Quaking and Gas Exchange in Leaves of Cottonwood (*Populus deltoides*, Marsh.)[1]

JOHN B. SHIVE, JR.,[2] AND KIRK W. BROWN
Soil and Crop Sciences, Texas A&M University, College Station, Texas 77843

ABSTRACT

Cottonwood (*Populus deltoides*, Marsh.) leaves are amphistomatous and have an adaptation in their petiole which allows them to oscillate in wind. A possible function of these oscillations in enhancing gas exchange was studied.

Cottonwood leaves were found to oscillate in the presence of wind velocities frequently encountered in nature. A pressure differential across the leaf was shown to result in bulk flow of air through that leaf. Oscillating a cottonwood leaf at frequencies found to occur in nature was found to increase the rate of O_2 flux through the leaf. The measured changes in boundary layer resistances during oscillations were found to be insufficient to account for the increased O_2 flux. Thus, the bulk flow of air through an oscillating cottonwood leaf results in a decreased total resistance which is typically 25% less than that of a still leaf.

Cottonwood leaves have adapted to quake or oscillate in the wind. Quaking is possible because of a flattened, nonrigid section of the petiole located just basal and perpendicular to the blade.

There are at least two possible functions of this adaption. Quaking may be a means of lessening wind damage, or movement of the blade might facilitate gaseous exchange. The latter possibility might occur by either a reduction of air boundary layer resistance or by facilitating a bulk flow of air through the leaves or by both mechanisms.

Woolley (9) calculated that bulk flow through corn leaves caused by a 7 m/sec wind could account for 0.016% of the observed transpiration. Slatyer and Bierhuizen (6) suggested that air movement by bulk flow does not occur in nature. Jarvis *et al.* (2) stated that "the exchanges of water vapour and carbon dioxide between leaf and atmosphere ... are commonly assumed to be diffusive in character." There are, however, numerous instances where gas has been forced through amphistomatous leaves (1-4). We have studied the effect of oscillation on gaseous exchange in cottonwood leaves to determine whether bulk flow of air through these leaves occurs.

MATERIALS AND METHODS

Measurements were made on fully expanded, attached leaves of mature *Populus deltoides* (Marsh.) trees. Influence of wind velocity, measured with a hot wire anemometer (Hastings air meter, model Rm-1), on the rate of oscillation was determined by photographing the leaves with a motion picture camera and later viewing them at slow speed.

The viscous or bulk flow of air containing 305 μl/l CO_2 through leaves was measured in the field with a leaf chamber similar to that of Mederski *et al.* (4). Leaves were sealed in the chamber with closed-cell Neoprene foam (Virginia Chemicals Inc., Portsmouth, Va.) gaskets. The leaf surface enclosed within the circular chamber was 17.3 cm^2, and flow was always from the adaxial to the abaxial surface. The air was bubbled through water with a resultant relative humidity of about 68%. Flow was measured with a rotameter.

Measurements of the flux of O_2 were used to test the effect of oscillations on gas movement through cottonwood leaves. The adaxial leaf surface was attached to the leaf cup (Fig. 1) which could be oscillated at a desired rate. The cup had internal dimensions of 5 × 5 × 2.9 cm in height and had a 1.5-cm-wide gasket. The gasket, consisting of closed-cell Neoprene foam, was glued to the cup with epoxy. The adhesive surface of the gasket was used to form a seal with the leaf.

The leaf cup was installed inside an outer chamber. The top of the outer chamber consisted of a Plexiglas non-flow-through water bath, and the bottom of wood painted white. The four remaining sides consisted of either Plexiglas or polyethylene film so that the entire leaf was enclosed and out of the wind. Tests were conducted in full sunlight. The leaf cup was attached to a rod which was oscillated by means of a motor mounted outside of the chamber. The oscillations of the surface of the cup has an arc of 180° about a line located 13 mm above the center of the leaf.

To determine O_2 flux through the leaf, N_2 containing 320 μl/l CO_2 was first forced into the leaf cup via the septum at the rate of 170 ml/min. The N_2 exited the leaf chamber either through the leaf or through the 40-cm long, 0.15-cm i.d. pressure release tube. The pressure release tube was long enough so that back diffusion had no influence on the O_2 concentration during the measurements. Once the concentration of O_2 measured with an O_2 electrode (Chemtronics LP-10 oxygen analyzer) reached a constant low level, the N_2 injection was terminated and the outer chamber closed. The rate of O_2 movement from the outer chamber through the leaf and into the cup was determined by the slope of the change in O_2 concentration with time. This in turn was used with the O_2 concentration gradient across the leaf to calculate the total resistance to transfer using the relationship:

$$r_T = \frac{C_o - C_i}{q} \qquad (1)$$

where r_T is the total resistance in sec/cm; C_o is the O_2 concentration outside the leaf cup, and C_i is the O_2 concentration inside the leaf cup, both in g/cm^3; and q is the flux of O_2 across the leaf in g/cm^2 sec.

The boundary layer resistance was evaluated by measuring the loss of water from wet blotting paper substituted for the leaf. The weight loss, corrected for losses during handling, was used to calculate the flux. The vapor pressure gradient was calculated from the wet bulb depression measured by a psychrometer and the blotting paper temperature measured with a thermocouple. The boundary layer resistance was calculated as:

[2] Present address: Department of Biology, Winthrop College, Rockhill, South Carolina 29733.
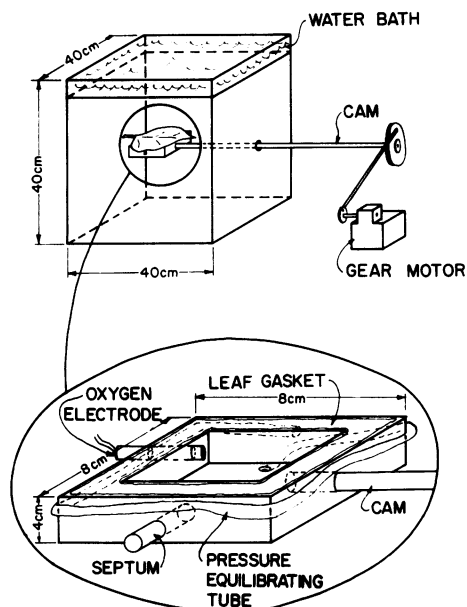
FIG. 1. Schematic diagram of the leaf cup enclosed in the outer chamber.

$$r_a = \frac{e_s - e_a}{q_e} \qquad (2)$$

where e_s is the vapor density at saturation for the temperature of the wet paper in g/cm^3, e_a is the vapor density for the air, and q_e is the flux of water vapor in g/cm^2 sec.

RESULTS AND DISCUSSION

Cottonwood leaves had a stomatal density of $9,420 \pm 550/cm^2$ on the adaxial surface and $20,180 \pm 1,490/cm^2$ on the abaxial surface. Microscopic observation of cross-sections indicated large connected intercellular spaces. Therefore, bulk flow of air through cottonwood leaves is feasible.

To test this feasibility further, pressures were applied across cottonwood leaves and the resultant air flows determined (Fig. 2). Woolley (8) has given a value for a maximum pressure differential across a leaf held "normal" to a wind of 7 m/sec of 570 dynes/cm^2 (0.57 cm H_2O). Although this pressure differential may never be reached across a cottonwood leaf, one can see from Figure 2 that if it were attained, a flow rate of at least 200 ml/$dm^2 \cdot$ min through the leaf would be possible. If the flow versus pressure curves are extrapolated they will strike at or close to the origin. Therefore we have concluded that if a pressure differential within the range of mm of H_2O occurs across a cottonwood leaf with open stomates, there will be bulk air flow through the leaf. The quaking of leaves in the wind results because of pressure differences however small they may be.

The rate of oscillation of cottonwood leaves with increasing wind speed was determined in the field. As can be seen in Figure 3, oscillation does not begin until the wind speed increases to about 1.2 m/sec. At wind speeds of above 2.4 m/sec, the oscillations do not occur about a single axis; instead the leaf rolls in addition to oscillating. Therefore, measurements on artificially oscillated leaves were taken in the range in which leaves oscillate in nature.

Leaves with open stomates were selected for study. After the leaf was in place on the leaf cup, N_2 was injected into the cup at a rate of 170 ml/min. This was sufficient to lower the O_2 concentration in the chamber to about 7%. Injection ceased and the change in O_2 concentration in the chamber was observed without oscillation. Total resistance was used as an indication of stomatal aperture. This was possible since, as will be shown, the boundary

layer resistance even of the still leaf in the chamber was a small fraction of the total resistance. About 5 min were required for the O_2 concentration to reach ambient levels. Nitrogen was again introduced into the chamber and immediately upon withdrawal of the N_2 source the leaf was set in motion at the desired oscillation rate. This series was repeated between three and seven times on each of the leaves tested. Each series ended with a final observation without oscillation. The entire set of measurements on each leaf lasted about 1 hr. Some leaves exhibited an increase in total resistance for the nonoscillation measurements with time indicating that the stomates were closing during the tests. Data from these leaves were not used.

Photosynthetic release of O_2 could also contribute to the increase in O_2 concentration in the leaf cup during the tests. Although photosynthetic rates were not measured, it is suggested that the rates may be of the order of that reported for Dogwood *Cornus flonda*, L. by Waggoner *et al.* (7). His rates at full sunlight are equivalent to an O_2 flux of 1.41×10^{-8} $g/cm^2 \cdot$ sec. Typical O_2 fluxes during the period for which the resistances were calculated were of the order of 5×10^{-7} $g/cm^2 \cdot$ sec. Even if one assumes that all of the photosynthetic O_2 flux was into the leaf cup, this flux would contribute only 2.8% of the change in concentration in the cup. Photosynthetic O_2 fluxes were probably of the same order of magnitude for the oscillating and nonoscillating leaf, minimizing their influences on the comparisons made here.

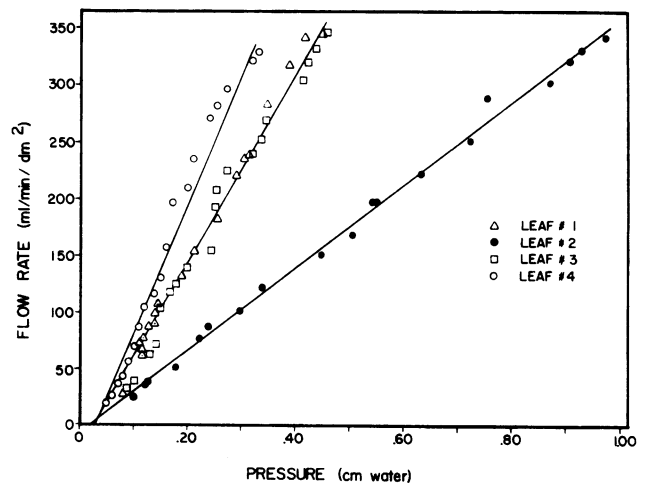Two typical sets of data showing total resistance as a function

FIG. 2. Flow rate as a function of pressure difference across cottonwood leaves. Flow was from the adaxial to the abaxial surface.
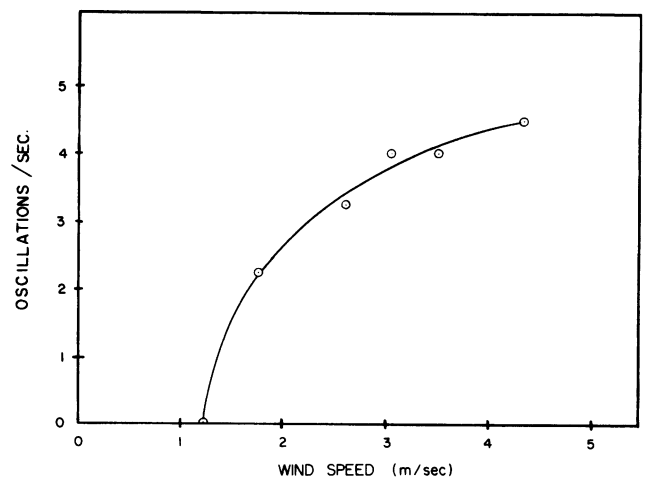

FIG. 3. Oscillation frequency of cottonwood leaves as a function of wind speed observed in the field.

of oscillation rate for leaves which did not exhibit stomatal closure are plotted in Figures 4 and 5. For all leaves tested the total resistances were lower when the leaves were oscillated than when they were still. In addition, the resistances appeared to decrease with increasing oscillation rate, but since the data are scattered only the average difference between oscillating and still leaves will be considered. The decrease in total resistance resulting from oscillation averaged 25%.

A portion of the change in total resistance may be the result of a change in the boundary layer resistance. Perrier et al. (5) reported an increase in boundary layer resistance with slight leaf flutter. Cottonwood leaves oscillate rather than flutter. The leaf cup movement was such that the edge of the leaf moved through an arc length of 9.2 cm. The boundary layer resistance at different oscillation rates was determined. In the "still" air inside the outer chamber, the wind speed was 13 cm/sec and the boundary layer resistances as measured averaged 1.9 sec/cm. The resistances decreased with increased oscillation rates to 0.76 sec/cm at 2.25

FIG. 6. Air resistance as a function of oscillation rate.

oscillations/sec. The evaporation of water probably rapidly increased the vapor pressure within the leaf cup. This may have greatly reduced or eliminated water loss inside the cup by evaporation. Therefore the boundary layer resistances to water transfer measured by this technique may be greater than the resistances which exist in the absence of the leaf cup. The values reported are therefore the maximum that would be expected for water. Oxygen, however, diffuses 1.78 times more slowly than water vapor. Thus, for comparison with the total resistances, the values shown in Figure 6 could be increased by this amount.

The decrease in total resistance resulting from oscillation ranged from 3.5 to 5.5 sec/cm, whereas the decrease in boundary layer resistance ranged from 0.5 to 2.2 sec/cm. Thus, the boundary layer resistance changes can account for only a fraction of the changes in total resistance. The remainder of the decrease in total resistance is apparently due to oscillation-induced bulk flow through the leaves.

We have given evidence for the bulk flow of gases through cottonwood leaves. The significance of the decreased transport resistances to CO_2 exchange is expected to be of the same magnitude as found here. Few species are equipped with adaptations which result in leaf oscillation. Those that are may benefit from the increased supply of CO_2; however, they may also suffer due to excessive transpirational losses.
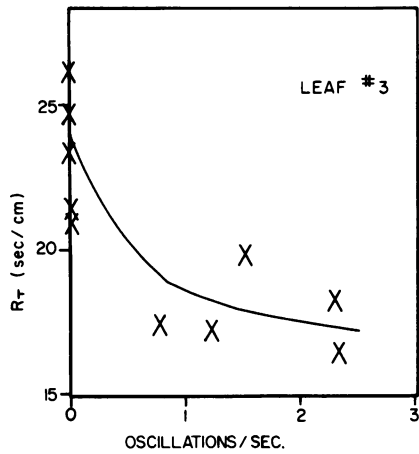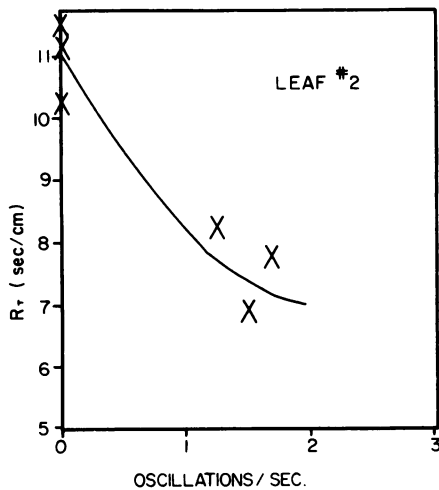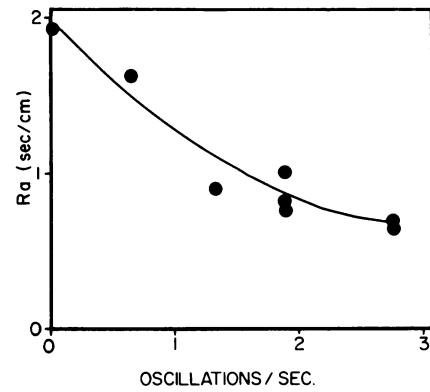

FIG. 4. Total resistance of a leaf with high resistance as a function of oscillation rate.

FIG. 5. Total resistance of a leaf with low resistance as a function of oscillation rate.

LITERATURE CITED

1. HEATH OVS 1939 Experimental studies of the relation between carbon assimilation and stomatal movement. I. Apparatus and technique. Ann Bot 3: 469–495
2. JARVIS PG, CW ROSE, JE BEGG 1967 An experimental and theoretical comparison of viscous and diffusive resistances to gas flow through amphistomatous leaves. Agric Meteorol 4: 103–117
3. LAKE JV, RO SLATYER 1970 Respiration of leaves during photosynthesis. III. Respiration rate and mesophyll resistance in turgid cotton leaves, with stomatal control eliminated. Aust J Biol Sci 23: 529–535
4. MEDERSKI HJ, LH CHEN, RB CURRY 1975 Effect of leaf water deficit on stomatal and nonstomatal regulation of net carbon dioxide assimilation. Plant Physiol 55: 589–593
5. PERRIER ER, A ASTON, TF ARKIN 1973 Wind flow characteristics on a soybean leaf compared with leaf model. Physiol Plant 28: 106–112
6. SLATYER RO, JF BIERHUIZEN 1964. Transpiration from cotton leaves under a range of environmental conditions in relation to internal and external diffusive resistances. Aust J Biol Sci 17: 115–130
7. WAGGONER PE, DN MOSS, JD HESKETH 1963 Radiation in the plant environment and photosynthesis. Agron J 55: 36–39
8. WOOLLEY JT 1961 Mechanisms by which wind influences transpiration. Plant Physiol 36: 112–114
9. WOOLLEY JT 1964 Water relations of soybean leaf hairs. Agric J 56: 569–571