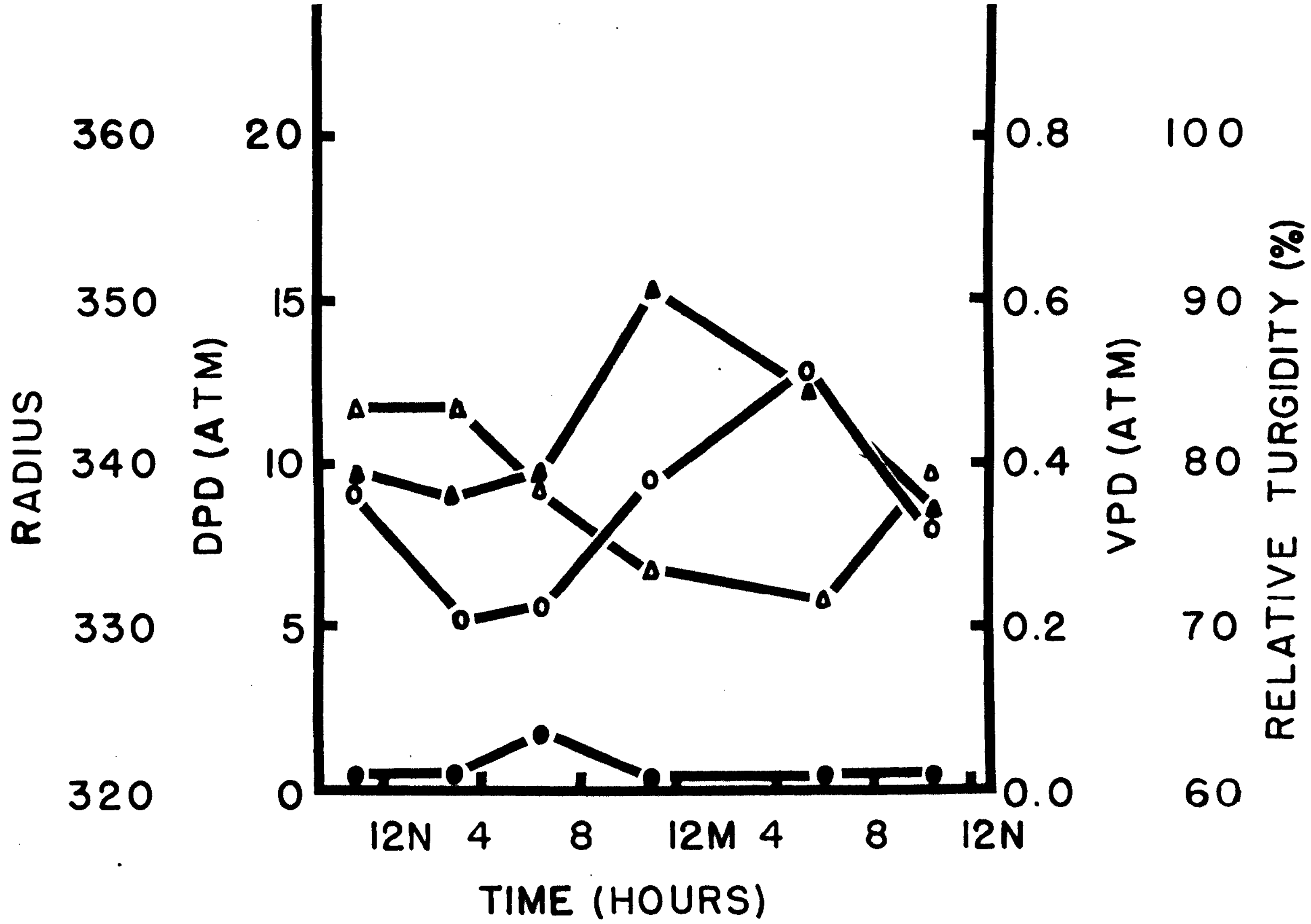

20
15
10
5
0
DPD (ATM)
360
350
340
330
320
RADIUS
12N
4
8
12M
4
8
12N
TIME (HOURS)

Fig. 2.--DPD, Relative Turgidity, and Radial Measurements for the Study Tree and Vapor Pressure Deficit of the Atmosphere From 11:00 A.M. May 1 to 10:30 A.M. May 2, 1965.

DPD (Atm)..........................●
Relative Turgidity (%).............▲
Radius.............................○
VPD (Atm)..........................△



RADIUS
360
350
340
330
320
DPD (ATM)
20
15
10
5
0
VPD (ATM)
0.8
0.6
0.4
0.2
0.0
RELATIVE TURGIDITY (%)
100
90
80
70
60
12N 4 8 12M 4 8 12N
TIME (HOURS)

Fig. 3.--DPD, Relative Turgidity, and Radial Measurements for the Study Tree From 10:30 A.M. May 8 to 10:30 A.M. May 9, 1965.

DPD (Atm)........................... ●
Relative Turgidity (%).............. ▲
Radius.............................. ○

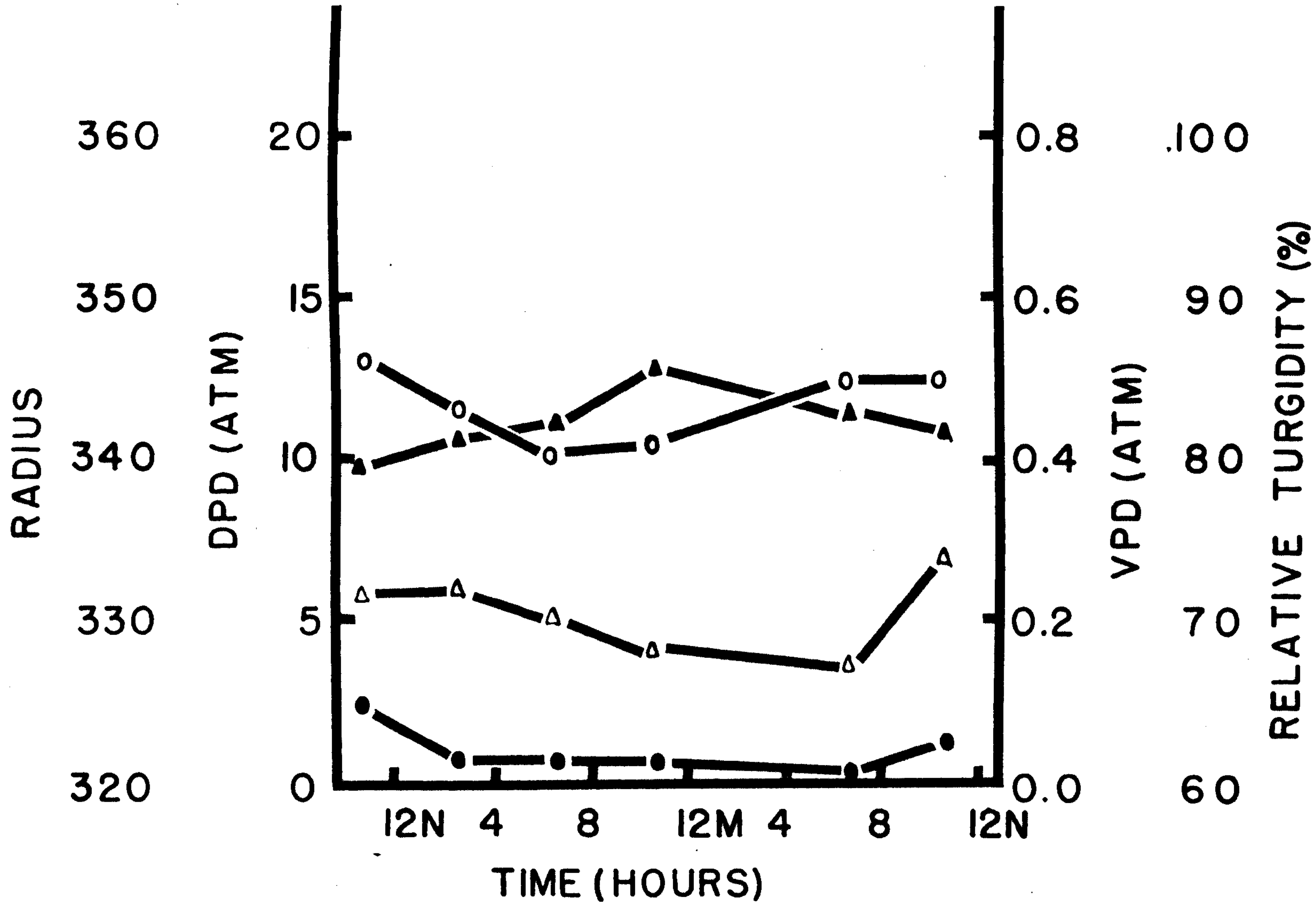

RADIUS
360
350
340
330
320
DPD (ATM)
20
15
10
5
0
VPD (ATM)
0.8
0.6
0.4
0.2
0.0
RELATIVE TURGIDITY (%)
.100
90
80
70
60
12N 4 8 12M 4 8 12N
TIME (HOURS)

Fig. 4.--DPD and Relative Turgidity for the Study Tree and Vapor Pressure Deficit of the Atmosphere From 10:40 A.M. May 15 to 7:30 A.M. May 11, 1965.

DPD (Atm)........................●
Relative Turgidity (%)............▲
VPD (Atm)........................△

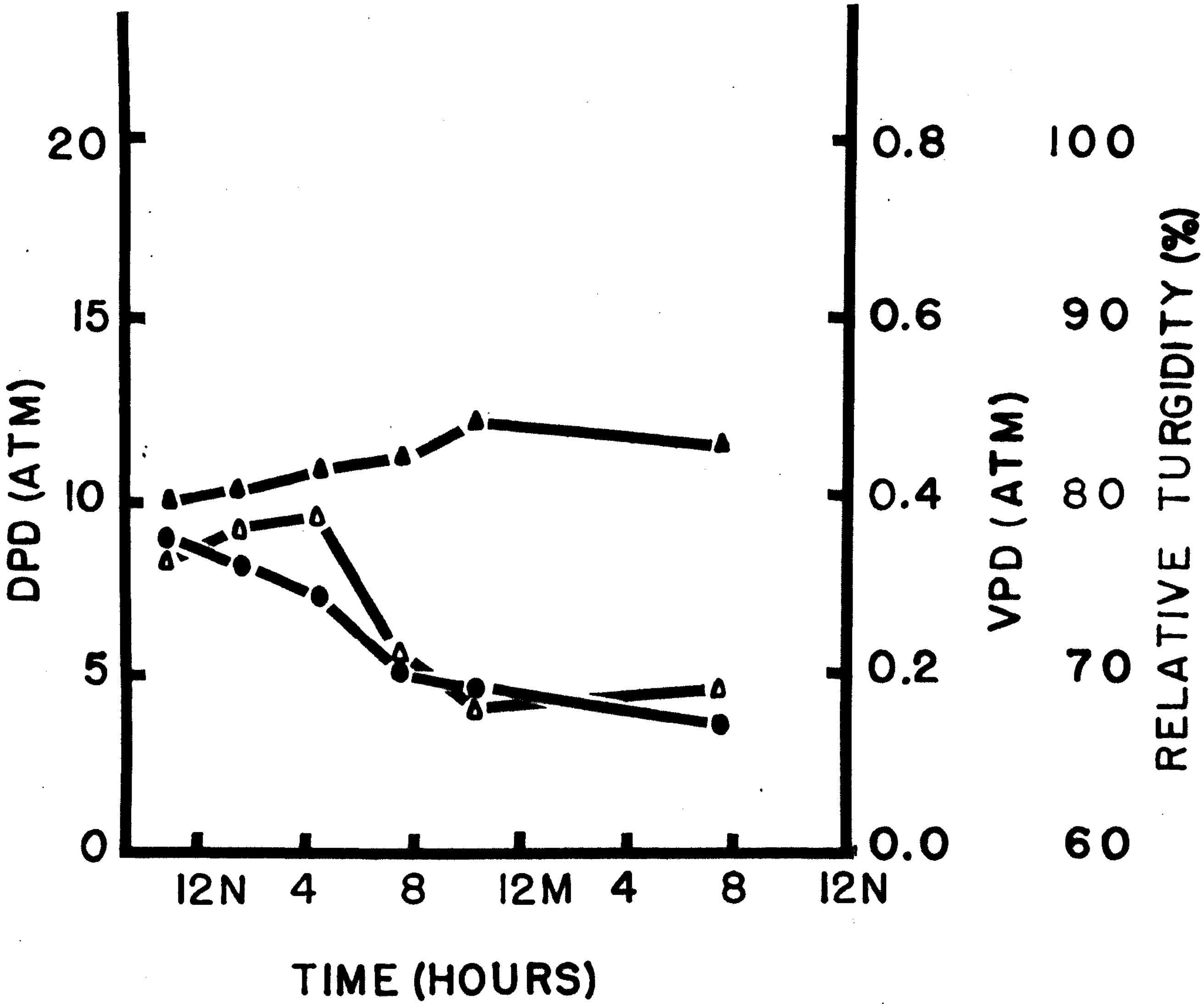
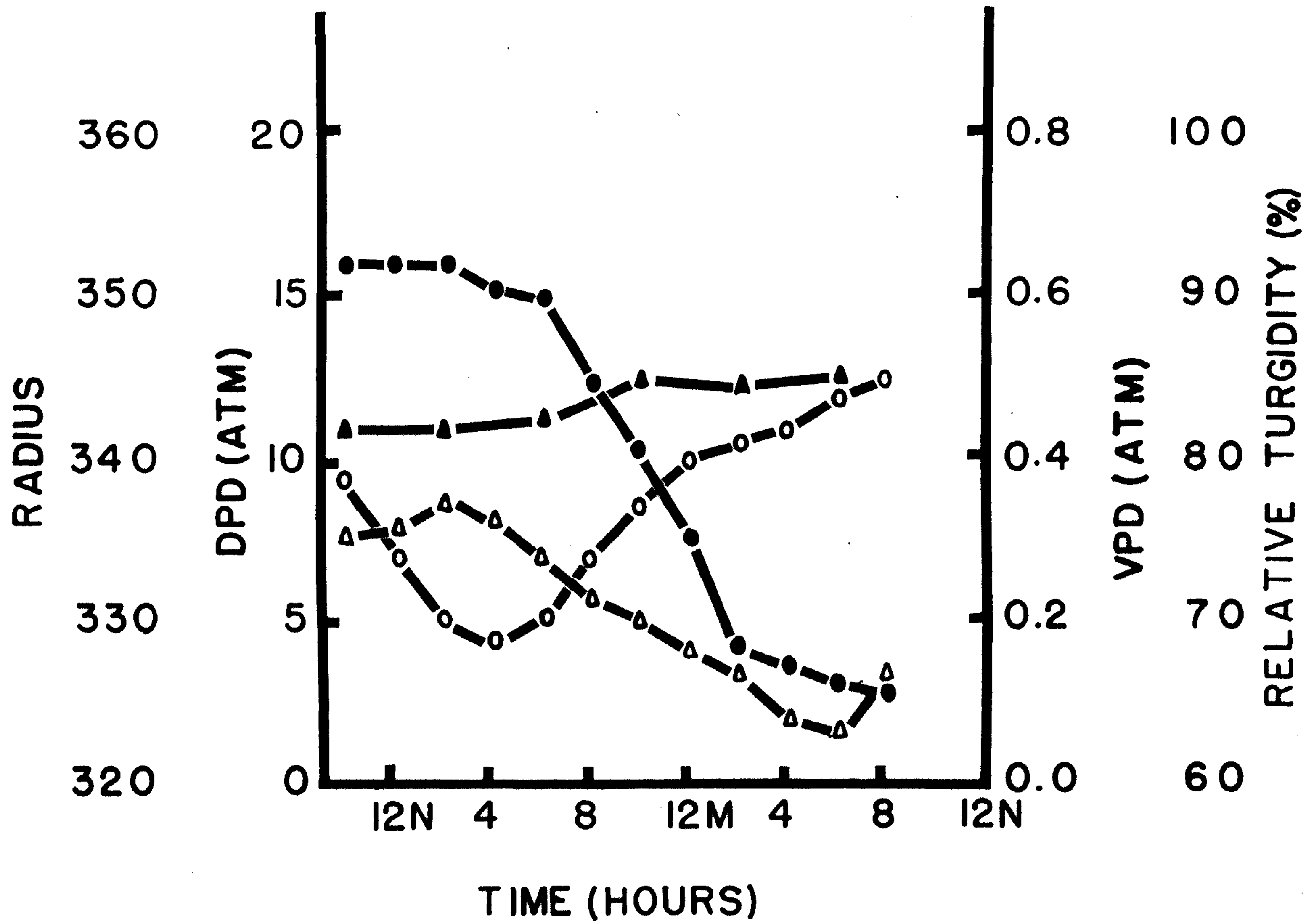

DPD (ATM)
VPD (ATM)
RELATIVE TURGIDITY (%)
TIME (HOURS)
0
5
10
15
20
0.0
0.2
0.4
0.6
0.8
60
70
80
90
100
12N
4
8
12M
4
8
12N

Fig. 5.--DPD, Relative Turgidity, and Radial Measurements for the Study Tree and Vapor Pressure Deficit of the Atmosphere From 10:30 A.M. May 22, to 8:30 A.M. May 23, 1965.

DPD (Atm)........................... ●
Relative Turgidity (%)............ ▲
Radius............................ ○
VPD (Atm)......................... △


RADIUS
360
350
340
330
320
DPD (ATM)
20
15
10
5
0
VPD (ATM)
0.8
0.6
0.4
0.2
0.0
RELATIVE TURGIDITY (%)
100
90
80
70
60
12N
4
8
12M
4
8
12N
TIME (HOURS)

The data collected on May 22 and 23 (Fig. 5) showed the greatest variation in DPD that was observed. The DPD remained above 16 atm. from 10:30 A.M. when sampling began, until 4:30 P.M. From 4:30 P.M. until 7:30 P.M. a gradual decrease occured. After 7:30 P.M. this decrease became more rapid until about 2:30 A.M. The decrease was less marked from 2:30 A.M. until 4:30 A.M. and from 4:30 until 8:30 A.M. when no significant change occured in DPD (Appendix Table 5).

An interesting pattern was observed in the DPD values for June 5 and 6 (Fig. 6). The samples at 2:00 P.M. and 4:00 P.M. showed DPD values significantly lower than those at either noon or 6:00 A.M. A significant rise in DPD was observed at 2:00 A.M. (Appendix Table 6).

No significant differences were observed for the DPD values on either June 12 and 13 (Fig. 7; Appendix Table 7) or June 19 and 20 (Fig. 8; Appendix Table 8). During both these sample periods the mean DPD never fell below 1.75 atm. and never rose above 4.65 atm. Even though statistical analysis showed that all mean DPD values for June 26 and 27 were not equal (Appendix Table 9), very little in the way of a pattern is discernible (Fig. 9). The rise in DPD from 3:00 A.M. to 6:00 A.M. and the drop from 6:00 A.M. to 8:00 A.M. are significant and unexpected changes.

Fig. 6.--DPD, Relative Turgidity, and Radial Measurements for the Study Tree and Vapor Pressure Deficit of the Atmosphere From Noon June 5 to 11:00 A.M. June 6, 1965.

DPD (Atm)........................●
Relative Turgidity (%)............▲
Radius...........................○
VPD (Atm)........................△

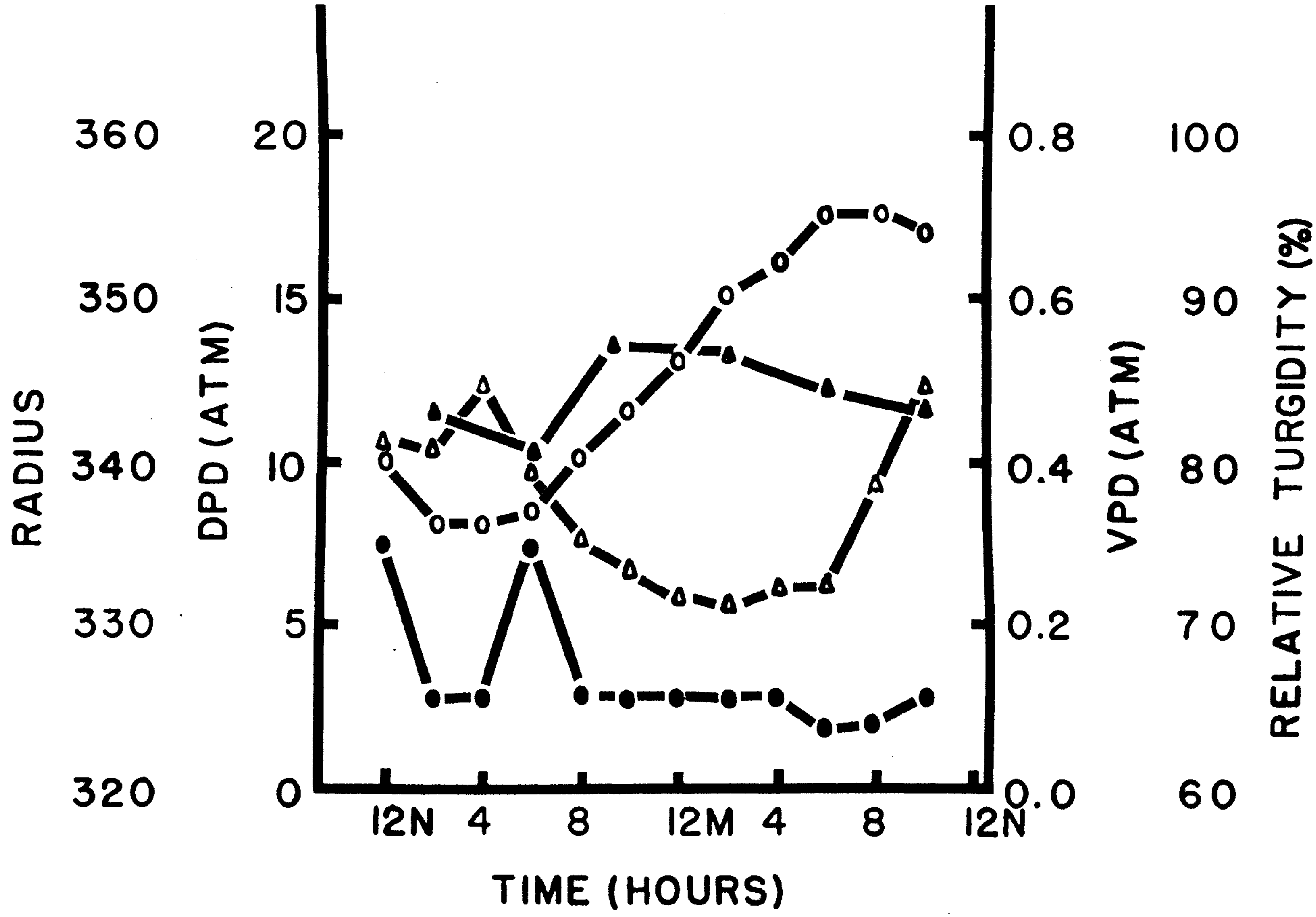

RADIUS
360
350
340
330
320
DPD (ATM)
20
15
10
5
0
VPD (ATM)
0.8
0.6
0.4
0.2
0.0
RELATIVE TURGIDITY (%)
100
90
80
70
60
12N
4
8
12M
4
8
12N
TIME (HOURS)

Fig. 7.--DPD, Relative Turgidity, and Radial Measurements for the Study Tree and Vapor Pressure Deficit of the Atmosphere From Noon June 12 to Noon June 13, 1965.

DPD (Atm)............................●
Relative Turgidity (%).............▲
Radius.............................○
VPD (Atm)..........................△

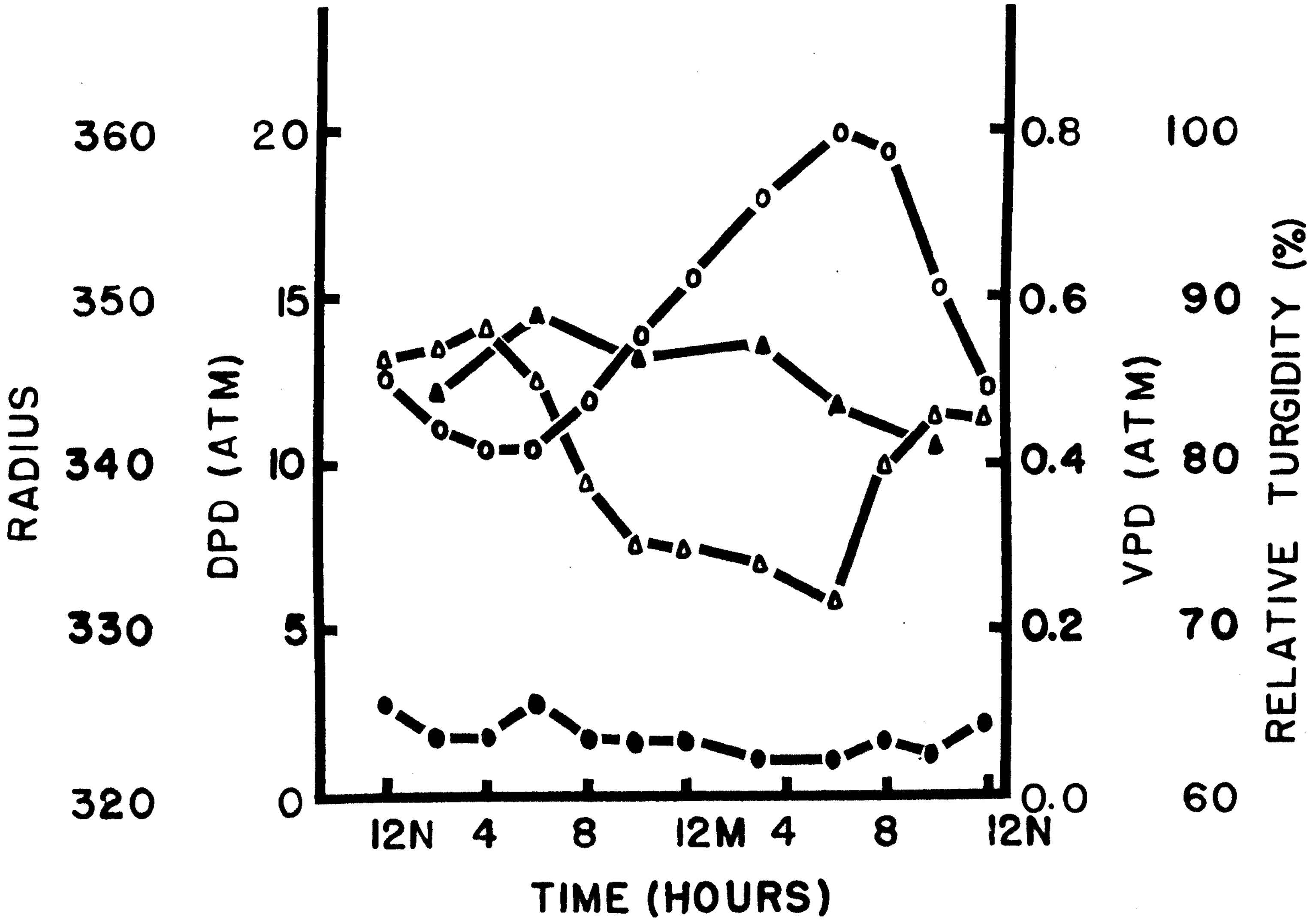

RADIUS
360
350
340
330
320
DPD (ATM)
20
15
10
5
0
0.8
0.6
0.4
0.2
0.0
VPD (ATM)
100
90
80
70
60
RELATIVE TURGIDITY (%)
12N
4
8
12M
4
8
12N
TIME (HOURS)

Fig. 8.--DPD, Relative Turgidity and Radial Measurements for the Study Tree and Vapor Pressure Deficit of the Atmosphere From 10:00 A.M. June 19 to 10:00 A.M. June 20, 1965.

DPD (Atm).......................... ●
Relative Turgidity (%)............ ▲
Radius............................ ○
VPD (Atm)......................... △

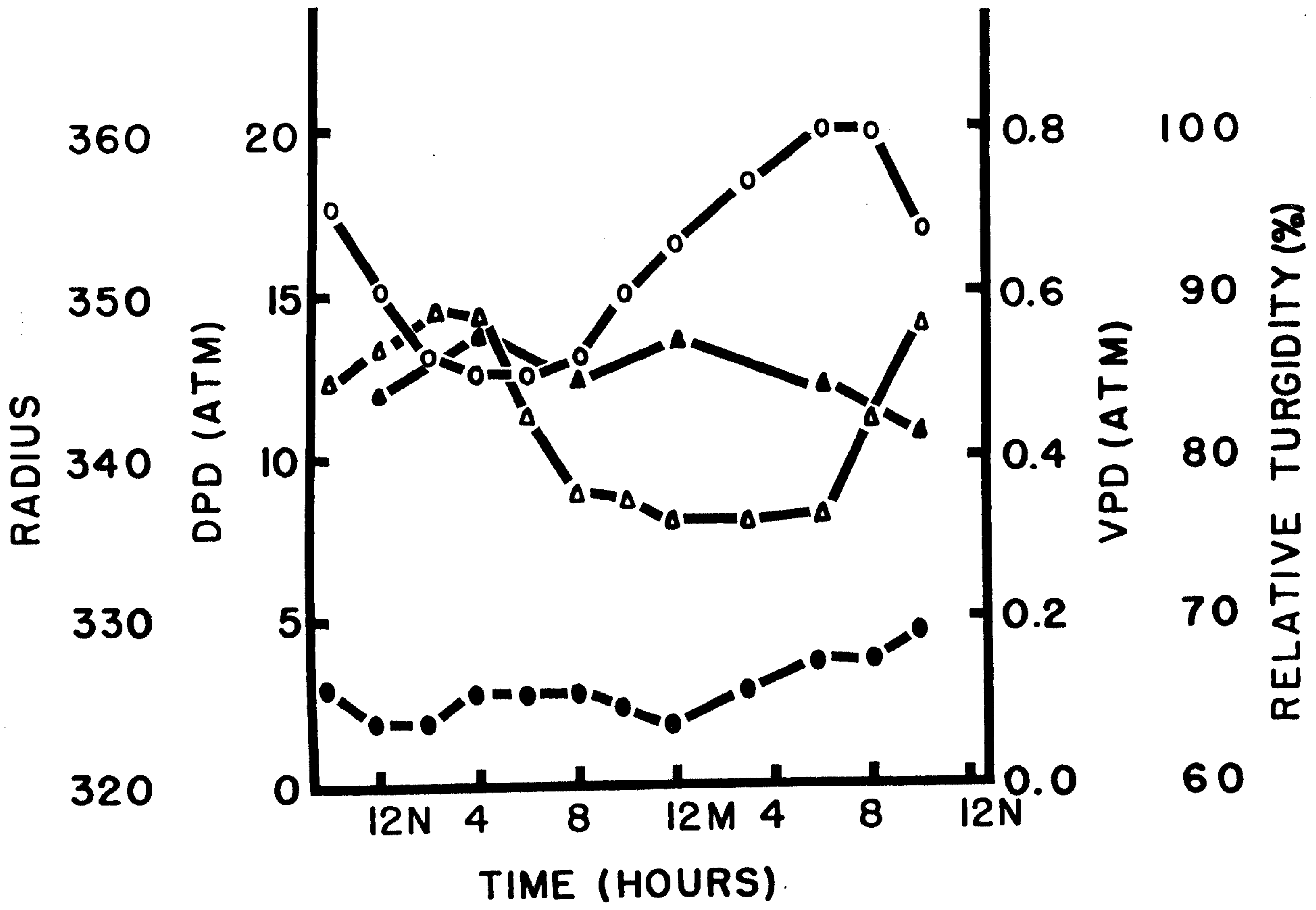
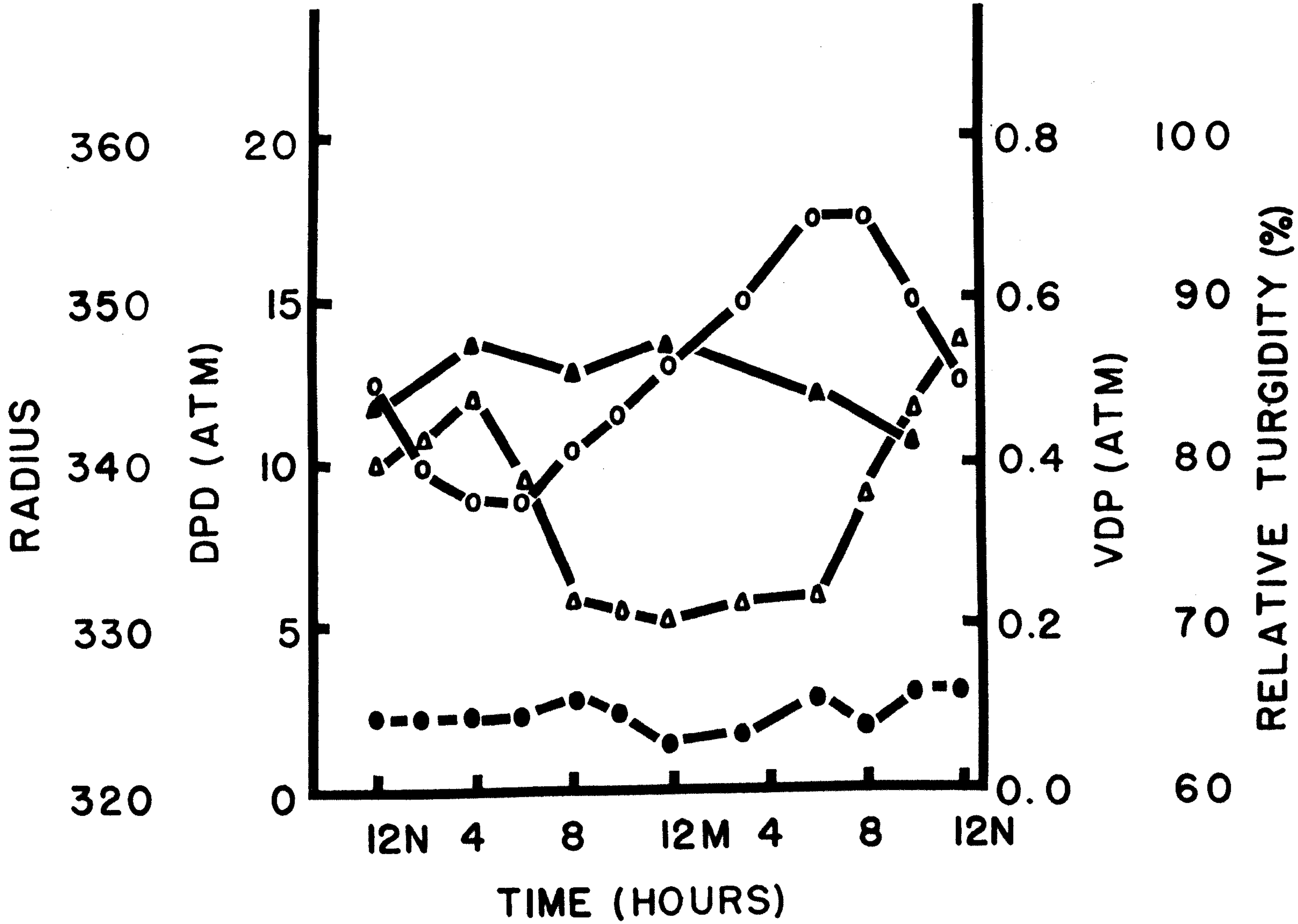

RADIUS
360
350
340
330
320
DPD (ATM)
20
15
10
5
0
VPD (ATM)
0.8
0.6
0.4
0.2
0.0
RELATIVE TURGIDITY (%)
100
90
80
70
60
12N
4
8
12M
4
8
12N
TIME (HOURS)

Fig. 9.--DPD, Relative Turgidity, and Radial Measurements for the Study Tree and Vapor Pressure Deficit of the Atmosphere From Noon June 26 to Noon June 27, 1965.

DPD (Atm)......................... ●
Relative Turgidity (%)............. ▲
Radius............................ ○
VPD (Atm)......................... △


RADIUS
360
350
340
330
320
DPD (ATM)
20
15
10
5
0
VDP (ATM)
0.8
0.6
0.4
0.2
0.0
RELATIVE TURGIDITY (%)
100
90
80
70
60
12N 4 8 12M 4 8 12N
TIME (HOURS)

Seasonal Variations in DPD

In order to present the seasonal variations in DPD the mean values for each of the 24 hour sample periods have been graphed for four different times of the day in Figures 10-13. The mean DPDs for noon (Fig. 10) remain at a low level until the first of May. After this date DPD increases, reaching a maximum on May 22. DPD then decreases until June 12 after which it remains fairly constant at a low level. It does not, however, return to the previous low which was observed prior to the first of May. The mean values for midnight and 6:00 P.M. follow essentially the same pattern (Figs. 11 and 12).

The pattern for the mean DPD values at 6:00 A.M. (Fig. 13) differs slightly from those of the other three times. The 6:00 A.M. maximum comes on May 16 rather than May 23. A marked rise also is apparent on June 20 which is not observed during other hours of the day.

Relation Between Relative Turgidity and DPD

Relative turgidity variations did not show as close a correlation with DPD variations as some researchers have reported (Weatherley and Slayer, 1957).

On May 1 and 2 (Fig. 2) both relative turgidity and DPD show greatest water stress during the daylight hours and least at 11:00 P.M. After this time, however, relative

Fig. 10.--DPD, Relative Turgidity, and Radial Measurements for the Study Tree at Noon and Soil Moisture From April 17 to June 26, 1965.

DPD (Atm)........................... ●
Relative Turgidity (%)............ ▲
Radius.............................. ○
Soil Moisture (Microamps)......... △

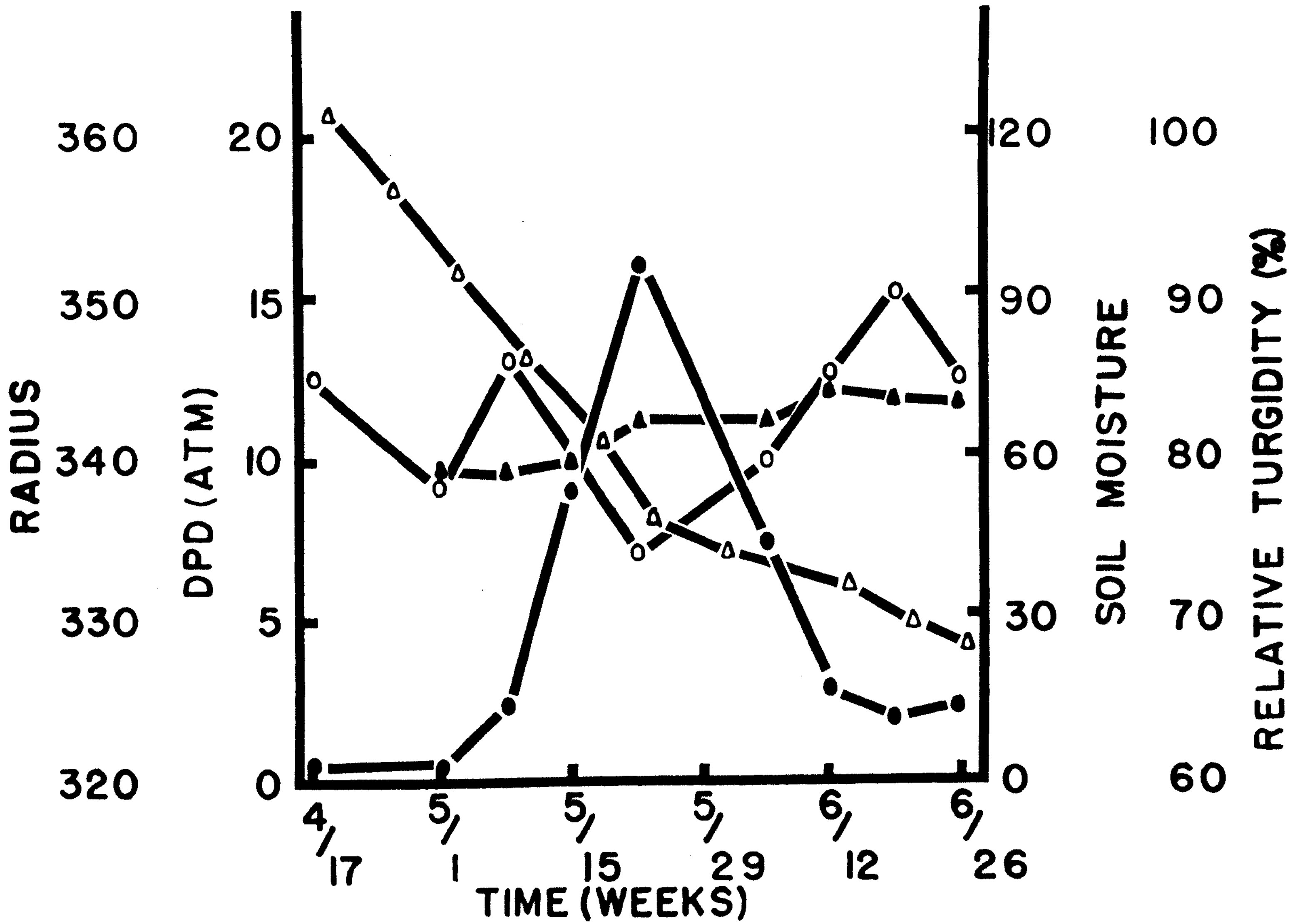

RADIUS
DPD (ATM)
SOIL MOISTURE
RELATIVE TURGIDITY (%)
TIME (WEEKS)
360
350
340
330
320
20
15
10
5
0
120
90
60
30
0
100
90
80
70
60
4/17
5/1
5/15
5/29
6/12
6/26

Fig. 11.--DPD, Relative Turgidity, and Radial Measurements for the Study Tree at Midnight and Soil Moisture From April 17 to June 26, 1965.

DPD (Atm).......................... ●
Relative Turgidity (%)............ ▲
Radius............................ ○
Soil Moisture (Microamps)......... △

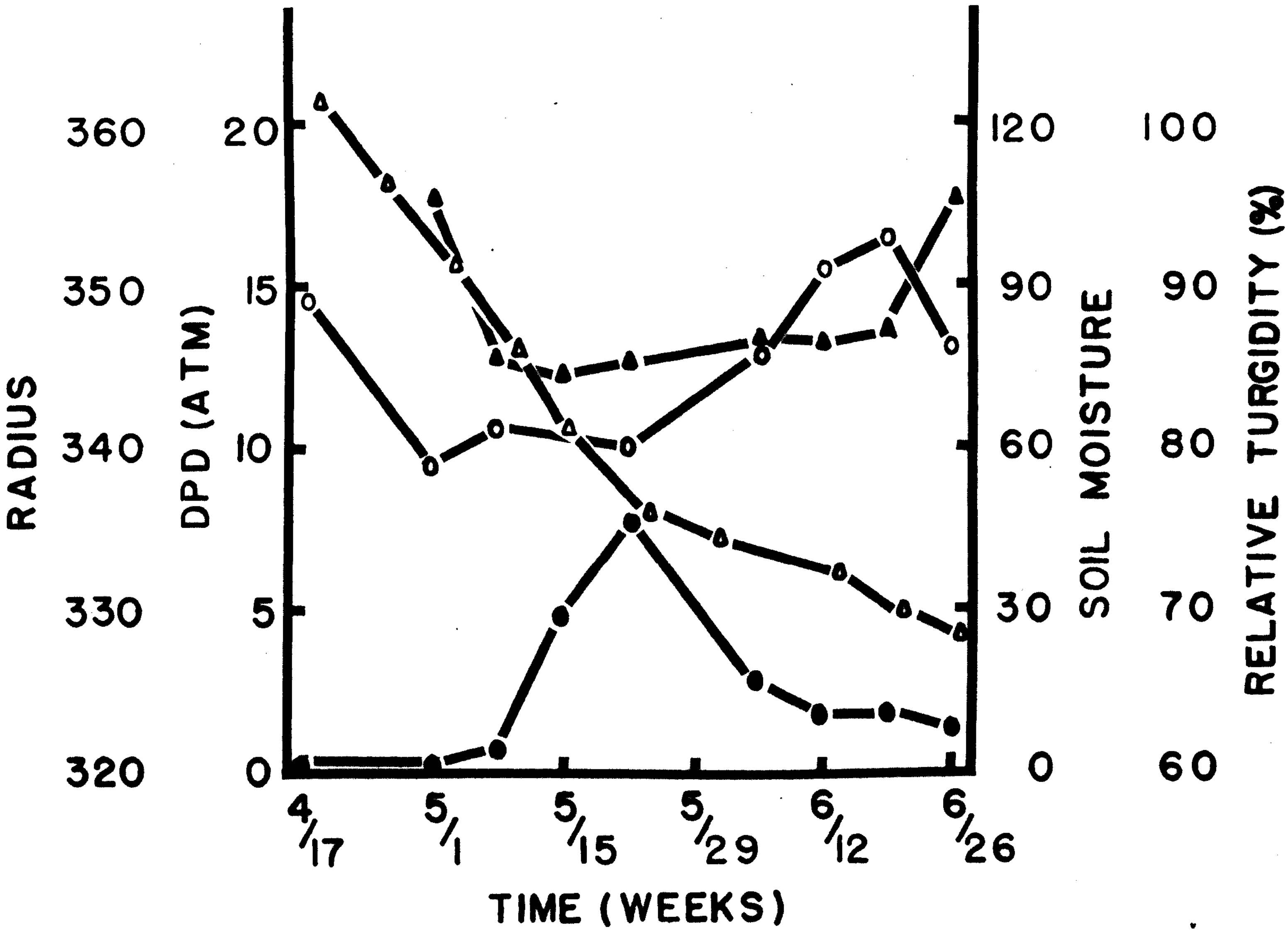

RADIUS
DPD (ATM)
SOIL MOISTURE
RELATIVE TURGIDITY (%)
360
350
340
330
320
20
15
10
5
0
120
90
60
30
0
100
90
80
70
60
4/17
5/1
5/15
5/29
6/12
6/26
TIME (WEEKS)

Fig. 12.--DPD, Relative Turgidity, and Radial Measurements for the Study Tree at 6:00 P.M. and Soil Moisture From April 17 to June 26, 1965.

DPD (Atm)........................●
Relative Turgidity (%)............▲
Radius............................○
Soil Moisture (Microamps).........△

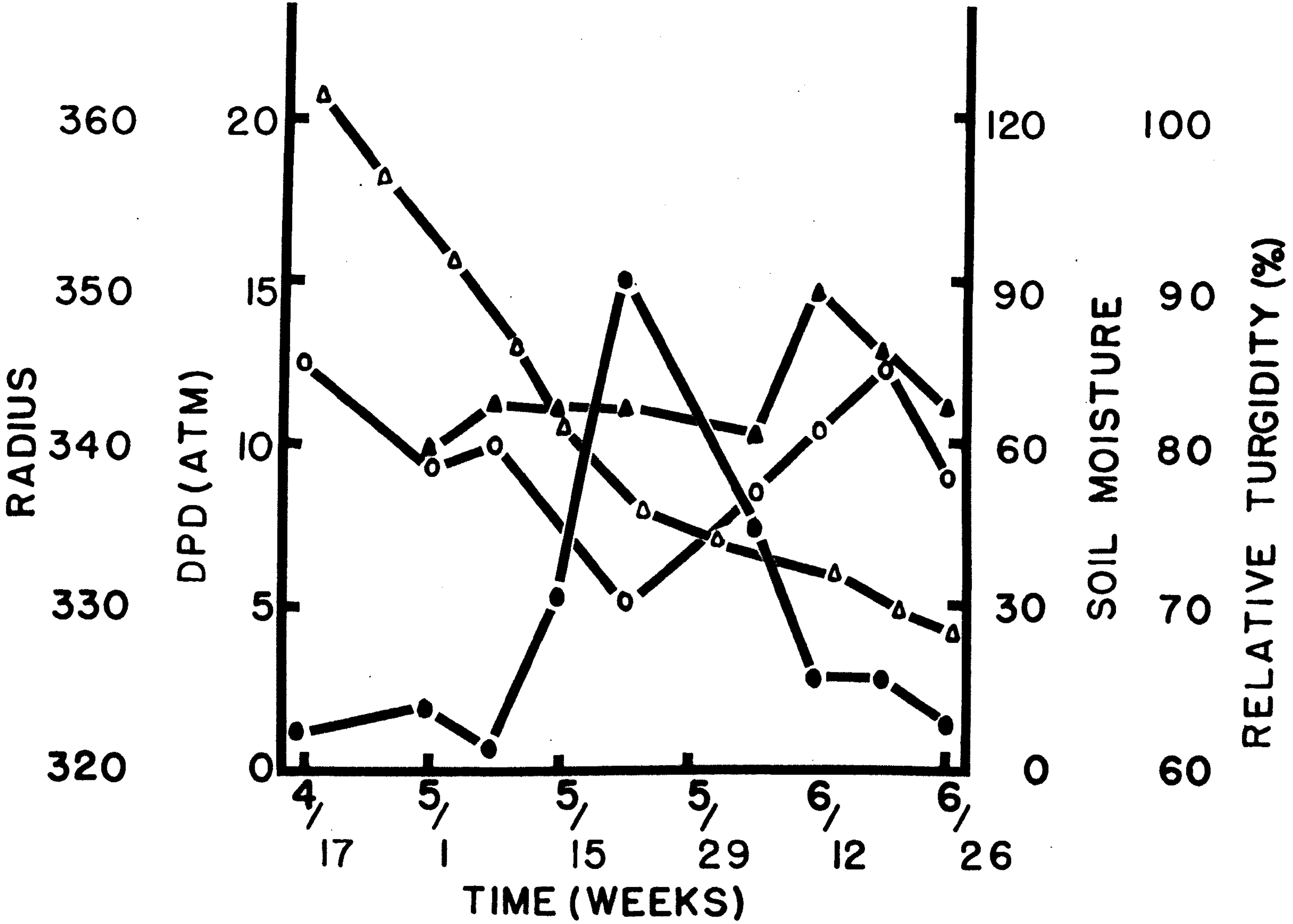
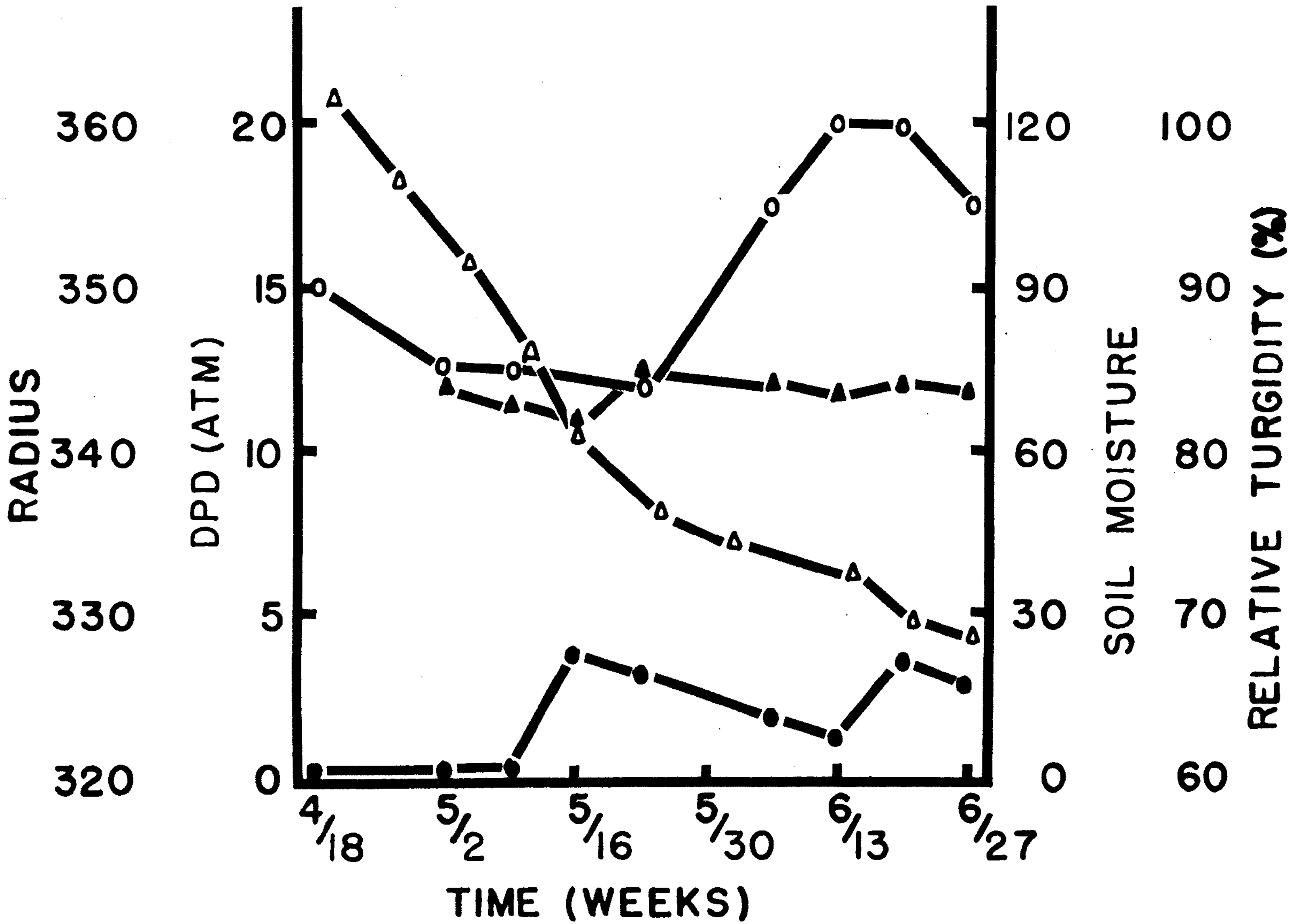

RADIUS
360
350
340
330
320
DPD (ATM)
20
15
10
5
0
SOIL MOISTURE
120
90
60
30
0
RELATIVE TURGIDITY (%)
100
90
80
70
60
4/17
5/1
5/15
5/29
6/12
6/26
TIME (WEEKS)

Fig. 13.--DPD, Relative Turgidity, and Radial Measurements for the Study Tree at 6:00 A.M. and Soil Moisture From April 18 to June 27, 1965.

DPD (Atm)........................ ●
Relative Turgidity (%)........... ▲
Radius........................... ○
Soil Moisture (Microamps)......... △

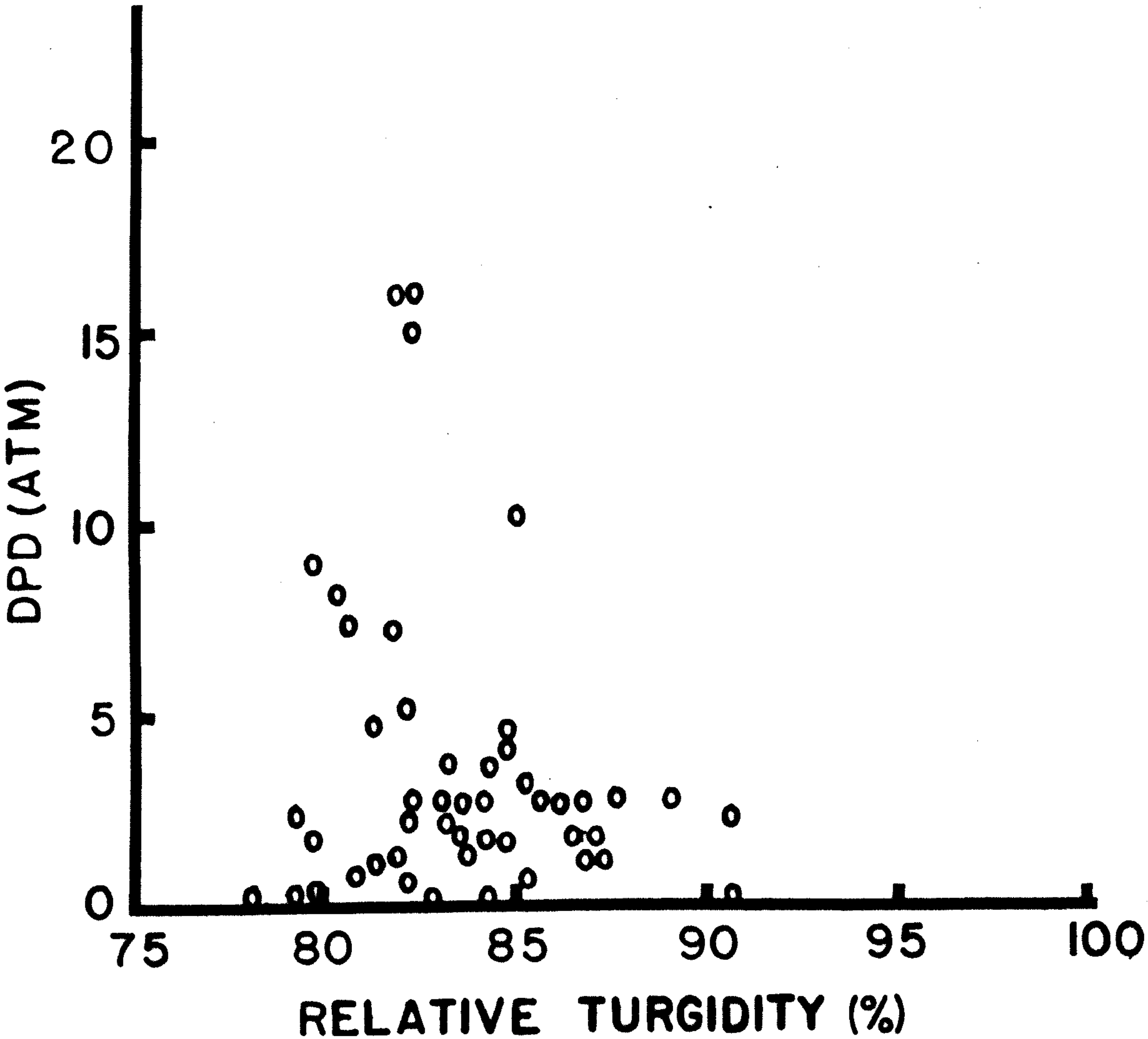

RADIUS
360
350
340
330
320
DPD (ATM)
20
15
10
5
0
SOIL MOISTURE
120
90
60
30
0
RELATIVE TURGIDITY (%)
100
90
80
70
60
4/18
5/2
5/16
5/30
6/13
6/27
TIME (WEEKS)

turgidity shows a steady decrease, but no corresponding increase appears in DPD. This same decrease in relative turgidity during the early morning hours appears during all sample periods for which relative turgidity was measured except for the period of May 22 and 23 (Fig. 5). During this period very little variation in relative turgidity could be found, although DPD showed the greatest variation of any period sampled. However, the mean relative turgidity values were significantly different at the 0.01 level. The only adjacent means which were significantly different were those at 6:30 P.M. and 10:30 A.M. (Appendix Table 13). The two measures of water stress seem to show the closest correlation during the June 19 and 20 sample period (Fig. 8). But during this period there were no significant differences between the mean values for either measure (Appendix Tables 8 and 16). The lack of a close relationship also can be observed on the graphs showing seasonal variations (Figs. 10-13). An even more apparent portrayal of this seeming lack of relationship can be seen in the plot of mean relative turgidity against the mean DPD values for the individual times (Fig. 14). This plot shows that a given DPD is not necessarily associated with a given relative turgidity.

Relationship Between Trunk Diameter Changes and DPD

During periods in which large variations in DPD are in evidence, such as the May 22 and 23 sample period, the

Fig. 14.--DPD Plotted as a Function of Relative Turgidity Values Obtained at the Same Sample Time.


DPD (ATM)
0
5
10
15
20
75
80
85
90
95
100
RELATIVE TURGIDITY (%)

trunk diameter changes appear to follow the same pattern as the DPD (high DPDs corresponding to small trunk diameters) (Fig. 5). The dendrograph trace does appear to lag slightly behind the DPD change, however. During the month of June when only slight DPD variations were detected, the trunk diameter changes continued to occur in about the same magnitude as during the periods of greater DPD variation. On these occasions the diameter changes followed essentially the same diurnal pattern as before (Figs. 6-9). The seasonal variations in trunk diameter follow the same pattern as the seasonal changes in DPD (Figs. 10-13). The increase in size after May 22 is probably a result of cambial activity and growth. Because of this change due to growth it was inpractical to attempt a correlation between trunk diameter and DPD by plotting the values of one as a function of the other.

Relationship of DPD to Vapor Pressure Deficit of the Atmosphere

On days when significant variations in DPD occured, the vapor pressure deficit of the atmosphere followed the same diurnal pattern as the DPD (Figs. 3-5). A lag of DPD behind vapor pressure deficit change was evident on June 5 and 6 (Fig. 6). During the sample periods when only slight DPD variations occured no relationship with the vapor pressure deficit was evident (Figs. 7-9). Relative turgidity, especially during the early morning hours, followed neither the trend in vapor pressure deficit nor the trend in DPD.

Relationship Between Soil Moisture and DPD

The seasonal variations in DPD show a close relationship to soil mositure up to June 5. From that time until measurements were stopped on June 27 the DPD did not relate to the soil moisture (Figs. 10-13).

Observations of Tree Growth

Buds began to open on the study tree on May 24, and the young needles were continuing to increase in size at the time the study was terminated. May 24 is about the same time the dendrograph readings began to indicate radial growth was taking place (Fig. 10).

DISCUSSION AND CONCLUSIONS

The results of this study indicate that in April while soil moisture was abundant no appreciable diurnal variations in water status of the needles occured. After the first of May when soil moisture began to decrease, diurnal variations in DPD began to occur. These diurnal variations increased in magnitude until about May 22 when growth apparently started. After growth began, the diurnal variations in DPD in the 1964 needles diminished even though soil moisture continued to decrease.

The increasing DPDs during May are obviously the result of decreased water content in the needles brought about by increasing vapor pressure deficits in the atmosphere and decreasing soil moisture. The high vapor pressure deficits probably resulted in rapid water loss through transpiration. Because the soil moisture was low, water absorption could not keep pace with this rapid loss thus creating a water deficit in the needles. This deficit caused the high DPD values. The close relationship between DPD and vapor pressure deficit of the atmosphere thus was established.

The decrease in DPD values and variations during the growing period indicates the occurence of different phenomena. Changes in DPD of a tissue can be attributed to: Changes in cell water content, changes in solute content, or changes in cell wall flexibility. Since only mature 1964 needles were used for DPD and relative turgidity determinations, changes in cell wall flexibility can be eliminated. The continually decreasing soil moisture makes it unlikely that the water supply to the needles was increasing. There remains only a decrease in solute content to account for the decreasing DPDs after May 23. This decreasing solute content was probably the result of two factors. The study tree was experiencing a period of low and even negative daily net photosynthesis during the month of June (Brown, 1965). Therefore, cell solutes were being used up almost as rapidly or even more rapidly than they were produced. In addition, the growth during this period probably resulted in increased translocation of material from the needles produced in 1964, dropping the solute content of these needles even lower.

If the relative turgidity technique actually measures the relative water content, as theory supposes it must, it should be controlled by the same factors which control DPD, that is water content, solute content, and cell wall flexibility. If these two measures of water status are controlled by the same factors some form of relationship should exist between them. This relationship need not be linear, however. A relationship which more closely approximates a logarithmic curve when the values of one are plotted as a function of the values of the other would cause slight changes in the value of one to correspond to large changes in the value of the other. The results of this study indicate that something approximating this logarithmic relationship may exist.

The technique used for estimating DPD does not give exact values, and only a range can be determined. With the solution ranges used in most of the tests an error of ± 0.5 atm. is possible. With this amount of error possible slight changes in DPD may not be detected. Some of the apparent lack of correlation, therefore, might be explained on the bases of undetected changes in DPD being accompanied by observable changes in relative turgidity.

Trunk diameter changes appear to offer a good means of estimating leaf tissue water stress. However, position changes associated with cambial activity must not be confused with changes in water status.

SUMMARY

The Schardakow method for estimating DPD was used to follow the seasonal and diurnal variations in water stress in the needles of ponderosa pine. Seasonal variations in DPD were found to correlate well with soil moisture except during the growing period. Changes in cell solute content appeared to play a greater role in DPD determination during the growing period than did soil moisture. Diurnal variations in DPD followed closely the diurnal variations of vapor pressure deficit in the atmosphere during periods in which DPD variations were in evidence. Relative turgidity measurements did not appear to correlate well with DPD values. This may have been partially due to the lack of a linear relationship between the two indicators of water stress. Trunk diameter changes correlated well with DPD values while diameter increase due to cambial growth was not occuring.

APPENDIX

TABLE 1

DPD Values in Atm for the Study Tree From Noon April 17 to 9:00 A.M. April 18, 1965

Time	Sample			Mean
	1	2	3	
12:00 N	0.7	0.7	0.7	0.7
4:00 P.M.	0.15	1.6	1.6	1.12
8:00 P.M.	0.15	0.15	0.7	0.33
12:00 M	0.7	0.15	0.15	0.33
5:30 A.M.	0.15	0.15	0.15	0.15
9:00 A.M.	0.15	0.15	0.15	0.15

F = 2.80 Not significant

TABLE 2

DPD Values in Atm for the Study Tree From 11:00 A.M. May 1 to 10:30 A.M. May 2, 1965

Time	Sample 1	Sample 2	Sample 3	Mean
11:00 A.M.	0.15	0.15	0.15	0.15
3:00 P.M.	0.15	0.15	0.15	0.15
6:30 P.M.	0.15	2.65	2.65	1.82
11:00 P.M.	0.15	0.30	0.15	0.20
6:00 A.M.	0.15	0.15	0.15	0.15
10:30 A.M.	0.30	0.15	0.15	0.20

F = 3.86 Significant at 0.05 level

1.82 <u>0.20 0.20 0.15 0.15 0.15</u> - A single line under two or more adjacent means indicates no significant difference between them.

TABLE 3

DPD Values in Atm for the Study Tree From 10:30 A.M. May 8 to 10:30 A.M. May 9, 1965

Time	Sample 1	Sample 2	Sample 3	Mean
10:30 A.M.	3.20	1.60	2.55	2.45
2:30 P.M.	0.70	0.70	0.70	0.70
6:30 P.M.	0.70	0.30	0.70	0.57
10:30 P.M.	0.70	0.30	0.70	0.57
6:30 A.M.	0.70	0.30	0.15	0.38
10:30 A.M.	0.70	0.70	2.70	1.37

F = 14.22 Significant at 0.01 level

2.45 1.37 0.70 0.57 0.57 0.38 - A single line under two or more adjacent means indicates no significant difference between them.

TABLE 4

DPD Values in Atm for the Study Tree From 10:40 A.M. May 15 to 7:30 A.M. May 16, 1965

Time	Sample			Mean
	1	2	3	
10:40 A.M.	9.00	9.00	9.00	9.00
1:30 P.M.	7.55	8.10	9.00	8.22
4:30 P.M.	6.55	7.55	7.55	7.23
7:30 P.M.	5.55	5.55	4.50	5.20
10:30 P.M.	4.65	5.55	3.60	4.60
7:30 A.M.	3.60	3.60	3.60	3.60

F = 38.67 Significant at 0.01 level

9.0 8.22 7.22 5.20 4.60 3.60 - A single line under two or more adjacent means indicates no significant difference between them.

TABLE 5

DPD Values in Atm for the Study Tree From 10:30 A.M. May 22 to 8:30 A.M. May 23, 1965

Time	Sample 1	Sample 2	Sample 3	Mean
10:30 A.M.	16.00	16.00	16.00	16.00
12:30 P.M.	16.00	16.00	16.00	16.00
2:30 P.M.	16.00	16.00	16.00	16.00
4:30 P.M.	16.00	15.00	15.00	15.33
6:30 P.M.	15.00	15.00	15.00	15.00
8:30 P.M.	13.05	11.00	12.95	12.33
10:30 P.M.	11.00	9.00	11.00	10.33
12:30 A.M.	9.00	6.95	6.95	7.63
2:30 A.M.	5.05	5.05	3.05	4.38
4:30 A.M.	5.05	3.05	3.05	3.72
6:30 A.M.	3.05	3.05	3.05	3.05
8:30 A.M.	3.05	3.05	3.05	3.05

F = 323.22 Significant at 0.01 level

16.0 16.0 16.0 15.33 15.0 12.33 10.33 7.63 4.38 3.72 3.05 3.05

A single line under two or more adjacent means indicates no significant difference between them.

TABLE 6

DPD Values in Atm for the Study Tree From Noon June 5 to 10:00 A.M. June 6, 1965

Time	Sample 1	Sample 2	Sample 3	Mean
12:00 N	7.45	7.45	7.45	7.45
2:00 P.M.	2.65	2.65	2.65	2.65
4:00 P.M.	2.65	2.65	2.65	2.65
6:00 P.M.	7.45	7.45	7.45	7.45
8:00 P.M.	2.65	2.65	2.65	2.65
10:00 P.M.	2.65	2.65	2.65	2.65
12:00 M	2.65	2.65	2.65	2.65
2:00 A.M.	7.45	2.65	2.65	2.65
4:00 A.M.	2.65	2.65	2.65	2.65
6:00 A.M.	2.65	2.65	0.15	1.82
8:00 A.M.	2.65	2.65	0.30	1.87
10:00 A.M.	2.65	2.65	2.65	2.65

F = 13.31 Significant at 0.01 level

7.45 7.45 4.25 2.65 2.65 2.65 2.65 2.65 2.65 2.65 1.82 1.82

A single line under two or more adjacent means indicates no significant difference between them.

TABLE 7

DPD Values in Atm for the Study Tree From Noon June 12 to Noon June 13, 1965

Time	Sample 1	Sample 2	Sample 3	Mean
12:00 N	1.75	1.75	4.65	2.72
2:00 P.M.	1.75	1.75	1.75	1.75
4:00 P.M.	1.75	1.75	1.75	1.75
6:00 P.M.	1.75	3.20	3.20	2.72
8:00 P.M.	1.75	1.75	1.75	1.75
10:00 P.M.	1.75	1.75	1.75	1.75
12:00 M	1.75	1.75	1.75	1.75
3:00 A.M.	0.30	1.75	1.75	1.27
6:00 A.M.	1.75	0.30	1.75	1.27
8:00 A.M.	1.75	1.75	1.75	1.75
10:00 A.M.	1.75	0.30	1.75	1.27
12:00 N	1.75	3.20	1.75	2.23

F = 1.42 Not significant

TABLE 8

DPD Values in Atm for the Study Tree From 10:00 A.M. June 19 to 10:00 A.M. June 20, 1965

Time	Sample			Mean
	1	2	3	
10:00 A.M.	4.65	1.75	1.75	2.72
12:00 N	1.75	1.75	1.75	1.75
2:00 P.M.	1.75	1.75	1.75	1.75
4:00 P.M.	1.75	4.65	1.75	2.72
6:00 P.M.	1.75	4.65	1.75	2.72
8:00 P.M.	1.75	4.65	1.75	2.72
10:00 P.M.	1.75	3.20	1.75	2.23
12:00 M	1.75	1.75	1.75	1.75
3:00 A.M.	1.75	1.75	4.65	2.72
6:00 A.M.	4.65	1.75	4.65	3.58
8:00 A.M.	4.65	4.65	1.75	3.58
10:00 A.M.	4.65	4.65	4.65	4.65

F = 1.39 Not significant

TABLE 9

DPD Values in Atm for the Study Tree From Noon June 26 to Noon June 27, 1965

Time	Sample 1	Sample 2	Sample 3	Mean
12:00 N	2.65	2.10	2.10	2.28
2:00 P.M.	2.10	2.10	2.65	2.28
4:00 P.M.	2.65	1.60	2.65	2.30
6:00 P.M.	2.10	2.65	2.10	2.28
8:00 P.M.	1.60	3.55	2.65	2.60
10:00 P.M.	3.55	1.60	2.10	2.41
12:00 M	1.10	1.60	1.60	1.43
3:00 A.M.	1.60	1.60	1.60	1.60
6:00 A.M.	2.65	2.65	3.55	2.95
8:00 A.M.	2.65	1.60	1.60	1.95
10:00 A.M.	3.60	1.65	3.20	2.82
12:00 N	3.60	2.65	2.65	2.97

F = 14.69 Significant at 0.01 level

2.97 2.95 2.82 2.60 2.41 2.30 2.28 2.28 2.28 1.95 1.60 1.43

A single line under two or more adjacent means indicates no significant difference between them.

TABLE 10

Relative Turgidity Values in Percent for the Study Tree From 11:00 A.M. May 1 to 10:30 A.M. May 2, 1965

Time	Sample			Mean
	1	2	3	
11:00 A.M.	77.79	78.33	82.40	79.50
3:00 P.M.	78.65	78.66	77.53	78.28
6:30 P.M.	80.10	80.68	78.98	79.92
11:00 P.M.	94.69	89.94	87.09	90.57
6:00 A.M.	85.74	83.72	83.76	84.41
10:30 A.M.	80.76	80.50	77.53	79.60

F = 14.69 Significant at 0.01 level

90.57 84.41 <u>79.92 79.60 79.50 78.28</u> - A single line under two or more adjacent means indicates no significant difference between them.

TABLE 11

Relative Turgidity Values in Percent for the Study Tree
From 10:30 A.M. May 8 to 10:30 A.M. May 9, 1965

Time	Sample			Mean
	1	2	3	
10:30 A.M.	79.52	80.08	78.70	79.43
2:30 P.M.	80.93	81.15	81.24	81.11
6:30 P.M.	79.85	83.09	83.86	82.26
10:30 P.M.	84.19	85.07	86.98	85.41
6:30 A.M.	85.51	82.63	80.64	82.93
10:30 A.M.	82.94	81.51	81.32	81.92

F = 0.14 Not significant

TABLE 12

Relative Turdigity Values in Percent for the Study Tree
From 10:40 A.M. May 15 to 7:30 A.M. May 16, 1965

Time	Sample			Mean
	1	2	3	
10:40 A.M.	79.98	79.94	79.89	79.94
1:30 P.M.	81.92	80.50	78.83	80.42
4:30 P.M.	84.13	81.94	79.37	81.81
7:30 P.M.	81.59	83.26	81.58	82.14
10:30 P.M.	83.82	85.26	85.27	84.78
7:30 A.M.	80.69	85.62	83.49	83.27

F = 3.44 Significant at 0.05 level

84.78 83.27 82.14 81.81 80.42 79.94 - A single line under two or more adjacent means indicates no significant difference between them.

TABLE 13

Relative Turgidity Values in Percent for the Study Tree From 10:30 A.M. May 22 to 6:30 A.M. May 23, 1965.

Time	Sample			Mean
	1	2	3	
10:30 A.M.	83.74	79.73	82.69	82.05
2:30 P.M.	81.99	82.78	81.50	82.09
6:30 P.M.	83.73	81.01	82.27	82.34
10:30 P.M.	85.09	86.40	83.93	85.14
2:30 A.M.	85.41	84.63	84.27	84.77
6:30 A.M.	86.09	84.89	84.46	85.15

F = 5.09 Significant at 0.01 level

85.15 85.14 84.77 82.34 82.09 82.05 - A single line under two or more adjacent means indicates no significant difference between them.

TABLE 14

Relative Turgidity Values in Percent for the Study Tree From 2:00 P.M. June 5 to 10:00 A.M. June 6, 1965

Time	Sample			Mean
	1	2	3	
2:00 P.M.	80.58	84.40	81.90	82.29
6:00 P.M.	83.17	73.86	85.01	80.68
10:00 P.M.	85.93	85.42	89.24	86.86
2:00 A.M.	85.36	87.60	85.08	86.01
6:00 A.M.	84.99	82.99	85.18	84.39
10:00 A.M.	84.71	80.92	83.81	83.15

F = 1.91 Not significant

TABLE 15

Relative Turgidity Values in Percent for the Study Tree
From 2:00 P.M. June 12 to 10:00 A.M. June 13, 1965

Time	Sample 1	Sample 2	Sample 3	Mean
2:00 P.M.	81.46	86.37	86.72	84.85
6:00 P.M.	89.97	89.12	88.10	89.06
10:00 P.M.	86.74	86.09	86.72	86.52
3:00 A.M.	84.87	87.06	89.82	87.25
6:00 A.M.	83.79	82.47	85.35	83.34

F = 7.22 Significant at 0.01 level

89.06 87.25 86.52 84.85 83.87 81.34

A single line under two or more means indicates no significant difference between them.

TABLE 16

Relative Turgidity Values in Percent for the Study Tree From Noon June 19 to 10:00 A.M. June 20, 1965

Time	Sample			Mean
	1	2	3	
12:00 N	83.35	87.45	80.55	83.78
4:00 P.M.	91.76	85.21	85.73	87.57
8:00 P.M.	86.78	86.25	83.93	85.65
12:00 M	84.72	90.58	86.32	87.21
6:00 A.M.	84.07	85.35	83.62	84.35
10:00 A.M.	78.69	82.10	83.22	81.34

F = 2.27 Not significant

TABLE 17

Relative Turgidity Values in Percent for the Study Tree From 2:00 P.M. June 26 to 10:00 A.M. June 27, 1965

Time	Sample			Mean
	1	2	3	
2:00 P.M.	81.42	86.28	82.67	83.45
6:00 P.M.	82.79	81.28	82.42	82.16
10:00 P.M.	69.98	86.59	94.44	90.52
3:00 A.M.	87.36	85.72	88.32	87.13
6:00 A.M.	85.38	82.36	83.89	83.87
10:00 A.M.	84.45	83.59	84.52	84.18

F = 0.28 Not significant

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