LEAF TEMPERATURES AND THE COOLING OF LEAVES BY RADIATION

OTIS F. CURTIS

(WITH SEVEN FIGURES)

There has been marked disagreement among plant physiologists relative to the effectiveness and importance of transpiration in cooling the leaves of plants. SMITH (**12**), CLUM (**4**), CURTIS (**5**), and others have concluded that the cooling effect is slight and rarely of importance in preventing excess heating, whereas, SHULL (**10**), EATON and BELDEN (**7**), ARTHUR and STEWART (**1**), CLEMENTS (**3**), and others have concluded that the cooling effect may be great. The latter investigators especially have claimed that the cooling effect is much greater than is commonly recognized. ARTHUR and STEWART, and CLEMENTS have claimed that the excessively high temperature of leaves, when they are inclosed in cellophane envelopes, or in glass chambers and exposed to strong light, is due to the fact that the cellophane or the glass effectively stops transpiration; while the failure of wilted, or vaselined leaves to rise in temperature more than 2° to 5° C. above those not so treated is due to the ineffectiveness of these treatments in preventing transpiration. As the writer pointed out in a recent paper (**6**), however, these investigators overlooked the fact that glass and cellophane are heat traps permitting the passage of visible radiation, but preventing much of the loss of heat by interfering with cooling by air currents, as well as by reducing loss by radiation in the infra-red. It was found that dry black paper showed similar marked rises in temperature when inclosed in cellophane envelopes, and in this case evaporation could play no part.

Although the effects of various factors upon leaf temperatures have been investigated by several workers, almost no attention has been given to the loss of heat by radiation in the infra-red. BROWN and ESCOMBE (**2**) speak of loss of heat by emission, and include loss by both conduction and radiation. In their preliminary discussion of a hypothetical case they state that the walls of the inclosure must be at the same temperature as the inclosed air, but, in the actual experiments cited, no mention is made of the wall temperature, and it is assumed that the air temperature is the same as that of the leaf's surroundings. It is also assumed that if the air temperature is equal to or exceeds that of the leaf, there will be no loss of heat from the leaf by radiation. They, WATSON (**13**), and other investigators seem to have failed to realize, that the oxygen and nitrogen of the atmosphere are almost transparent to radiation in the infra-red, and that in such an atmosphere leaves may become cooler than the air about them, owing to radiation to cooler objects, or to space at a distance; or warmer owing to receipt of radiant energy from them.

It is well known that on a clear night leaves or other objects at or near the surface of the earth may become cooler than the air about them because of radiation. Under these conditions dew or frost is likely to form on them. It is also well known that clouds will act as a blanket, largely preventing such loss of heat by radiation. The maximum radiation at earth temperature (293° C. absolute) occurs at wave lengths of about 10 μ. Although water vapor has a band of relative transparency at about 10 μ, for the range from 1.4 to 20 μ, water is almost opaque, more so than any other known substance. This accounts for the blanketing effect of clouds. At night they radiate (or reflect) back to the earth much of the infra-red that is radiated to them. In the daytime they absorb some infra-red directly from the sun, part of which also is radiated to objects at the earth's surface.

This effect of clouds led the writer to believe that possibly the low temperature for leaves in sunlight, which EATON and BELDEN (**7**) reported for cotton in Arizona, might be accounted for by the fact that these measurements were made in a region with very low humidity, for it has been found by FOWLE (**8**) that water vapor has strong absorption bands in much the same region of infra-red as has liquid water.

Experimentation

In order to test the effectiveness of radiation in cooling leaves, a preliminary experiment was carried out with bits of black paper 1 cm. square exposed to radiant energy in a chamber where the gas in the chamber, and the temperature of the chamber walls, could be controlled.

The chamber consisted of a thin walled, cylindrical, tinned, and blackened tank, 18 cm. in diameter and 28 cm. deep. It was submerged in a large water bath so that only about a centimeter of the upper rim extended above the water. This water bath served to keep the lateral walls and the bottom of the chamber at approximately constant temperature. Radiant energy from a 500-watt lamp, placed at a distance of about 50 cm., entered from above through a circular opening 7.5 cm. in diameter. In the experiment a single sheet of black paper, which is somewhat transparent to infra-red, and itself radiates when heated by visible radiation, was clamped over the circular opening so as to prevent loss of the contained gases.

Thermocouples were held in position at different levels in the chamber by tying them to threads stretched between two wooden rods projecting vertically downward from the cover. Strips of black needle paper, 22 mm. long and 10 mm. wide, were folded double and one edge folded over about 2 mm. to hold the edges together. These squares of black paper were slipped over the thermocouples and so adjusted as to be exposed at right angles to the incident radiation.

For making the temperature readings, thermocouples made of copper and constantan wire of no. 30 gauge were used. (No. 36 gauge wires would have been preferable, especially for thin leaves.) The standard junction was placed in a thermos bottle filled with ice and distilled water. The equipment used consisted of a Leeds and Northrup Type K-2 potentiometer, a portable galvanometer (no. 2420B), a standard cell, and two ordinary 1.5-volt dry cells. These were all mounted in a shallow box which could be carried into the field. With this outfit temperature can be read to about 1/20° C., but no attempt was made to read closer than 1/10° C., because leaves often change in temperature more than fifty times this amount in 10 to 15 seconds. For making leaf temperature readings the thermocouple wires, which extended about a centimeter beyond the insulation, were threaded through the leaf so that the thermocouple junctions as well as that part of the wires back to the insulation would touch the leaf surface. I find this method far superior to that of MILLER and SAUNDERS (9), or of EATON and BELDEN (7) for following changes in specific leaves. A comparison of the methods will be discussed later.

In measuring the temperature of the paper squares placed at different levels in the chamber and exposed to radiant energy, it was found that there were no differences in temperature in dry and nearly saturated air. It immediately became apparent that this was due to the fact that too little water vapor was present in so small a chamber to have any marked effect. At the temperatures used, the chamber could contain only 20 to 30 mg. of water vapor per liter. A depth of only about 9 cm. of gas separated the thermocouples from the walls. A gas was then sought which could be used in much higher concentrations than water vapor, and which also had strong absorption in the infra-red. Carbon dioxide was found to be suitable. The experiment was therefore repeated with the chamber filled with CO_2 at atmospheric pressure in order to compare its effect with air. Curves showing readings of such an experiment are presented in figure 1.

The temperature of the water bath rose slightly during the experiment so that the second set of readings for the bath, although parallel to the first set when CO_2 was in the chamber, was somewhat higher. To correct for this, the experiment was repeated in the reverse order, that is, air was used first, followed by CO_2. Similar differences were found, but greater by the amount of difference in the bath temperatures. Except for this slight difference both sets of curves were exactly the same.

The paper squares became warmer by about 3° C. in the atmosphere of CO_2 than they did in air. This is probably due to the fact that the CO_2 is absorbing some of the infra-red coming directly from the lamp as well as

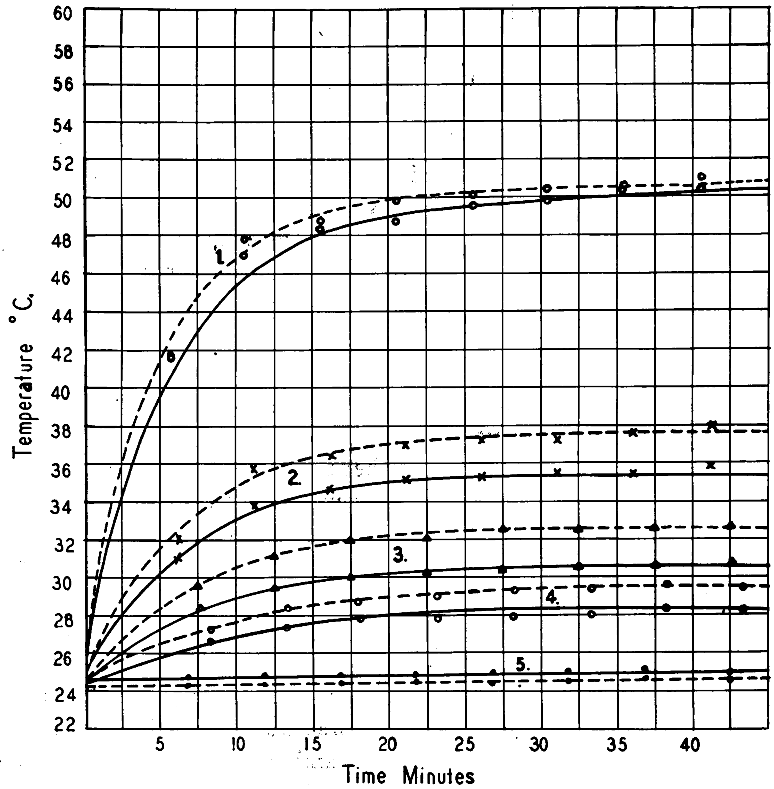

FIG. 1. Curves showing the temperatures of squares of black paper in an atmosphere of CO_2 as compared with one of air. Solid lines represent temperatures in air; broken lines, temperatures in CO_2. No. *1*, thermocouple touching black paper closing opening of chamber; *2*, square in chamber 1 cm. from paper at top; *3*, square in chamber 2 cm. from paper at top; *4*, square in chamber 5 cm. from paper at top; *5*, temperature of bath in which chamber was submerged.

that radiated to it from the paper squares, while the air, being transparent, does not act as a warming blanket but allows the heat to be radiated more easily to the walls of the chamber. It is recognized that the rate of heat removal from the squares by conductance would be slightly less in CO_2 than in air because the relative heat conductance of CO_2 is about 0.6 that of air, but estimates indicate that this would account for less than one per cent. of the difference obtained.

In order to test the effectiveness of heat loss from leaves by radiation in the infra-red, a simple apparatus was set up by which a cold surface could be placed near the leaves.[1] A narrow tank 6.5 cm. wide, 41 cm. deep, and

[1] This part of the investigation was performed at the University of California at Berkeley where facilities were supplied by the Division of Plant Nutrition.

41 cm. long was made of galvanized iron. In the center of the two opposite faces a hole 5 cm. in diameter was cut. These holes accommodated rubber stoppers through which glass tubes 3 cm. in diameter and 10 cm. long were inserted. All sides of the tank were insulated by sheets of "celotex" 1 cm. thick. One face of the metal box was blackened with a mixture of lamp black and varnish in order to make a good absorbing or radiating surface. On this face the sheet of celotex was so adjusted as to be easily removable. A microscope lamp placed at the tube opening at the back of the box served to supply the radiant energy. In operation, the box was filled with crushed ice and water. The cold blackened surface of the box represents a clear sky; the lamp, the sun; and the movable celotex shield, a cloud or atmosphere rich in water vapor.

In a representative experiment cut leaves of *Coprosma baueri* with thermocouples inserted in them were placed 23 cm. from the front face of the cold box. One leaf was so placed that it would receive light through the opening in the cold box, while another was placed a few centimeters to one side so as to receive no light. A bare thermocouple for measuring the air temperature was placed at the same distance from the box but was shielded from it by a small square of celotex 2×2 cm. placed about 2 cm. from the thermocouple. A second bare thermocouple was placed at the same distance from the cold box, but not shielded from it. Temperature readings were made at 5-minute intervals. In this series the temperatures of six couples were recorded. Two of the curves, one for air temperature, and the other for a second leaf are not included in the figure as they ran parallel to those here given. It took about 2 minutes to read the six temperatures. Although the time interval for any given thermocouple was 5 minutes, because they were always read in the same order, the actual time of reading did not coincide for the different thermocouples. To eliminate difficulties in drawing the curves all points in these and subsequent curves are placed as if all were taken at the same time. The data are presented in figure 2.

In this experiment the front face of the cold box was covered at first by the celotex shield. At point *1* the light was turned on; at point *2* the door of the laboratory was opened and the draft of cold air caused a temporary drop in temperature of all the thermocouples. At point *3* the door was opened again with the same results. At point *4* the celotex shield was removed from the cold box, which resulted in a fall in temperature of both lighted and shaded leaves, a slight drop in the bare thermocouple which could radiate to the cold surface, but no change in the air temperature as indicated by the bare thermocouple which was shielded from the cold box. At point *5* the shield was replaced on the face of the cold box, which resulted in an abrupt rise of leaf temperature accompanied by only a slight and gradual rise in air temperature. At point *6* the door was again opened, re-

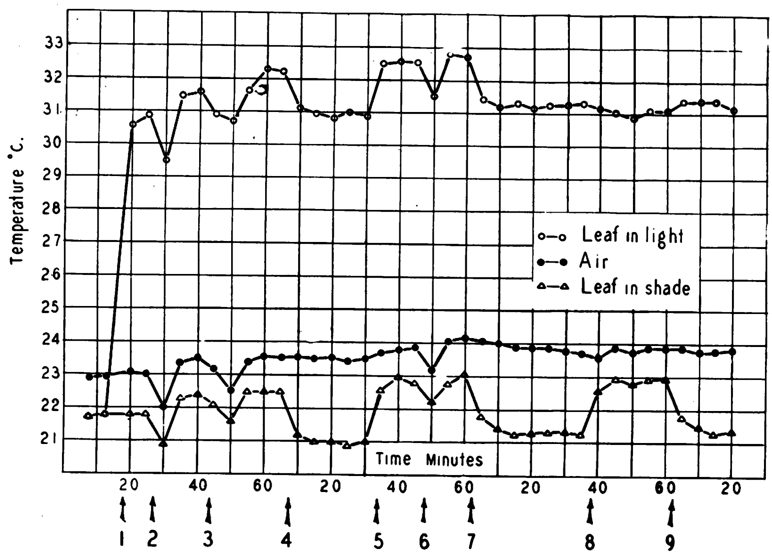

FIG. 2. Cooling of leaves by radiation to a cold box: point *1*, light was turned on and leaf receiving the light rose in temperature; *2*, *3*, and *6*, door of the laboratory was opened, and cool air lowered the readings for all thermocouples; *4*, shield was removed from cold box. (Note drop in temperature of leaves but not the air); *5*, shield replaced on cold box; *7*, shield removed; *8*, large sheet of glass shielded the cold box; *9*, glass removed.

sulting in a cooling draft of air. At point *7* the shield was again removed, with the resultant sudden drop in leaf temperature. The slow drop in air temperature was probably due to the loss of heat from the many surrounding objects by radiation to the cold box, and the slight cooling of the air by conduction. At point *8* a large sheet of glass was placed in front of the cold box in place of the celotex shield. The temperature of the leaf in the light dropped slightly, while the temperature of the leaf in the shade rose abruptly. This rise in temperature of the shaded leaf is undoubtedly due to the failure to lose heat to the cold box by radiation. In like manner the glass must have prevented loss by radiation from the leaf in the light, but to an approximately equal extent it also reduced the radiant energy reaching the leaf from the light, for there was no hole through the glass shield as there was through the celotex shield. At point *9* the glass was removed and the temperature of the leaf not in the light again dropped, as was expected.

Another experiment was carried out in the controlled environment chamber at Berkeley, which Professor A. R. DAVIS placed at the writer's disposal. The chambers were so constructed that the air temperature, humidity, air flow, and light intensity were under accurate control. In this case a potted strawberry plant, and rooted leaves of citrus growing in a nutrient solution in quart jars were used. One thermocouple (no. 1) was placed in the dark where the air was entering the chamber. Another thermocouple (no. 2) was placed at the level of the leaves but exposed to direct light and not shielded from the cold box. Thermocouples (nos. 3, 4) were placed in strawberry and citrus leaves. Other thermocouples were placed in other leaves but the readings ran parallel to those here presented so they are omitted. Until near the end of the experiment, the relative humidity was kept constant at 36 per cent. and the air flow was constant at about 30 feet per minute near the leaves. In this experiment the light did not come through the tube in the cold box, but ten 500-watt lamps were shining on the plants from outside of the glass walls of the control chamber. The cold box with the insulating shield over its face was placed 27 cm. from the leaves and thermocouples. Only thermocouple no. 1 was below and completely shielded from the cold box. Readings were taken every 5 minutes. The data are presented in figure 3.

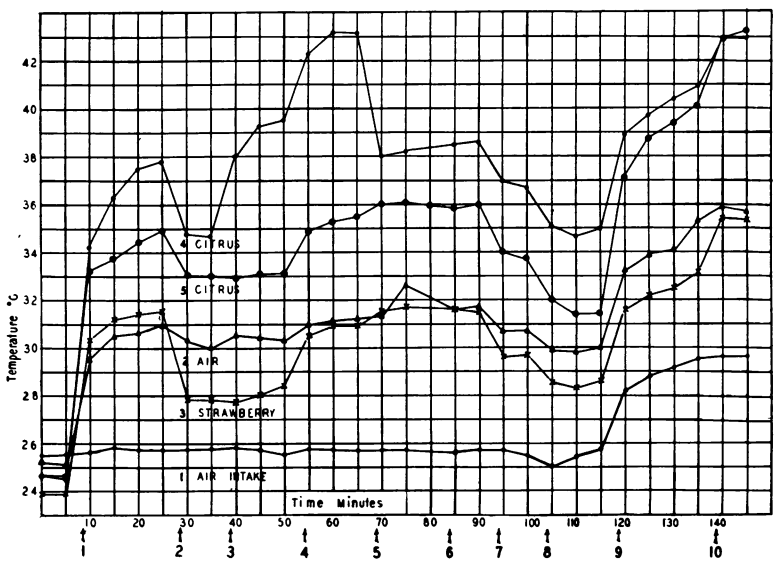

FIG. 3. Cooling of leaves by radiation to a cold box. First two readings all thermocouples in the dark. Nov. 30, 1934. At point *1*, lights were turned on; *2*, shield removed from cold box; *3*, cellophane envelope slipped over citrus leaf no. 4; *4*, shield replaced on cold box; *5*, cellophane envelope removed from citrus leaf and placed on thermocouple in the air; *6*, cellophane removed from no. 2 and placed behind no. 4 which accounts for its slow rise; *7*, shield removed from cold box; *8*, rate of air flow considerably increased; *9*, air flow completely stopped; *10*, shield replaced on cold box.

The first few readings were taken in darkness. At point *1* the lights were turned on, and the temperature of the leaves rose abruptly. At point *2* the shield was removed from the cold box and the temperature of the leaves dropped abruptly although the air temperature, even that of the freely exposed thermocouple, changed but slightly. At point *3* a cellophane envelope was placed over the citrus leaf (no. 4) causing abrupt rise in leaf temperature. At point *4* the shield was placed over the cold box. At point *5* the cellophane envelope was removed from the citrus leaf and placed over the bare thermocouple. At point *6* the cellophane was removed from the bare thermocouple (no. 2) and placed behind leaf no. 4, which accounts for its slight rise. At point *7* the shield was again removed from the cold box. At point *8* the rate of air flow was considerably increased but the amount of increase was not measured. At point *9* the air flow was completely stopped and the temperature in all cases rose abruptly. At point *10* the shield was replaced on the cold box. From these experiments it is obvious that the temperature of objects at a distance may markedly affect the temperature of the leaves, and this effect is independent of the air temperature in the vicinity of the leaf.

In order to test the effect of radiation to the sky on the temperature of leaves, thermocouples were threaded into leaves of an orange tree at Riverside, California.[2] This experiment is somewhat complicated by the fact that the leaves had previously been whitewashed with lime to determine the effect of this treatment on leaf temperature; but similar behavior was obtained with unsprayed leaves, and since this same tree was used on a cloudy day for comparison these data rather than others are here presented. The experiment was performed on the afternoon of January 3, 1935. There were a few light clouds in the sky and by the time this particular set of readings began, at 3:40 P.M., the sun was low in the west and soon was hidden behind the clouds. Thermocouples were inserted into three leaves on the northeast side of the tree where they were exposed to the sky but shielded from the sun by the remainder of the tree. For the most part, the air movement was not strong. The thermocouple for reading air temperature was hung fairly close to the leaves. Three others, hung in various parts of the tree, when read at various intervals were found to read about the same as this one but were not read so regularly. The temperature readings were made mostly at 1-minute intervals. The data are presented in the curves in the upper part of figure 4.

At the beginning it is apparent that the three leaves were cooler than the air by about one degree. At point *1* a cardboard shield about 40 cm. wide × 50 cm. long was held at a distance of about 50 cm. from the leaves to shield them from the sky. The leaf temperatures immediately rose to approximately that of the air. At point *2* the shield was removed and the

[2] The writer is indebted to Professors H. S. REED and E. T. BARTHOLOMEW for supplying facilities for this work at the Citrus Experiment Station.

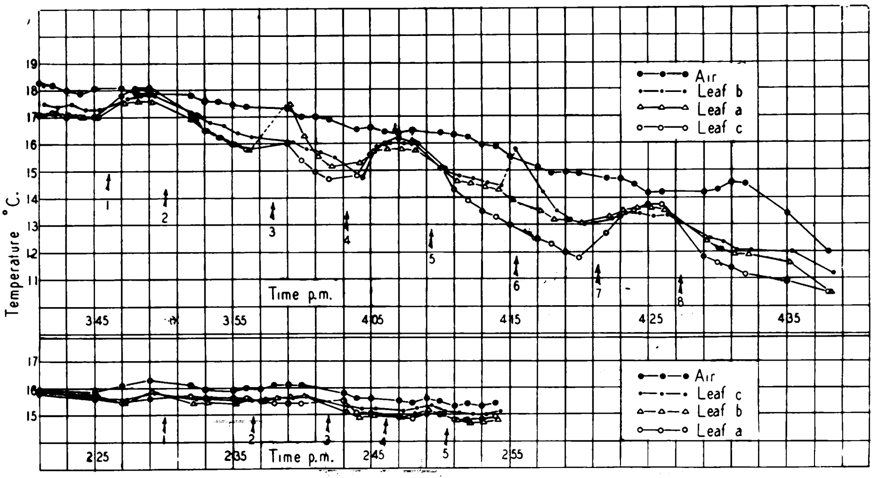

FIG. 4. Radiation to sky from citrus leaves on clear and cloudy days compared. Upper curves, data on a clear day: Up to point *1*, leaves freely exposed to the sky and cooler than the air. Points *1*, *4*, *7*, leaves shielded from sky; *2*, *5*, *8*, shield removed; *3*, lime wiped from leaf *a*; *6*, lime wiped from leaf *b*. Lower curves, data on a cloudy day: Points *1*, *4*, leaves shielded from the sky; *2*, *5*, shield removed; *3*, lime wiped from leaf *a*.

leaf temperatures immediately dropped below that of the air. At point *3* the lime was wiped from leaf *a*. Leaf *c* was close to leaf *a* and the handling of *a* and partial shading of *c* accounts for the brief rise in temperature. At point *4* the leaves and free thermocouple were again shielded from the sky, and this resulted in a rise in leaf temperature. At point *5* the shield was again removed. At point *6* leaf *b* was wiped free from the whitewash. At point *7* the leaves were shielded from the sky and there was a rise in leaf temperature. At point *8* the shield was again removed and this was followed by the expected fall in leaf temperature. The shield was again replaced and again removed with response similar to those just recorded.

The next day, January 4, the sky was completely overcast with clouds and the experiment was repeated, using similar leaves from the same side of the tree. The temperature readings are given on the curves in the lower part of figure 4. At the beginning the leaves were open to the sky. At points *1* and *4* the leaves were shielded from the sky as on the previous day, and at points *2* and *5* the shield was removed. At point *3* leaf *a* was wiped free from lime. It is clear that on this cloudy day the presence or absence of the cardboard shielding or not shielding the leaves from the sky had almost no effect upon the leaf temperatures.

It seems that on the cloudy day there was little cooling by radiation to a cold sky, while on a clear day the leaf temperatures were greatly influenced by radiation to the sky. A similar fall in temperature when the leaves were exposed to the sky, and a rise to air temperature when shielded from the sky were observed for leaves of *Quercus wislizenii* on the top of Mt. Diablo near Berkeley, California, on October 19. Similar data were also obtained for leaves of *Chenopodium* sp. on top of Mt. Rubidoux at Riverside, California. At this time there was such a heavy wind blowing that it was difficult to hold the paper for recording the readings, and to keep the thermocouples in place. In spite of this wind the leaves were cooler than the air by approximately 2° C. when not shielded from the sky, and practically the same as the air temperature when shielded from the sky but not from the wind.

That air movement may have a marked effect on leaf temperature, when

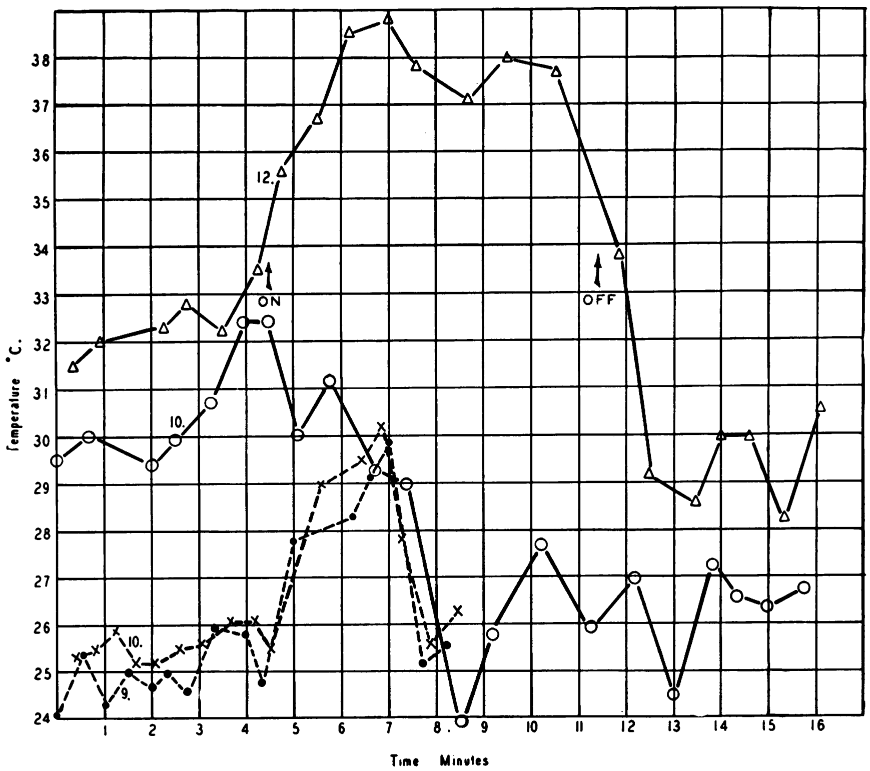

FIG. 5. Curves showing rapidity of change in leaf temperature when light is constant and air currents vary. Berkeley, Calif., Oct. 10, 1934. Broken lines: two thermocouples threaded into the same leaf. Solid lines: no. 10, indicates natural fluctuations owing to changes in air current; no. 12, leaf inclosed in cellophane envelope at "on," envelope removed at "off." Note marked rise in temperature and relatively slight drop coinciding with minimum temperature of freely exposed leaf.

the leaves are in direct sunlight and therefore much warmer than the air, has been noted by a number of investigators, notably, SMITH (**12**) and CLUM (**4**). Additional data are here given to show the rapidity of the fluctuation over time intervals that are, for the most part, shorter than those previously reported.

The data for figure 5 were obtained from leaves of *Pitosporum undulatum* on the campus of the University of California at Berkeley. The broken lines give the readings of two thermocouples threaded into the same leaf. Thermocouple no. 9 was so threaded that the tip of the thermocouple lay on the upper surface of the leaf, while thermocouple no. 10 was so threaded that the tip lay on the under surface. The readings were made first with one thermocouple and then with the other in rapid succession. The time of each reading was recorded by a stop-watch. Air temperature readings were made just before and at the end of this run and were 20.0° and 19.7° C.

The solid lines of figure 5 represent readings taken from this same leaf (to which thermocouples nos. 9 and 10 were attached) and also from a second leaf (no. 12) over which a cellophane envelope was placed and removed at the times indicated by arrows. These readings were made shortly following those just described, and the air temperatures, at the beginning and end, were 19.7° and 19.9° C.

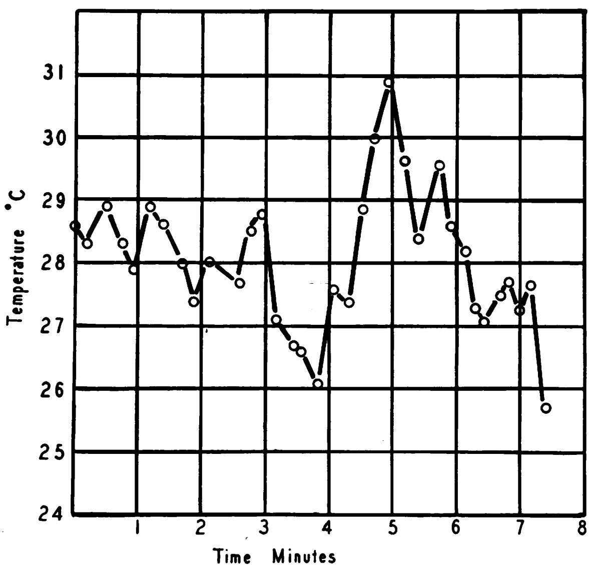

FIG. 6. Curve showing rapidity of natural changes in temperature of a leaf due to varying air currents. Air temperature immediately preceding these readings was 20.5° C., immediately afterwards, 19.7° C.

The readings for the curve in figure 6 were made immediately before those for thermocouples nos. 9 and 10 of figure 5. In this case, the temperature changes taking place in a single leaf were followed as rapidily as possible. On the average, 4.3 readings per minute were made over a period of 7.5 minutes. At the beginning the air temperature was 20.5° C., at the end 19.7° C.

The leaves were in direct sunlight for these three sets of curves and the light intensity seemed constant. With the exception of the leaf temporarily inclosed in a cellophane envelope, the temperature fluctuations seemed entirely due to fluctuations in rates of air movement. Since the leaves were so much warmer than the air it is obvious that changes in rate of air movement would greatly affect their temperature. No attempt was made to keep a careful record of air movement but it was noted in all three sets of curves that the air was quiet at the points of maximum temperature and a breeze was evident at the minimum points. It is to be noted that leaf no. 12 when inclosed in a cellophane envelope showed only a slight drop in temperature when its mate showed the minimum. This time coincided with the maximum breeze.

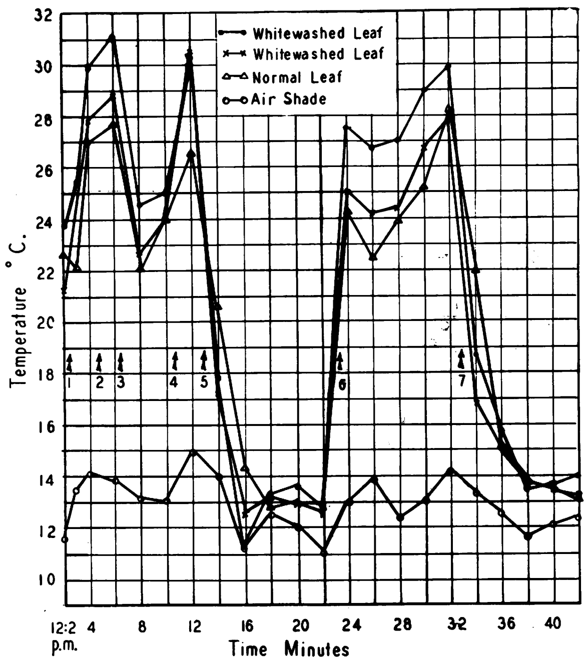

FIG. 7. Temperature changes in citrus leaves, outdoors, Jan. 6, 12: 2 to 12: 44 P.M. At point *1*, a slight breeze was noticeable; *2*, it was quiet; *3*, a breeze was again noticeable; *4*, more quiet; *5*, leaves were shaded from sun by sheet of cardboard; *6*, shade was removed; *7*, leaves were again shaded. At 12: 48, shade was removed but all temperatures fluctuated between 11° and 15° as a cloud shut off direct sunlight.

The data for figure 7 were taken on Jan. 6, 1935, from orange leaves at Riverside. In this experiment the temperatures of six thermocouples were recorded every 2 minutes, and part of the time temperatures of eight thermocouples were recorded. Curves for only 4 of these thermocouples are presented in the figure. The rapidity and degree of temperature change, changes in rate of air movement, and the effect of shading are particularly striking.

The writer and his students have frequently observed that, when measuring in a potometer the transpiration of leafy shoots exposed to strong artificial light, the transpiration is often reduced when the shoot is vigorously fanned. This, to the uninitiated, is contrary to expectation because one expects the rapid air movement to increase transpiration. When one realizes, however, that the fanning may cause a drop in leaf temperature of from a few to 10° C. or more, the marked drop in vapor pressure of the leaf owing to its fall in temperature can easily be seen to account for the decreased transpiration, and the divergent responses of leaves and evaporimeters to air currents.

In the voluminous literature dealing with various factors influencing transpiration, it seems that the importance of the effect of leaf temperature upon the process has been too little recognized. A failure to recognize that the leaf temperatures may be far different from the air temperature and that they may fluctuate over short time intervals, as indicated in figures 5, 6, and 7, has led in many cases to misinterpretation of data, particularly in relation to the effects of stomatal movement, relative humidity, and air movements. A change of only 1° to 2° C. in leaf temperature, for example, may bring about a change in vapor pressure gradient between the leaf and the atmosphere equivalent to changing the external humidity as much as 5 to 14 per cent. Assuming that at the beginning the leaf has the same temperature as the air and that the intercellular spaces remain saturated,[3] a rise in temperature of the leaf to 1° C. above the air temperature would be comparable, in its effect on transpiration, to lowering the external humidity by 5.5 to 6.9 per cent. over the temperature range between 40° and 10° C. On the same assumption, a rise of leaf temperature of 5° C. would have an effect on the vapor pressure gradient comparable to lowering the external humidity by 30.1 to 38.7 per cent., and a rise of 10° C. to a lowering of humidity by 65.5 to 90.0 per cent. For example, raising the leaf temperature from 10° to 11° C. would be

[3] With the large exposure of cell surfaces within the leaf and the short distances involved, the relative humidity is likely to remain close to 100 per cent., and in the deeper tissues probably rarely drops below 95 per cent. because the turgor deficit (suction tension) in equilibrium with 95 per cent. relative humidity would be of the order of that of a solution with an osmotic concentration equivalent to seventy atmospheres, and leaves rarely approach this concentration.

equivalent, in its effect on the vapor pressure gradient between leaf and air, to lowering the external humidity by 6.9 per cent. (that is from 100 to 93.1 per cent. or 60 to 53.1 per cent., etc.); while raising the leaf temperature from 40° to 41° C. would be equivalent to lowering the external humidity 5.5 per cent. Within the range of temperature between 10° and 40° C. if the leaf has the same temperature as the air and the air humidity is 65 per cent., transpiration would increase more by raising the leaf temperature 10° C. than would result from lowering the air humidity to 0 per cent., because raising the leaf temperature 10° C. would be equivalent to lowering the external humidity 65.5 to 90 per cent., depending on whether the original temperature was 40° or 10° C.

One of the commonest mistakes found in the literature and texts dealing with transpiration is the claim that a rise in air temperature increases transpiration because it lowers the relative humidity of the atmosphere, or increases its vapor pressure deficit. The change in relative humidity or vapor pressure deficit of the atmosphere around the leaf, however, when it is brought about by a rise in temperature of the atmosphere, does not lower the vapor pressure of the atmosphere and has no tendency whatever to increase transpiration unless the leaf also is heated, and this heating of the leaf alone is responsible for the increased transpiration. In other words, lowering the relative humidity of the atmosphere or increasing its vapor pressure deficit by raising its temperature is not responsible for increased transpiration.

In experiments performed by the writer, only a few of which are here reported, he has in no case found leaf temperatures in direct sunlight to be below that of the air surrounding them. MILLER and SAUNDERS (**9**), and EATON and BELDEN (**7**), however, have reported leaf temperatures in strong direct sunlight to be close to, and in many cases even below that of the surrounding air. It has been suggested that these low temperatures, especially those of EATON and BELDEN, are due to the fact that the experiments were carried out in such an arid environment that transpiration was sufficiently rapid to cause the marked cooling of the leaf below air temperature. When transpiration was greatly reduced by withholding water, the leaf temperatures rose only about 2 to 5° C., or approximately the same amounts observed by CLUM (**4**), and SMITH (**12**), who worked under more humid conditions and who found leaf temperatures in direct sunlight often 10° to 15° C. above air temperature. As reported in an earlier paper (**6**), it seemed possible that the lower temperatures reported by MILLER and SAUNDERS (**9**), and EATON and BELDEN (**7**) might be largely due to greater loss by radiation in the drier regions in which these investigators worked. Although the evidence presented in the present paper indicates that this loss by radiation to a clear sky, especially when the amount of water vapor in the air is low, may be appreciable, the amount of such cooling by radiation even with increased cooling by greater transpiration, probably does not fully account for the low leaf temperatures reported by these investigators. The writer has obtained rather clear-cut evidence that particularly the methods used for determining the air temperatures may have been faulty.

MILLER and SAUNDERS (9) measured leaf temperatures by mounting one junction of the thermocouple on cork tipped clamps with which the leaf was grasped. Using a similar clamp, the writer has made many readings, comparing them with those of a thermocouple threaded into a leaf. The experimental procedure was first to read the thermocouple threaded into the leaf, then the one attached to the clamp and held in the air but shaded from the light, then this same couple held on the surface of the leaf. The three readings could be made in about 30 seconds or less. Data from such experiments in artificial light are presented in table I. The leaf

TABLE I

COMPARATIVE READINGS OF LEAF TEMPERATURES OBTAINED WITH THERMOCOUPLES EITHER THREADED INTO LEAF, OR PLACED ON LEAF SURFACE ACCORDING TO METHOD OF MILLER AND SAUNDERS

LEAVES AND LIGHT INTENSITY	AV. NO. READINGS	TEMPERATURE				
		THERMO-COUPLE IN LEAF	CLAMP IN AIR	CLAMP ON LEAF	AIR SHADE	LEAF MINUS CLAMP ON LEAF
		°C.	°C.	°C.	°C.	°C.
Bryophyllum in strong light	20	38.3	29.0	35.3	25.6	3.0
Apple in strong light	18	32.5	27.9	28.8	25.9	3.7
Bryophyllum in diffuse light	5	22.6	23.8	23.5	23.2	– 0.9
Apple in diffuse light	2	21.4	23.8	23.0	23.2	– 1.6

temperature readings with the cork tipped clamp were always[4] intermediate between the temperature of the clamp when held in the air and that of the thermocouple inserted in the leaf. Therefore when the leaves were warmer than the air, as in strong sun or artificial light, the readings with the clamp were too low, while when the leaves were in diffuse light and cooler than the clamp in air readings, the readings with the clamp on the surface of the

[4] If the clamp was so held, however, that the cork face of the jaw opposite the thermocouple was held in direct light, then, especially with thin leaves, when a leaf was grasped with the clamps the temperature was higher than either the leaf or the thermocouple because the cork was heated.

leaf were too high. As was expected, the leaf readings with the clamp were more nearly correct with the thick leaves of *Bryophyllum* than with the thin leaves of apple where the heat retaining capacity of the leaves is less (see last column in the table).

In several instances MILLER and SAUNDERS (9) report leaf temperatures in direct sunlight as lower than the air temperatures. The writer has yet to find in his experiments such readings under natural conditions. In comparing the readings of a bare thermocouple hanging free in the shade with those of a thermocouple in the cork tipped clamps when so placed that the thermocouple was shaded by the cork, the writer found that the thermocouple touching the cork, although shaded, was consistently warmer than that hanging free. For example, in a series of fourteen readings each, a thermocouple in the cork jaws of the clamp but shaded from direct light by the cork showed an average temperature of 30.7° C. This was the method used by MILLER and SAUNDERS in obtaining air temperatures. A second thermocouple, about 2 cm. behind and in the shade of a vertical wooden pot label, showed an average temperature of 28.0° C. A third thermocouple in direct light read 29.9° C. A fourth thermocouple, 2 cm. behind and in the shade of a vertical apple leaf read 28.5° C. A fifth thermocouple threaded into the leaf read 33.0° C. When left in the same position but in the breeze of an electric fan, averages of 5 readings each gave the following temperature readings: 26.1°, 25.4°, 26.7°, 25.8° and 27.3° C. From these data as well as those of table I it is evident that the thermocouple shaded by the cork but in contact with it was usually 2 to 3° C. warmer than one held in the shade at a distance of one or two centimeters from the shading object. It seems from this that the air temperature readings of MILLER and SAUNDERS were too high and therefore that the leaves in direct sunlight were probably not cooler than the air as their data would indicate.

EATON and BELDEN (7) did not measure actual leaf temperature but attempted to compare leaf temperature with that of the air by placing one junction of the thermocouple in contact with the leaf and leaving the other in the air. The direction and amount of swing of the galvanometer were taken as measures of the direction and amount of temperature difference between the leaf and the air. In making the readings they placed one junction on the surface of the leaf and quickly folded the two halves of the leaf against the junction by the use of cork tipped clamps. This should give a fairly accurate measure of the leaf temperature because the thermocouple was in contact only with the leaf surfaces. It would seem a desirable method for measuring temperatures of large numbers of leaves but is valueless for following temperature changes of any given leaf with natural or artificial environmental changes, and, furthermore, the effect of brief shading has not been determined.

What seems to be the most serious weakness in the method, as EATON and BELDEN used it, is that, to get the air temperature, this junction was "protected from the direct rays of the sun by two slightly separated slips of white paper." Their description of this paper arrangement is not sufficiently clear to enable one to follow it exactly. The writer has attempted to test the effect of a similar arrangement based on their description, including figure 2 of their article. In an experiment performed indoors using ordinary mercury thermometers, placing one between two slips of paper, and comparing the temperature of this thermometer with that of another in direct sunlight, using a third thermometer with a blackened bulb (blackened by dipping in shellac and then lamp black), and a fourth thermometer shielded by a vertical white card placed 5 cm. from the bulb, the writer found readings of the sort given in table II. In this experiment

TABLE II

COMPARISON OF TEMPERATURE READINGS WHEN MERCURY THERMOMETERS ARE VARIOUSLY SHADED FROM SUNLIGHT, INDOORS. THERMOMETERS MOSTLY IN A ROOM WITH SUNLIGHT COMING THROUGH A WINDOW. ALL READINGS BETWEEN 4 AND 4:30 P.M. DURING MAY. AVERAGES OF 2 TO 7 READINGS ARE GIVEN. VERTICAL COLUMNS NUMBERED 1 TO 4 REPRESENT DIFFERENT DAYS

THERMOMETER IN RELATION TO SUNLIGHT	TEMPERATURE			
	1	*2*	*3**	*4*
	°*C.*	°*C.*	°*C.*	°*C.*
Thermometer shielded from direct sunlight by vertical white card at distance of 5 cm.	27.1	26.0	....	24.8
Bare thermometer in direct sunlight	32.4	28.5	13.1	27.0
Thermometer shielded by horizontal strips of white paper†	37.5	32.5	16.0	30.4
Excess over that in direct sunlight	5.1	4.0	2.9	3.4
Excess over air	10.4	6.5	....	5.6
Thermometer with blackened bulb	43.0	37.0	....	36.4

* Placed on window ledge outside, where there was a strong wind.

† Method used was similar to that of EATON and BELDEN for obtaining air temperature.

the use of white paper strips, close to but not touching the thermometer, resulted in temperature readings averaging 2.9° to 5.1° C. higher than those of the thermometer directly exposed to the sun, and 5.6° to 10.4° C. higher than the truer air temperatures.

Similar experiments were performed with thermocouples out-of-doors.

The data of a typical set-up are summarized in table III. Readings were taken every two or three minutes. The temperatures showed many changes associated chiefly with changes in air currents. But in no case did the temperature curve of any given treatment cross that of a different treatment. That is, the bare thermocouples (nos. 3 and 5) were always warmer than the one shaded by a wooden stick (no. 1) and always cooler than any of those shielded on both sides by white paper (nos. 4, 6, and 7). Although the paper shields were open both at the side and the end and did not touch the thermocouples, they served to trap the heat and give excessively high readings. It seems probable that the air junctions in the experiments of EATON and BELDEN were also at temperatures higher than the air and therefore the leaves in direct sunlight were not as cool as indicated in their readings. The claim, therefore, of MILLER and SAUNDERS, and EATON and BELDEN that leaves in direct sunlight are often cooler than the air seems questionable.

TABLE III

COMPARISON OF TEMPERATURES OF THERMOCOUPLES WHEN VARIOUSLY SHADED FROM DIRECT SUNLIGHT, OUT-OF-DOORS. TEMPERATURE READINGS FROM 3: 43 TO 5: 17 P.M. JULY 17, 1935. AVERAGES OF 25 CONSECUTIVE READINGS ARE GIVEN

NUMBER	THERMOCOUPLE	TEMPERATURE				
	RELATION TO SUNLIGHT	MAX.	MIN.	AV.	AV. EXCESS ABOVE AIR	MAX. EXCESS ABOVE AIR
		°C.	°C.	°C.	°C.	°C.
1	Thermocouple shielded by vertical wooden pot label 2 cm. wide at a distance of 2 cm. Assumed to be air temperature	31.4	26.9	29.6	0.0	0.0
2	Shielded by vertical strip of white paper at a distance of 2 cm.	32.4	29.5	31.3	1.7	4.4
3	Bare thermocouple (near no. 4)	34.7	30.8	32.5	2.9	5.6
4*	Thermocouple shielded by horizontal strips of white paper	41.7	35.3	37.7	8.1	12.2
5	Bare thermocouple (near no. 6)	34.9	27.7	31.8	2.2	4.5
6*	Thermocouple shielded by horizontal strips of white paper	37.8	32.5	34.8	5.2	8.0
7*	Thermocouple shielded by horizontal strips of white paper	39.4	33.4	36.6	7.0	10.7

* Method used similar to that of EATON and BELDEN for obtaining air temperature.

Discussion

Although those who have investigated thermal emissivity of leaves have mentioned the loss of heat by radiation as well as by conduction to the atmosphere, in those reports which the writer has read, the assumption is made that there will be no loss of heat by radiation unless the leaf is cooler than the atmosphere around it. The fact that the air is mostly transparent to infra-red radiation and that plant tissues may lose or receive heat by radiation to or from distant objects does not seem to be generally recognized by botanists. The temperature of the walls of a chamber may have a marked effect upon the temperature of leaves of a plant within that chamber which is entirely independent of the temperature of the air within the chamber. This in turn will influence the various physiological processes in the plant. Therefore for interpretation of certain physiological experiments, air temperature readings alone may be highly misleading. The cooling of plants at night below air temperature is undoubtedly chiefly due to loss by radiation. This cooling may lead to condensation of moisture on leaf surfaces and may thus modify turgor relations, water loss, and infection by bacteria and fungi. Such condensation does not often occur in greenhouses, even though the humidity is high, because the glass tends to prevent this loss of heat by preventing radiation to the sky.

Many papers have been published in which the effects upon transpiration of various spray residues and dusts have been reported. The fact that these materials often appreciably alter the temperature of the leaves, and therefore influence both transpiration and other processes including resistance to the toxic effects of the applied materials, seems often overlooked. Data on this phase are accumulating and will be published later.

Several writers have claimed that, if it were not for the cooling effect of transpiration, leaves would be quickly killed in direct sunlight because of excess heating. It is true that transpiration invariably tends to lower the temperature of the transpiring leaf but the data obtained by various investigators indicate that this lowering of temperature commonly amounts to less than 2° to 5° C. There are several other factors concerned in the prevention of excess heating. The angle of exposure to incident radiation will obviously greatly affect absorption of radiant energy, and therefore the temperature. SHULL (**10**) has demonstrated that with many plants 25 per cent. or more of the light within the visible spectrum is reflected even when the incident radiation is normal to the leaf surface. Photographs taken with radiation in the near infra-red indicate that many plants also reflect much of the radiant energy within this range of shorter infra-red, for they appear white in such pictures. When leaf temperatures exceed that of the air there may be considerable loss by conduction (WATSON, **13**), especially when the air is in motion (BROWN and ESCOMBE, **2**). There is also loss by radiation to cooler objects near or far, or, when the sky is clear, to space or to cold gases, especially CO_2 and H_2O. Plant temperatures therefore may be greatly influenced by water in the atmosphere, either as clouds or vapor, at a great distance from the plant because of the influence of this water on the receipt or loss of infra-red radiation. This effect may be totally independent of the effect on transpiration of water vapor close to the leaf, and independent of the effects of clouds on the visible radiation reaching the plant. The relative importance of these various methods of dissipating heat varies greatly with the environment of the plant as well as the condition within the leaf, including also its surface. It is possible to control conditions so that any one of the more important factors, such as conduction, reduced absorption,[5] reradiation or transpiration may play a dominant rôle in preventing excessively high leaf temperatures. Often transpiration is assumed to be the only factor, or the major factor, in preventing excessive heating. There seems to be no justification for such an assumption. The available evidence points strongly to conduction to the atmosphere and reduced absorption as of major importance under natural conditions.

For the experiments reported in this paper one may well question what part transpiration played in determining the temperatures observed. Transpiration may have played a small part in some cases but the part was relatively so small that slight changes in air currents, angle of incidence, and light intensity undoubtedly would greatly overshadow any such effects. Furthermore, in several instances cut leaves, in which transpiration was practically zero, and dry pieces of black paper, showed responses to the various treatments exactly comparable to those of the attached leaves. It seemed therefore entirely useless to attempt to determine transpiration rates in these experiments.

Summary

1. Leaf temperatures may be considerably influenced by exchange of infra-red radiation between the leaf and other materials near or at a distance from it. There may also be loss of heat by radiation to space. These effects are independent of the temperature of the air in the vicinity of the leaf because the oxygen and the nitrogen of the air are almost transparent to infra-red radiation.

2. It has been demonstrated, both under laboratory and field conditions,

[5] Both changes in angle of incidence and reflectivity of surface may influence absorption.

that leaf temperatures may be rapidly changed several degrees by allowing or preventing radiation to cold objects or to space.

3. Rapid and great changes in temperature of leaves in direct sunlight are also brought about by natural or artificial changes in rates of air flow or light intensity. The presence of water in the atmosphere either as vapor or clouds may influence plant temperatures through its effect on infra-red radiation.

4. Data, which have been taken by various investigators to demonstrate that leaves in direct sunlight may be cooler than the air, are questioned on the basis that the readings for air temperatures were probably too high.

CORNELL UNIVERSITY
ITHACA, NEW YORK

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