THE TEMPERATURE OF LEAVES OF PINUS IN WINTER[1]

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I. INTRODUCTION

There is evidence to show that the food reserve of decidous trees is at a maximum in autumn at the fall of the leaves, and that there is a gradual decrease in reserve material during the winter months to a minimum in the spring. For trees with persistent leaves, on the contrary, there is evidence to show that there is a gradual *increase* in reserve food during the winter, and that the maximum is not reached until just before the swelling of the buds in spring. Accepting the evidence as true leads to the conclusion that, while deciduous trees maintain their existence during the winter at the expense of the reserve food, trees with persistent leaves produce, by photosynthesis during the same season, food material not only for their maintenance, but in quantities sufficient for an accumulation of reserve. How they are able to do this in cold climates where the temperature rarely rises far above 0° C., and where the mean temperature for the winter months is several degrees below 0° C. is a problem that has not been solved.

It has been shown by investigators that broad leaves, *i. e.*, leaves of deciduous trees, exposed to tropical insolation and leaves exposed to summer insolation in temperate regions, may attain in still air a temperature 16° C. above the shade temperature of the air. Assuming that a similar condition holds for trees with persistent leaves, such as the conifers, during the cold days of winter, may not this offer a solution to the problem suggested above?

While a number of investigators have definitely determined the effect of solar radiation upon broad leaves for tropical regions, and for summer conditions in temperate regions, no such work has been done to find its effect upon persistent leaves under winter conditions. It was to fill this gap, *i. e.*, to determine the effect of solar radiation upon the temperature of persistent leaves under winter conditions,

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and its possible bearing upon photosynthesis and the accumulation of reserve food material during the same season, that this investigation was undertaken. The work was carried on in the Botanical Department of the University of Michigan during the winter months of 1912–1913 and 1913–1914. The problem was suggested to the author by Professor F. C. Newcombe, and was carried to completion under his supervision. To him my sincere thanks are due for helpful suggestions and kindly criticism. Grateful acknowledgment is also made to Professor H. M. Randall of the department of physics for valuable suggestions and help in setting up the apparatus, and for apparatus loaned by him; and to Professor N. H. Williams of the department of physics for the use of his laboratory and for helpful advice given.

II. Historical

The papers of particular interest for the consideration of the problem under discussion may be grouped under three heads: (1) the internal temperature of foliage leaves; (2) photosynthesis at low temperatures; (3) accumulation of reserve food material by evergreen trees in winter.

1. *The Internal Temperature of Foliage Leaves*

Of interest here, merely because it is the first record of an investigation to determine leaf temperatures that could be found in botanical literature, is a paper by Rameaux (21) published in 1843. This investigator placed neighboring leaves, attached to the stems, one upon another until the layer was sufficiently thick to prevent any light from passing through, and then bent the layer around a mercury thermometer. No record of leaf temperatures is given, however, since the investigation was chiefly concerned with finding the temperature of stems.

Schumacher (27) was the next to attempt a determination of leaf temperatures. His method consisted in placing a thermometer against the lower side of a leaf exposed to solar illumination. At least two serious objections may be raised to this method: (1) Assuming a difference in temperature between the leaf and the surrounding air, only the small portion of the mercury bulb in contact with the leaf would be influenced by the leaf temperature; (2) the rays passing through the leaf would tend to warm the mercury regardless of the leaf temperature.

Askenasy (1) in 1874 made observations on the temperature attained by succulent plants when exposed to solar radiation. *Sempervivum* and *Opuntia* were used for this purpose. A mercury thermometer was laid against the upper surface of the leaf, or inserted in a cut made for that purpose. With the thermometer in the shade registering 31° C., the leaves of *Sempervivum* attained a temperature of 43.7° to 51.2° C., an excess of 20.2° C. over the air temperature. With leaves of *Opuntia* he obtained a temperature of 15° C. above the shade temperature. Thin leaves (*Aubrietia* and *Gentiana*) on the other hand reached a temperature of only 7° C. above that of the air. The difference in temperature attained by succulent and by thin leaves he ascribes to two causes: (1) the lower rate of transpiration of the succulent leaves; (2) their massive structure, exposing less surface in proportion to mass than thin leaves expose.

Worthy of mention because of the method employed is an investigation by Stahl (29) to determine the difference in temperature between the red and non-red parts of variegated leaves. Stahl seems to have been the first to apply a thermo-electric method to determine leaf temperatures. His apparatus consisted of a thermo-couple of German silver and copper, and a mirror galvanometer read by means of scale and telescope. The junctions were made spatulate in form and were pushed into the leaf lamina. Variegated succulent leaves were used. The source of light was a gas flame. Since no absolute temperatures are given his work needs no further mention here.

Under tropical insolation, Ewart (5) obtained with leaves of *Vanilla* and *Hoya* temperatures of 45° and 50° C. respectively. The leaves were suddenly bent around and pressed against a delicate mercury thermometer originally a little below the expected temperature. The results obtained compare fairly well with those obtained by Askenasy.

Ursprung (31) in the fall of 1901 made observations on the temperature of both succulent and thin leaves under natural illumination. The observations were made in the Basel Botanical Garden at temperatures ranging from 14° to 28° C. Ursprung rejected the thermoelectric method on the ground that the direct reading of temperatures with a mercury thermometer was more simple, and because of the difficulty of getting an instrument sufficiently sensitive over a wide range of temperatures. Thermometers with small cylindrical bulbs and graduated to .5 degrees over a range of 10° to 50° C. were used.

For finding the temperature of thin leaves, the thermometer was placed on the upper surface of the leaf. The sides of the leaf were folded over with the midrib as an axis, and fastened with a light wooden clamp. In handling, the leaves were kept from contact with the fingers by using a pad of wadding. In the case of succulent leaves a small hole, the exact diameter of the thermometer bulb, was bored and the bulb inserted. The results obtained for succulent leaves under strong solar illumination confirmed the findings of previous investigators, *i. e.*, for *Opuntia* 43.3° C., *Mamillaria* 43.5° C., and for *Sempervivum* 49.6° C. These were the maximal temperatures. The air temperatures were 27.5°, 28°, and 27.1° C. respectively. The temperatures found for thin leaves were much lower, *Ulmus montana*, *Betula alba*, and *Saxifraga crassifolia*, showing maxima of 0.7°, 2.3°, and 8.1° C. respectively, above the air temperature. Ursprung ascribes the lower temperature of thin leaves, as did Askenasy, to the very large surface exposed in proportion to the total mass of the leaf.

In 1905 four important papers appeared, important because more refined methods were used in the determination of leaf temperatures than had been employed by previous investigators. Of these, one, prepared by Miss Matthaei (14), was communicated to the Royal Society of London by F. Darwin in 1903. Miss Matthaei, in the course of her researches on vegetable assimilation and respiration, found it necessary to determine the internal temperature of the leaves used. For this purpose detached leaves of cherry laurel (*Prunus Laurocerasus*) held in a special leaf chamber and placed in a constant temperature bath, were exposed to light of varying intensity from an incandescent gas lamp. For strong illumination, a powerful Keith burner was used. The leaf was protected from direct heating effect by a system of circulating water. The temperatures were determined by means of a very fine thermo-couple of copper and constantan. One junction was inserted in the midrib of the leaf, the other, insulated by a rubber tube, was placed in a water bath the temperature of which could be varied at will. The electromotive force produced by the difference in temperature at the two junctions was read by means of a Thomson mirror-galvanometer, about ½ ohm in resistance. The deflections were read directly on the scale; no refinements, such as the use of a telescope, were considered necessary. This apparatus was found by calibration to be sensitive to 0.1° C. The temperatures were not read directly by means of the galvanometer, but by a zero method which was to adjust the temperature of the bath containing the control junction until the galvanometer showed no deflections. The temperature of the bath then indicated the leaf temperature. This method was easily accurate to within .5° C., which was considered sufficient for the purpose.

Under strong illumination from the powerful Keith burner, leaves of cherry laurel reached a temperature of 10° C. or more above the temperature of the bath.

The second of the above mentioned papers was presented before the Royal Society of London in March, 1905, by Brown and Escombe (4). The paper deals with investigations on the physiological processes of green leaves. It is interesting in this connection because of the method employed to determine leaf temperatures. The temperatures were arrived at by complicated calculations involving (1) the coefficient of absorption of radiation, (2) the specific heat of the leaf, (3) the energy expended in photosynthesis and respiration, (4) the thermal emissivity of the leaf, and (5) the effect of the wind velocity. Both attached and detached leaves of *Helianthus annuus* and *Senecio grandifolius* were used. Under full solar illumination, a maximum temperature difference between leaf and air of only 2° C. was found by this method. This work was done at air temperatures of 15° to 27° C.

In strong contrast to the results of Brown and Escombe are those obtained by Blackman and Matthaei (2) in their investigations of vegetable assimilation and respiration. Determinations of leaf temperatures under natural illumination, both with the leaf in open air and enclosed in a glass case, were made thermo-electrically. The apparatus and method used were identical with those used by Matthaei (14). For experiments in the open air detached leaves of cherry laurel were stretched on a frame, the leaf stalk dipping in a well of water. The thermo-junction was inserted in the midrib. Under brilliant insolation, temperatures varying from 7° to 16° C. above the shade temperature of the air were obtained. In diffuse light the leaves were found to be from 1° to 3° C. above the air temperature. Of the two methods—the complicated calculations of Brown and Escombe and the thermo-electric method of Blackman and Matthaei—the latter seems by far the more trustworthy. The sources of error are very much reduced.

In confirmation of the results obtained by Blackman and Matthaei are those obtained by Smith (28) in Ceylon. The apparatus and methods employed by Smith were practically the same as those used by Blackman and Matthaei and, therefore, need no further description. His results may be summarized in part as follows: (1) Thermo-junctions give the same result whether inserted in the lamina or in the midrib of the leaf; (2) "in still air, with the black bulb in vacuum thermometer at from 55° to 62° C., the air temperature in the shade being 25° to 28° C., leaves, whether thick and fleshy, or thin and pliable, when placed normal to the sun's rays, may reach a temperature of 15° C. above that of the surrounding air;" (3) "in the shade such leaves have an internal temperature varying from 1.5° C. below to 4° C. above that of the surrounding air;" (4) thickness and texture of leaf have little effect, but thick leaves require more time to reach the final temperature and cool off more slowly; (5) air currents and transpiration are important factors in reducing leaf temperatures.

2. *Photosynthesis at Low Temperatures*

While it has long been recognized that photosynthesis is influenced by the temperature to which the plant is exposed, comparatively little work has been done to determine the relationship between them. This is especially true of photosynthesis at low temperatures, such as prevail during the winter season in cold temperate regions. Until within recent years only a few more or less isolated determinations of the lowest temperature at which photosynthesis begins have been made.

Among the first investigators of photosynthesis at low temperatures was Boussingault (3) who observed an evolution of oxygen by *Pinus laricio* at a temperature of 0.5° to 2.5° C., and by meadow grasses at 1.5° to 3.5° C. It is interesting to note that Boussingault took into account the effect of solar radiation upon the leaf temperature. The plants with which he experimented were placed on the north side of a wall to protect them from the sun's rays during the experiment.

Heinrich (8) found that in *Hottonia palustris* carbon-dioxide assimilation began at 2.2° R., while Kreusler (11), experimenting with *Phaseolus vulgaris*, *Ricinus communis*, *Prunus Laurocerasus*, and *Rubus*, observed an assimilation of CO_2 at temperatures of − 0.9°, − 0.6°, − 2.2°, and − 2.4° C. respectively.

Jumelle (9), as a result of experiments with *Evernia Prunastri*, *Picea excelsa*, and *Juniperus communis*, makes the assertion that these plants, when exposed to sunlight at temperatures as low as $-30°$ to $-40°$ C., absorb CO_2 and evolve oxygen, while respiration ceases at $-10°$ C. He suggests that the absorption of heat along with the light rays by the exposed leaves may prevent the cell sap from being entirely frozen at even these low temperatures and that, in consequence, assimilation may proceed.

Pfeffer (20) offers in criticism of Jumelle's results the following: "Since, however, all respiration ceases at $-10°$ C. to $-12°$ C., it is manifestly impossible that any assimilation of carbon dioxide can take place at $-40°$ C., for CO_2 assimilation is a vital process involving protoplasmic activity." Jumelle's methods are generally considered faulty by later investigators, and not much credence is placed in his results. For criticism of his methods the reader is referred to Matthaei (15) and to Ewart (7).

Miyaké (18) has found that the leaves of a large number of evergreen plants, including trees, shrubs, and herbacous plants growing in the vicinity of Tokyo, contain more or less starch during the winter. To determine whether this starch was the product of photosynthesis in winter, or whether it was stored there as suggested by Sachs (25), he excluded light from several plants (*Thea japonica*, *Fetsia japonica*, *Cinnamomum Camphora*, *Pinus Thunbergii*, and *Abies firma*), some in the open, others in a dark chamber the temperature of which varied between 1° and 7° C., until the starch had disappeared, and then exposed them to sunlight. Microscopical tests showed the reappearance of starch within five hours after exposure. The temperatures were: for *Thea*, minimum 2.6° C., maximum 8.6° C., mean 3.1° C.; for *Fetsia*, minimum 0.8° C., maximum 9.7° C., mean 3.4° C. He concludes that starch is formed by photosynthesis in winter and that its translocation occurs in the same season. This is further evidence, not only of photosynthesis in winter, but also of the accumulation of reserve material. The temperatures given were taken from the records of the Meteorological Observatory of Tokyo, and, presumably, are shade temperatures and, therefore, do not represent the true temperature of the leaf. As will be shown later, the absorption of the sun's radiations by the leaf will increase the internal temperature of the leaf from 3 to 10 degrees Centigrade on bright winter days.

The next contribution of importance was by Ewart (6). In a paper on assimilatory inhibition he devotes a part to experiments on assimilation at low temperatures. He used the bacterium method.

With this method the lowest temperatures at which determinations can be made is approximately 1° C. Parts of plants that were growing in the open and had been exposed for several weeks to temperatures often reaching – 15° C. were thawed and examined at 1° C. The following plants among others, although most of their leaves remained alive, showed no power of assimilation at 1° C.: *Ilex Aquifolium*, *Buxus sempervivens* var. *arborescens*, *Pinus montana*, *Taxus baccata*, *Thuya occidentalis*, and *Juniperus Sabina*. Experiments were also made with tropical, subtropical and water plants. His results are summarized as follows: "It appears that all evolution of oxygen ceases in tropical plants between 4° C. and 8° C.; in warm temperate, subtropical and water plants between 0° C. and 2° C., whilst in cool temperate, arctic, and alpine plants assimilation only ceases when the plants are frozen, *i. e.*, at a few degrees below 0° C." The last case is, presumably, an inference, since he offers no experimental proof to substantiate it. He ascribes the cessation of assimilation in cool temperate, arctic, and alpine plants to physical causes, *i. e.*, the withdrawal of water from the protoplasm to form ice crystals and the consequent desiccated condition of the tissue.

The most important contribution to the question under consideration was made by Matthaei (14). Determinations of the rate of assimilation through a range of temperatures from – 6° C. to 45° C. were made. The leaves of cherry laurel, *Prunus Laurocerasus* var. *rotundifolia*, were used for this purpose. Her work differs in two respects from that of all previous investigators: (1) In that careful attention was given to keeping the material under uniform conditions before the experiment; (2) in that precautions were adopted for obtaining the true internal temperature of the leaf. The leaf temperatures obtained and the method of determining them have already been briefly stated. Of the results obtained those which are of particular interest here are:

1. The minimum at which assimilation could be observed. This was – 6° C. Disregarding Jumelle's finding as untrustworthy, this is the lowest temperature at which photosynthesis has been observed. The author further suggests that, for such cold-enduring plants as the conifers, assimilation may take place at temperatures considerably lower.

2. The assimilation curve. This curve shows the maximal amount of assimilation at all temperatures from – 6° C. to 43° C. From

− 6° C. to 38° C. the curve is convex to the temperature abscissa, the maximal amounts increasing rapidly as the temperature increases. For example, the maximal amounts increase from 0.2 mmg. of CO_2 per hour for 50 sq. cm. of leaf surface at − 6° C. to 3.8 mmg. at 9° C. The conclusion is that, other conditions being favorable, assimilation increases directly with the temperature; that for each temperature there is a definite amount of assimilation beyond which a further increase in light intensity produces no effect except in so far as it increases the internal temperature of the leaf. A greater assimilation can be obtained only by increasing the temperature. The author considers temperature, therefore, as the fundamental condition governing assimilation, intensity of light as well as percentage of CO_2, since they are always present in sufficient quantities, being of secondary importance.

3. *Accumulation of Reserve Food Material by evergreen Trees in Winter*

In 1904 Sablon (23) published the results of his investigations on the reserve material of deciduous trees. He found that the reserve carbohydrates of these trees reached a maximum in autumn at the fall of the leaves at the end of the period of active assimilation. During the winter the reserve decreased a little, while in the spring during the formation of new shoots there was a decided diminution—a fall to the minimum. Two years later (24) he published the results of an investigation of the reserve materials of evergreen trees (les arbres a feuilles persistantes). The species used were *Quercus Ilex*, *Pinus laricio*, *Larix europoea*, and *Evonymus japonicus*. The determinations in both investigations were made by chemical analysis. The results obtained in this investigation were strikingly different from those obtained with deciduous trees. Instead of the maximum appearing in autumn, there is a constant increase in reserve material during the winter, and a maximum is reached only at the beginning of spring. To quote directly: "Pendent l'hiver, en effet, la végétation est suspendu, par conséquent la dépense de réserve est faible; d'autre part l'assimilation du carbone se poursuit et l'on sait que l'abaissement de la température affaiblet beaucoup mains l'assimilation que la respiration. Il est donc naturel que l'hiver soit pour les arbres à feuilles persistantes une périod de formation de réserve." In other words, in trees with persistent leaves photosynthesis is not only sufficient for the maintenance of the tree, but there is actually an increase in the reserve material during the "rest period" so called. Mer (17) thirty years earlier working with the leaves of *Hedera* came to a similar conclusion. The experiments of both of these investigators were made with material growing in the open—Mer at Paris, Sablon at Toulouse. Unfortunately neither gives any data as to temperatures. How far their results may be applied in a given locality depends upon the factors governing photosynthesis in that locality. That they hold for the greater part of Japan has been shown conclusively by Miyaké (18) in the investigations cited above.

III. Methods

A. *Preliminary Work in 1912–13*

1. *Material and Location.*—Since the purpose of this investiagtion was to find the internal temperature of pine leaves in winter under as nearly natural conditions as possible, cut branches were avoided and leaves *in situ* used. As best suited for the purpose, the species *Pinus laricio austriaca* Endl. was selected. The leaves of this species are, in cross section, the largest of the conifer leaves available in this locality.

The tree used during the preliminary work is about 2.5 meters high and is located in the university arboretum about a mile from the university campus. A small shed was built near the tree to house the apparatus.

2. *Method.*—The character of the leaves and the conditions under which the work was to be carried out made a thermo-electric method the only method possible. In the preliminary work an attempt was made to interpret directly into temperature differences, by means of a d'Arsonval galvanometer, telescope, and scale, the electromotive force produced by the difference in temperature of two thermo-junctions, one embedded in the leaf tissue, the other in a thermos-bottle kept at a known temperature—usually at 0° C. This method was, however, found unsatisfactory. The changes in the resistance of the lead wires and the wires connecting the leads with the galvanometer in the shed, as well as the changes in resistance in the galvanometer itself, due to changes in atmospheric conditions, made new calibrations necessary not only each day, but sometimes several times a day. After a thorough test this method was abandoned.

B. Final Experiments

1. *Material and Location.*—When the work was resumed in the autumn of 1913 the station in the arboretum was abandoned. An Austrian pine growing on the university campus was selected for the final experiments. This tree is about 40 years old and about 15 meters high. It is protected from direct winds on the north and west by the library, and on the south by the physics laboratory. To give the operator access to the leaves and to hold the outdoor part of the apparatus, a wooden platform 4 meters high was constructed. Upon this platform a wooden screen was set up to protect the apparatus from the sun's rays. Three pairs of heavy insulated copper wires connected the platform with the ground floor of the physics laboratory where the measuring apparatus was kept.

2. *Method.*—The first two months were spent in trying out various methods. A potentiometer method was finally adopted as best suited for the purpose. The principle of the method consists in opposing over the slide wire of a Wheatstone bridge the fall of potential due to a suitable current from a cell against the electromotive force produced by the difference in temperature between the two junctions, one of which is in the leaf. By moving the sliding contact, the portion of the bridge wire included in the galvanometer circuit (*A* to *B*, figure 1) may be changed until the fall of potential over this portion is equal and opposite to the resultant E.M.F. due to difference in temperature of the junctions. This condition is indicated by a zero deflection of the galvanometer. The displacement along the wire per degree temperature difference is determined empirically by placing the junctions in baths of known temperature.

The great advantage of this method over the first one employed is that, since it is a zero method, no current flows in the galvanometer circuit and variations in resistance due to temperature changes and other causes may be neglected. Furthermore, its accuracy is independent of any assumption of proportionality between galvanometer deflection and current.

3. *Apparatus.*—The apparatus in its essential parts consisted of a slide wire Wheatstone bridge, galvanometer, storage cell, resistance boxes, rheostat, and voltmeter. Figure 1 shows the arrangement. The galvanometer used was of the d'Arsonval type with a resistance of 30.6 ohms, and was made by the Eberbach and Son Co., of Ann Arbor, Michigan. The Wheatstone bridge was made by the same

firm. The cell used to furnish the current for the potentiometer circuit (II, figure 1) was an ordinary storage cell with an E.M.F. of 2 volts. This cell proved entirely satisfactory, giving a uniform current throughout the experiments. As a check upon the cell, a Weston voltmeter was connected across the terminals of the potentiometer

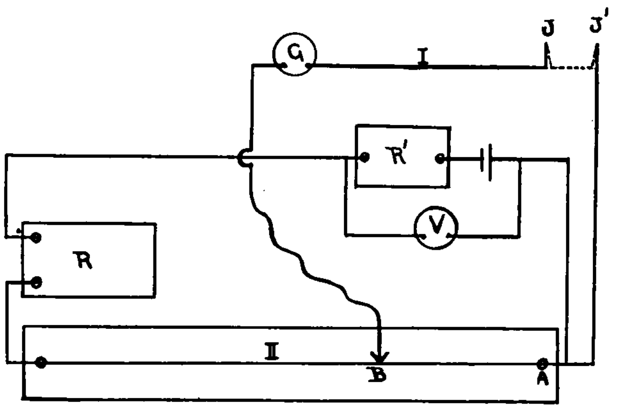

Figure 1.
I Galvanometer Circuit.
II Potentiometer Circuit.
B Sliding Contact.
G Galvanometer
J, J' Thermo-junctions
V Voltmeter
R, R' Resistance Boxes.

circuit. By throwing a knife switch, the voltage applied to this circuit of constant resistance could be measured, and any variations or weakening of the cell detected. Variations could be corrected by varying the resistance of a small rheostat which was placed between the cell and the potentiometer. It was not found necessary to use it however.

4. *Thermo-Junctions.*—The thermo-junctions were made of *advance* (a trade name for constantan, which is an alloy of copper and nickel) and copper wire obtained from the Driver, Harris Co., of Harrison, N. J. The advance wire was 0.07 mm. in diameter, the copper slightly

larger $-$ 0.09 mm. The wires were carefully soldered, and all junctions having rough or thick joints rejected. A thin coating of shellac was given the junctions to protect them against oxidation and any possible action of the leaf juices.

5. *Method of Insertion into the Leaf.*—The leaves of *Pinus laricio austriaca* grow in bundles of two. The leaf in cross section represents roughly a semi-circle in outline about 1.5 mm. in its shortest diameter. To insert the junctions into the leaf at temperatures ranging from 0° to $-$ 17° C. was attended with considerable difficulty and many junctions were broken, especially in the beginning of the experiments. The procedure was to thread the lead wire through a very fine steel needle and draw the wire through the leaf until one of the junctions was embedded in the tissue. To prevent too great a loss of heat by conduction along the lead wires, as much of the wire as possible should be embedded in the leaf tissue. Drawing the wire through at right angles to the long axis of the leaf would not, therefore, give the best results. Drawing the wire through the leaf lengthwise was found impracticable because of the firmness of the tissue. Attempts to do this usually resulted either in the splitting of the epidermis, or the breaking of the leaf. Placing the junction and lead wires between two leaves fastened together flat surface to flat surface did not give good results. The method finally adopted was to fasten the two leaves together by means of two single turns of very fine wire placed about 1 cm. apart, the wire covered with white insulation. The leads were drawn through both leaves at an angle of 45° with their long axis. Care was observed to leave the junction embedded in the leaf toward the sun and as near its center as possible. This gave a contact surface of about 1 mm. for the advance lead wire and from 3 to 4 mm. for the copper—the better conductor of the two. The second junction was left exposed to the air and shaded from the sun's rays by a wooden screen. The junctions, therefore, registered directly the differential temperature between leaf and surrounding air.

6. *Position of the Leaf.*—The leaves of the pines assume no definite position with relation to the sun's rays. In all experiments, unless otherwise stated, a leaf normal to the sun's rays, or as nearly normal as could be found, was selected. Two sets of junctions, each in a different leaf, were constantly in use—the one a check upon the other. A double-pole double-throw switch on the table beside the operator made it possible to read the temperatures of the two leaves in rapid

TABLE I.

CALIBRATION OF APPARATUS

Temperature			Bridge Reading in Cm.	Displacement per Degree C. Temp. Diff.	Average Displacement per Degree Temp. Diff. in Cm.	Degrees C per Cm. Displacement
Junction A	Junction B	Temp. Diff.				
−9.82°	−15.40°	5.58°	44.6	7.99		
−9.82	−15.10	5.28	42.1	7.97		
−9.81	−15.00	5.19	41.5	7.99	8.00	0.1250°
−7.30	−14.85	7.55	60.7	8.04		
−7.18	−14.70	7.52	60.4	8.03		
−4.87	−10.40	5.53	44.7	8.08		
−4.94	−10.00	5.06	41.0	8.10		
−5.00	− 9.92	4.92	39.8	8.09	8.10	0.1234
−5.11	− 9.68	4.57	37.1	8.12		
−5.13	− 9.65	4.52	36.7	8.12		
0	− 6.52	6.52	53.6	8.20		
0	− 6.58	6.58	54.0	8.21		
0	− 6.60	6.60	54.3	8.23		
0	− 6.60	6.60	54.2	8.21	8.22	0.1216
0	− 5.65	5.65	46.5	8.23		
0	− 5.60	5.60	46.0	8.21		
0	− 5.50	5.50	45.4	8.25		
0	− 5.45	5.45	45.0	8.25		
5.00	0	5.00	41.6	8.32		
5.00	0	5.00	41.6	8.32		
5.00	0	5.00	41.5	8.30		
5.07	0	5.07	42.0	8.28		
5.28	0	5.28	43.8	8.28	8.30	0.1205
5.48	0	5.48	45.4	8.29		
5.62	0	5.62	46.5	8.27		
7.70	0	7.70	64.2	8.34		
3.00	0	3.00	25.0	8.33		
13.25	10.00	3.25	27.6	8.49		
13.52	10.00	3.52	29.9	8.52		
14.60	10.00	4.60	39.2	8.52		
14.61	10.00	4.61	39.3	8.52	8.50	0.1176
14.67	10.04	4.63	39.4	8.51		
14.80	10.14	4.66	39.6	8.50		
13.33	9.75	3.58	30.3	8.46		
26.20	18.61	7.59	65.8	8.64		
26.20	18.62	7.58	65.6	8.64		
26.20	18.62	7.58	65.6	8.64		
26.20	18.64	7.56	65.5	8.66		
26.20	18.64	7.56	65.5	8.66	8.65	0.1156
26.62	18.68	7.94	68.8	8.67		
27.27	18.68	8.59	74.3	8.64		
27.26	18.71	8.55	74.0	8.65		
27.95	18.72	9.23	80.0	8.67		
27.90	18.72	9.18	79.5	8.66		

TABLE I.—*Continued*

Temperature			Bridge Reading in Cm.	Displacement per Degrees C. Temp. Diff.	Average Displacement per Degree Temp. Diff. in Cm.	Degrees C. per Cm. Displacement
A	*B*	Temp. Diff.				
23.57	20.00	3.57	31.1	8.71		
23.54	20.00	3.54	30.9	8.73		
23.49	20.05	3.44	30.0	8.72		
23.40	20.05	3.35	29.2	8.72	8.71	0.1148
23.36	20.05	3.31	28.9	8.73		
25.15	20.15	5.00	43.4	8.68		
26.10	20.15	5.95	51.8	8.70		
26.13	20.18	5.95	51.9	8.72		
26.22	20.20	6.02	52.3	8.69		

succession. By comparing fresh leaves with others in which the junction had remained embedded for several days, it was found that the same leaf could be used 3 or 4 days in succession without any appreciable effect upon the results.

7. *Calibration of Apparatus.*—In calibrating the apparatus the junctions were tied to the bulbs of the thermometers, the leads separated from one another by small glass tubes. Junctions and thermometers were then thrust into glass tubes containing kerosene oil and the tubes immersed in constant temperature baths. The leads of the junctions were connected with the apparatus by means of copper wires and copper binding posts. By means of resistance boxes the current from the cell was reduced until a displacement on the bridge of 100 cm. was equivalent to a temperature difference at the junctions of approximately 12° C. Readings were taken with the colder junction at temperatures varying from 18° to 20° C., while the warmer junction ranged from 0.5° to 10° C. higher. More than 50 readings gave an average displacement on the bridge of 8.66 cm. per degree centigrade temperature difference, or 0.1155° C. per centimeter displacement. But experiments showed that this factor could not be used for temperature differences at 0° C. and below, the error varying from 0.05° to 0.5° C. Calibrations were therefore made at various points through a temperature range of 35 degrees, with the colder junction at − 15°, − 10°, − 5°, 0°, 10°, 18° and 20° C., the warmer junction varying from three to eight degrees higher in each case. Standard thermometers, one graduated to 0.2° C. the other to 0.1° C. were used for temperatures from 0° to 20° C. The low temperatures were obtained by means of two Beckmann thermometers. With these the temperatures could be read without lifting the bulb in the freezing mixture. The results are given in Table I.

If these values are plotted against the temperatures as ordinates, a curve is obtained which, for all practical purposes is a straight line, the deviation at − 5° C. being negligible. From this curve (figure 2), by interpolation, values can be obtained for any temperature between − 20° and 20° C. The two columns of figures at the right of figure 2 contain these empirical numbers with the computed numbers interpolated.

8. *Sensitiveness of Apparatus.*—The galvanometer was found readily sensitive to a displacement on the bridge wire of two millimeters. Taking the factor obtained for 0° C. as an example, the apparatus is sensitive to $.2 \div 8.30 = 0.024°$ C., which is amply sufficient for the purpose of this investigation. The apparatus may be made still more sensitive by decreasing further the current from the cell and increasing the sensitiveness of the galvanometer correspondingly.

9. *Accuracy of the Method.*—To determine whether the theoretical sensitiveness of the apparatus would hold in practice, tests were made in December and January, and again in March at the close of the experiments. The method consisted in placing the junctions in baths of known temperatures, finding the corresponding displacement on the bridge wire, computing the temperature by applying the proper factor obtained from the curve, and then comparing the calculated with the actual temperature difference. The results are given in Table II.

Table II shows representative readings taken from a large number. The average error of the December and January readings is only 0.0155°; the greatest for any one reading 0.055°. For March the average error is 0.0233°; the greatest 0.056°.

10. *Uniformity of the Junctions.*—Table III gives the results of an experiment to test the uniformity of the junctions used. Two sets of junctions were placed in the same baths. By throwing a switch, changes from one set to the other could be made in rapid succession. A number of other tests gave results similar to those in the table.

The greatest difference in displacement is 2 mm. This, at the temperature difference given (5.04°) represents an error of 0.023° C., or .4 per cent.

11. *Sources of Error.*—The possible sources of error in this method are: (1) Variation in the current due to weakening of the cell; (2) the

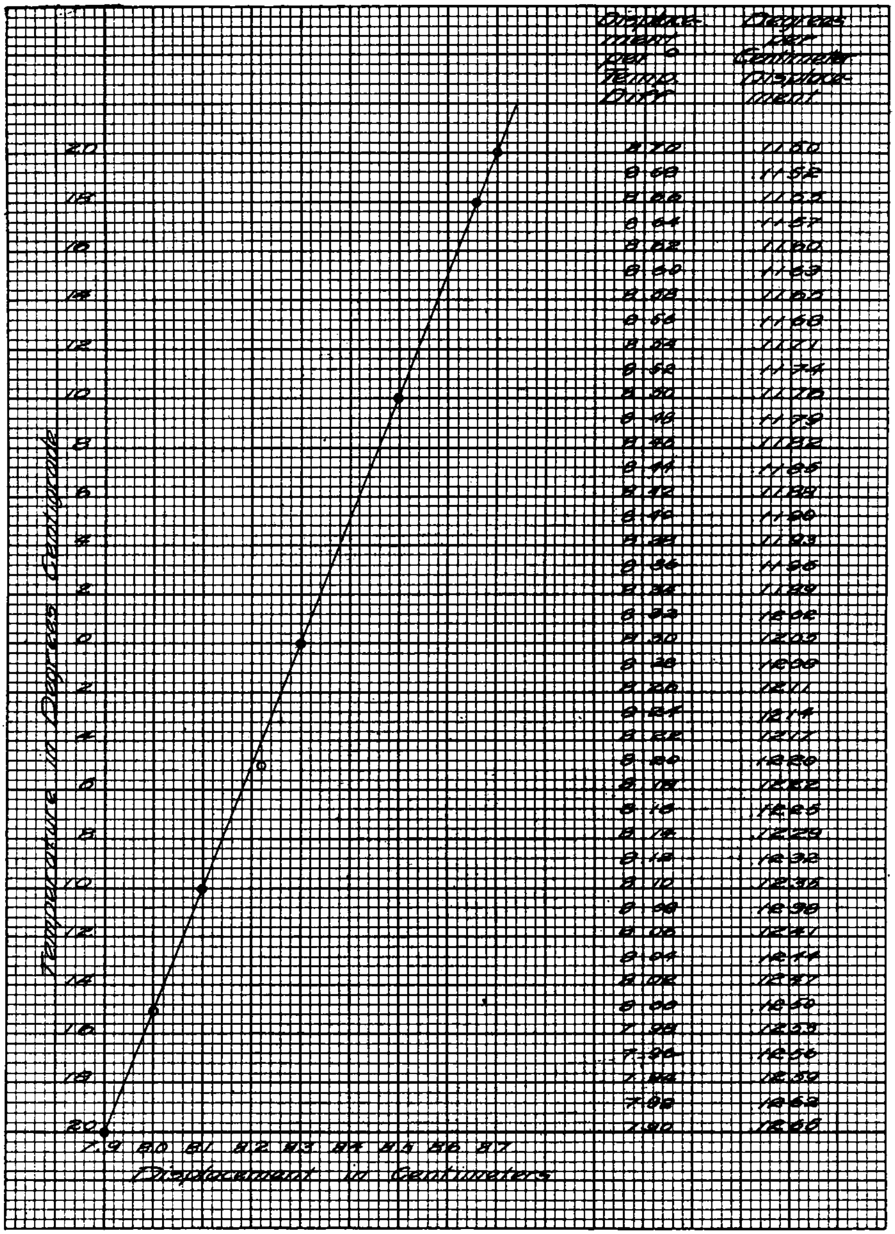

FIG. 2 Curve showing displacement in centimeters on wheatstone bridge. The temperatures from zero down the column are all minus.

TABLE II

Date	Temperature			Displacement in Cm.	Calculated Temp. Diff. in Deg. Cent.	Error
	A	*B*	Actual Difference			
Dec. 27	24.53°	18.38°	6.15°	53.2	6.149°	0.001°
	24.52	18.39	6.13	52.9	6.115	0.015
	26.25	18.40	7.85	68.3	7.895	0.045
	24.65	18.85	5.80	50.2	5.803	0.003
	24.62	18.85	5.77	49.8	5.757	0.013
	23.35	18.90	4.45	38.6	4.462	0.012
	23.32	18.93	4.39	38.0	4.392	0.002
Dec. 28	20.21	18.04	2.17	18.8	2.173	0.003
	21.86	18.02	3.84	33.2	3.838	0.002
	19.19	18.16	1.03	8.9	1.029	0.001
	19.13	18.15	.98	8.5	.983	0.003
Jan. 5	8.00	0.00	8.00	66.7	8.037	0.037
	5.00	0.00	5.00	41.6	5.013	0.013
	2.97	0.00	2.97	24.7	2.976	0.006
Jan. 11	−7.40	−14.68	7.28	58.4	7.293	0.013
	−7.18	−14.70	7.52	60.4	7.543	0.023
	−7.05	−14.00	6.95	55.6	6.950	0.000
	−9.25	−16.67	7.42	58.7	7.365	0.055
	−9.80	−17.03	7.23	57.3	7.198	0.032
	−5.05	−10.00	4.95	39.9	4.924	0.026
					Average error	0.0155
Mar. 22	4.15	0	4.15	34.2	4.118	0.032
	4.18	0	4.18	34.8	4.190	0.010
	4.28	0	4.28	35.7	4.298	0.018
	4.38	0	4.38	36.4	4.383	0.003
	4.45	0	4.45	36.6	4.406	0.056
	4.56	0	4.56	37.9	4.563	0.003
	4.77	0	4.77	39.7	4.789	0.019
	5.18	0	5.18	42.8	5.153	0.027
	5.34	0	5.34	44.2	5.322	0.018
	5.45	0	5.45	45.0	5.418	0.032
	5.50	0	5.50	46.0	5.538	0.038
					Average error	0.0233

formation of secondary couples; (3) heat due to wounding of the leaf tissue; (4) loss of heat by conduction along the lead wires.

(1) *Variation of the Current from the Cell.*—To guard against any variation of the current from the cell, a Weston voltmeter and a rheostat were connected across the terminals of the potentiometer circuit as already described. The simple throwing of a switch enabled the operator to detect any change in the voltage applied to the potentiometer circuit. Corrections could then be made by varying the resistance of the rheostat.

TABLE III
COMPARISON OF JUNCTIONS

Date	Temperature			Displacement in Cm.		Diff. in Mm.
	A	*B*	Diff.	Junct. No. 1	Junct. No. 2	
Jan. 3	22.85°	20.42°	2.43°	21.0	20.9	1
	22.90	20.42	2.48	21.5	21.4	1
	23.04	20.48	2.56	22.2	22.1	1
	24.10	20.53	3.57	31.0	31.0	0
	24.10	20.53	3.57	31.0	31.0	0
	24.09	20.55	3.54	30.8	30.7	1
	25.60	20.56	5.04	43.7	43.5	2
	25.57	20.57	5.00	43.4	43.4	0
	26.58	20.56	6.02	52.3	52.3	0
	26.55	20.60	5.95	51.9	51.8	1
Jan. 4	20.28	19.24	1.04	9.0	9.0	0
	19.60	19.21	.39	3.4	3.3	1
	19.45	19.15	.30	2.7	2.6	1
	19.50	19.17	.33	2.9	2.9	0
	29.80	19.04	10.76	93.2	93.2	0
	29.78	19.04	10.74	93.1	93.0	1

(2) *The Formation of Secondary Couples.*—Any difference in the composition of the metals at the connections, or any slight difference in the composition of the metal in the wires themselves may, if there is a difference in temperature at those points, cause the formation of secondary couples. For the purpose of this investigation the latter case may be neglected, as the error arising from this source would be exceedingly small. To guard against secondary couples at the connection of the lead wires with the heavy copper wires, copper binding posts were used and the joints placed as closely together as practicable to insure the same temperature for both. The connections with the apparatus in the laboratory were all under uniform temperature conditions throughout the experiments and, consequently, the danger from secondary couples at those points was reduced to a minimum.

(3) *Heat Due to the Wounding of the Leaf Tissue.*—The development of heat in wounded tissue is due to an increased respiration of the injured part. Tiessen (30) found that the rise in temperature due to wounding increases with the extent of the wound; that its duration varies from one half to three days; and that its absolute value varies from 0.02° to 0.08° C. with an average of 0.04° C. Richards (22) has shown that a curve plotted for the heat developed in wounded tissue corresponds in the main to that of the respiration intensity under the

same conditions. Now since respiration is but feeble at 0° C. and decreases rapidly as the temperature falls [Maximow (16), Matthaei (14)], and since nearly all the readings were taken at 0° C. and below, and since the wound made in the leaf was very small, any increase in temperature due to wounding would not be appreciable.

(4) *Loss of Heat by Conduction Along the Lead Wires*.—This was, in all probability, the source of greatest error and could not be entirely overcome. As already stated, two leaves were fastened together and the lead wires drawn through them at an angle in order to give as large a contact surface as possible. To determine what the loss from this source might be, the following experiment was made. A small glass tube 15 cm. long with a bore of 5 mm. was furnished with two side arms and two minute openings. Three thermo-junctions, such as were used in taking the leaf temperatures, were inserted in this tube as shown in figure 3. Through this tube kerosene oil was siphoned from a bath kept at a temperature of 10° C. above the room temperature. The leads of junction 1 were in contact with the heated oil the entire length of the tube, and this junction should therefore record accurately the temperature of the flowing oil. The leads of junction 2, on the other hand, were in contact with the oil for a distance of .5 mm. to 1 mm. for the advance lead and 4 mm. for the copper—a condition similar to that of the junction in the leaf. By connecting junctions 1 and 2 with the potentiometer, any difference in temperature between these junctions due to loss of heat by conduction from junction 2 could be measured. By connecting junctions 1 and 3 in the same way the temperature gradient between the flowing oil and the surrounding air could be determined. A three-way switch enabled the operator to measure both in rapid succession. Repeated trials gave an average displacement on the bridge for junctions 1 and 3 of 84.5 cm. which at the room temperature was equivalent to a temperature difference of 9.7° C. Junctions 1 and 2 gave an average displacement of .36 cm. This repre-

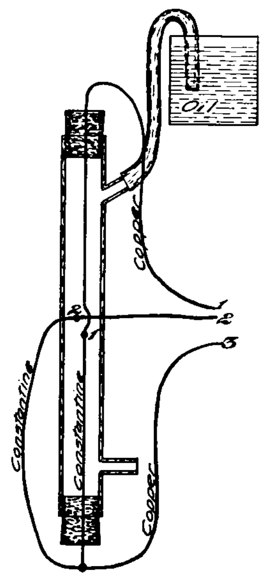

FIG. 3. Showing the details of the three thermo-junctions.

sents a temperature difference between these junctions of 0.04° C., *i. e.*, enough heat is lost by conduction from junction 2 to reduce its temperature 0.04° C. below the true temperature of the oil. When it is borne in mind that the temperature gradient between air and oil in this experiment was 9.7° C., and that the maximum temperature gradient between leaf and air under natural conditions was 8.83° C. and the average considerably below this, it is evident that the error arising from loss of heat by conduction along the lead wires is also negligible. Furthermore it is compensated for in part by the very small increase in temperature due to wounding.

(5) *Absorption of Radiation by the Junction in the Leaf.*—It may have occurred to the reader that the rise in temperature indicated by a junction placed in a leaf exposed to direct sunlight may be due in part to the absorption of radiation by the junction itself. Smith (28) has shown that this is not true. By alternately shading a junction by means of a small piece of pith and exposing it to direct sunlight, he found that direct sunlight had no effect upon the junction whatever. He concludes from his experiment that "the rise of temperature of a junction registered when it is placed in a leaf exposed to direct sunlight must all be due to the absorption of radiation by the leaf, and no part of it to the absorption of radiation by the junction itself." Smith's result was accepted by the author and no experiments were made to verify it.

12. *Meteorological Data.* (1) *Air Temperature.*—In the earlier experiments the air temperature was obtained with a mercury thermometer graduated to degrees Centigrade. Later a registered thermometer graduated to .1° C. was used. No attempt was made to read the air temperature beyond one tenth degree. The thermometers were hung behind the screen upon the platform.

(2) *Solar Radiation.*—For purposes of comparison, the intensity of the solar radiation was also taken. For this a black bulb in vacuum thermometer graduated to the Fahrenheit scale was employed. It was placed on the platform near the leaf. For the sake of uniformity the readings were converted into degrees Centigrade.

(3) *Velocity of the Wind.*—For this a self-registering anemometer making contact every one tenth mile was used. The miles of wind per five minute periods could be determined. The anemometer was placed upon the platform near the leaf; the registering device in the laboratory.

(4) *Relative Humidity.*—The relative humidity was obtained from the records of the university observatory situated about one half mile from the campus. The values given represent the average from 7 a.m. to 7 p.m.

IV. Experimental Data

A. Leaf Temperature under Winter Conditions

The collection of data began early in January. Of the mass of data obtained only a part can be given. The results shown by the tables following in the text may be taken as representative.

The readings, as a rule, were taken from one half to three minutes apart for a period of five to ten minutes. Then the air temperature, radiation, and the wind velocity were recorded for that period. To save space, the average of the readings for the period is given, as a rule. In a few cases all the readings are given to show the rapidity of temperature changes within the leaf.

The readings of the black bulb in vacuum thermometer are the maxima for the period unless otherwise indicated.

The wind velocity given in column 9 is the average for the period as recorded by the anemometer on the platform and has only general value. Since the tree, partly sheltered from direct winds by the neighboring buildings, was subject to sudden gusts and eddy currents, some of which were vertical and did not, therefore, affect the anemometer, the velocity given does not necessarily represent the true velocity at the moment the leaf temperatures were taken.

Column 4 in the tables gives the differential temperature between the leaf and the shade temperature of the air. The values are obtained by multiplying the bridge readings by the factor (see figure 2) indicated by the shade temperature given in column 5. Column 8 gives the actual temperature of the leaf. The values are obtained by adding the differential temperature to the air temperature. Column 7 gives the difference between the shade temperature and that recorded by the black bulb in vacuum thermometer—a better standard for comparison than the values in column 6. In general, the differential temperature between leaf and air increases as the radiation increases. When this is not the case, an explanation can usually be found by referring to the wind velocity recorded in column 9.

The data presented here are given to show: (1) the effect of full sunlight; (2) the effect of one fourth to one half full sunlight; (3) the effect of diffuse light; (4) the leaf temperature at night; (5) the effect of strong air currents; (6) the temperature of leaves at different angles to the sun's rays.

(1) *The Effect of Full Sunlight.*—Unfortunately no data on the effect of full sunlight in still air could be obtained. Low temperature, still air, and full sunlight are a combination of conditions that rarely obtains. The nearest approach to these conditions was found on February 24. The data obtained are given in Table IV.

TABLE IV

February 24, 1914

Clear. Light breeze. Relative humidity 87%

1	2	3	4	5	6	7	8	9
Time of Observation	No. of Observations	Aver. Bridge Reading in Cm.	Calculated Temp. Diff.	Shade Temp.	Black Bulb in Vacuum	Diff. Columns 5 and 6	Actual Leaf Temp.	Wind Velocity Miles per Hr.
9.00– 9.02	4	26.1	3.26°	−15.0°	5.6°	20.6°	−11.74°	1.2
9.21– 9.24	4	48.4	6.04	−14.1	14.4	28.5	− 7.06	1.2
9.28– 9.33	7	44.4	5.54	−14.0	20.0	34.0	− 8.46	2.4
10.02–10.04	4	60.4	7.51	−13.0	20.6	33.6	− 5.49	.4
10.50–10.55	7	44.0	5.46	−12.2	25.6	37.8	− 6.74	.8
11.00	1	56.0	6.96				− 5.54	
11.005	1	37.2	4.52				− 7.98	
11.01	1	50.8	6.31				− 6.19	
11.015	1	38.2	4.75				− 7.75	
11.02	1	64.0	7.95	−12.5	28.3	40.8	− 4.55	1.2
11.025	1	59.6	7.41				− 5.09	
11.03	1	46.5	5.78				− 6.72	
11.04	1	40.0	4.97				− 7.53	
11.05	1	54.0	6.71				− 5.79	
11.08–11.12	4	58.1	7.21	−12.0	28.9	40.9	− 4.79	1.2
11.25–11.32	8	56.5	7.00	−11.1	28.9	40.0	− 4.10	.9
11.29–12.35	7	57.6	7.11	−10.2	29.4	39.6	− 3.09	.5
2.35– 2.40	8	41.5	5.13	−10.0	11.7	21.7	− 4.87	.3
		Averages	6.04	−12.4		33.8	− 6.36	1.0

With the shade temperature of the air varying from − 15° to − 10° C. the black-bulb thermometer registering from 20.6° to 40.9° C. higher, and the wind velocity varying from 0.3 to 2.4 miles per hour, the average differential temperature between leaf and air for the entire time during which the readings were taken was 6.04° C., *i. e.*, the leaf maintained, under the conditions given, a temperature of 6.04° C. higher than the air. This is shown by the averages of columns 4, 5, and 8. The maximum temperature difference for the day was 7.95° C.

The following Table V shows a maximum leaf temperature of 8.83° above that of surrounding air, the air temperature in this series of observations being considerably higher than that shown in Table IV.

TABLE V

February 27, 1914

Clear. Light breeze. Relative humidity 66.5%

1	2	3	4	5	6	7	8	9
Time of Observation	No. of Observations	Aver. Bridge Reading in Cm.	Calculated Temp. Diff.	Shade Temp.	Black Bulb in Vacuum	Diff. Columns 5 and 6	Actual Leaf Temp.	Wind Velocity Miles per Hr.
8.00[2]	5	5.7	.69°	– 2.0°	7.2°	9.2°	–1.31°	1.2
9.15	4	18.6	2.24	0	18.9	18.9	2.24	1.2
9.25	5	16.4	1.97	0.8	20.6	19.8	2.77	3.6
9.33	8	32.5	3.90	1.5	23.9	22.4	5.40	1.0
10.05	5	46.9	5.60	3.0	24.4	21.4	8.60	1.2
10.54	1	50.5	6.02	4.0	29.3	25.3	10.02	1.2
10.55	1	66.5	7.93				11.93	
10.555	1	73.0	8.71				12.71	
10.56	1	74.6	8.83				12.83	
10.565	1	58.5	6.98				10.98	
10.57	1	61.2	7.30				11.30	
10.58	1	63.0	7.52				11.52	
10.59	1	57.0	6.80				10.80	
11.05	5	28.1	3.35	4.2	31.7	27.5	7.55	2.4
12.34	6	18.5	2.20	5.1	32.2	27.1	7.30	2.4
		Average	3.82	2.66			6.48	

The conditions under which the results in Table VI were obtained differ somewhat from those of the preceding Table IV. The air temperature averaged 3.85° C. lower and the average wind velocity was .7 miles per hour greater. Also the difference between the shade temperature and that recorded by the black-bulb thermometer was 2.7° C. lower. Under these conditions the average differential temperature between leaf and air was 3.56° C. and the maximum 5.19° C.

(2) *The Effect of One Fourth to One Half Full Sunlight.*—That a decrease in the intensity of solar radiation, other conditions remaining

[2] Not included in the averages.

TABLE VI

February 12, 1914

Clear. Moderate breeze. Relative humidity 86.5%

1	2	3	4	5	6	7	8	9
Time of Observation	No. of Observations	Aver. Bridge Reading in Cm.	Calculated Temp. Diff.	Shade Temp.	Black Bulb in Vacuum	Difference Columns 5 and 6	Actual Leaf Temp.	Wind Velocity Miles per Hr.
9.55	1	40.6	5.12°	−19.0°	12.8°	31.8°	−13.88°	1.2
10.20	1	30.0	3.78	−18.1	12.8	30.9	−14.32	1.2
10.48	4	27.8	3.49	−17.2	16.1	33.3	−13.71	2.4
10.58	5	34.2	4.30	−17.0	20.0	37.0	−12.70	1.2
11.05	6	41.4	5.19	−16.0	22.2	38.2	−10.81	1.2
11.46	4	30.0	3.76	−16.0	20.0	36.0	−12.24	2.4
12.26	6	31.8	3.98	−15.8	20.6	36.4	−11.82	1.8
12.36	7	37.0	4.64	−16.2	21.2	37.3	−11.56	1.8
1.38	4	20.3	2.54	−15.5	13.9	29.4	−12.96	1.8
1.47	4	30.7	3.84	−15.0	12.8	27.8	−11.16	1.8
1.56	8	19.3	2.41	−15.2	11.7	26.9	−12.79	1.8
1.36	4	15.4	1.93	−15.0	5.6	20.6	−13.07	1.2
2.50	2	10.5	1.31	−15.2	3.3	18.5	−13.89	1.8
2.54[3]	1	6.5	.81	−15.2	3.3	18.5	−14.39	1.8
		Average	3.56°	−16.25		31.1	−12.68	1.7

constant, is followed by a decrease in the differential temperature between leaf and air needs, of course, no proof. Nevertheless the tables given are of interest since they show the actual temperatures of the leaf under the conditions existing. Results are given in Tables VII, VIII and IX where the column headings are the same for all tables.

TABLE VII

January 16, 1914

Hazy. Light breeze. Relative humidity 93%

1	2	3	4	5	6	7	8	9
Time of Observation	No. of Observations	Aver. Bridge Reading in Cm.	Calculated Temp. Diff.	Shade Temp.	Black Bulb in Vacuum	Difference Columns 5 and 6	Actual Leaf Temp.	Wind Velocity Miles per Hour
11.10	5	21.3	2.54°	5.0°	25.6°	20.6°	7.54°	No data
11.40	6	15.9	1.90	5.2	25.6	20.4	7.10	
11.58	2	15.9	1.90	5.5	25.6	20.1	7.40	
12.30	5	18.2	2.17	5.7	25.6	19.9	7.87	
12.40	6	20.4	2.42	5.8	27.0	21.2	8.22	
12.50	7	26.8	3.18	6.0	27.8	21.8	9.18	
1.10	3	18.9	2.25	6.5	27.5	21.0	8.75	
1.23	7	18.2	2.17	5.3	26.7	21.4	7.47	
1.35[4]	6	8.2	.97	5.2	26.1	20.9	6.17	
		Average	2.17	5.58		20.8	7.74	

[3] Leaf in shadow; not included in the averages.

[4] Leaf in shadow.

Table VIII

January 25, 1914

Approximately one half full sunshine. Light breeze. Relative humidity 78.5%

1	2	3	4	5	6	7	8	9
9.45	1	22.5	2.77°				−5.73°	
9.47	1	21.5	2.65				−5.85	
9.48	1	20.3	2.50	−8.5°	16.7°	25.2°	−6.00	1.2
9.49	1	20.0	2.46				−6.04	
9.50	1	25.7	3.17				−5.33	
9.53	1	26.8	3.30				−5.20	
11.10	1	26.9	3.31				−4.69	
11.11	1	33.7	4.14				−3.86	
11.12	1	36.3	4.46	−8.0	20.0	28.0	−3.54	0.8
11.15	1	36.3	4.46				−3.54	
11.20	1	32.5	3.99				−4.01	
11.22	1	36.7	4.51				−3.59	
		Average	3.47	−8.25		26.6	−4.78	

Table IX

February 2, 1914

Approximately one fourth full sunshine. Breeze moderately strong. Relative humidity 83.5%

1	2	3	4	5	6	7	8	9
Time of Observation	No. of Observations	Aver. Bridge Reading in Cm.	Calculated Temp. Diff.	Shade Temp.	Black Bulb in Vacuum	Difference Columns 5 and 6	Actual Leaf Temp.	Wind Velocity Miles per Hr.
10.34	1	24.8	3.00°	−1.0°	20.0°	21.0°	2.00°	
10.40	5	14.5	1.75	−0.8	22.2	23.0	.95	4.8
11.00	4	14.0	1.69	−0.5	22.2	22.7	1.19	4.8
11.15	5	11.5	1.39	0	17.8	17.8	1.39	4.8
11.46	5	13.5	1.63	0	18.3	18.3	1.63	4.8
11.55	3	16.1	1.94	0.2	19.2	19.0	2.14	3.7
12.36	3	10.9	1.31	1.0	16.7	15.7	2.31	3.2
1.25	3	18.9	2.27	1.8	19.7	17.9	4.07	3.6
1.31	4	21.5	2.58	2.0	22.2	20.2	4.58	3.6
2.34	3	11.0	1.39	2.5	19.4	16.9	3.89	3.6
		Average	1.89	0.52		19.25	2.41	

With approximately one fourth of full sunlight, and with a light breeze blowing, the maximum differential temperature obtained was 3.18° C. and the average 2.17° C. (Table VII); with approximately the same radiation (compare column 7, Tables VII and IX) and a moderate breeze blowing, the maximum is 3.0° C. and the average only 1.89° C.; with approximately one half of full sunlight (Table VII) and a light breeze, the maximum is 4.51° C. and the average 3.47° C., as compared with a maximum of 7.95° C. and an average of 6.09° C. under full sunlight (Table IV).

(3) *The Effect of Diffuse Light.*—Even on dark, cloudy, winter days, pine leaves absorb sufficient radiant energy to maintain a temperature slightly above that of the air. On a few very dark days the potentiometer gave zero displacement, indicating that the leaf temperature was the same as that of the air, but, as a rule, the leaf was found to be from 0.34° C. to a little more than 2° C. higher than the air temperature, depending upon the brightness of the diffuse light. In only one case was the leaf temperature found to be lower than that of the air during the hours of daylight. This occurred on January 29, when the air temperature was comparatively high. The average for the days given in Table X is 0.95° C.

TABLE X

January 18, 1914

Cloudy. Light breeze. Relative humidity 77%

1	2	3	4	5	6	7	8	9
Time of Observation	No. of Observations	Aver. Bridge Reading in Cm.	Calculated Temp. Diff.	Shade Temp.	Black Bulb in Vacuum	Diff. Columns 5 and 6	Actual Leaf Temp.	Wind Velocity Miles per Hr.
12.30	9	9.6	1.16°	−2.2°	9.4°	11.6°	−1.04°	
12.48	3	8.2	.99	−2.0	7.2	9.2	−1.01	
		Average	1.08	−2.1			−1.02	

January 23, 1914

Cloudy. Breeze moderate. Relative humidity 100%

1	2	3	4	5	6	7	8	9
10.15	5	11.0	1.31°	4.0°	17.8°	13.8°	5.31°	1.2
10.33	6	4.9	.58	5.1	14.4	9.3	5.68	2.4
1.15	5	5.1	.61	6.0	15.6	9.6	6.61	2.4
		Average	.83	5.03			5.86	

February 19, 1914

Cloudy. Breeze moderate. Relative humidity 89.5%

1	2	3	4	5	6	7	8	9
12.38	5	12.9	1.58°	−6.0°	12.8°	18.8°	−4.42°	3.0
1.30	5	17.8	2.17	−5.5	17.2	22.2	−3.33	2.4
		Average	1.88	−5.75			−3.87	

March 22, 1914

Cloudy. Light breeze

1	2	3	4	5	6	7	8	9
8.40	6	2.8	.34°	−0.8°	7.2°	8.0°	−0.46°	
12.30	7	5.6	.67	1.4	9.4	8.0	2.07	
1.30	1	0	0	1.0	2.0	1.0	1.00	
		Average	.34	.53			.87	

(4) *The Leaf Temperature at Night.*—Throughout February and a part of March readings were taken at six and ten p.m. The results obtained are represented by the values given in Table XI. A few readings show no difference in temperature between the leaf and the air, but, as a rule, the leaf is from 0.1° to 0.7° C. colder than the air.

TABLE XI

Date		Bridge Read.		Computed Temp. Diff.		Air Temp.		Rel. Humidity	Atmospheric Conditions
		6 PM.	10 PM.	6 PM.	10 PM.	6 PM.	10 PM.	7 PM.	
Feb.	7	−2.0[5]	−2.5[5]	0.25°	0.32°	−10.0°	−11.0°	80%	Clear; wind light.
"	8	0	−2.0	0	0.25	−18.5	−20.0	67	Clear; wind strong.
"	9	−1.0	−2.5	0.13	0.31	−10.0	− 9.5	74	Clear; wind strong.
"	10	−2.8	0	0.35	0	−12.0	−14.0	55	Wind light 6 P.M.; Calm 10 P.M.
"	11	−2.5	−2.5	0.31	0.32	−16.0	−19.5	77	Wind moderate.
"	12	−2.0	−2.5	0.25	0.32	−17.0	−19.0	73	Wind moderate.
"	13	0	−1.5	0	0.19	−13.0	−14.0	75	Cloudy; wind moderate.
"	16	−1.5	−1.2	0.19	0.15	−10.0	−12.0	81	Cloudy; wind moderate.
"	19	−5.0	−3.6	0.62	0.45	− 9.0	−12.0	88	Clear; calm.
"	25	−3.5	−6.0	0.45	.73	− 7.0	−10.0	44	Clear; calm.
Mar.	5	−1.0	−1.5	0.12	0.18	0	− 2.0	78	Cloudy; wind light.
"	6	−0.5	0	0.06	0	0.5	0	73	Cloudy; wind light.
"	7	−0.3	0	0.04	0	− 1.5	− 4.0	100	Snowing; wind light.
			Average	0.21	0.25				

(5) *Effect of the Wind in Reducing the Leaf Temperature.*—The effect of the wind in reducing the leaf temperature is well illustrated in Tables XII and XIII. The average differential temperature between leaf and air for the two tables is 2.93° C. as compared with 6.04° C. in Table IV. A part of this reduction in differential tempera-

[5] Negative sign under bridge reading indicates that the current was reversed and that the leaf was colder than the air.

ture is due, no doubt, to a difference in intensity of insolation, column 7 of Table IV showing slightly higher values than the corresponding columns in Tables VI, XII and XIII. But the difference in the intensity of insolation is slight and can account for only a small part of the reduction. The wind, therefore, is the important factor.

TABLE XII

February 1, 1914 .

Clear. Strong wind.[6] Relative humidity 71%

1	2	3	4	5	6	7	8	9
Time of Obser-vation	No. of Obser vations	Aver. Bridge Readings in Cm.	Computed Temp. Diff.	Shade Temp.	Black Bulb in Vacuum	Diff. Columns 5 and 6	Actual Leaf Temp.	Wind Velocity Miles per Hr.
12.35	3	17.4	2.11°	−3.0°	28.6°	31.6°	−0.89°	6.0
12.45	6	22.1	2.68	−3.1	29.0	32.1	−0.42	6.0
1.50	11	27.0	3.28	−3.5	29.2	32.7	−0.22	6.0
1.58	5	23.8	2.89	−3.2	20.0	23.2	−0.31	4.8
		Average	2.74	−3.2		29.9	−0.46	

March 2, 1914

Relative humidity of 90%

1	2	3	4	5	6	7	8	9
8.52	7	15.4	1.91°	−12.2°	9.4°	21.6°	−10.29°	4.8
9.36	4	17.1	2.12	−11.3	21.1	32.4	− 9.18	4.8
10.06	8	23.0	3.83	− 8.5	27.2	35.7	− 4.67	5.0
11.00	1	20.0	2.46	"	"	"	− 6.04	3.6
	1	10.5	1.29	"	"	"	− 7.21	"
	1	7.5	.92	"	"	"	− 7.58	"
	1	22.6	2.78	"	"	"	− 5.72	"
	1	26.5	3.26	"	"	"	− 5.24	"
	1	13.2	1.62	"	"	"	− 6.88	"
	1	19.0	2.34	"	"	"	− 6.16	"
	1	7.0	.86	"	"	"	− 7.64	"
	1	22.5	2.77	"	"	"	− 5.73	"
	1	39.3	4.83	"	"	"	− 3.67	"
11.05	1	28.0	3.44	"	"	"	− 5.06	"
12.31	8	16.8	2.06	− 6.5	26.1	32.6	− 4.44	4.8
		Average	2.61	− 9.4		31.6	− 6.93	

The effect of gusts of wind is shown in the rapid fluctuations in the differential temperature for the period 11.00 to 11.05, Tables IV and XIII. Fluctuations of 2° and 3° C. occur within one half minute.

[6] Wind velocity, University Observatory record, Feb. 1, 15 miles per hour; March 2, 26 miles per hour.

TABLE XIII

February 8, 1914

Clear. Strong wind.[7] Relative humidity 71%

1	2	3	4	5	6	7	8	9
Time of Observation	No. of Observations	Aver. Bridge Reading in Cm.	Calculated Temp. Diff.	Shade Temp.	Black Bulb in Vacuum	Diff. Columns 5 and 6	Actual Leaf Temp.	Wind Velocity Miles per Hr.
9.45	2	16.7	2.09°	−15.5°	10.0°	25.5°	−13.41°	6.0
10.15	1	20.2	2.48	−14.5	11.1	25.6	−12.02	6.0
10.37	7	24.0	3.00	−14.5	15.6	30.1	−11.50	6.0
10.47	7	23.1	2.87	−14.5	17.2	31.7	−11.63	6.0
10.56	5	30.1	3.75	−14.3	18.2	32.5	−10.55	4.8
11.04	6	34.5	4.30	−14.0	19.8	33.8	− 9.70	6.0
11.45	7	32.8	4.09	−14.2	19.9	34.1	−10.11	6.0
12.17	12	38.7	4.83	−13.8	22.2	36.0	− 8.97	6.0
1.38[8]	8	28.7	3.58	−13.8	22.2	36.0	−10.22	6.0
		Average	3.44	−14.34		31.7	−10.90	

These fluctuations by no means represent all the changes in the leaf temperature. In fact, the changes were so rapid that it was not possible to adjust the sliding contact quickly enough to record them all. A somewhat nearer approach toward recording all the fluctuations was made in the following way: The galvanometer was calibrated at the existing temperature in terms of displacement along the bridge wire. The sliding contact was held at a fixed point, and the galvanometer deflections read every five seconds for a period of two minutes, an assistant indicating the periods and recording the deflections as read. To insure that the deflections should be due solely to changes in the leaf temperature, the second junction was enclosed in a thermos-bottle and kept at a constant temperature. The results are graphically represented by figure 4.

One series of observations and measurements was made on a detached branch with cut end immersed in water, and the preparation protected from the wind by a thin cloth screen except on the south side. The results, given in the following table, show that in quiet air the temperature of the leaf may rise to 10° above that of the surrounding air.

In making up the averages the average readings for the periods are taken.

[7] Wind velocity, university observatory record, 18 miles per hour.
[8] Leaf in shadow for a part of the period.

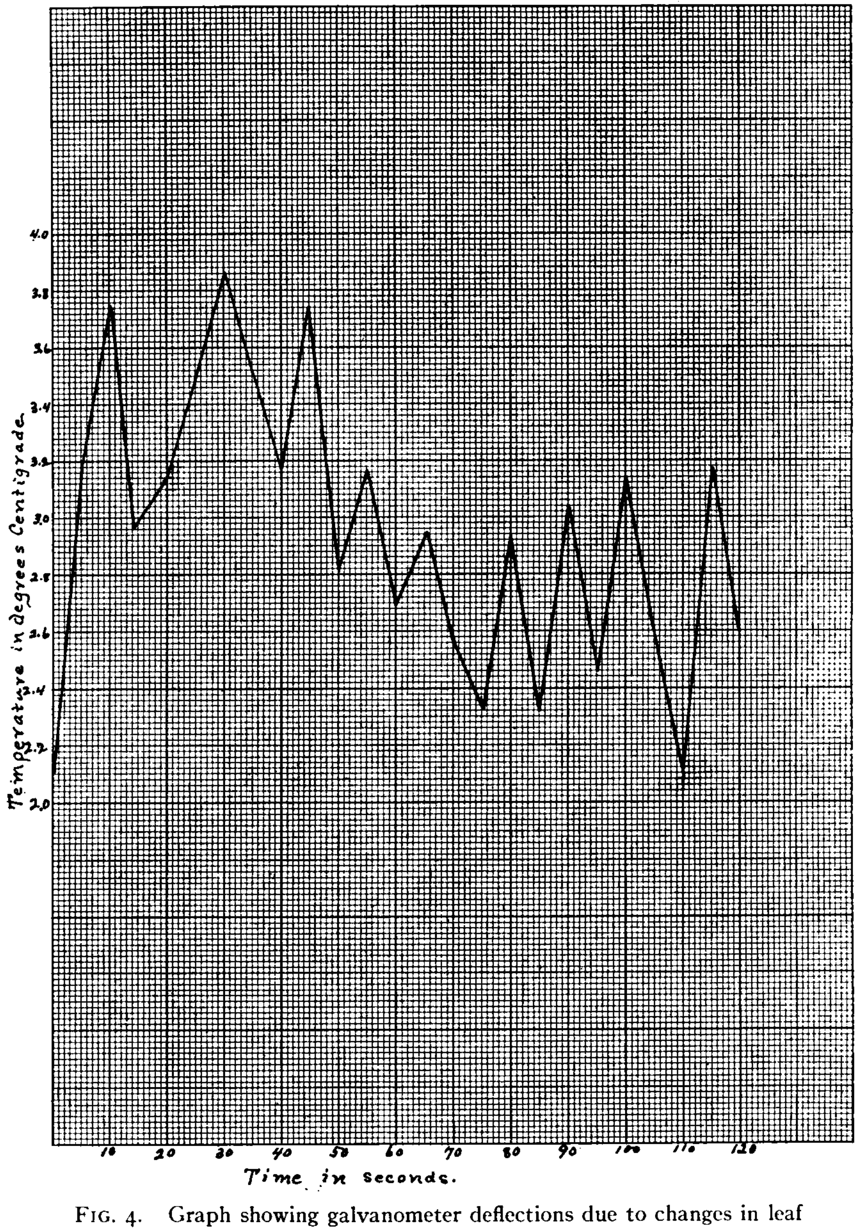

FIG. 4. Graph showing galvanometer deflections due to changes in leaf temperature.

TABLE XIV

March 10, 1914

Clear. Breeze light. Relative humidity 76%

Detached branch partially protected against air currents by cheese cloth screen.

1	2	3	4	5	6		8
Time of Observation	No. of Observations	Aver. Bridge Reading in Cm.	Calculated Temp. Diff.	Shade Temp.	Black Bulb in Vacuum	Diff. Columns 5 and 6	Actual Leaf Temp.
10.45	1	64.0	7.69°				9.69°
	1	50.5	6.07				8.07
10.46	1	63.8	7.67				9.67
10.47	1	73.0	8.77	2.0°	32.2°	30.2°	10.77
10.48	1	85.8	10.31				12.31
10.49	1	82.0	9.86				11.86
10.50	1	75.0	9.02				11.02
11.47	1	74.0	8.83				13.03
	1	71.5	8.53				12.73
11.48	1	61.0	7.28				11.48
	1	77.0	9.17				13.37
	1	74.2	8.85	4.2	35.0	30.8	13.05
11.50	1	79.4	9.47				13.67
	1	79.4	9.47				13.67
	1	73.0	8.71				12.91
11.51	1	74.4	8.88				13.08
12.40	1	75.5	8.98				14.48
	1	80.0	9.52				15.02
12.41	1	63.5	7.56				13.06
	1	66.0	7.85				13.35
12.42	1	71.5	8.51				14.01
	1	69.5	8.27	5.5	36.7	31.2	13.77
12.43	1	76.4	9.09				14.59
	1	65.0	7.73				13.23
12.44	1	75.0	8.93				14.43
	1	61.8	7.35				12.85
12.45	1	76.5	9.10				14.60
12.54	1	82.0	9.76	5.5	36.7	31.2	15.26
12.55	1	85.2	10.12				15.62
1.05	1	83.0	9.88				14.88
	1	64.5	7.68	5.50	35.0	30.0	12.68
1.06	1	79.5	9.46				14.46
1.07	1	72.5	8.63				13.63
		Average	8.91	4.44			13.35

(6) *The Temperature of Leaves at Different Angles to the Sun's Rays.*—Finally an experiment was made to determine the difference in temperature between two leaves at different angles to the sun's

rays—one at approximately 45°, the other at 90°. For this purpose a cut branch, partially protected from the wind by a screen of white cheese cloth, was exposed to solar illumination. The screen was open at the top to prevent the enclosed air from becoming heated. Doubtless there was some reflected radiation, but, since the leaves were side by side within the enclosure and therefore under the same conditions, this did not affect the results. These are given in Table XV. Other attempts in which the differential temperatures of the two leaves were read alternately in rapid succession gave similar results.

TABLE XV

March 5, 1914

Temperature of leaves at different angles

	Time of Observation	Aver. Bridge Reading in Cm.	Calculated Temp. Diff.	Shade Temp.	Black Bulb in Vacuum
Angle 45°	2.15	45.4	5.29°	14.0°	36.1°
		49.8	5.80		
		46.3	5.39		
		48.0	5.59		
		38.6	4.50		
		43.0	5.01		
		31.0	3.61		
	2.20	35.5	4.14		
	Average	42.2	4.92		
Angle 90°	2.25	58.9	6.86°	14.2°	36.0°
		64.2	7.47		
		64.5	7.51		
		57.1	6.65		
		49.0	5.71		
		47.0	5.48		
		54.5	6.35		
		50.0	5.83		
	2.30	54.6	5.36		
	Average	55.5	6.36		

B. Direct Evidence of Photosynthesis in Winter

An attempt was made to obtain direct evidence of photosynthesis under winter conditions by examining for starch content the leaves of the various conifers growing in the university arboretum. The leaves were collected in early morning and again in late afternoon of clear days. They were kept in 75 per cent alcohol and later examined microscopically. Thin sections were placed on a slide and treated with absolute alcohol and ether to remove the fats, and then with a solution of chloral-iodine and potassium iodide. During the autumn and through December the leaves of *Pinus laricio austriaca* Endl. only were examined. Later other species were added. From five to ten leaves were examined in each case.

In the leaves of *Pinus laricio austriaca* starch remained abundant in mesophyll, endodermis, and transfusion tissue throughout October and November. But leaves collected December 2, after a period of seven dark, rainy days—maximum temperature for the entire period 14° C. and the mean 6.7° C.—showed, when examined, no starch in the mesophyll and only a small amount in the endodermis. Leaves collected from the same branch December 4—maximum temperature 11.6° C. and the mean 6.7° C.—showed a small amount of starch in the mesophyll, endodermis, and transfusion tissue. On December 11, the temperature, in the meantime, having dropped to a minimum of − 7° C. and a maximum of 3° C., the starch had entirely disappeared from all the tissues. Starch was again found on December 12 in the mesophyll, endodermis, and transfusion tissue, and in greater abundance on the following day, the temperature having risen to a maximum of 12 ° C.

Since the temperature on December 4 was colder by several degrees than that of the preceding days, the reappearance of starch could not be due to a regeneration from sugar already present in the leaf, but must have been the result of photosynthesis. On December 13, however, the maximum temperature had risen 9° C. above that of December 11, and the reappearance of starch may have been the result, in part at least, of a regeneration of starch from the sugar present in the leaf, due to an increase in temperature.

When next examined, December 20, starch had entirely disappeared from the mesophyll, though a small amount still remained in the endodermis and in the transfusion tissue. By January 15 the leaves were entirely free from starch with the exception of an occasional group of hyaline mesophyll cells, where it was evidently stored.

Throughout January, February, and early March leaves of a number of conifers were collected and examined, but no further conclusive evidence of photosynthesis was obtained. Some of the species examined retained starch in the mesophyll in greater or less abundance throughout the winter, but no increase in quantity, even after a comparatively warm bright day, could be detected microscopically. In other species groups of hyaline cells filled with large starch granules were observed more or less regularly. These groups usually appeared immediately below the epidermis. No explanation is attempted. The author hopes to make this a subject for further investigation.

While no conclusive evidence of starch formation was observed after December 13, it does not follow that all photosynthetic activity had ceased. Carbohydrates may have been formed and used or translocated as fast as formed. It merely indicates that photosynthesis was not sufficiently active under the conditions that obtained during January and February to result in the production of starch in the leaf.

The species examined and the results obtained are as given below.

No starch: *Pinus strobus* L.

More or less starch:

Juniperus communis L.	*Thuya occidentalis* L.
Juniperus virginiana L.	*Picea Abies* (L.) Karst.
Tsuga canadensis (L.) Carr.	*Abies balsamea* (L.) Mill.

Starch in groups of hyaline cells:

Pinus laricio austriaca Endl.	*Pinus ponderosa* Laws.
Pinus sylvestris L.	*Pinus Banksiana* Lamb.

These results do not agree with those of Schulz (26) and Lidforss (13). The former maintains that the leaves of all gymnosperms except the Gnetaceae contain no starch in winter; the latter states as a universal rule that all green plant cells are free from starch during the winter months. Evidently their results do not hold for southern Michigan just as they do not hold for the warmer portions of Japan as was shown by Miyaké (18). This problem should be given more extended investigation.

V. Summary

The data presented above show that evergreen conifer leaves, even under winter conditions, through the absorption of radiant energy, maintain temperatures from 2° to 10° C. higher than the surrounding air. The maximum obtained under brilliant illumination and with a light breeze blowing was 8.83° C. (Table V). In still air the temperature difference is considerably higher. This was shown

by an experiment in which the leaf was partially protected against air currents. Under these conditions a differential temperature of 10.31° C. was obtained (Table XIV). Under less brilliant illumination and stronger air currents the differential temperature is correspondingly less. Even diffuse light, according to its brightness, will increase the leaf temperature from 0.5° to 2° C. For February, the coldest month of the year, the average differential temperature between leaf and air—650 readings in all, taken between the hours of 8 a.m. and 3 p.m. and under all kinds of weather conditions, cloudy days as well as days of sunshine—was 3.06° C.

The differential temperatures in the winter season, as was to be expected, are considerably less than those obtained by previous investigators for broad leaves under summer and tropical insolation, namely, from 7° to 16° C. The cause of the difference is to be sought in the lower rate of respiratory changes (Molisch (19)), the lower intensity of solar radiation, and in the greater loss of heat by convection, air currents being, as a rule, more constant and stronger during the winter season. Though smaller in winter, the differences are, nevertheless, of sufficient magnitude to become an important factor in photosynthesis.

It should also be remembered that the differential temperatures as found in this investigation are those of the leaf as a whole, and not necessarily those of the chloroplasts. It is the chloroplasts that absorb the most of the radiant energy; the temperature of the leaf is due to radiation and conduction from the chloroplasts. It is entirely probable, therefore, that the chloroplasts have a temperature considerably higher than that of the leaf as a whole.

Recalling briefly the more important facts of the evidence at our disposal concerning photosynthesis at low temperatures, we have:

(1) Evidence of an accumulation of reserve food material through the winter in trees with persistent leaves as found by Sablon; (2) confirmatory evidence both of photosynthesis and of an accumulation of reserve food in winter by evergreen leaves as found by Miyaké; (3) evidence of photosynthesis at − 6° C. as the result of very careful work by Matthaei; (4) the finding of Ewart that a number of evergreen shrubs and trees including conifers, after having been exposed for some time to a temperature often falling below − 15° C. had no power of assimilation when tested at 1° C.

The results obtained by Ewart appear to contradict those of

Miyaké and Matthaei. In making comparisons it should be borne in mind, however, that Matthaei's material had previously been kept at a uniform temperature from 10° to 16° C., and that Miyaké's experiments were made at Tokyo where the mean temperature for the three winter months is 3.8° C. and the minimum − 6.5 (Kusano (12)), while the plants from which Ewart obtained his material had been exposed for three weeks to temperatures falling below − 15°C. Ewart ascribes the inability of these plants to assimilate CO_2 at 1° C. to the inhibiting effect of the extreme temperature to which they had been exposed. The same plant material, when brought to a temperature of 15° C., showed weak assimilation within a few hours and quite active assimilation within eight hours to one day. The long latent period of recovery, according to Ewart, indicates that the exposure had nearly reached the plant's limit of resistance. Unfortunately Ewart does not state how long the tests for assimilation at 1° C. lasted. One gains the impression that the tests were of short duration. It is entirely possible that, had the plants been exposed to a temperature of 1° C. for a longer time, the inhibiting effect of the previous extreme temperature would have been overcome and assimilation begun. The contradiction between Ewart's results on the one hand and those of Matthaei and Miyaké on the other is, therefore, more apparent than real.

Bearing in mind the assimilation curve obtained by Matthaei, the application of the results of the present investigation becomes at once apparent. Kanitz (10) has shown that the law of van't Hoff (32), that for every rise of 10° C. the rate of reaction is doubled or trebled, holds for the results obtained by Matthaei for temperatures between 0° and 37° C. assuming other conditions favorable. For temperatures from − 6° to 0° C. the rate of increase is very much greater. The assimilation curve in Matthaei's work shows an increase in assimilation from 2 mmg. of CO_2 per 50 sq. cm. per hour at − 6° C., to 18 mmg. at 0° C.,—an increase of 900 per cent. Since an increase of 6° C. in the temperature of the leaf due to the absorption of radiant energy is not at all uncommon and higher temperature differences are often found, the increase in assimilation resulting therefrom is of very great importance and goes far toward explaining the accumulation of reserve food material by evergreen trees.

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