

Short Communication

Importance to Gas Exchange of Mass Flow of Air through Leaves

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ABSTRACT

A reanalysis of results from a recent paper on the effect of oscillation on gas exchange through leaves of cottonwood (*Populus deltoides*, Marsh) is presented. Mass flow of air through the leaf cannot account for the observed increase in gas exchange during oscillation in that experiment. Consideration of various published data shows that in the field, mass flow will not constitute more than a few per cent of the total exchange for most agricultural crops, but may be a significant part of the exchange for the leaves of tall trees, as they can be exposed to high winds.

In a recent paper, Shive and Brown (8) considered the possibility that in high winds, mass flow of gas through leaves of cottonwood could contribute significantly to the total gas exchange. We wish here to reconsider their experimental measurements, and by considering their own and other published work, determine whether such mass flow can be important in nature.

Shive and Brown (8) sealed single leaves of cottonwood (*Populus deltoides*, Marsh.) to one side of a leaf chamber, and measured the effect of oscillating the chamber on the rate of O₂ transfer between the inside and outside of the chamber. The O₂ concentration inside the chamber was initially reduced to about 7% by flushing with N₂. The subsequent rate of increase of O₂ concentration in the chamber can be expressed as the sum of diffusive and mass flow components:

$$\left(\frac{d[O_2]_i}{dt}\right) \cdot V/A = ([O_2]_o - [O_2]_i)/(r_s + r_b) + KP([O_2]_o - [O_2]_i) \quad (1)$$

where [O₂]_o is the O₂ concentration outside the chamber, [O₂]_i the O₂ concentration inside the chamber, A the leaf area (m²), V the chamber volume (m³), r_s the resistance to diffusion of O₂ from one side of the leaf to the other (s m⁻¹), r_b the boundary layer resistance to O₂ diffusion (s m⁻¹), P the pressure difference across the leaf (Pa), and K the conductivity of the leaf to mass flow of gas (m s⁻¹ Pa⁻¹). Shive and Brown (8) found that the total resistance to O₂ transfer decreased by up to 550 s m⁻¹ at their highest rate of oscillation, whereas the boundary layer resistance decreased by a maximum of 220 s m⁻¹.

The importance of mass flow relative to diffusive flow is given by the ratio, α , of the second term to the first term on the right side of equation 1, i.e.

$$\alpha = KP(r_s + r_b)$$

The value of α depends upon the stomatal aperture, because the viscous flow resistance of stomata increases more rapidly than the diffusion resistance as the stomata close (3, 5). The mass flow contribution to gas exchange will therefore be greatest when the diffusion resistance is low. Shive and Brown (8) selected leaves

with open stomata and, from their results, values of 1.2×10^{-5} m s⁻¹ Pa⁻¹ for K and 1.2×10^3 s m⁻¹ for r_s + r_b would seem typical for cottonwood leaves, giving $\alpha = 1.4 \times 10^{-2}$ P, with P in Pa.

P is more difficult to determine, but is usually (9) taken to be less than or equal to the pressure difference which would be produced if air at velocity u were halted at the leaf surface, i.e. $P = \rho u^2$, where ρ is the air density. For Shive and Brown's oscillating chamber, the mean pressure difference thus calculated is $\frac{1}{2} \rho x^2 w^2$, where 2x is the length of the leaf perpendicular to the axis of oscillation, and w the angular frequency of the oscillation. For their chamber x was 2.5 cm, and the maximum mean pressure difference of 0.06 Pa. At this pressure the value of α is only 10⁻³, much too small to explain the change in gas exchange rate observed.

It should be noted that contribution of mass flow to gas exchange should increase rapidly with oscillation frequency, as $\alpha \propto w^2$. The results Shive and Brown present (their Figs. 5 and 6) do not show any significant effect of oscillation frequency when it is increased from 0.8 to 2.3 s⁻¹.

Two effects may have contributed to the observed increase in diffusion rate, although it is not possible to quantify either of them. First, the leaf surface is likely to have been able to make small movements, e.g. in response to the "centrifugal" force that will act on the leaf as the chamber oscillates. Because the axis of oscillation is not in the plane of the leaf, there will be a component of this force perpendicular to the leaf surface with a magnitude per unit area of about 1.0 Pa taking the leaf density to be 0.3 kg m⁻². The leaf movements will tend to increase and decrease the chamber volume, moving air into and out of the chamber through any available viscous flow path. The pressure equilibrating tube offers a possible path, and, calculating from the tube dimensions given by Shive and Brown, the viscous flow resistance of the tube is five times less than that of the leaf. However, the maximum pressure involved cannot exceed the 1.0 Pa calculated above and this would lead to only a 1% increase in gas exchange.

The second effect which would contribute to the increase in gas exchange is a decrease in the boundary layer resistance at the leaf surface inside the chamber during oscillation. Shive and Brown's results show that at their maximum oscillation rate the resistance to O₂ transfer of the boundary layer external to the chamber is decreased. The oscillations will also cause air movements within the chamber. As the leaf surface will be accelerated to speeds of up to 30 cm s⁻¹ more than twice each second, the boundary layer thickness at the leaf surface inside the chamber will be decreased significantly compared to the chamber dimensions (6). The resulting decrease in resistance could approach the measured decrease in the external resistance, i.e. 220 s m⁻¹. If so, the observed effects on O₂ diffusion could be completely explained by effects on the boundary layer resistances.

Woolley (9) calculated that bulk flow through a corn leaf in a 7 m s⁻¹ wind could account for less than 0.016% of the observed transpiration, and we have argued that mass flow was not signif-

Table I. Values for α/P : the ratio of mass flow to diffusive flow per unit of differential pressure

Where the source offers a range of values, the value for open stomata is given here. The units of r_s+r_a are $s\ m^{-1}$

Species	α/P Pa^{-1}	Source
<u>Populus deltoides</u> Marsh.	1.4×10^{-2}	(8)
<u>Gossypium hirsutum</u> L.	1.2×10^{-3}	(3)
<u>Triticum aestivum</u> L.	2.5×10^{-2} (theoretical)	(5)
<u>Citrus sinensis</u> Osbeck	8.7×10^{-4} (r_s+r_b)	(7)
<u>Gossypium barbadense</u> L.	2.3×10^{-4} (r_s+r_b)	(1)
<u>Zea mays</u> L.	10^{-8} (r_s+r_b)	(9)

icant in Shive and Brown's experiment—partly because the effective wind speeds were very low. Using various published data (Table I) values for α can be calculated at much higher wind speeds (or pressures) to show whether mass flow is in fact negligible in all situations. Some of the data do not include measurements of the diffusive resistance, and, for comparison, values may be assumed to be in the range 200 to 2000 $s\ m^{-1}$. The values of α from the various publications differ greatly, the largest value being 8.7×10^{-4} (r_s+r_b) P obtained by Sherriff (7). The smallest is that found by Woolley (9), being at least three orders of magnitude less than the other values. Using Shive and Brown's results, α

could be as large as 0.84, i.e. mass flow could account for 46% of transpiration, in a 7 $m\ s^{-1}$ wind, and such a windspeed can occur in a tall tree such as cottonwood.

Within most agricultural crops, growing to heights of 1 to 2 m, winds do not often exceed 1.0 $m\ s^{-1}$ (4), except in particularly exposed locations. An average speed near the top of the crop of 0.5 $m\ s^{-1}$ is likely and at this speed the contribution from mass flow would be only 0.4%. Even for the largest values of α in Table I, the contribution of mass flow at this windspeed would not be greater than a few per cent.

In conclusion, we have shown that the contribution of mass flow to the gas exchange of leaves could be greater than was suggested by Woolley (9) and may be significant on occasions for tall trees. However, the circumstances in which it would constitute a significant part of the gas exchange for most agricultural crops are so extreme that mass flow may be neglected. For all crops the principal effects of wind on gas exchange will be via changes in the aerodynamic resistance to diffusion, and at high wind speeds, leaf damage (2).

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