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LIGHT INTENSITY AND TRANSPIRATION[1]

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(WITH ONE FIGURE)

Introduction

While it is well known that light intensity plays an important rôle in the determination of water loss from plants, our knowledge of this matter is purely qualitative. The present paper deals with an attempt to find some simple means of physically determining the intensity of solar radiation with reference to its effect on plant transpiration. While the results to be here brought forward do not possess that degree of completeness that we are wont to expect in the fields of physics and chemistry, yet they emphasize the quantitative aspect in the study of the external factors which influence plants in the open, and they seem to place in the hands of ecologists of a quantitative turn of mind a somewhat ready means of approximating the physical magnitude of one of the most important, and at the same time most baffling, of the environmental conditions with which they have to deal.[2]

The total amount of transpirational water loss from a plant, for any given period, may be considered as a summation of the effects of the evaporating power of the air and of the radiant energy absorbed throughout the period, modified by certain secondary

[1] Botanical Contribution from the Johns Hopkins University, No. 21.

[2] The pressing need for methods of evaluating the various external factors which affect plants has been emphasized in a paper read before the Botanical Society of America in 1908. See Plant World **12**:41–46. 1909; and Amer. Nat. **43**:369–378. 1909.

effects of these conditions and by certain responses to other conditions. One secondary effect of variations in light intensity is seen in the opening of stomata when many plants are transferred from darkness to diffuse or stronger light. These openings close, or tend to close, in many plants when light gives place to darkness or to very dim light. But there seems to be no evidence for thinking that stomatal movement is at all marked as long as the intensity of illumination is above a certain minimum, about what is known as weak diffuse light. Of course they close with wilting under any light conditions (see LLOYD, *Publ. 82* of the Carnegie Institution).

Another secondary effect of high evaporation conditions, whether caused by direct sunlight or by dryness of the air, etc., is the removal of water from the leaves at a rate more rapid than its rate of entrance, so that the cells are plasmolyzed and general wilting occurs. It is probable that this effect is felt long before actual wilting is to be observed; whenever transpiration surpasses the rate of water supply to the transpiring tissues it must be supposed that a gradual lowering of the vapor tension of the water films held in the moist cellulose walls will ensue, just as a semi-dry piece of filter paper will exhibit a much lower vapor tension than a similar piece saturated. Long before plasmolysis occurs we should expect to find that the capillary menisci of the cell membranes abutting upon the internal atmosphere of the leaf would become more and more concave, and would perhaps break and retreat into the pores of the membrane. In the one case, the vapor tension of the water film, in the other their actual superficial extent should be reduced. It may thus come about that an increase in the evaporating power of the air or of solar insolation might produce, by its very accelerating influence, a retardation in the transpiration rate. Such a phenomenon is common in soils, where an increase in the rate of water loss above the rate of diffusion of water to the soil surface causes the water films to retreat into the soil and thus *decreases* the rate of water loss. It is thus that the "dust mulch" is produced, by which *adaptation* the soil seeks to reduce water loss in a dry time! A measurable falling off in the relative transpiration rate, occurring in the forenoon, when the evaporating power of the air and the light intensity are both still increasing in their daily march, is exhibited in certain of the transpiration graphs of *Publ. No. 50* of the Carnegie Institution. These occurrences may well be due to the phenomenon just suggested, which may be termed *incipient wilting*. If the process were carried far enough, actual wilting would of course ensue. If incipient wilting be the true cause of this sort of fall in transpiration, without any appreciable stomatal closure, it should make itself manifest by a gradual fall in the gross water content of the leaves themselves, which should become more marked as evident wilting was approached. It is seen, then, that either stomatal closure or this hypothetical incipient wilting must act to decrease the equivalent evaporating surface of plants. By equivalent evaporating surface is here meant a free water surface which would evaporate the same amount of water as the plant, at the same place and for the same period.

Since the secondary effects of variations in light intensity through the photosynthetic process may be safely regarded as negligible in the present state of our inquiry, they will not be considered here. We may therefore assume that (for short periods having light intensities continuously adequate to prevent the closure of stomata, and with transpiration rates and a moisture supply which do not produce incipient wilting) the plant is virtually to be looked upon as an *integrating atmometer*, automatically summing the various increments of water loss from moment to moment as these fluctuate in magnitude. It might therefore be expected that a physical atmometer exposed at the side of a plant should exhibit the same march of the evaporation rate as that evidenced in the transpiration of the plant, providing of course that suitable corrections of the observed rate be applied, to adequately account for any and all internal changes in the organism which were influential in reducing the effective or equivalent evaporating surface of the latter. It is on this general supposition that the methods used in this study are based.

To keep logically and spatially within bounds, I shall here consider the effects of changes in the intensity of illumination between strong diffuse light and direct sunshine, thus once for all avoiding the question of marked stomatal movement. The stomata in my experiments are supposed to be open, in the day condition, throughout. I shall also limit my considerations to short periods of time, at least to short periods in strong light, thus aiming at an avoidance of the problem of incipient wilting as above set forth. The former of these problems has been touched upon already (see *Science* N.S. **29**:269–270. 1909), and the full consideration of it should make another title. The second problem, of incipient wilting, cannot be experimentally considered at the present time.

The specific problem which now holds our attention is, then, Is it possible by any simple means to estimate quantitatively the various light intensities to which plants in the open are subjected and so to sum the effects of these as to be able approximately to calculate the variations in transpiration thus brought about, and the total transpiration for the longer period in which these variations occur? It is obvious that the solution of such problems as this is of the utmost importance in establishing a basis for a scientific agriculture. Also, such problems lie at the bottom of considerations of the factors determining plant distribution, and it must be through their solution that ecology may at length emerge from the descriptive and classificational stage in which, for the most part, it now finds itself. The importance of our present inquiry is exceeded only by its difficulty.

Apparatus and methods

To attack the problem outlined above it was necessary to measure the water loss from experimental plants under different light intensities, and to compare the various rates thus obtained with readings taken, for the same periods and exposures, upon whatever physical instruments were available for the estimation of light intensity. For the plants, the ordinary method of weighing potted and sealed specimens was resorted to. A number of different instruments for determining light intensity were tested. I shall proceed first to a discussion of these instruments.

Since the intensity of solar radiation varies from time to time, even for short periods, as on a partly cloudy day, our great desideratum in the present connection is an instrument or method for automatically obtaining an integration of this factor for a given time period. One such device was available at the inception of this work, another was devised.

1. The Hicks solar radio-integrator (obtainable from J. HICKS, Hatton Garden, London) consists of a glass vacuum chamber, the upper portion of which (a spherical bulb) is about half filled with dark-colored alcohol and exposed to the light. The alcohol vapor produced by the absorption of energy by the dark surface is condensed in a lower bulb and collected in a still lower burette-like, graduated tube. The condenser and receiver are shaded during operation, and readings are obtained from time to time on the amount of alcohol distilled into the tube. The instrument is occasionally to be inverted and the collected alcohol replaced in the exposed bulb, an operation made possible by a bent tube connection between the two bulbs. The rate of distillation depends of course on the difference between the vapor tension of the alcohol in the upper bulb and that obtaining in the shaded part of the apparatus. The shaded part nearly maintains the temperature of the surrounding air, while the exposed bulb tends to be warmed by the sunshine. Thus this instrument causes the sun's rays to perform work in vaporizing alcohol and furnishes a means of measuring the work accomplished in terms of the amount of the liquid accumulating in the graduated tube. It is thus seen to be self-integrating.

2. Various lines of experimentation had shown that the porous cup atmometer, a self-integrating device for estimating the evaporating power of the air (see *Publ. No. 50* of the Carnegie Institution), is measurably affected by sunshine; that, *ceteris paribus*, it loses more water in direct sunlight than in shade. The difference in rate so produced, however, is not as great as that observed in plants under the same varied conditions of illumination. Considering this fact, it occurred to me that it should be possible to modify the porous cup in such manner as to cause it to absorb a greater proportion of the sun's energy, and thus render the ratio of its readings in light and shade more nearly like those obtained from the plant. The instrument already integrates the influx of energy, in terms of the amount of water evaporated, and the contemplated alteration should involve only the coloring of the porous evaporating surface so as to increase its power to absorb radiant

energy. After numerous preliminary tests this possibility was achieved.

The porous cups are now furnished in a dark-colored clay, a deep, grayish brown, and these cups show a marked increase in light-absorbing power over the ordinary white ones.

3. Another light-absorbing cup was obtained by coating the white form with a thin layer of washed lampblack. Common lampblack is boiled in distilled water, allowed to cool and settle, and the water decanted as well as possible. This process is repeated three to five times, and furnishes a clean, insoluble, and impalpable black powder, in the form of an aqueous paste. The latter may be diluted and applied to the cups with a small brush. This application should be made *after* the cup is filled and ready for operation, as the absorption of water by the surface when thus arranged is sufficient firmly and quickly to fix the carbon layer in place, and the latter is never allowed to become drier than it is destined to be in the actual operation of the instrument. The cup cannot be handled by the coated surface without injury, but it is a simple matter to renew the coating if such injury occurs. These coated cups operate in essentially the same manner as the permanently colored ones. As used in these tests, the white, brown, and black cups were installed on burettes, essentially as figured in *Publ. No. 50* of the Carnegie Institution.

4. The black bulb thermometer *in vacuo* (the one used was obtained from the Kny-Scheerer Co., New York) is essentially an ordinary glass-mercury thermometer, the bulb of which is blackened and inclosed in a thin glass vacuum bulb. It is exposed to the light for a short time period and the rise of the temperature of the bulb noted as the reading. The instrument must be shaded and must come to air temperature between observations. It is seen that the light absorbed by this instrument is made to do the work of expanding the mercury, the amount of expansion occurring in a specified time being the measure of the energy absorbed.

The devices for light estimation thus far mentioned all depend upon the *heating* effect produced by the absorbed light. Another group of instruments, all following the principle of the Bunsen-Roscoe "photometer," depend upon the chemical effect produced by the absorbed rays. These instruments now make use of some form of photo-sensitized paper, and the reading is either the length of time required to produce a certain standard shade of color in the paper, or the depth of color produced by an exposure of a certain length. WIESNER's instrument (see his *Lichtgenuss der Pflanzen*) belongs to this class. They are not photometers in any true sense, but really actinometers, measuring only the actinic effect of the light. The paper may be modified so as to give sensitiveness in any part of the spectrum, but the region to which they are sensitive is always rather limited, and the sensitiveness is not uniform throughout this region. Another obstacle in their operation comes from the difficulty of procuring proper standard colors; a third arises from the fact that the comparison of the color produced with the standard depends to a great extent upon the observer's judgment, the sensitiveness of his retina, etc. Two forms of actinometer were tested in this work. They were exposed to the action of the light till the sensitive paper attained the shade of the standard, the record being made in seconds.

5. The simplest form of actinometer for our estimations is the Wynne exposure meter, for sale by most dealers in photographic goods. It is very convenient to use, the paper therefor is apparently carefully standardized, and with each package of paper is furnished a slip of non-fading standard color suited to that particular lot of paper.

6. The other instrument of this class to which we had recourse is the Clements actinometer, a modification of the Wiesner type of instrument, using any form of photographic paper which the user may wish. It is described by CLEMENTS in his *Research methods in ecology*. As there recommended, I used "solio" printing out paper, and made my own standard color (water colors, afterward varnished), which was no easy task. As will be shown in the records of these tests, there is no doubt that this method is as satisfactory in operation as that of the Wynne, but the former is somewhat more difficult. I have had evidence, moreover, that the "solio" brand of paper is rather more apt to alter with age (at least in a warm climate) than the Wynne paper.

Since all of these instruments, both thermal and actinic, depend for their records upon the absorption of incident radiations, it is essential that the angle of incidence of the impinging light be always the same. But the direction of incidence of the sun's rays is constantly changing throughout the day, and varies, for the same hour, from day to day. It is therefore necessary to consider this matter in the operation of any and all forms of absorbing instruments. The Hicks instrument cannot be adjusted in this regard, for the main absorbing surface is the meniscus of alcohol in the upper bulb.

The porous cup atmometer possesses a cylindrical absorbing surface, modified slightly at the closed end of the cup, which latter part may readily be removed from operation by a suitable covering if desired. I am convinced that the error involved from the curved end of the cup, however, is negligible in this sort of estimation. The form of cup used was the usual one, the modification recently described by TRANSEAU (BOT. GAZ. 49:459. 1910) would no doubt be as efficient for our purpose. To receive the sunlight always at the same angle, the cups are so placed that their long axis is perpendicular to the direction of light incidence at noon, the common plane of sun and cylinder being vertical. When so arranged the sun virtually rotates about the cup, its rays always illuminating one-half of the surface only, and falling always vertically upon a longitudinal line through the center of the lighted area. The position of the lighted area on the cup is constantly changing, but since all sides of the cup are supposedly equivalent, this introduces no complication. The position of the instrument will of course vary with the sun's altitude, that is, with latitude and season, but may readily be determined from an almanac or by simple observation at high noon. Actual tests showed clearly that the vertical cup, as ordinarily used, fails to record proper intensities of sunshine at and about noon, for at that time only a small portion near the tip receives perpendicular radiation. Of course in high latitudes the vertical position would not introduce so great an error as nearer the equator, and the error in winter would be less than in summer. The black bulb thermometer is to be exposed in the same way as the cups.

The photographic papers were always exposed by hand, so placed that they received perpendicular rays from the direction of the sun at the time of observation.

As to the portion of the entire radiation which is absorbed by these various instruments, it is possible to say very little at the present time. It is fairly certain that portions of all the various wave-lengths of light, as well as of the infra-red and ultra-violet, are absorbed by the thermal instruments. On the actinometers we may be as certain that little effect is produced outside the actinic rays. Since the heating effect is the one which we are interested in at present, because our inquiry deals with the evaporation of water from green leaves, it is obvious that on a-priori grounds the thermal instruments are to be regarded as the most reliable. The quantitative statement of this whole matter must be left to some future time.

One other theoretical point may be mentioned here with reference to the interpretation of the results obtained with these instruments. It must be borne in mind that other factors besides radiation intensity are active in the control of evaporation, both from the porous cup and from the plant. Thus, in the night time the evaporation rate and that of transpiration are by no means *nil*, while the readings of the instruments which do not deal with evaporation will vanish at that time. From this fact we may expect the differences between two light intensities as shown by the non-evaporating instruments to be much greater than those shown by the evaporating ones. The latter always record the rate *without* light influence *plus* that due to light, the former can show no rate without the influence of radiant energy. It is possible so to manipulate the porous cup as to obtain readings from it directly comparable to those from the black bulb thermometer, but this cannot be entered into here.

Experimentation

It was my good fortune to be able to spend the summer of 1910 at the Desert Laboratory, Tucson, Arizona, under auspices of the Department of Botanical Research of the Carnegie Institution of Washington. During this period, and with the assistance of Dr. William H. Brown, now of the Michigan Agricultural College, a number of lines of inquiry which had been previously begun were continued, the matters considered in the present paper forming a portion of our operations. Without the enthusiastic cooperation of Dr. BROWN, the amount of experimentation and other work accomplished would have been much smaller, and the quality less satisfactory.

In the three series of tests to be presented, the plants stood upon a table in the open, the instruments being arranged in their immediate vicinity, so that the whole group of plants and instruments occupied a space perhaps 40 or 50 cm. square. Reduced light intensities were obtained by placing over the group, at a height of something less than a meter above the table, a cloth screen about a meter square, supported by a light wood frame and four light wood supports at the angles. The screen was always so placed that all the objects of the experiment were well within the shadow; they never received any direct sunshine while the shade was in position. The burettes of the atmometers and the tube of the radiometer projected below the table, so that the active portion of all instruments was always at approximately the same height from the table (and distance below the screen) as the plant foliage. The plants were 10–20 cm. in height; they had been lifted from the open soil several weeks previously and had been carefully accustomed to full sunlight. All had grown appreciably since potting, were leafy and apparently in good condition. They were in tinned sheet iron cylinders, some 8 or 10 cm. in diameter and about as high, which, during the experiments, were sealed by the application of prepared modeling clay over the soil surface and over the drainage openings at the base.

The plants were weighed and the instruments read at intervals of one-half hour, or as nearly so as possible. Where the time period was greater or less than 30 minutes, the data have been corrected to this time period. Weighings were made in the house, each plant remaining out of its proper position only long enough for this operation. In every test, after two half-hour periods of sunlight, there followed two similar periods under shade, these being in turn followed by two more periods of sunshine. The black bulb thermometer was covered most of the time by a loosely fitting cylinder or sheath of asbestos board, open at both ends to allow air circulation. When a reading was to be taken, this sheath was removed far enough to expose the scale, and a reading of the shade temperature was taken. Then the sheath was completely removed and the rise of temperature which took place in a single minute was noted. The photographic instruments were operated by exposure in the hand, close to the plants, a stop watch being used to determine the length of time needed to produce darkening of the sensitive paper to the degree of the standard color, a bit of which was attached to the case of the instrument, directly adjoining the exposure opening. All instruments and plants had been in full sunshine for an hour or more at the beginning of an experiment. Wind velocity was taken, and shade temperatures, but since these data show no relation to the resulting transpiration ratios, they need not be reproduced here. Throughout the tests there was always some air motion and never a high wind, the velocity varying from 0.2 or 0.3 to 2.0 or 3.0 miles per hour. The temperature varied from about 30 to 35° C. The plants used were *Physalis angulata* L. var. *Linkiana* Gray, *Xanthium commune* Britton, and *Martynia louisiana* Mill. They will be referred to merely by the generic names.

Results

The first series of observations extended from 8:00 A.M. to 1:00 P.M., August 9, 1910. A plant of *Physalis*, one of *Xanthium*, and the three porous cup atmometers (brown, black, and white) made up the series of objects. During the second hour the shade used was of white "8-ounce cotton duck" or tent canvas. During the fourth hour the shade was of a single thickness of "cheesecloth." The data from this series are given in table I.

To study, in a general way, the comparative effects of shade on the rates of water loss of the different objects, it is expedient to reduce each series of figures to relative values. We may take the datum for period 4 as unity in each case, and form the new series by dividing this datum into each of the remaining data. Graphs of these derived quantities are given in fig. 1, all of them passing through the common point (unity) at period 4. These graphs are thus directly comparable as to the relative heights of their ordinates

The periods of shade are denoted on the graphs by a broad black line below.

The graphs show merely a general and qualitative agreement between the rates of water loss from the various objects. It is quite evident that the white cup fails to show nearly as great fluctuations with light and shade as do the plants. On the other hand, the brown and black atmometers agree fairly well with each other

TABLE I

Period	Exposure	Losses per 30 mins., grams or cc.				
		Physal.	Xanth.	Brn. atm.	Blk. atm.	Wht. atm.
1......	Open	2.1	3.4	3.2	3.7	2.0
2......	Open	3.0	4.2	4.3	4.7	2.8
3......	Canvas shade	1.7	2.4	4.1	3.4	2.4
4......	Canvas shade	1.7	2.4	2.1	2.9	2.4
5......	Open	2.7	3.9	3.5	3.8	2.4
6......	Open	5.1	4.5	4.0	5.0	3.1
7......	Cheesecloth shade	3.0	3.2	3.3	4.0	2.9
8......	Cheesecloth shade	1.9	3.7	2.5	3.7	2.3
9......	Open	3.2	4.1	3.7	4.8	3.4
10......	Open	3.5	4.2	4.1	5.3	3.5

and with the plants. The *Physalis* plant lost an inordinate amount in period 6, the brown cup lost what appears as too much in period 3, and the behavior of the *Xanthium* plant in the last three periods is unusual; otherwise the agreement in the different ordinates is about what should be expected. Attention may be called to the general ascent of the series of three maxima for two of the instruments, showing clearly the gradual increase of the sun's intensity from 8:00 A.M. to 1:00 P.M. Also, with the thinner shade neither of the plants and neither of the dark instruments exhibit such a fall in rate of water loss as they do in the denser shade. We may now turn to the quantitative relations shown by these series of data.

Since the use of two different shades really constitutes two separate tests, we may consider the observations for the first six periods as test I, and those for the last six as test II, there being a common period of sunshine for the two tests. If now we calculate the ratios of the two sun periods, respectively, in each test, to those of the shade period intervening, we shall obtain quantitative measures of the relations which we wish to study in detail. But it is obvious that the first half-hour in any condition fails to give as clear an expression of the response to that condition as does the second half-hour, there usually being a more or less marked

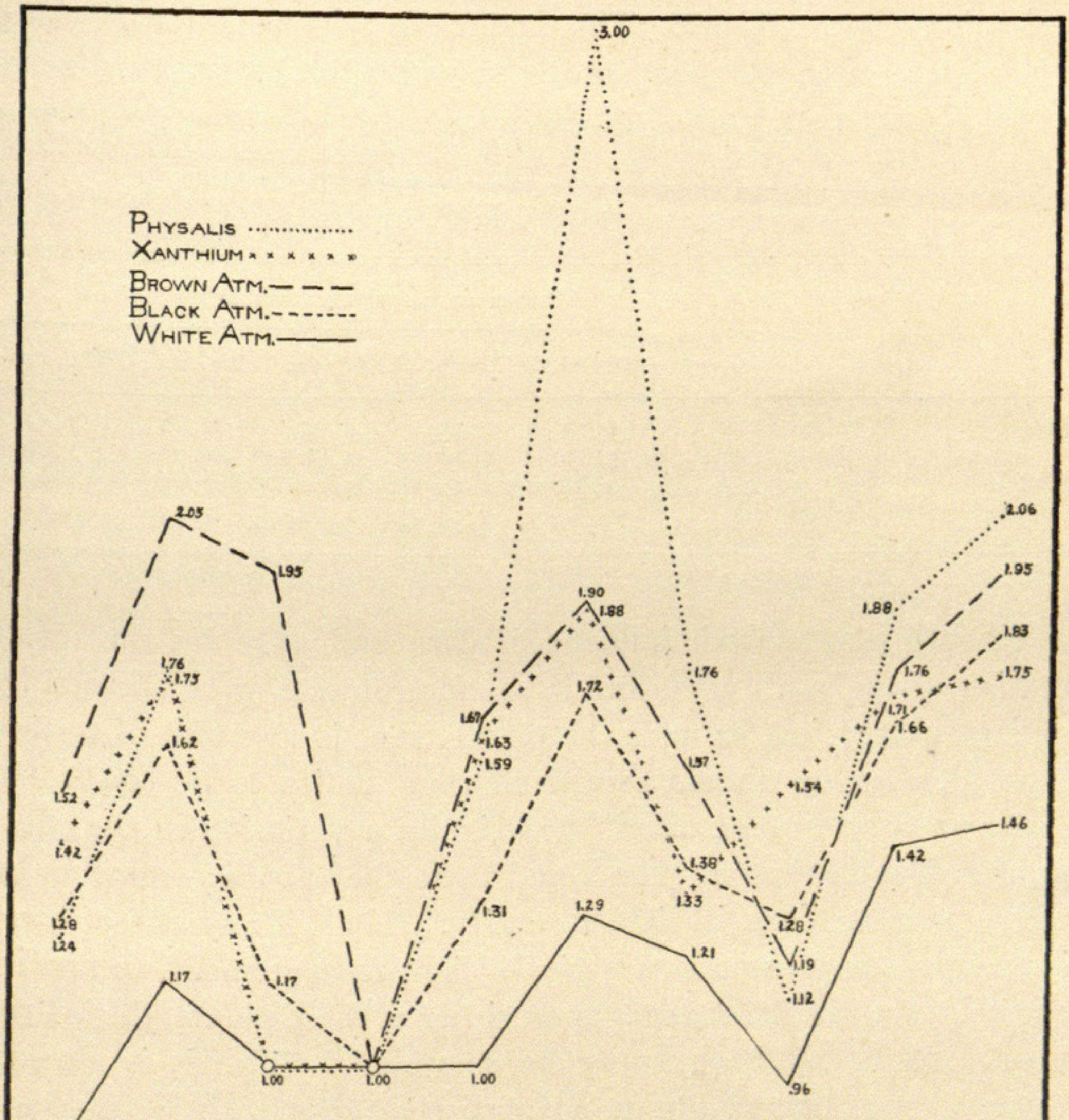

FIG. 1

lag of effect behind cause; therefore we need give attention only to the second period in each condition. Thus a period of 30 minutes is allowed to elapse after each change of conditions before use is made of the data obtained. This is a common method for the treatment of such changes in physics as well as physiology. The two *second* half-hour periods of sunshine will be termed the *first* and *second sun exposures*, the second half-hour of shade giving us the measure for the *shade exposure*. All of the sun-shade ratios are given in table II. Examples may make the procedure of their derivation more evident. The first ratio of test I for *Physalis* is 3.0÷1.7, or 1.76. The second ratio for the brown atmometer in test II is 4.1÷2.5, or 1.64, etc.

TABLE II

		Sun-shade ratios of rates of water loss				
		Physal.	Xanth.	Blk. atm.	Brn. atm.	Wht. atm.
Test I (canvas)	1st sun exp.	1.76	1.75	2.05	1.62	1.17
	2d sun exp.	3.00	1.88	1.90	1.72	1.29
Test II (cheesecloth)	1st sun exp.	2.68	1.22	1.60	1.35	1.35
	2d sun exp.	1.84	1.14	1.64	1.43	1.52

If both plants were influenced alike and only by the direct heating of the sun's rays, and if the instruments were affected by radiant energy just as were the plants, that is, per unit of surface exposed, then we should expect all these ratios to be equal. In so far as they are not equal, they signify a variation in the effect produced upon the two plants and upon the three instruments by the same alterations in light intensity. Thus, if any one of these instruments were used as a basis for light measurement, to predict the influence of light changes upon either of these plants, the instrumental result must obviously be corrected. Since it is already clear that the two plants do not entirely agree in their sun-shade ratios, it will be necessary to find correction coefficients, not simply for each instrument, but *for each instrument for each plant*. From the sun-shade ratios of table II have been calculated the correction constants, by which the ratio of any instrument for any period is to be modified (multiplied) so as to equal the corresponding ratio for either plant, and these coefficients are given in table III. As an example of the method of derivation, the first coefficient of correction for the black atmometer in reference to *Physalis* (test I) is

1.76÷1.62, or 1.09. Each pair of coordinate coefficients for each test is averaged, also, in the table.

TABLE III

		Correction coefficients					
		Brown atmom.		Black atmom.		White atmom.	
		Physal.	Xanth.	Physal.	Xanth.	Physal.	Xanth.
Test I	1st sun exp...	0.86	0.85	1.09	1.08	1.50	2.33
	2d sun exp....	1.58	0.99	1.74	1.09	1.50	1.46
	Average.....	1.22	0.92	1.42	1.09	1.50	1.90
Test II	1st sun exp...	1.69	0.76	1.99	0.90	1.99	0.90
	2d sun exp....	1.12	0.70	1.29	0.80	1.21	0.75
	Average.....	1.40	0.73	1.64	0.85	1.60	0.83

The second series of observation (test III) was carried out from 10:00 A.M. to 1:00 P.M., August 11. The shade here used was of two thicknesses of cheesecloth. Three plants were used, one of each of the forms above mentioned, but different specimens, and one of *Martynia louisiana*. Besides the three atmometers, all of our other instruments were operated in this series. We may neglect the losses for the first half-hour periods of each exposure, since they are not to be used in calculating the different ratios. The rates of loss, or in the case of non-evaporating instruments the averages of two readings taken at the beginning and end of the second half-hour of each exposure, are given in table IV, and the corresponding coefficients of correction in table V. There was almost no discrepancy shown between the first and second readings of the non-evaporating instruments; the conditions for the half-hour were sensibly constant. In the case of the two photographic papers the ratios are of course inverted, since the light intensity must vary inversely as the time required to produce the given depth of color.

A third series (test IV) was carried out on August 12, from 10:00 A.M. to 1:00 P.M. The plants were similar to those of test III, but were different individuals; the shade was of canvas, as in test I. For this series only the final coefficients of correction and their averages need be given. They may be found in table VI.

TABLE IV

Test III	Losses and readings per 30 minutes: Physal. (gm.)	Xanth. (gm.)	Martyn. (gm.)	Brown atm. (cc.)	Black atm. (cc.)	White atm. (cc.)	Integr. (cc.)	"Solio" (sec.)	Wynne (sec.)	Black therm. (deg. cent.)
1st sun exposure.....	3.45	3.98	3.12	2.9	3.7	2.2	3.00	34.5	2.4	6.7
Double cheesecloth shade............	2.88	3.48	2.70	2.6	2.6	2.2	1.71	95.0	5.5	3.0
2d sun exposure.....	4.35	4.05	3.54	3.3	4.5	2.7	2.95	38.0	2.15	6.5

TABLE V

Test III	Coefficients of correction					
	Brown atmometer			Black atmometer		
	Physal.	Xanth.	Martyn.	Physal.	Xanth.	Martyn.
1st sun exposure ...	1.07	1.02	1.04	0.85	0.80	0.82
2d sun exposure....	1.19	0.91	1.03	0.87	0.67	0.76
Average..........	1.13	0.97	1.04	0.86	0.74	0.79
	White atmometer			Integrator		
	Physal.	Xanth.	Martyn.	Physal.	Xanth.	Martyn.
1st sun exposure ...	1.20	1.14	1.16	0.69	0.65	0.66
2d sun exposure....	1.23	0.94	1.07	0.87	0.67	0.76
Average..........	1.22	1.04	1.12	0.78	0.66	0.71
	"Solio" paper			Wynne paper		
	Physal.	Xanth.	Martyn.	Physal.	Xanth.	Martyn.
1st sun exposure ...	0.44	0.41	0.42	0.52	0.50	0.51
2d sun exposure....	0.60	0.46	0.52	0.59	0.45	0.51
Average..........	0.52	0.44	0.47	0.56	0.48	0.51
	Black thermometer					
	Physal.	Xanth.	Martyn.			
1st sun exposure ...	0.54	0.51	0.52			
2d sun exposure ...	0.70	0.53	0.60			
Average	0.62	0.52	0.56			

TABLE VI

Test IV	Coefficients of correction					
	Brown atmometer			Black atmometer		
	Physal.	Xanth.	Martyn.	Physal.	Xanth.	Martyn.
1st sun exposure . . .	1.38	1.09	0.99	1.38	1.09	0.99
2d sun exposure. . . .	1.53	1.26	0.97	1.46	1.21	0.93
Average.	1.46	1.18	0.98	1.42	1.15	0.96
	White atmometer			Integrator		
	Physal.	Xanth.	Martyn.	Physal.	Xanth.	Martyn.
1st sun exposure . . .	1.99	1.58	1.43	0.43	0.34	0.31
2d sun exposure. . . .	1.23	1.68	1.29	0.69	0.57	0.44
Average.	1.61	1.63	1.36	0.56	0.46	0.38
	"Solio" paper			Wynne paper		
	Physal.	Xanth.	Martyn.	Physal.	Xanth.	Martyn.
1st sun exposure . . .	0.21	0.16	0.15	0.43	0.34	0.31
2d sun exposure. . . .	0.25	0.21	0.16	0.51	0.43	0.33
Average.	0.23	0.18	0.15	0.47	0.39	0.32
	Black thermometer					
	Physal.	Xanth.	Martyn.			
1st sun exposure . . .	0.40	0.31	0.29			
2d sun exposure . . .	0.49	0.40	0.31			
Average	0.45	0.36	0.30			

Finally, in table VII are brought together all the average coefficients from the preceding tables, together with *their* averages, for each plant for the whole investigation. This second average gives us a coefficient that may be taken to represent each instrument with reference to each plant. The average of the three different coefficients thus obtained for each instrument is given in the last column of the table. The latter average may perhaps represent the correction to be applied to each instrument for plants in general. Of course the latter statement is a pure assumption, based on the gratuitous supposition that plants in general may be found to average up, in their sensitiveness to light intensity, as did the three which happened to be used in these tests.

TABLE VII

Instrument	Coefficients of correction					Average	
	Plant	Test I	Test II	Test III	Test IV	For plant	For instr.
Brown atm.....	Physal......	1.22	1.40	1.13	1.46	1.30	1.09
	Xanth......	0.92	0.73	0.97	1.18	0.95	
	Martyn.....	....	....	1.04	0.98	1.01	
Black atm	Physal......	1.41	1.64	0.86	1.42	1.33	1.06
	Xanth......	1.09	0.85	0.74	1.15	0.96	
	Martyn.....	....	....	0.79	0.96	0.88	
White atm.....	Physal......	1.92	1.60	1.22	1.61	1.59	1.36
	Xanth......	1.48	0.83	1.04	1.63	1.25	
	Martyn.....	....	....	1.12	1.36	1.24	
Integr.........	Physal......	....	....	0.78	0.56	0.67	0.59
	Xanth......	....	....	0.66	0.46	0.56	
	Martyn.....	....	....	0.71	0.38	0.55	
"Solio" paper..	Physal......	....	....	0.52	0.23	0.38	0.33
	Xanth......	....	....	0.44	0.18	0.31	
	Martyn.....	....	....	0.47	0.15	0.31	
Wynne paper ..	Physal......	....	....	0.56	0.47	0.52	0.46
	Xanth......	....	....	0.48	0.39	0.44	
	Martyn.....	....	....	0.51	0.32	0.42	
Black therm....	Physal......	....	....	0.62	0.45	0.54	0.47
	Xanth......	....	....	0.52	0.36	0.44	
	Martyn.....	....	....	0.56	0.30	0.43	

Conclusions

In the last section have been brought forward the results of an experimental attempt to determine what sort of corrections must be applied to the data furnished by the seven instruments tested, in order that we may obtain from these data the sun-shade ratios of the transpiration rates as actually exhibited by the different plants. Four tests, each furnishing two sun-shade ratios for each plant, have been carried out. In all, we have eight tests for *Physalis* and the same number for *Xanthium*, but only four for *Martynia*. It is safe to assume that the full sunshine for the three days of this inquiry was approximately the same; all tests continued through about the same part of each day. It is quite obvious that in other regions the results might have been different, but I am convinced that the present data would agree fairly well with those for the hottest summer days in most parts of the United States. It is to be remembered, however, that the work was done in the arid region, albeit in the moist season, and that humidity has not yet been investigated with reference to its quantitative effect on plant transpiration. In the absence of a better method for describing weather conditions, it may be stated that the temperature varied within the limits 30–35° C., and the sky was not without haze, though clouds were rare. We have considered nothing weaker than strong diffuse light, that obtained under a screen of tent canvas. The plant stomata were probably always in the day condition throughout these experiments, and incipient wilting, if it occurred, was probably not generally a controlling factor in the transpiration rates.

Several different shade intensities were included in the tests, but an inspection of the tables will convince one that the fluctuations in the correction coefficients do not appear to be related to any particular shade. In the following derivation of conclusions all tests will be considered as tentatively equivalent, and no attempt to weight the averages will be made. The coefficients of correction will be treated as the main criterion for judging of the relative degrees of sensitiveness of the plants and instruments toward variations in light intensity.

1. Considering all coefficients (tables III, V, and VI, not the averages) with values between 0.90 and 1.10, inclusive, as equal to unity, we see that *all* of those greater than unity have reference to the porous cup atmometers. The other instruments *always* recorded greater differences between the two light intensities than did any of the plants. To study the distribution of the different forms of coefficient more in detail we may proceed to classify them in each of these two groups of instruments. The frequencies of occurrence of coefficients less than, equal to, and greater than unity, for the three atmometers and the three plants, are presented in table VIII. For example, there are six coefficients greater than one occurring for the brown atmometer and *Physalis*, only one for

Xanthium, and none for *Martynia*. The last column of the table gives the total number of comparisons made.

TABLE VIII

Instrument	Plant	C 1	C=1	C 1	Total
Brown atm....	Physal..........	1	1	6	8
	Xanth..........	3	4	1	8
	Martyn.........	0	4	0	4
Black atm	Physal..........	2	1	5	8
	Xanth..........	3	4	1	8
	Martyn.........	2	2	0	4
White atm....	Physal..........	0	0	8	8
	Xanth..........	1	2	5	8
	Martyn.........	0	1	3	4

2. From table VIII we derive the generalization that for all cups, under all test conditions, *Physalis* shows the most frequent occurrence of coefficients greater than unity. *Martynia* shows the least frequent occurrence of these. *Physalis*, therefore, is usually more sensitive to light changes than the cups; the other two plants are generally equally sensitive or less so.

3. For the white cup, for all plants, and under all test conditions, the great majority (16 out of 20) of the coefficients are greater than unity. This cup is generally not as sensitive to light variations as are the plants.

4. The brown and black atmometers agree in giving mainly coefficients for *Physalis* which are greater than unity, while for the other plants they are equal to or less than unity; see 2.

Turning now to an analysis of the coefficients of the other instruments, we may treat them as we have the atmometers, only classifying them as less than, equal to, or greater than 0.50 instead of 1.00. We may consider as equal to 0.50 all coefficients from 0.40 to 0.60, inclusive. Table IX presents the classification on this basis.

5. It appears from this array of figures that the integrator gives predominance to coefficients greater than 0.50, while the other instruments give them equal to or less than 0.50.

6. "Solio" paper shows the strongest tendency to give coeffi-

cients less than 0.50, but half of those derived from this instrument are equal to 0.50.

TABLE IX

Instrument	Plant	C<0.50	C=0.50	C>0.50	Total
Integrator	Physal.	0	1	3	4
	Xanth.	1	1	2	4
	Martyn.	1	1	2	4
"Solio" paper	Physal.	2	2	0	4
	Xanth.	2	2	0	4
	Martyn.	2	2	0	4
Wynne paper	Physal.	0	4	0	4
	Xanth.	1	3	0	4
	Martyn.	2	2	0	4
Black therm	Physal.	0	3	1	4
	Xanth.	1	3	0	4
	Martyn.	2	2	0	4

7. From the Hicks integrator and the black bulb thermometer evidence is again presented that *Physalis* is more sensitive to light changes than either of the other plants, and it is suggested that *Martynia* may be somewhat less sensitive than *Xanthium*.

From the grand averages of table VII we may derive some approximate notion of the values to be taken, in general, as correction constants in the operation of these instruments. It must be borne in mind that the data are inadequate and the conclusions tentative in the extreme.

8. *Physalis* appears to be about a third more sensitive than the two dark cups, which agree well together. *Xanthium* and *Martynia* appear nearly to equal these cups in sensitiveness. The average correction factor for all three plants is 1.075.

9. *Physalis* appears to be about 60 per cent, the other two plants only about 25 per cent, more sensitive than the white cup. The average correction factor for the white cup is 1.36.

10. All three plants are somewhat more than half as sensitive as the Hicks solar radio-integrator, the average correction for which is 0.59; see 5 above.

11. The Wynne actinometer and the black thermometer agree well in showing a sensitiveness about double that of the plants,

more than double for *Physalis* and less than double for the others.

12. The Clements instrument, with "solio" paper, seems to be generally about three times as sensitive as are these plants, somewhat more than this for *Xanthium* and *Martynia*, somewhat less for *Physalis*. From these averages it appears more sensitive than by the method of frequencies; see 6 above.

On the whole, we may conclude that the black and brown atmometers and the Hicks integrator have shown themselves to be valuable instruments for estimating the solar intensity, so far as transpiration is concerned. They should be suitable for the comparison of light intensities in different habitats, etc., and they are especially to be recommended on account of their power of automatic integration, and also on account of the fact that they all give their results in terms of vaporization of a liquid, thus resembling the plant in its transpiration activity. The black bulb thermometer recommends itself as the best of the non-integrating devices. The photographic papers are not to be highly recommended as used in this inquiry, mainly on account of their failure to record effects of other than restricted wave-lengths. They may be modified so as to be more available, and may, possibly in their present form, be even more valuable than the other instruments here tested, when the effects of light variations on *photosynthesis* rather than transpiration are to be determined.

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