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Temperatures and Transpiration Resistances of *Xanthium* Leaves as Affected by Air Temperature, Humidity, and Wind Speed[1]

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ABSTRACT

Transpiration and temperatures of single, attached leaves of *Xanthium strumarium* L. were measured in high intensity white light (1.2 calories per square centimeter per minute on a surface normal to the radiation), with abundant water supply, at wind speeds of 90, 225, and 450 centimeters per second, and during exposure to moist and dry air. Partitioning of absorbed radiation between transpiration and convection was determined, and transpiration resistances were computed.

Leaf resistances decreased with increasing temperature (down to a minimum of 0.36 seconds per centimeter). Silicone rubber replicas of leaf surfaces proved that the decrease was due to increased stomatal apertures. At constant air temperature, leaf resistances were higher in dry than in moist air with the result that transpiration varied less than would have been predicted on the basis of the water-vapor pressure difference between leaf and air.

The dependence of stomatal conductance on temperature and moisture content of the air caused the following effects. At air temperatures below 35 C, average leaf temperatures were above air temperature by an amount dependent on wind velocity; increasing wind diminished transpiration. At air temperatures above 35 C, leaf temperatures were below air temperatures, and increasing wind markedly increased transpiration. Leaf temperatures equaled air temperature near 35 C at all wind speeds and in moist as well as in dry air.

The partitioning of energy between the heat dissipation processes of a leaf, transpiration and convection, depends on environmental factors, including the radiation impinging upon a leaf and the moisture content, movement, and temperature of the air. The partitioning of energy also depends on leaf shape and orientation and on the physiological responses of the leaf to changes in the environment. The latter processes affect the leaf's orientation toward the source of radiation and the magnitude of the stomatal diffusion resistances for water vapor. Thus, environment affects the distribution of energy between transpiration and convection directly and indirectly. The temperature difference between the leaf and the air is related to the sign and magnitude of heat exchange by convection, and thus, ultimately, convection may have an influence on the rates of the metabolic processes occurring within the leaf.

The direct, physical relationships between environmental parameters and the terms of the energy budget of a leaf are in principle well understood. They can be described by solving the equation of energy balance of a leaf (2, 7, 8). We have little quantitative knowledge, however, of the extent to which physiological responses within the leaf affect the distribution of energy between transpiration and convection. The recent review by Gates (2) on transpiration and leaf temperature demonstrates that no new fundamental insights into the control of the energy exchange of leaves by the environment have been gained during the past dozen years. Furthermore, this review does not go beyond a guess that changes in the internal diffusion resistances of plants may serve to regulate leaf temperature. Studies in stomatal physiology have so far yielded equally little information which could be expressed quantitatively, generalized, and then utilized to predict physiological control of energy partitioning (5).

We undertook this investigation in order to find out whether the partitioning of energy between transpiration and convection is significantly controlled by changes in the transpiration resistance within the leaf occurring in response to changes in the physical environment of the leaf. We restricted our investigation to a variation of temperature, moisture content, and movement of the air. The experiments were done under strictly controlled conditions with only one environmental factor changing at a time. This was accomplished by conditioning air in a growth chamber and then cycling it through a closed loop wind tunnel. The experiments were conducted with single attached leaves optimally supplied with water. A high light level was chosen because we felt that a high energy input into the leaf would permit us to determine energy partitioning more accurately. We also felt that the operation of physiological regulation processes in the leaf, if they occur, would become more conspicuous under this condition than with a lower energy input.

THEORY

Leaf temperatures can be measured directly; transpiration resistances cannot. Diffusion resistances in the leaf can, however, be estimated from measurements of transpiration, leaf and air temperature, and moisture content of the air, and from determinations of the diffusion resistance of the boundary layer of the air at the leaf surfaces (7).

The sum of the diffusion resistances for water vapor (transpiration resistances) is

$$\Sigma r = r_l + r_a = \frac{60\, c_p \rho\, (E_l - e)}{Va} \quad [\text{sec cm}^{-1}] \qquad (1)$$

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All symbols are defined in the Appendix. The diffusion resistance within the leaf can be estimated if the diffusion resistance of the boundary layer is determined separately and subtracted from the sum. This procedure produces an error if the diffusion resistances within the leaf differ between the upper and lower epidermis (6, 7). Since the stomatal density in the leaves we used for our experiments was about equal in the adaxial and abaxial epidermises, we did not find it necessary to apply a correction to the leaf resistances computed according to equation 1.

We determined boundary layer resistance by exposing black, dry leaf models in the wind tunnel to known radiation flux densities and wind speeds, and recording the temperatures of the models. Since in the stationary state, heat gains and losses balance each other, we can write

$$\epsilon_v J_v + J_i = (T_m - T_a)\frac{c_p\rho}{r_a/60} \quad [\text{cal cm}^{-2}\,\text{min}^{-1}] \tag{2}$$

Equation 2 is thus simplified

$$r_a = \frac{60\,(J_n)}{(T_m - T_a)\,c_p\,\rho} \quad [\text{sec cm}^{-1}] \tag{3}$$

The exchange of infrared radiation between the leaf model and the walls of the wind tunnel can be estimated from the temperature distribution in the system and its geometry. The model was in the center of the rectangular cross section of the wind tunnel and viewed the ceiling (or the floor) of the tunnel under an angle of 2α. The exchange of infrared radiation is then

$$J_i = \epsilon_i h_i\,\{(T_c + T_f - 2T_w)\sin\alpha + 2(T_w - T_m)\} \quad [\text{cal cm}^{-2}\,\text{min}^{-1}] \tag{4}$$

with $h_i = 4\epsilon_i\sigma T^3$[cal cm^{-2} min^{-1} °C^{-1}] (derived from the Stefan-Boltzmann Law) where T is the mean of the absolute temperatures at which the processes occur.

The loss of heat by transpiration, V, can be determined by measuring water loss (g) and multiplying the result by the enthalpy of evaporation. Transpiration can also be determined as

$$-V = J_n + C \quad [\text{cal cm}^{-2}\,\text{min}^{-1}] \tag{5}$$

with

$$J_n = \epsilon_v J_v + J_i \tag{6}$$

and

$$-C = \frac{60 c_p\rho\,(T_l - T_a)}{r_a} \tag{7}$$

J_i is determined for the leaf by equation 4 with T_l substituted for T_m.

When transpiration resistances have been obtained, they can be used to compute leaf temperature and heat losses by transpiration for various environmental conditions according to the following formulae (8):

$$T_l = T_a + \frac{J_n\,(r_a + r_l)/60 c_p\,\rho - E(1-\phi)/a}{(r_a + r_l)/r_a + (\mathrm{d}E/\mathrm{d}T)/a} \quad [°\text{C}] \tag{8}$$

$$-V = \frac{\Delta e\,c_p\rho}{(r_a + r_l)/60} \quad [\text{cal cm}^{-2}\,\text{min}^{-1}] \tag{9}$$

and

$$-V = \frac{J_n \mathrm{d}E/\mathrm{d}T + 60 c_p\,\rho E(1-\phi)/r_a}{a(r_a + r_l)/r_a + \mathrm{d}E/\mathrm{d}T} \quad [\text{cal cm}^{-2}\,\text{min}^{-1}] \tag{10}$$

MATERIALS AND METHODS

Xanthium strumarium L. was cultivated according to Salisbury (11). The plants were 60 days old when they were used. All leaves tested were 6.4 cm across the widest part, and there was only one leaf per root system. The water supply to this leaf was therefore better in our experiments than would be expected under field conditions.

Leaf, air, and wet bulb temperature, and water loss due to evaporation from the single leaf were measured inside the test section of a wind tunnel which formed a closed loop with a growth chamber (12) so that air passed from the growth chamber through the test section of the wind tunnel and back into the growth chamber. Wind speed could be controlled accurately between 72 to 500 cm sec^{-1}. Wind was measured by a Hastings air meter (range from 0 to 500 cm sec^{-1}).

The wet bulb temperature of the air in the test section of the wind tunnel was determined by a hand aspirating psychrometer (Bendix) as well as a 40-gauge thermocouple sewn into a small cotton wick The output of the thermocouple psychrometer was continually recorded.

The moisture content of the air could not be controlled precisely, but by using either a dryer or a humidifier built into the growth chamber, two levels of humidity could be obtained. At air temperatures between 3 and 5 C, relative humidity was 100% for moist air and 40% for dry air; at temperatures between 35 and 40 C, it was 70% for moist air and 10% for dry air.

The leaf was irradiated with light from a 2.5-kw high pressure xenon arc lamp filtered through a Schott IR-6-U filter with an infrared-reflecting coating. This combination gave a band of radiation between the wave lengths 0.38 and 0.71 μm. The light was reflected into the test section of the wind tunnel from a surface which had been covered with crinkled aluminum foil in order to give a wider area of uniform irradiance at the leaf surface. The area of uniform irradiance in the wind tunnel was approximately 7 cm in diameter. Variations in light intensity in this area were less than 10%. In all experiments the irradiance was approximately 1.25 cal cm^{-2} min^{-1} impinging upon a surface normal to light which corresponded to about 87 mw cm^{-2} and was, with respect to total energy, about equal to full sunlight at noon in summer in middle latitudes. With respect to energy effective in photosynthesis, however, this irradiance was roughly equivalent to twice full sunlight.

The spectral absorptivity of the *Xanthium* leaves was determined by measuring the spectral distribution of transmissivity and reflectivity with an integrating sphere attached to a Zeiss PMQ II spectrophotometer according to

$$\epsilon_v = 1 - (\tau_\lambda + \gamma_\lambda) \tag{11}$$

The *Xanthium* leaves absorbed 0.70 of the filtered xenon light.

Water loss was measured continuously by weighing on a Mettler K-T balance. A potted plant with all leaves but one excised was sealed with two layers of polyethylene bags and masking tape which covered the entire length of the stem and petiole, leaving only the leaf lamina exposed. Water loss was determined per unit leaf surface. (A 1-cm^2 leaf has 2 cm^2 of surface). The leaf outline was taken before and after each experiment, and the amount of growth was divided by the number of hours in the experiment so that a correction for growth could be applied for any time interval during the experiment. Loss of heat by transpiration (V) was calculated by multiplying the rate of evaporation (g/t) obtained by weighing by the heat of vaporization of water (L) at the leaf temperature and by dividing by twice the area within the leaf outline (A).

$$V = \frac{gL}{tA} \quad [\text{cal cm}^{-2}\,\text{min}^{-1}] \tag{12}$$

Direct evidence on stomatal aperture was obtained from silicone rubber replicas made according to a method described by Sampson (13). Photomicrographs were made from the cellulose acetate positives of the rubber impressions.

The leaf models needed for determining boundary layer resistances were made for us by Mr. F. F. Fischer of Aspen, Colorado,

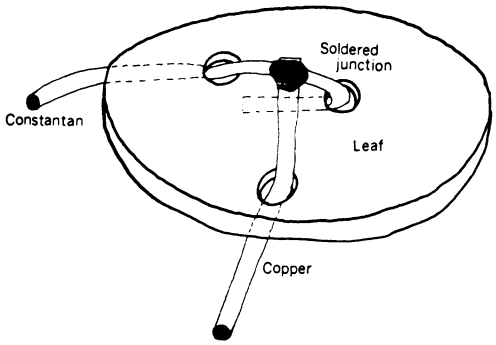

FIG. 1. Method of attaching copper-constantan thermocouples to the leaf. The soldered junction is pressed to the leaf surface and secured by an extension of the constantan lead beyond the junction. This extension is passed through the leaf and bent backward in the shape of a hook.

by electroplating *X. strumarium* leaves thinly with copper as practiced by some jewelers. The models were sprayed with flat black paint. Their absorptivity for visible light was measured to be 0.98.

The temperatures of the models and leaves were measured with 40-gauge (0.079-mm) thermocouple wire attached at intervals of 1.3 cm beginning 0.5 cm from one edge across the widest part of the leaf. The method of attachment of the thermocouple to the leaves is illustrated in Figure 1. After a number of preliminary experiments, it was found that two thermocouples, each located halfway between the midvein and edge of the leaf, gave a good approximation (± 0.5 C) of the leaf temperature as measured by a Stoll-Hardy radiometer. Temperature differences between the upper and lower surfaces of the leaves were generally less than 0.3 C, the upper surface always having the higher temperature.

Execution of the Experiment. The leaf models were exposed horizontally (held by thin wires) to a constant irradiance (1.25 cal cm^{-2} min^{-1}) and to varying wind speeds while the temperatures of the leaf models, as well as of the air and the walls of the test section, were recorded.

Experiments with live leaves were begun at low temperature with low humidity and a given wind velocity. After the temperature within the test section and the leaf had equilibrated, the weight of the plants was recorded, and the record of the leaf, air, and wet bulb temperature was taken for the succeeding hour. At the end of this hour, plant weight was again recorded. Equilibration required about 1½ hr when the temperature of the air was raised by 10 C, but only about 10 min when only the wind velocity changed. Leaf temperature was considered to be constant if a change of no more than 1 C occurred during the run. This temperature and humidity treatment was repeated at the two remaining wind velocities tested. Temperature was then changed to the next higher step until the highest temperature (about 43 C) was reached. The air in the chamber was then humidified to the highest possible level and the temperature of the air was lowered in steps. The experiment was replicated three times.

RESULTS

Boundary Layer Resistance as a Function of Wind Speed. At wind speeds (u) below approximately 200 cm sec^{-1}, the boundary layer resistance (Fig. 2) of a leaf model measuring 6.4 cm wide followed a relationship

$$r_a = 7.5(u^{-0.58}) \quad [\text{sec cm}^{-1}] \tag{13}$$

Above $u = 200$ cm sec^{-1}, this changed into

$$r_a = 23(u^{-0.82}) \quad [\text{sec cm}^{-1}] \tag{14}$$

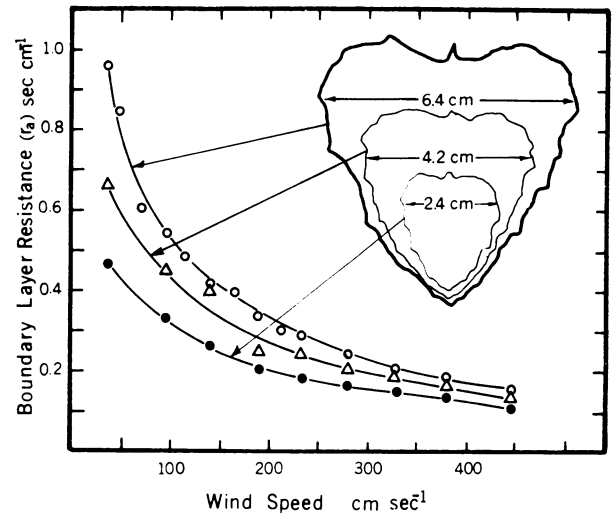

FIG. 2. The dependence of the boundary layer resistance (r_a) of *X. strumarium* leaf models upon leaf size and wind velocity. The models were made by copper plating live leaves.

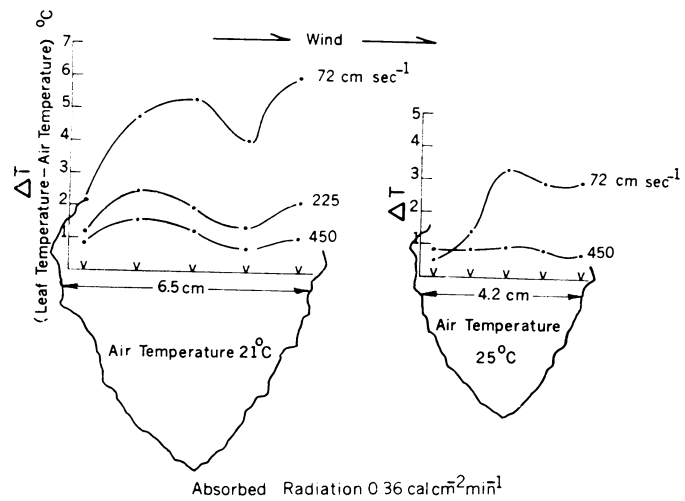

FIG. 3. Temperature distribution across leaves of two sizes at different wind speeds. The wind velocity is indicated for each curve.

which means that a transition from nearly laminar to turbulent flow occurred at a comparatively low Reynolds number (Re $\approx$ 7000). Corresponding observations were made with the smaller leaf models, and boundary layer resistances decreased with decreasing model size (Fig. 2). At wind speeds below 100 cm sec^{-1}, size dependence was larger than predicted by the theoretical square root relationship, indicating a contribution of free convection to convective heat transfer between leaf model and air. For computing heat exchange by convection from the leaves used in the experiments, the regression equations derived from the data obtained with leaf models were used to estimate boundary layer resistances. The computed functions are entered in Figure 2 as curves.

Leaf Temperatures. In some experiments leaf temperatures were measured at five locations across each leaf separately for the upper and lower surfaces. They were averaged for each location and plotted as differences with respect to air temperature ($\Delta T = T_l - T_a$) for those wind speeds and two leaf sizes in Figure 3. A temperature minimum in the leeward half of the leaf was a distinctive feature, particularly at low wind speeds.

The departure of the average leaf temperature from air temperature depended on wind speed and air temperature. At all

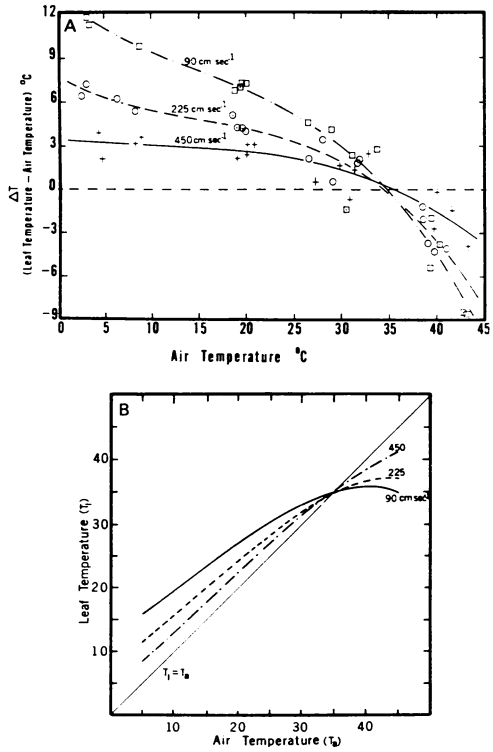

FIG. 4. a: Dependence of the temperature difference between leaf and air upon air temperatures at wind speeds of 90 (⊡), 225 (⊙), and 450 (+) cm sec^{-1}. b: Leaf temperature as a function of air temperature. Curves are transposed regression curves of part a.

wind speeds, leaf temperature was very close to air temperature when air temperature was 35 C. Below 35 C, the leaves were warmer than air; above 35 C, the leaves were cooler. Wind speed affected the magnitude of the temperature difference between leaf and air but not its sign (Fig. 4a). There was no difference in the general behavior of the leaves between dry and moist air at air temperature below 35 C, but above 35 C, leaves were cooler in dry air than in moist air at each wind speed. The regression equations and their coefficients of determination (r^2) for Fig. 4a were:

$$\Delta T_{90} = 13.1 - 0.52T_a + 0.018T_a^2 - 0.00040T_a^3 \quad r^2 = 0.95$$

$$\Delta T_{225} = 7.7 - 0.36T_a + 0.016T_a^2 - 0.00037T_a^3 \quad r^2 = 0.95$$

$$\Delta T_{450} = 3.5 - 0.069T_a + 0.0038T_a^2 - 0.00013T_a^3 \quad r^2 = 0.75$$

The relationship of leaf temperature to air temperature, as predicted by the regression equations, is shown in Figure 4b.

Transpiration and Convection in Relation to Air Temperature and Wind Speed. The partitioning of energy between convection and transpiration is shown in Figure 5. Heat loss by transpiration (V) increased rapidly with temperature. Net radiation (J_n) varied by as much as 25% through the range of air temperatures studied because of variations in the long wave radiation component as wall and leaf temperature changed. Energy losses by convection and transpiration are, therefore, not expressed as absolute fluxes but relative to net radiation. Hence, each data point is either convection C(cal cm^{-2} min^{-1}) per unit J_n(cal cm^{-2} min^{-1}) or transpiration V(cal cm^{-2} min^{-1}) per unit J_n. The average value of J_n was 0.38 cal(cm^{+2} leaf surface and min)$^{-1}$. The average of the sum of convection and transpiration accounted for 0.90 of J_n, with a variation between 0.8 and 1.2.

Wind affected the partitioning of energy. When leaf temperature was above air temperature, increasing wind caused increased convective heat loss and decreased transpiration. When leaf temperature was below air temperature, increasing wind caused convection to add energy to the leaf but also increased energy loss through transpiration.

Transpiration in Relation to Water Vapor Pressure Difference. Transpiration (V) should be proportional to the water vapor pressure difference (Δe) between leaf and air, provided the diffusion resistances remain constant (equation 9). Both V and Δe were plotted as functions of air temperature in moist and dry air in Figure 6; the data were measurements taken at wind speed 90 cm sec^{-1}. Similar results were found for wind speeds 225 and 450 cm sec^{-1}. Transpiration and water vapor pressure difference were not linearly related to each other; this indicates a change in the transpiration resistance within the leaf (with temperature). Furthermore, transpiration into moist and into dry air was approximately the same (Fig. 6). Although water vapor pressure differences were about twice as large in dry air as in moist air at the same air temperature, transpiration into dry air was on the average only between 1.05 and 1.20 times that into moist air. This observation suggests that changes in the diffusion resistances within the leaf occurred in response not only to temperature changes but also to changes in atmospheric humidity or to changes in the transpiration stream.

Leaf Resistances. Leaf resistances (r_l) were computed according to equations 1 and 3. Transpiration resistances decreased with increasing leaf temperature and with increasing moisture content of the air (Fig. 7). The values obtained for dry air scattered widely, and only a linear regression was meaningful. It was, however, possible to fit second order polynomials to the data obtained in moist air. The estimating equation for all data in moist air taken together had a maximum near 20 C.

The estimating equations are as follows: For dry air

$$r_l = 7.95 - 0.18T_l$$

For moist air, at each wind speed

$$r_{l_{90}} = 5.03 - 0.198T_l + 0.00224T_l^2$$

$$r_{l_{225}} = 1.02 + 0.0595T_l - 0.00185T_l^2$$

$$r_{l_{450}} = -0.0592 + 0.224T_l - 0.00489T_l^2$$

For moist air at all wind speeds taken together

$$r_l = 0.292 + 0.1397T_l - 0.00342T_l^2$$

For moist air, only the curve for all data together is plotted in Figure 7.

As computed from the estimating equations, the Q_{10}s of the decrease in the leaf resistance with temperature were approximately 2.1 in dry air and 1.7 in moist air; both values were computed for the temperature range between 25 and 35 C.

Stomatal Apertures. Photomicrographs of cellulose-acetate positives from silicone-rubber replicas were made. Stomatal apertures in the upper and lower epidermis of leaves of *X. strumarium* were clearly wider at 30 C leaf temperature than at 14.6 C, although detailed measurements were not made.

DISCUSSION

The experimental results show clearly that transpiration resistance changes with changes in the environment, and that these responses do affect the partitioning of energy between transpiration and convection. This becomes apparent in our experiment in three ways: (*a*) In transpiration increasing with temperature beyond the increase caused by the increased steepness of the water vapor pressure function (Fig. 6). This leads to an increased importance of transpirational cooling with increasing temperature and a stabilization of leaf temperature at high air temperatures (Fig. 4b). (*b*) In a crossover from leaf temperatures above air temperature to below air temperature near 35 C for all wind

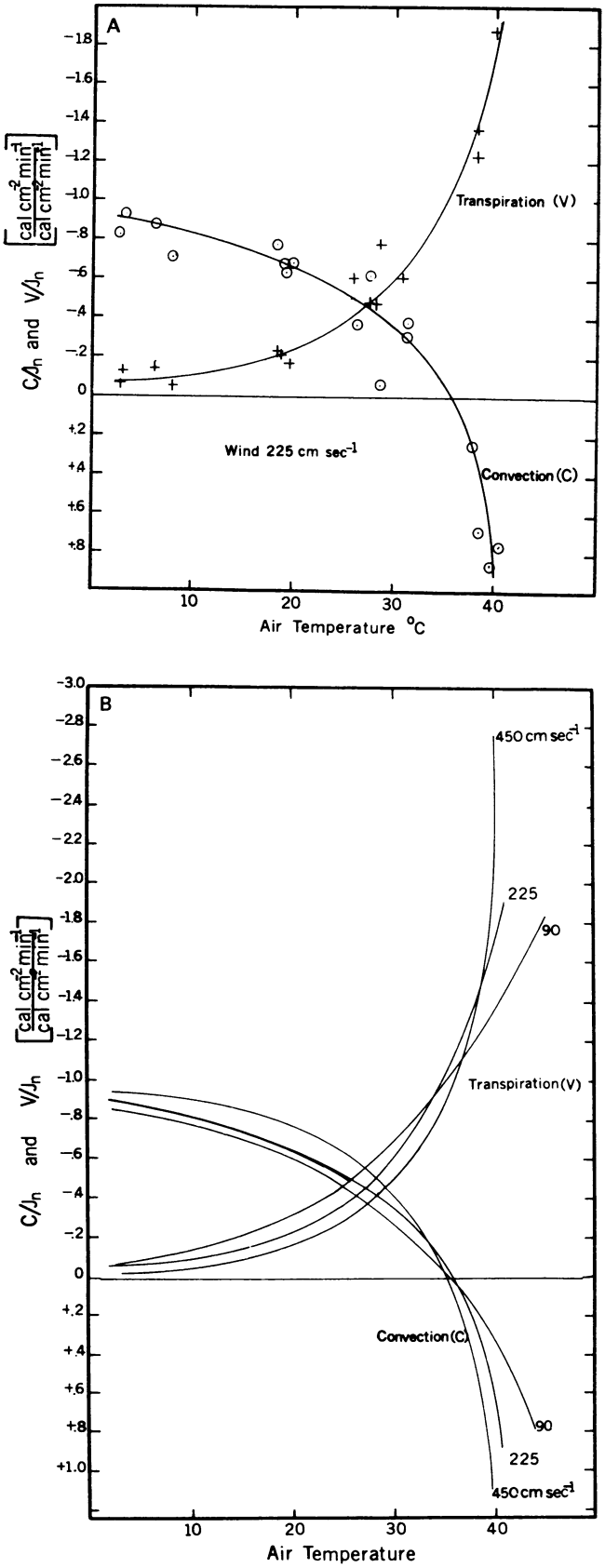

FIG. 5. a: The partitioning of the net radiation between convection (⊙) and transpiration (+) at a constant wind speed of 225 cm sec^{-1}. Signs + and − mean energy absorbed or dissipated by the leaf. The total energy exchange by these two processes was on the average 90% of net radiation. The experimental error is of the order of 10%. b: Partitioning of net radiation as a function of wind speed and air temperature. Summary for wind speeds 90, 225, and 450 cm sec^{-1}.

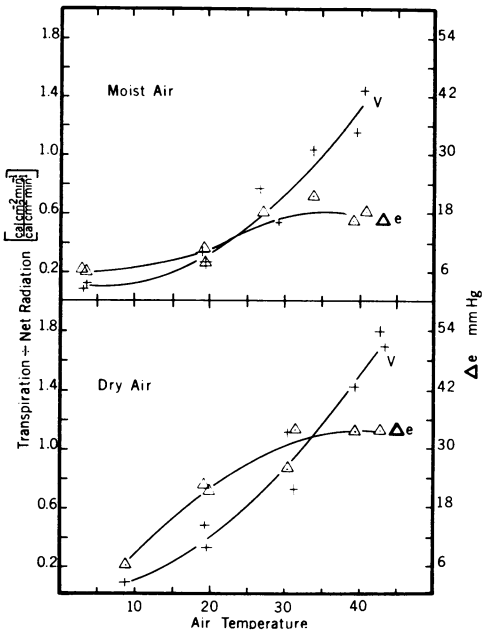

FIG. 6. The relationship between the ratio of energy losses by transpiration to net radiation (+) and water vapor pressure difference between leaf and air (△) in moist and dry air.

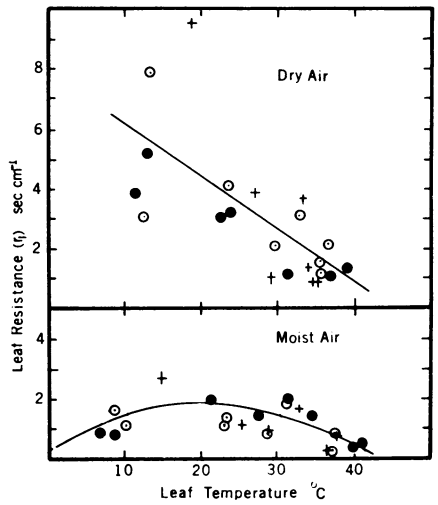

FIG. 7. Leaf resistance (r_l) as a function of leaf temperature in moist and dry air. The data for dry air at three wind speeds, 90 (+), 225 (⊙), and 450 (●) cm sec^{-1} could not be meaningfully separated, and the regression line is for all data taken together. In moist air, however, it was possible to fit separate second order equations to the data for 225 (⊙) and 450 (●) cm sec^{-1} wind. The curve shown here is for all data and is similar to the individual curves for 225 and 450 cm sec^{-1}.

speeds (Fig. 4). (*c*) In an apparent independence of the magnitude of transpiration from the moisture content of the air, provided air temperature and net radiation remain constant (Fig. 6).

Leaf Resistance Dependence on Temperature. The magnitude of the leaf resistances computed from our data was low, thus indicating that most of the water loss occurred through open stomates. Participation of stomates is also indicated by the Q_{10} of

stomatal conductance. We found a Q_{10} of 1.7 (for moist air) and 2.1 (for dry air) for the decrease in leaf resistance between 25 and 35 C. These values agree sufficiently well with the Q_{10} of 1.6 to 1.8 found in humidified air for stomatal conductivity for CO_2 in *Zea mays* (10) or of 1.5 for stomatal aperature in *Vicia faba* (14). Noteworthy is the decrease of the leaf resistance below 20 C at wind speeds of 225 and 450 cm sec^{-1} in moist air (Fig. 7). A similar phenomenon was observed at low temperatures (below 20 C) in leaf sections of *Zea* which were well supplied with water (10).

Feedback of Transpiration on Leaf Resistance. At constant air temperature, transpiration changes were less than proportional to the water vapor pressure difference between leaf and air (Fig. 6). It appears that transpiration was regulated. A similar observation of nearly the same magnitude of transpiration into dry or into moist air was made on *Z. mays* (10) and interpreted as resulting from a feedback of transpiration to the stomata through the water potential drop the transpiration stream produces in the leaf tissue.

Control of Leaf Temperature and Partitioning of Energy by the Leaf Resistance. With increasing temperature an increasing share of the radiation absorbed by a leaf is dissipated by transpiration, at least as long as water supply to the leaf is sufficient (Fig. 5). The two causes for this increase in water loss can be described quantitatively: the dependence of dE/dT on temperature can be read from water vapor pressure tables; the change of leaf resistance with temperature is described by the estimating equations derived from our data obtained with *Xanthium* (Fig. 7). Estimating equations of the temperature dependence of stomatal conductance in *Z. mays* have also been given (10).

The temperature at which transpiration compensates net radiation and leaf temperature equals air temperature may be anywhere on the temperature scale; its location depends on the magnitudes of net radiation, saturation deficit of the air, boundary layer resistance and leaf resistance (equation 8). Observations show, however, that temperatures of strongly insolated leaves fall below air temperature only at higher temperature levels (this paper, Refs. 1–4, 15). The value of dE/dT is usually too low and leaf resistances are usually too high at low temperatures to allow transpiration to balance a net radiation of a magnitude of 0.4 cal cm^{-2} min^{-1} which would occur in full sunlight.

The common crossover point of leaf temperature which in our experiments occurred near 35 C for three wind speeds and two humidity levels (Fig. 4) can be explained as resulting from the feedback of transpiration on leaf resistance. Compensatory changes in leaf resistance make transpiration relatively independent of the moisture content of the air (Fig. 6), and of the influence of wind at temperatures between about 32 and 38 C (Fig. 5b). In this temperature range there seems to be one ceiling value of transpiration for each temperature level. As a consequence there is only one value of net radiation which can be balanced by transpiration for each temperature level. If transpiration balances net radiation, the leaf is at air temperature. Since transpiration does not change with wind and moisture content of the air, the air temperature at which the temperature difference between leaf and air is zero should be independent of wind speed and moisture content of the air as long as net radiation remains constant.

Leaf temperature will not rise in linear proportion to either an increase in net radiation or in air temperature because dE/dT increases and leaf resistance decreases with increase in temperature. As a result, transpiration will exceed net radiation, and leaf temperature will drop below air temperature above the temperature of the crossover point. Leaf temperature may remain rather constant if air temperature rises above 35 C, particularly if wind speed is low (Fig. 4b). At air temperatures above 40 C, leaf resistances are of the magnitude of the boundary layer resistance, and transpiration is strongly dependent on wind speed. The combined effect of changes in dE/dT and leaf resistance, with increasing temperature, on leaf temperature and transpiration can be roughly estimated by introducing leaf resistances computed from the regression equations given in this paper into equations 8 and 9.

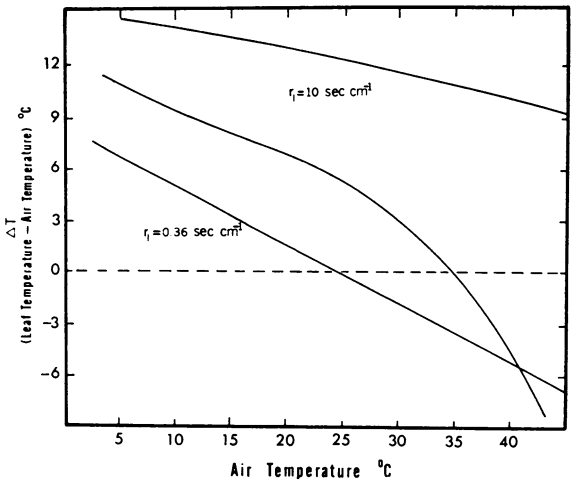

FIG. 8. The estimated dependence of temperature difference between leaf and air (ΔT) as computed for a high and low leaf resistance (10.0 and 0.36 sec cm^{-1}) in a *X. strumarium* leaf measuring 6.4 cm across. Wind velocity was taken to be 90 cm sec^{-1}, relative humidity 50%, and net radiation 0.38 cal cm^{-2} min^{-1}. The middle curve is taken from Figure 4 and is ΔT measured in wind 90 cm sec^{-1} in both moist and dry air.

Ecological Consequences of Changes in Leaf Resistance with Temperature. The occurrence of a single crossover point was recognized by Linacre (4) in a number of previously published leaf temperatures. Linacre found that in sunlight and with good water supply, leaf temperatures tended to equal air temperatures at about 33 C. Gates (1) found a similar phenomenon in two species of *Mimulus*, the leaves of which were at air temperature near 30 C, and in several other species kept in growth chambers. The transition from positive to negative temperature differences between leaf and air occurred between 30 and 40 C. Gates concluded that the diffusion resistance within the leaves must have declined with temperature.

The increase in stomatal conductivity with increasing temperature may be beneficial to the plant because it effectively prevents overheating of the leaves as long as there is sufficient water available to support a large transpiration stream. We have calculated the possible range of leaf temperatures for *Xanthium* for air temperatures between 5 and 45 C, net radiation of 0.375 cal cm^{-2} min^{-1}, relative humidity 50%, and wind speed 90 cm sec^{-1}, using the highest and lowest leaf resistances we found in our experiments (Fig. 8). We concluded that at air temperatures around 45 C, leaf temperatures may be as much as 10 C below air temperature when the air humidity is low. This can have an important effect on net exchange of CO_2. Leaf temperature of 35 C might permit a high rate of net photosynthesis, whereas one of 45 C will most probably restrict the rate to the compensation point.

Leaf temperatures several degrees below air temperature can also be observed in the field if air temperatures are high. *Xanthium* plants growing near Prosser, Washington, beside a well watered corn field had leaf temperatures between 22 and 25 C when the air temperature was 19.5 C, and when air temperature was 35.5 C, leaf temperature was between 25 and 28 C. *Xanthium* plants beside an irrigation ditch in Arizona had leaf temperatures between 27 and 29 C, when air temperature was 36.0 C. Leaf impressions with silicone-rubber showed the stomates to be wide open. In all cases, larger leaves departed further from air tem-

perature than did smaller leaves whether they were above or below air temperature. Leaf width ranged from about 5 to 18 cm.

Effective transpirational cooling at high air temperatures has been observed also in other species in the field, on irrigated sorghum (15) and on several species growing in oases in North Africa (up to 15 C below air temperature of 50 C) (3).

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APPENDIX

We use the following symbols and dimensions (all values expressed relative to unit area are per unit area of leaf surface; leaf surface is twice the area circumscribed by the leaf outline):

A = area of evaporating surface [cm^2]
a = psychrometric constant; in this investigation approximately 0.43 [torr C^{-1}] (1500 m above sea level)
C = convection [cal cm^{-2} min^{-1}]
c_p = specific heat of air at constant pressure [cal g^{-1} C^{-1}]
E = saturation water vapor pressure at air temperature [torr]
E_l = saturation water vapor pressure at leaf temperature [torr]
e = water vapor pressure of air = ϕE [torr]
Δe = water vapor pressure difference between the leaf and the air = $E - e$ [torr]
dE/dT = first derivative of the water vapor pressure function with respect to temperature [torr C^{-1}]
g = water evaported from leaf [g]
h_i = heat transfer coefficient for infrared radiation = $4\epsilon_i\sigma T^3$ [cal cm^{-2} min^{-1} C^{-1}]
J_i = net infrared radiation [cal cm^{-2} min^{-1}]
J_v = irradiance with visible radiation [cal cm^{-2} min^{-1}]
J_n = $\epsilon_v J_v + J_i$ = net radiation [cal cm^{-2} min^{-1}]
L = latent heat of vaporization [cal g^{-1}]
Re = Reynolds number [dimensionless]
r_a = diffusion resistance of the boundary layer for water vapor [sec cm^{-1}]
r_l = diffusion resistance of the leaf for water vapor [sec cm^{-1}]
T = temperature level at which the heat transfer processes occur [K]
T_a = air temperature [C]
T_c = temperature of ceiling of wind tunnel [C]
T_f = temperature of floor of wind tunnel [C]
T_l = leaf temperature [C]
T_m = model temperature [C]
T_w = temperature of wall of wind tunnel [C]
ΔT = difference between leaf and air temperatures [C]
t = time [min]
u = wind speed [cm sec^{-1}]
V = transpiration = gL/tA [cal cm^{-2} min^{-1}]
α = ½ of the angle under which the ceiling (or the floor) of the wind tunnel appears to the leaf (or the leaf model [deg])
ϵ_i = absorptivity, emissivity for infrared radiation [dimensionless]
ϵ_v = absorptivity, emissivity for visible radiation [dimensionless]
ϕ = relative humidity [dimensionless]
ρ = density of air [g cm^{-3}]
γ_λ = reflectivity at wave length λ [dimensionless]
σ = 8.26×10^{-11} [cal cm^{-2} min^{-1} C^{-4}]: Stefan-Boltzmann constant
τ_λ = transmissivity at wave length λ [dimensionless]