(Table 1). Furthermore, bilirubin solutions do not decrease the oxygen-carrying capacity of intact red cells (*13*).

The magnitude of the Bohr effects in human fetal hemoglobin and that of rhesus monkeys are similar (*14*), but the fact that the infusions of alkaline solvent alone did not change the oxygen concentration measured by the electrode indicates that the lowered oxygen concentration in the tissues was not secondary to a shift in the dissociation curve for hemoglobin caused by a change in *p*H.

Kernicterus was reproduced in newborn monkeys by combining the effects of hyperbilirubinemia with antecedent injury—that is, asphyxia, and the clinical manifestations of it were more severe than those produced by asphyxia alone (*4*, p. 56). In conjunction with those observations, our findings support a hypothesis that high serum bilirubin concentration in vivo may result in a decrease in the concentration of oxygen in the tissues, and thereby make cells more susceptible to the inward diffusion of bilirubin. This effect may precede the intracellular action of bilirubin on oxygen uptake and phosphorylation.

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17 March 1963

Transpiration: Its Effects on Plant Leaf Temperature

Abstract. *A definite and significant temperature gradient exists over the area of a tomato leaflet and is apparently due to the variation in transpiration across the leaflet. Transpiration is most effective at low velocities of air movement, but when the velocity increases, convection becomes the dominant factor. Leaves in which the stomata are allowed to open naturally in response to light attain temperatures about 5°C lower than leaves in which the stomata are forced to remain closed.*

Despite the fact that the phenomenon of transpiration has been the object of a great deal of study (*1*) there remains some uncertainty about the magnitude of its role in determining the temperature of the plant leaf. Schull (*2*) concluded that transpiration played a significant part in temperature regulation since he found it to be the foremost means of energy dissipation. Curtis and Clark (*3*), however, stated that the influence of transpiration on leaf temperature is slight. Similarly, Ansari and Loomis (*4*) concluded that the effects of transpiration are small, and that convection and radiation are the major factors in heat exchange. Most recently, Wolpert (*5*), through a theoretical analysis, showed that under normal conditions transpiration could account for approximately one-fourth of the heat removed from a leaf, indicating that transpiration is at least a significant factor in the heat exchange phenomena of leaves.

In view of this lack of agreement, additional work on the role played by transpiration in the temperature regulation of plant leaves was necessary. We carried out such a study using the tomato plant, *Lycopersicon esculentum*, L. Leaf temperature was determined by inserting a thermocouple made from two 36-gauge wires under the lower epidermal surface of the tomato leaflet, the insertion depth being about 1 cm in a direction parallel to the leaf surface. This insertion technique caused some local cell damage but, in comparison with other techniques, proved to be most accurate and reliable. The environment for these experiments was a growth chamber in which the relative humidity was maintained at a constant 50 percent. Air velocity and light were varied so that their individual effects on the leaf temperatures could be determined.

The existence of a temperature gradient across a tomato leaflet was established by measuring temperatures at five or six selected locations over the surface of several leaflets under otherwise constant conditions. Equivalent temperatures at corresponding locations were verified, so that the data from the several leaflets could be correlated. The results of a typical isothermal plot are illustrated in Fig. 1. Environmental conditions for these tests were 24.2°C, still air, and illumination at 660 lumen/m^2 (60 ft-ca). The temperature variation over the leaflet in this instance was approximately 1.0°C, the leaflet being coolest near the midrib and warmest near its extremities. With one notable exception, the results for all other leaflets tested under the same environmental conditions were virtually the same, within ±0.1°C. Those leaflets which had started to dry out and become yellow had a much smaller temperature gradient, often less than 0.5°C in magnitude. Also, the average temperature of these leaflets was nearer room temperature. No significant variation in leaf temperature (that is, no greater than 0.1°C) was noted from one leaflet to another, from one leaf to another, or from one plant to another when the temperatures were measured at corresponding locations on leaflets of tomato plants in the same condition.

Next, two series of tests were made in which a fan and ducting arrangement were used to produce a controlled velocity of air over the leaflets. In the first series of tests a high light intensity [24,750 lumen/m^2 (2250 ft-ca)] was obtained by using a 1000-watt incandescent bulb in a reflector placed about 30 cm from the leaflet. In the second series of tests the light intensity was much lower, 605 lumen/m^2 (55 ft-ca), which is equivalent to normal indoor lighting. Since the air temperature was held constant for each test, it was a suitable reference with which to compare the changes in leaflet temperature. Thus, the results presented in Fig. 2 are the temperature differences between the leaflet and air, plotted against wind velocity.

In curve 1, Fig. 2, the equilibrium temperature is much lower than in curves 2 and 3, because the leaflet was heated to 21°C above the room temperature of 25°C by the incandescent bulb which caused some wilting. In curve 6 the response was more accentuated than in curves 4 and 5 because the thermocouple in this test

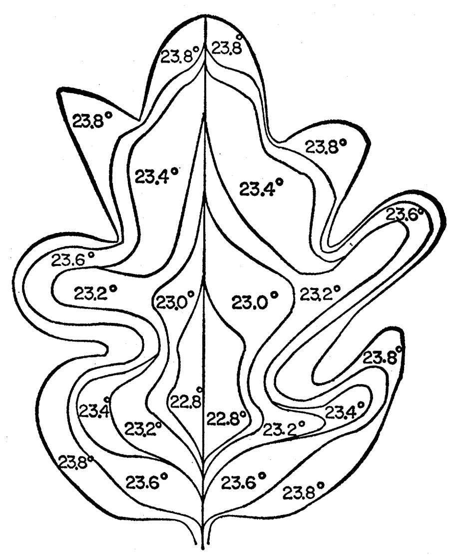

Fig. 1. A plot of temperature variation over a tomato leaflet kept in still air at a temperature of 24.2°C.

was not placed exactly in the center of the region of maximum temperature variation over the leaflet, but nearer to the center of the leaflet itself.

Figure 2 shows that there is a functional relationship between the temperature of a leaflet and wind velocity, since transpiration is always cooling the leaflet and convection is always moving the leaflet temperature toward room temperature. From velocities of 0 to about 6 km/hr, transpiration is a dominant mode of heat transfer since, under these conditions, transpiration

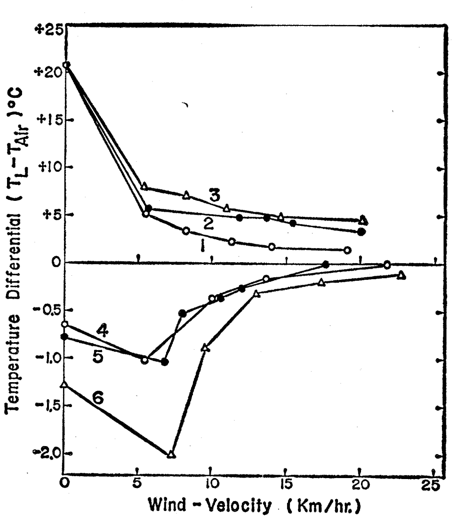

Fig. 2. A plot of the difference between leaf temperature and air temperature against wind. Note that the scale for the negative portion of the abscissa has been expanded. Curves 1, 2, and 3 show the result of tests performed on leaflets subjected to high light intensity, and curves 4, 5, and 6 show results obtained with leaflets exposed to normal indoor light.

decreases leaf temperature whether the leaflets are above or below air temperature. From velocities of 6 km/hr to approximately 21 km/hr, convection is the dominant mode of heat transfer because, under these conditions, the leaflets approach room temperature regardless of their initial temperature. Wind velocities above approximately 21 km/hr do not further alter the temperature of the leaflet.

The second environmental parameter investigated was the effect of light on leaf temperature. In particular, this study concerned the reaction of leaf temperature to an abrupt increase in light intensity from 0 to 29,700 lumen/m^2 (2700 ft-ca). Tomato plants were moved into the dark for 2 hours before the experiment, during which time two thermocouples were inserted into the underside, in the mid-region of the temperature gradient across two separate leaflets. For comparison, one leaflet was painted with a solution of sodium azide ($10^{-3}M$) to prevent opening of the stomata (*6*) and hence suppress transpiration. The solution was allowed to dry before any measurements were made. Examination of leaflets with a microscope verified that the stomata remained closed on the azide-treated leaflets under the conditions of these experiments.

After the light was turned on, the temperatures of the two leaflets were recorded every 2 minutes (Fig. 3). Air velocity over the leaflets was less than 1 km/hr. The leaflet treated with sodium azide rose to a maximum temperature and remained practically constant, decreasing only slightly with time. The untreated leaflet rose to a similar maximum temperature but after about 6 minutes it decreased markedly, reflecting the opening of the stomata and the associated increase in heat exchange by transpiration. Microscopic observation of untreated tomato leaflets under similar conditions revealed that the stomata achieved the opened state after about 5 to 10 minutes of exposure to light. Temperature measurements were continued and showed that, after about 17 minutes, the temperature was lowered approximately 5°C by the stomatal action. The leaflet with closed stomata was unable to maintain such a temperature differential. The magnitude of the effects of transpiration is therefore qualitatively indicated by the temperature difference between the transpiring and nontranspiring leaflets.

Three conclusions may be drawn

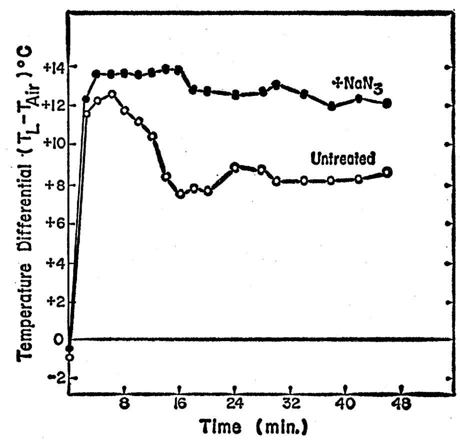

Fig. 3. Temperature changes in leaves upon being exposed to light. The upper curve shows the response when the stomata were kept closed by sodium azide, and the lower curve shows the response of leaves with normal, operational stomata.

from our results. (i) Transpiration appears to establish a temperature variation over the area of the leaflet. Since the lowest temperatures are maintained near the leaf veins, they can be presumed to be due to the greater transpiration there. (ii) The transpiration component of heat exchange increases with increasing wind velocities up to about 6 km/hr (under the conditions used in our experiments), and as velocities rise beyond this value, transpiration becomes a decreasingly important factor in heat transfer. (iii) Light amplifies the part played by transpiration in heat transfer by causing stomatal opening, and in our tests accounted for leaf temperatures being 5°C lower than when transpiration was suppressed. These measurements emphasize the variability and importance of the transpirational component of heat transfer by leaves.

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