THE STOMATA AND TRANSPERSION OF OAKS

L. Edwin Yocum

(WITH TWO FIGURES)

Introductory

Stomata and transpiration are of fundamental importance in the water relations of plants. It is evident that the loss of moisture in transpiration is equally as important as absorption of water by the root system in plant survival. Our mesophytic plants must have stomatal protection against excessive loss of moisture during drought. This is of paramount importance to us in our conservation work, where trees are being used as windbreaks, and to conserve moisture. Most of our knowledge regarding stomata has to do with herbaceous plants, as indicated by texts in plant physiology (Miller, 7, and others). Growth habits and therefore soil conditions are not the same for leaf formation on herbaceous plants as on trees. On trees most of the leaves grow simultaneously in the spring while on herbaceous plants they appear over a longer period. In herbaceous plants stomata are commonly on both leaf surfaces, but tree leaves have them usually only on the lower surface.

Nearly all the water loss of plants occurs through the stomata. Some is lost through the epidermis, and since the upper epidermis has thicker cell walls, it is probable that a little more water loss occurs through the lower than through the upper epidermis. Water passes freely through the stomata when open; in fact Brown and Escombe (2) have shown that water may be lost through the stomata as rapidly as though it were evaporating from a free water surface instead of through many small pores. Sayre (12) has shown that the rate of transpiration depends more on the perimeter of the opening, than on its area, which is very important in the study of partly closed stomata. It is evident from their shape that the beginning of closure changes the perimeter very little, and only the last few per cent. of closure will in many cases affect the transpiration rate, as found by Jeffreys (4).

Methods

The relation of the stomata to transpiration was measured by the cobalt chloride paper method, since it seemed to offer a more accurate measure than the actual observational measurement of the final stages of closure in percentages. Mature leaves on one to three year old Q. palustris, Q. rubra, and Q. prinus seedlings grown outdoors, some in pots and some in seed beds, were used. Readings were taken at intervals of two hours or less over twenty-four hour periods.

705
Stomatal counts were made on fresh leaves of the above seedlings and from mature leaves from trees with the aid of the "ultropak" microscope at 500× magnification. Reed (10) has shown that immature leaves of citrus have many more stomata per mm.² than mature ones. At least ten leaves were used from two or more trees of each species. The trees were isolated individuals or at the edge of a group where they were freely exposed to light and wind. To select trees within a group would reduce the number of stomata, as Salisbury (11) found the number to decrease with the protection of the forest.

The stomata were counted in a rectangle 200 µ by 150 µ, except in the case of the willow oak at 10 places on each leaf, or a total area of 0.3 mm.² per leaf. Areas having veins thirty µ or more in width were avoided. In order to get the average number of stomata, five counts were made on each side of the midrib as follows: near the base of the leaf; near the midrib at the center of the leaf; near the center of the halfleaf; the edge opposite this point; and near the tip. Counts were made on willow oak leaves only at the base, middle, and tip.

**Results**

During the day, with adequate soil moisture the cobalt chloride paper reacted over the lower epidermis in one twentieth to one tenth the time required over the upper epidermis. At sunset the reaction time of the lower epidermis quickly changed to about one half the time on the upper side, but at sunrise it returned to daytime rates. Seedlings¹ grown in a seedbed in 1931 during a very dry period, when the soil moisture was below the wilting coefficient near the surface and a little above the wilting coefficient deeper in the soil, were found to have their stomata closed all day as indicated by their transpiration. The cobalt chloride paper required two hours or longer to change color on the lower surface and usually a little longer on the upper, due to the difference in epidermal cell walls. If they were entirely closed it was thought that carbon dioxide would be prevented from entering and that photosynthesis would be retarded. Leaves tested with iodine for starch at 4:00 p.m. on bright days gave a negative test for starch. A second seedbed was watered artificially and showed a high rate of transpiration and an abundance of starch in the leaves. Two days after a heavy rainfall the seedlings in the dry bed showed rapid transpiration and photosynthesis. A negative test for starch on a day favorable for photosynthesis appears to be a good test for all day total stomatal closure.

The differences in stomatal numbers for various parts of the same leaf were small, but the base of the leaves always had the fewest stomata; and in nearly all cases the region near the midrib had a lower number than the

¹ Results of studies made while employed by the Allegheny Forest Experiment Station, Philadelphia, Pa.
other parts of the leaf. No consistent differences were noted in the middle, edge, and tip counts, but in the total count the edge and tip were nearly 0.25 per cent. greater than the middle; the midrib, nearly 2, and the base, nearly 8 per cent. less. That is, in a general way the smallest number was found at the leaf base, and it increased toward the tip and edges of the leaf. Shaded leaves on mature trees and on seedlings always had fewer stomata than insolated leaves.

Stomata are small but very numerous and the guard cells may cover more than fifty per cent. of the surface as is shown by *Q. triloba* (fig. 1), and forty per cent. in the case of *Q. palustris* (fig. 2). Small areas of *Q. triloba*

![Fig. 1. Q. triloba Michx., stomata and epidermal cells in an area of 0.0036 mm²](image1)

![Fig. 2. Q. palustris DuRoi, stomata and epidermal cells in an area of 0.0036 mm²](image2)

have an average of more than nineteen hundred per mm², and the average for all counts was 1192 per mm². This is exceeded to the writer’s knowledge only by ADAMSON’s (1) report of *Veronica cookiana*, 2200. Other species of *Veronica* had an average number of 250 to 400 per mm². Fully opened stomata of *Q. triloba* are about five μ long and one μ wide, or about

<table>
<thead>
<tr>
<th>TABLE I</th>
<th>STOMATAL NUMBERS FOR Quercus SP. PER MM²</th>
</tr>
</thead>
<tbody>
<tr>
<td>TREES</td>
<td></td>
</tr>
<tr>
<td>PIN</td>
<td>BLACK RED</td>
</tr>
<tr>
<td>497</td>
<td>580</td>
</tr>
<tr>
<td>SEEDLINGS</td>
<td></td>
</tr>
</tbody>
</table>

This is exceeded to the writer’s knowledge only by ADAMSON’s (1) report of *Veronica cookiana*, 2200. Other species of *Veronica* had an average number of 250 to 400 per mm². Fully opened stomata of *Q. triloba* are about five μ long and one μ wide, or about
one per cent. of the total surface of the leaf. Table I gives the average stomatal numbers for trees of eight species, and three seedlings.

Stomatal counts were made at different elevations on two species of oaks, *Q. palustris* at 7, 17, and 60 feet, and *Q. velutina* at 7, 14, and 30 feet, taken from all sides of exposed trees. The results were similar for the two species. The data given for *Q. palustris* in table II are the average of 100 or more counts for each elevation. The number per mm.\(^2\) for each elevation is within three per cent. of the average number and while at 7 feet high the averages are higher, it is probably not significant.

In order to examine further the relation of elevation to stomatal number the shoot of a three year old *Q. palustris* seedling was removed at the ground level in the winter, and a single sprout allowed to grow the following spring. On July 19, the sprout was forty-four inches tall. Stomatal counts were made at eight inch intervals from the ground as follows:

<table>
<thead>
<tr>
<th>Height from the ground, inches</th>
<th>Stomata per mm.(^2)</th>
</tr>
</thead>
<tbody>
<tr>
<td>8</td>
<td>410</td>
</tr>
<tr>
<td>16</td>
<td>430</td>
</tr>
<tr>
<td>24</td>
<td>450</td>
</tr>
<tr>
<td>32</td>
<td>503</td>
</tr>
<tr>
<td>40</td>
<td>533</td>
</tr>
</tbody>
</table>

The leaves at the forty inch level were mature and had developed during July. This shoot had developed its leaves progressively as is common for herbaceous plants.

**Discussion**

The transpiration rate of the oaks studied showed that the stomata normally remain open throughout the day but close at sunset. With low soil moisture the stomata may remain closed all day even to the extent of preventing photosynthesis. This action of the stomata is very important as it indicates a maximum transpiration rate when soil water is available, justifying the statement sometimes made that "trees are our natural humidifiers"; and when soil water is so limited that many herbaceous plants would be seriously injured or killed, trees may resist drought for some time
because of the action of their stomata. Thus in addition to improving the physical conditions of the soil for the retention of soil moisture the oaks give off water rapidly when it is abundant in the soil but withhold it during drought. Magness (5) has reported similar drought reactions for apple trees in the eastern states, and finds that there is a cessation of growth of fruit, but that the stomata rarely remain open later than noon on bright clear days, regardless of the soil moisture conditions.

This difference in afternoon stomatal condition suggests interesting questions regarding the rate of photosynthesis in apples and oaks. Is the rate much higher for apples in the morning than for oaks, or is the total amount greater for oaks? Of equal interest and perhaps more important to conservationists is the "water requirement" of trees, or as Maximov (6) prefers to state it, the "efficiency of transpiration." Are we more interested in the maximum humidifying power of the plant or in the maximum plant material produced with the available water? Scarth (13) has discussed the problem of the stomatal influence on transpiration and photosynthesis.

The stomatal counts for the species recorded were made during the summer of 1934. During the previous six months, December to May, inclusive, the total rainfall was greater than normal by more than six inches; during only two months, January and April, was it slightly below normal, according to the U. S. Weather Bureau records for Washington. Excessive rainfall during the spring tends to decrease the stomatal numbers, according to Hirano (3); therefore the frequencies given in table I are lower than the number to be found during a dryer spring. The number of stomata found on trees growing in a dense forest would probably be lower because of the high percentage of shaded leaves, which were found to have fewer stomata. Hirano (3) points out some ecological relationships to stomatal numbers in citrus. The oak species examined in this study have not indicated a well defined ecological relationship; however, the three species having the greatest frequency grow on dry soil.

Trees generally have a higher stomatal frequency than shrubs or herbaceous plants as found by Salisbury (11), Raber (9), and others. Citrus has been studied extensively by Hirano (3), Oppenheim (8), and Reed (10), who found a frequency often more than 500 per mm.² and a distribution similar to that found in oaks. No record has been noted of a group of species with as high stomatal frequencies as are found here in the oaks.

Salisbury (11), Yapp (14), and others have found a rapid increase in the stomatal numbers as the leaves are higher on the stem. Reed (10) finds a certain relationship on long stems of citrus but not on short ones. Maximov (6) describes Yapp's work under the heading "Leaf structure in relation to water," but follows the suggestion of Zalenski that the later leaves

Downloaded from www.plantphysiol.org on January 5, 2018.
have more water deflected to the lower leaves, causing a greater osmotic pressure in the upper leaves, producing more stomata. It has been shown by Hirano (3) that the amount of spring rainfall has more influence on stomatal number than has annual rainfall. Herbaceous plants grow their leaves during several months. In Yapp's (14) study of Spiraea, illustrations are given from March to June, inclusive, during which time the external conditions favor the increase of transpiration as new leaves develop, but normally the soil moisture becomes less. This would cause the osmotic pressure of the leaf cells to become greater and the leaves to become more xeromorphic, with increased stomata. The difference in height would have relatively no effect compared with the difference in the resistance which the soil offers to water loss in early spring and in the dryer summer period. This would seem to explain the fact that stomatal frequency varies so little on the Q. palustris tree with a height of sixty feet since the leaves all developed with nearly the same soil moisture; but a seedling of the same species has thirty per cent. more stomata at forty inches than it has thirty-two inches lower on the same stem.

Summary

1. The stomata of oaks are functional and may remain completely closed during a drought.
2. Stomatal frequencies on eight species of oaks are all high, and on Q. triloba, the highest, the frequency is exceptionally high.
3. Stomatal numbers do not appear to increase with height on mature, exposed trees, but they do appear to increase on indefinitely growing stems.

DEPARTMENT OF BOTANY
THE GEORGE WASHINGTON UNIVERSITY
WASHINGTON, D. C.

LITERATURE CITED