SEASONAL AND DIURNAL CHANGES IN THE WATER CONTENTS
AND WATER DEFICITS OF BARTLETT PEAR LEAVES

WM. B. ACKLEY
WASHINGTON AGRICULTURAL EXPERIMENT STATION, PULLMAN, WASHINGTON

It is general knowledge that the water content of deciduous leaves usually decreases as the season advances. It has also been noted that the water deficit fluctuations of such leaves are often more pronounced early in the growing season when these parts are young and succulent than later when they are older and harder. The seasonal changes in the actual weights of the water and dry matter components of leaves, however, are less commonly understood.

Leaf samples are comparatively easy to pick, dry and weigh. For this reason, the water content of leaves is often used to indicate water changes within plants. Knight (5) found slight diurnal variations in water contents of leaves of the plants he tested in the area of southeastern England. Livingston and Brown (7) found large diurnal changes in the water contents of the desert plants with which they worked. Miller (9) made frequent periodic water content determinations on the leaves of corn and sorghums in his studies of the water relations of these crop plants. Maximov (8), Stanescu (12), Kramer (6), and Wilson, Bogess, and Kramer (14) have also reported on the fluctuations in the water contents of plants.

Stocker (13) devised a measurement of water deficits by which he related the amount of water needed to bring a leaf to full saturation, or zero deficit, to the total amount of water in the leaf at saturation. The resulting ratio figure was multiplied by 100 and expressed as a percentage. Stocker used such a measurement to obtain a comparison of the water deficits existing in the leaves taken at different periods of the day from plants growing in widely separated climatic zones. Oppenheimer and Mendel (10), Halma (3, 4), Compton (1), and Runyon (11) have reported on the use of similar measurements to determine changes in the water deficits of plants.

During the past five years the Department of Horticulture of the State College of Washington has conducted a study of certain water relationships of Bartlett pear trees. A portion of this study included the measurement of the seasonal and diurnal fluctuations in the leaf water contents and water deficits and the weight changes of the leaf constituents responsible for these fluctuations.

MATERIALS AND METHODS

As a source of leaf materials, eight bearing Bartlett pear trees were selected for this study. These trees were located in one orchard block at the Tree Fruit Experiment Station, Wenatchee, Washington. The leaf samples were taken from non-bearing fruit spurs near the periphery of the trees. An effort was made to limit the number of leaves removed from any one spur to not more than two during the entire sampling season.

In determining seasonal changes, the samples dates covered six 6-day periods spaced at three-week intervals from May 15 to September 2, 1950. The samples were taken between 2:00 and 2:30 P.M. each day from four sides of each tree and at three levels—5, 10, and 15 feet from the ground. To determine diurnal changes, leaf samples were taken at 4-hour intervals during six 32-hour periods spaced throughout much of the 1950 growing season. Four leaves were selected from each tree near the five-foot level at each sampling time.

The leaves were transported from the field to the laboratory in weighing cans and immediately weighed for "field weight" measurements. The leaf samples were then arranged in racks and lowered into an enclosed constant-temperature water bath for saturation. The racks held the leaves in such a position that the end of the petioles were under water. The samples were left in the water bath for 18 hours at 22°C. After obtaining the "saturated weight" the leaves were dried at 100°C for 24 hours and the "dry weight" determined. Water contents, as percent dry weight, and water deficits, as percent of the water at saturation, were calculated according to the formulas:

\[
\text{Water content} \% = \frac{\text{field weight} - \text{dry weight}}{\text{dry weight}} \times 100
\]

\[
\text{Water deficit} \% = \frac{\text{saturated weight} - \text{field weight}}{\text{saturated weight} - \text{dry weight}} \times 100
\]

The trees were irrigated at frequent intervals throughout the growing season, an attempt being made to keep the soil moisture ample at all times. As indicated by tensiometer measurements, there was no practical difference in the availability of moisture to the trees between any two of the sampling periods.

RESULTS AND DISCUSSION

SEASONAL CHANGES: The results of this portion of the study are presented graphically in figures 1 and 2. Each weekly average indicated represents 12 leaves from each of 8 trees on each of 6 days, or a total of 576 leaves.

Figure 1 illustrates the increase in leaf weight occurring during the season. The decrease noted at the last sampling period should not be interpreted to mean that individual leaves actually decreased in weight between the last two sampling periods. During the week of August 13 to 19, temperatures and humidity conditions were extremely severe. By August 28 approximately one-fifth of all the leaves had fallen prematurely, and a fourth of the remaining leaves showed dry brown areas typical of transpiration injury. The samples were selected from the ap-
The average of the three leaves were smaller apparently uninjured leaves and evidently these leaves were smaller than those selected at the earlier dates.

Figure 1 also illustrates the relative amounts of the three measured components which make up the total weight of a leaf at saturation: (1) dry matter, (2) water in the leaves at sampling time, and (3) water taken up by the leaves in the saturation period. After the leaves reached full development, or after the first sampling period, total weight increases were due primarily to increases in the dry matter component. After the leaves reached full development, the amount of water occurring in them did not vary to any large extent. At the earlier sampling periods the leaves took up more water, even though they were smaller, than later in the season.

It is evident that the seasonal water content reductions illustrated in figure 2 were due, for the most part, to increases in dry matter and not to decreases in the water component. The seasonal water deficit changes shown in figure 2 indicate that age of leaf is of extreme importance in the evaluation of these measurements. The high water deficit value found at the first sampling period cannot be related to environmental conditions at that time, whereas the water deficit values observed during the next four sampling periods appear to reflect increasing transpirational losses due to increasing temperatures and decreasing relative humidities.

**Diurnal Changes:** The results of these tests are summarized in table I. The seasonal changes in water contents and water deficits previously discussed are immediately apparent. In fact, these seasonal changes were so large as to make over-all seasonal averages of little value. The diurnal changes, however, were remarkably uniform between any two corresponding sampling periods.

As indicated by these data, and as shown in figure 3, minimum water contents were found to occur around 2:00 P.M. each day. The samples taken at 2:00 A.M. were found to have the highest water content values. The differences between these extremes were generally larger early in the season, particularly at the first sampling period before the leaves had reached full development. At this time the leaves had a much lower dry matter content and small changes in the water component caused relatively large changes in the water dry matter ratios.

The diurnal water deficit values, when plotted as in figure 4, showed opposite fluctuations, the maximum values occurring around 2:00 P.M. and the minimum values around 2:00 A.M. It is of special interest to note that the minimum water deficits, as measured, never reached zero, even under the conditions of low night time temperatures common in the Wenatchee, Washington, area. This observation emphasizes the fact that artificial leaf saturation under conditions of unrestricted water uptake in a near-saturated atmosphere is not comparable to usual field conditions.
Table I
DIURNAL CHANGES IN THE WATER CONTENTS AND WATER DEFICITS OF BARTLETT PEAR LEAVES DURING SIX 32-HOUR PERIODS SPACED THROUGHOUT THE 1950 GROWING SEASON

<table>
<thead>
<tr>
<th>Sampling dates</th>
<th>Sampling times</th>
<th>Water contents as % dry weight</th>
<th>Water deficits as % of the water at saturation</th>
</tr>
</thead>
<tbody>
<tr>
<td>May 19-20</td>
<td>2 P.M. 6 P.M. 10 P.M. 2 A.M. 6 A.M. 10 A.M. 2 P.M. 6 P.M. 10 A.M. 2 P.M. 6 P.M. 10 A.M.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>May 19-20</td>
<td>251.6 255.5 268.6 280.3 276.8 259.6 246.5 254.4 267.7</td>
<td></td>
<td></td>
</tr>
<tr>
<td>June 9-10</td>
<td>172.8 174.7 182.7 191.5 175.9 173.4 173.1 178.2 180.9</td>
<td></td>
<td></td>
</tr>
<tr>
<td>June 28-29</td>
<td>151.1 153.6 166.2 167.2 163.6 153.9 152.8 165.1 166.7</td>
<td></td>
<td></td>
</tr>
<tr>
<td>July 20-21</td>
<td>140.5 142.2 151.3 153.1 148.6 142.2 140.7 145.8 154.2</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Aug. 8-9</td>
<td>135.9 140.3 147.1 153.6 152.8 141.7 135.9 143.1 148.2</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Aug. 28-29</td>
<td>134.7 138.7 142.1 146.2 137.4 135.6 137.9 145.8 145.8</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Curtis and Clark (2) have pointed out that small changes in water content can cause relatively large changes in water content figures when the calculations are based on dry weights. A critical review of the diurnal changes in the actual weights of the components responsible for the water contents presented in table I indicates that these figures were influenced by changes in both of the factors concerned. As the water component decreased during the day, the dry matter component was found to increase. During the night, as the amount of water in the leaf increased, the dry weight decreased. Thus the diurnal extremes of water contents were accentuated by simultaneous and inverse changes of the two components involved.

SUMMARY
A study was conducted to measure the seasonal...
and diurnal fluctuations in the water contents and water deficits of Bartlett pear leaves. The results indicated that there was a general reduction in the leaf water content, as calculated on a dry-weight basis, during the growing season. The results also indicated, however, that this reduction was caused by an increase in the dry matter content and not by a decrease in the water component.

Minimum water contents and maximum water deficits of pear leaves were observed to occur around 2:00 P.M. each day. Maximum water contents and minimum water deficits were observed around 2:00 A.M. each day. The differences between the diurnal extremes of leaf water content were generally larger early in the growing season, particularly when the leaves were young and succulent. These extremes appeared to be due to inverse changes in both the dry matter and water components.

Since the actual amount of water in a leaf may or may not accompany changes in calculated leaf water contents, as indicated by the results of this study, the term "water content" or even "water content on a dry-weight basis" may be somewhat misleading unless the weights of the individual components involved are also considered. The results also indicate that only after leaves reach nearly full size can water deficit changes be related to environmental conditions.

This work was aided in part by grants from the Northwest Canners Association and the Washington State Soft Fruit Commission.

LITERATURE CITED

THE PHYSICAL ENVIRONMENT OF CHLOROPLASTS AS RELATED TO THEIR MORPHOLOGY AND ACTIVITY IN VITRO \(^{1,2}\)

JOHN H. McCLENDON \(^3\)

HOPKINS MARINE STATION, STANFORD UNIVERSITY, PACIFIC GROVE, CALIFORNIA, AND DEPARTMENT OF BOTANY, UNIVERSITY OF MINNESOTA, MINNEAPOLIS, MINNESOTA

Various authors have commented recently on the relative worth of different procedures for the isolation of intracellular structures such as mitochondria, nuclei and chloroplasts. (Recent reviews are 13, 50). Many workers have considered one or another aqueous medium adequate and proper for the study of the biochemical system in question, while others maintain

\(^1\) Received March 10, 1954.

\(^2\) The investigations reported here were supported by the Office of Naval Research (contracts No. ONR 51A(00) with Stanford University and No. 160-030 with the University of Minnesota) and by the Graduate School, University of Minnesota.

\(^3\) Present address: Department of Agricultural Chemistry, University of Delaware, Newark, Delaware.

that non-aqueous liquids are the only known media which prevent changes in the distribution of proteins, nucleic acids, etc. upon disintegration of the tissue \((1, 14)\). While granting the usefulness of non-aqueous media in some cases, an aqueous medium is obviously necessary to maintain a natural environment, except perhaps for seeds and other naturally desiccated bodies. However, aqueous media used successfully by some have in other cases proven inadequate, either on a different tissue or organism, or by different criteria on the same tissue and organism. For example, some animal nuclei when isolated into certain aqueous media with little change in microscopic appearance have been shown to have lost half of their dry weight \((14)\).