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MECHANISMS BY WHICH WIND INFLUENCES TRANSPIRATION [1]

JOSEPH T. WOOLLEY

SOIL & WATER CONSERVATION RESEARCH DIVISION, AGRICULTURAL RESEARCH SERVICE, U. S. DEPARTMENT OF AGRICULTURE, & DEPARTMENT OF AGRONOMY, UNIVERSITY OF ILLINOIS, URBANA

Although the amount of transpiration from a leaf is predominantly a function of the amount of energy received by the leaf, wind can influence the manner in which the leaf loses energy, and thus can affect transpiration significantly. Wind influences transpiration by removal of the so-called "layer" of saturated air from the surface of the leaf, and also by changing the temperature of the leaf. Bange (1) showed that in the isothermal case the stimulation of transpiration by wind could be accounted for quantitatively by theoretical calculations involving the removal of the layer of saturated air. Thermal effects of wind on transpiration are more difficult to evaluate, since any change in transpiration rate will usually be accompanied by a secondary temperature change, but wind does have one direct effect on the leaf temperature. The increased mass of air brought into contact with the leaf by wind tends to bring the leaf temperature closer to the air temperature, regardless of whether the leaf be warmer or colder than the air.

Certain other mechanisms of wind action appear to be possible or have been mentioned in the literature as possibilities, and therefore deserve investigation. These mechanisms are:

I. Decrease in air pressure on the lee side of the leaf, causing increased evaporation on this side.

II. Ventilation of intercellular spaces, caused by actual passage of air through amphistomatous leaves.

III. Bending of the leaves in the wind, causing compression of the intercellular spaces and consequent pumping of saturated air out of the stomata.

These three mechanisms are the subject of this paper.

I. DECREASE IN AIR PRESSURE. Maximov (5) mentioned that wind may cause a reduced pressure on the lee side of a leaf, causing increased evaporation on that side, and Gaumann and Jaag (4) invoke this same mechanism to account for part of their substomatal transpiration. Putting aside the fact that a reduced pressure on one side of the leaf would usually be compensated for by an increased pressure on the other, we can estimate the possible magnitude of this effect by considering a leaf held normal to a wind which is blowing 7 meters second^{-1} (ca. 15 miles/hr). Such a wind could cause a maximum pressure differential of about 570 dynes cm^{-2} between the two sides of the leaf. This 570 dynes cm^{-2} would be less than 0.06 % of the difference between atmospheric pressure and the vapor pressure of water. Therefore the rate of transpiration could not be increased by more than 0.1 % by such a pressure differential.

II. VENTILATION THROUGH AMPHISTOMATOUS LEAVES. Measurements made by a modification of the Darwin and Pertz (2) porometer technique indicate that a pressure of 10^4 dynes cm^{-2} may force a maximum of 10^{-3} cm^3 of air per second through 1 cm^2 of a corn leaf when the stomata are open. Thus a 7 m second^{-1} wind, causing a pressure differential of 570 dynes cm^{-2} between the sides of the leaf, might force as much as 5.7 × 10^{-5} cm^3 of air per second through each square centimeter of a corn leaf.

Miller and Coffman (9) found that corn plants in the field often transpired as much as 5.5 × 10^{-6} g of water per square cm of leaf per second (200 g m^{-2} hr^{-1}). If the relative humidity inside the leaf were 100 % and that outside of the leaf were 50 %, an exchange of 3.6 × 10^{-1} cm^3 of air per cm^2 of leaf sur-

face would be required each second to account for this transpiration. The air exchange forced by a 7 m second^{-1} wind, then would be sufficient to account for only 0.016 % of the observed transpiration.

III. PUMPING BY LEAF BENDING. Both the older and the recent literature (6, 7, 8, 10) have numerous references to the possibility that the change of volume of intercellular space as leaves bend in the wind might pump gases out of the stomata and thus increase transpiration. The only experimental work bearing upon this pumping action seems to be that of Eberdt (3), who found that leaves which were allowed to flutter in moving air lost about 10 % more water than did fixed leaves. Unfortunately, Eberdt's description and data permit neither an evaluation of possible artifacts nor a statistical analysis.

Leaves actually undergo very little bending in the wind. The maximum rate of bending of corn leaves, for instance, seems to occur at wind speeds of 7 to 10 meters second^{-1}. Stronger winds break and tear the leaves. There are two types of leaf motion—a slow flexing of most leaves with a period of about two seconds and a radius of curvature changing between limits such as 30 cm and 50 cm, and a rapid flutter of a few leaf tips with a period of as little as 0.25 seconds and a radius of curvature of 3 cm or more.

With a 3-cm radius of curvature, the stretching of the outer surface or the compression of the inner surface of a corn leaf 0.018 cm thick would be 0.6 %. If all of this stretching or compression took place in the intercellular space, the maximum possible volume change would be 10^{-4} cm^3 of air per cm^2 of leaf. At four cycles per second, 4×10^{-4} cm^3 of air would be exchanged each second. This would be only 1/9th of 1 % of the 3.6×10^{-1} cm^3 cm^{-2} second^{-1} of air exchange necessary for the transpiration rate observed by Miller and Coffman. Thus the pumping action of leaf bending theoretically could not account for a significant portion of the transpiration.

EXPERIMENTAL

Sections from the tip portions of corn leaves were harvested in the field and kept in polyethylene bags until they were used. These sections were 16 cm long, and the average widths were 6.3 cm and 8.5 cm at the tip and basal ends, respectively. Two leaf sections, designated A and B, were fastened by rubber bands to leaf holders, one of which is shown diagrammatically as figure 1. A fan and a lamp were arranged to give a wind velocity of 5 m second^{-1} and a light intensity of 40 lux on both leaf sections. Temperature was not controlled, and ranged between 28° C and 32° C. A motor was arranged so as to flex each leaf. Four 3-minute runs were made with each pair of leaf sections. In the first and third runs leaf section A was the "fast" leaf, flexing at 4 cycles per second and leaf section B was the "slow" leaf, flexing at one cycle per second. In the second and fourth runs, A was the slow leaf and B was the fast leaf. Leaf
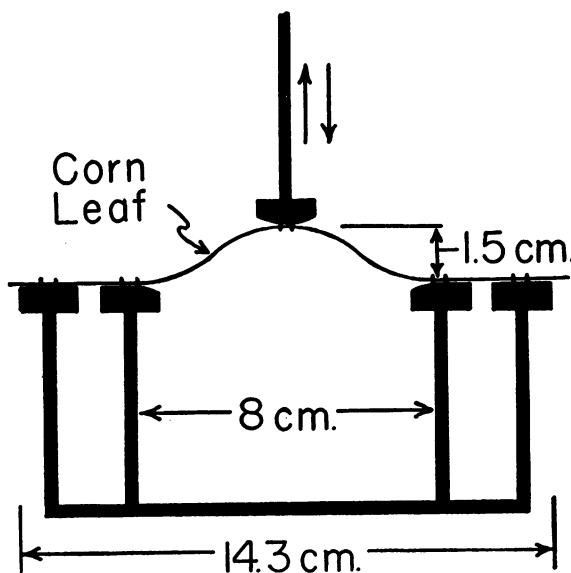

FIG. 1. Leaf on leaf holder (diagrammatic).

weights were taken initially and after each run, and the data were analyzed statistically to determine if there was a significant difference between the amount of water lost by the fast leaves and that lost by the slow leaves. Theoretical calculations indicated that the fast leaves should transpire no more than 0.13 % faster than the slow leaves. A similar experiment was conducted without a fan, as a test of the method.

RESULTS & CONCLUSIONS

In 60 individual runs, the fast leaves lost 0.33 % more water than did the slow leaves, but this difference was far from being statistically significant. The variability was such that the least significant difference would have been 3 %, so we can say with some degree of assurance only that the fast flexing would not increase the transpiration by as much as 3 % under these conditions.

In 32 individual runs without the fan the fast leaves lost 6.2 % more water than did the slow leaves. This difference was statistically highly significant. Such a difference would be expected even in the absence of a pumping action, because the flexing would stir the air in the vicinity of the leaf.

SUMMARY

The following three mechanisms by which wind might possibly increase transpiration have been explored theoretically:

I. Increase in transpiration caused by a decrease in air pressure on the lee side of the leaf.

II. Ventilation of amphistomatous leaves by air passing through the leaf by way of the stomata and intercellular spaces.

III. Pumping action of changes in volume of intercellular spaces as leaves bend in the wind.

It is concluded from theoretical considerations that none of these mechanisms could account for as much as 1 % of the transpiration of corn leaves.

The pumping action of leaf bending was also investigated experimentally by means of an apparatus which flexed leaves in a stream of air. The flexing did not cause as much as a 3 % difference in the transpiration.

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ACTION SPECTRA OF LIGHT-SATURATED PHOTOSYNTHESIS [1]

G. C. McLEOD

DEPARTMENT OF PLANT BIOLOGY, CARNEGIE INSTITUTION OF WASHINGTON, STANFORD, CALIFORNIA

At low light intensities the rate of photosynthesis is directly determined by the intensity and color of the light absorbed. It is only slightly influenced by temperature and carbon dioxide concentration.

At high light intensities a saturation is reached so that a further increase in the light intensity does not increase the rate of photosynthesis. Typical curves of photosynthetic rate versus intensity are given by Rabinowitch (12). The photosynthetic rate at saturating intensities is determined by the temperature, carbon dioxide concentration, and the physiological state of the plant. It has generally been supposed to be independent of the wavelength of the light.

This paper deals with the photosynthetic rate at different wavelengths above the level of light saturation, but below intensities causing photochemical damage to the plant. Contrary to expectation there was structure in the action spectrum of photosynthesis at saturating light intensities.

METHODS

The polarographic apparatus used for measuring the rate of oxygen evolution by photosynthesis was patterned after Haxo and Blinks (7) as modified by Haxo and Fork (8) for use with suspensions of unicellular algae.

A 1,000 w General Electric projection lamp, and a high-pressure water-cooled mercury lamp (PEK Labs, Palo Alto, Cal.) served as sources of light. An image of each lamp was focused simultaneously on the platinum electrode by large condensor lenses and mirrors. Adjustment of the light intensity was made with variable voltage transformers. Interference filters were combined with colored glass filters to give reasonably monochromatic light (ca. 10 mμ half band-width). Infrared radiation was removed with water and "Calflex" infrared reflecting filters.

The unicellular algae, *Chlorella pyrenoidosa* Chick (a chlorophyte), *Phormidium persicinum* (Reinke) Gomont (a cyanophyte), and the chrysophyte *Botrydiopsis alpina* Visher were used. Chlorella was cultured in Knop's solution in a continuous culture apparatus (9); Phormidium was cultured in a modified sea water medium (11) under daylight illumination and, Botrydiopsis was cultured on Bristol's agar medium under continuous illumination from two 15 w fluorescent tubes.

Cells from the culture of Chlorella were centrifuged and diluted with their respective media to 25 cmm/cc. This suspension was pipetted onto the platinum electrode at the bottom of a well 0.25 mm deep, and covered with a piece of moistened dialyzing