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Author(s): A. L. Bakke

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STUDIES ON THE TRANSPIRING POWER OF PLANTS AS INDICATED BY THE METHOD OF STANDARD IZED HYGROMETRIC PAPER

By A. L. BAKKE

(*With two Figures in the Text*)

I. INTRODUCTION

The well-known cobalt paper method of Stahl (**18**), employing hygrometric paper which is blue when dry and white or slightly pink when a certain amount of moisture has been absorbed, is well suited to comparative tests of the transpiring power of different plants, if the tests are made with the same paper and at the same temperature. In seeking a means for comparing the transpiring power of a leaf surface with the power of a free water surface to give off water by evaporation, Livingston (**11**) conceived the idea of a standard evaporating surface, the power of which to give off water to the hygrometric cobalt chloride paper was compared directly with the similar power possessed by the leaf surface in question. He placed a square of the prepared paper across the mouth of a small glass vial filled with water to approximately 1 mm. from the top, and noted the time required for the paper to change from blue to pink. A paper square already in the moist condition (pink) was used as a colour standard in this determination. By placing a square of the same paper, in the dry condition (blue), upon a leaf at approximately the same time, observing the time elapsing before this paper attained the standard pink colour, and comparing the latter time with the length of the corresponding interval as observed over the free water surface, a definite measure of the transpiring power of the leaf surface was obtained, in terms of the evaporating power of the free water surface blanketed by a millimetre layer of air. This measure, being the ratio of the water surface time to the leaf time, was designated by Livingston as the *index of transpiring power* of the given leaf surface.

To avoid some of the difficulties arising from the use of the free water surface, Mr E. M. Harvey, working with Livingston in 1912, made use of saturated blotting paper as standard evaporating surface¹. The two ends of a strip of ordinary blotting paper were passed downward through two parallel slits (about 3 cm. apart) in the metal screw cap of a small glass bottle, the ends dipping into water contained in the bottle and a portion of the paper (kept moist by capillarity) lying flat upon the upper surface of the cap between the slits. The unoccupied portion of the cap surface was covered with blotting paper of the same thickness

¹ Renner (**15**) had shown that such a paper surface gives off water by evaporation at the same rate as does a free water surface.

as the moist strip, but made waterproof by treatment with shellac. A vulcanite plate 1 mm. in thickness was then sealed to the metal cap so as to lie directly upon the blotting paper. The vulcanite plate had two circular openings 8 mm. in diameter and about 1 cm. apart, so placed as to expose two circular areas of the moist paper strip just beneath the plate. The apparatus was completed by a glass plate covering the vulcanite. In operation, a slip of the hygrometric paper was gummed at its margin to the lower side of the glass plate, in such a position as to lie over one of the circular openings in the vulcanite. This slip assumed and retained the pale pink colour of the paper in its moist condition, water being absorbed from the saturated blotting paper surface just a millimetre below. When the pink colour had been attained by this comparison slip the glass was momentarily raised and a second slip of the test paper in its dry condition was placed over the second opening in the vulcanite, this slip being thus parallel to and 1 mm. from the blotting paper below. The glass cover was immediately replaced and the time required for the second slip of test paper to attain the same colour as that of the comparison slip was observed by means of a stop watch. The test slip and the comparison slip were seen by the observer, lying side by side beneath the glass plate. To avoid the disturbing factor introduced by the margins of the paper slips which extended beyond the limits of the circular openings below, the glass cover was itself covered by a piece of black paper, gummed in place, this having two circular openings so situated as to lie directly over the circular openings in the vulcanite when the glass plate was in position.

The Livingston method of applying the slips of hygrometric paper to plant surfaces makes use of a spring wire clip, shaped somewhat like a Mohr pinch cock, the wire loop becoming the handle in the present case and the movable ends being extended by two small glass plates which lie face to face when the clip is closed. These plates separate, but remain nearly parallel, when the wire loop of the clip is compressed. The leaf to be tested is placed between the two glass plates of a clip, with a slip of the hygrometric paper held between one of the plates and the leaf surface. The colour change in the paper is observed through the glass. It has been found generally desirable that a considerable pressure be exerted by the clips, thus reducing the influence of external air conditions upon the time of colour change of a paper slip held, by this pressure, between the leaf and one of the glass plates. If the pressure is too great, however, some injury is apt to be imparted to delicate leaves. Brass spring wire, 1.29 mm. in diameter (B and S gauge 16), has proved very satisfactory.

Livingston has emphasized the considerations that both internal and external conditions are effective in determining transpirational water loss from plant surfaces and that the problem of the control of the rate of transpiration is much more complex than has generally been appreciated. Various forms of atmometers furnish measurements which are useful in determining the various influences upon transpiration of the external atmospheric conditions, wind, temperature, solar insolation, etc., but the quantitative analysis of the influence of internal factors is less readily accomplished. The transpiration rate as measured for a particular time period is of course to be regarded as resulting from both external and internal conditions during that period. External conditions remaining the same, an old

leaf has a different transpiration rate from that of a younger one; this must be due to the influence of internal conditions. Leaves receiving the sun's rays at different angles transpire at different rates, even though they may be alike internally, for here the external conditions differ. The transpiring power of plant surfaces (or its reciprocal, the retardation offered to transpirational water loss from such surfaces) is, of course, an internal condition. Livingston has measured this power and determined its mode of daily variation by means of his ratio of relative transpiration and also by his method of standardized cobalt chloride paper, and the two methods appear to give generally concordant results. The ratio of the time required for colour change of the hygrometric paper over the standard water surface, to the corresponding time required for the same change when the paper is applied to the plant surface, has been termed by Livingston, as has been mentioned, the *index of transpiring power*.

Livingston has presented sufficient evidence to show the possibilities of the method of standardized cobalt chloride paper in comparisons of the transpiring power of different leaf surfaces at the same time and of the same surface at different times, and it was the writer's problem to test the method upon a large number of plant species and upon different individuals of the same species. From these studies presented below, it is possible to begin the consideration of foliar xerophytism in its quantitative aspect, an aspect hitherto neglected in ecological writings. Evidence is also presented in these studies bearing upon the alterations in foliar transpiring power induced by wilting and by ageing of the leaves, and some information on the value of the method here employed, in comparing drought resistance in different agricultural plants as far as foliar structures are concerned, is also here brought out.

This work was made possible through the kindness of the Director of the Department of Botanical Research of the Carnegie Institution of Washington, who placed at the writer's disposal the facilities of the Desert Laboratory at Tucson, Arizona, during July, August and part of September, 1913. It is a pleasure to state that the experimentation was carried on under the direction of Professor Burton E. Livingston, who followed the work throughout and made many helpful suggestions at various times. I am also grateful to Professor Geo. F. Freeman, of the University of Arizona, for extending to me the use of his Laboratory for Plant Breeding, and to Professor J. J. Thornber, also of the University of Arizona, for the verification of the numerous species studied.

II. EXPERIMENTATION

1. Method

The method of standardized cobalt chloride paper here employed was essentially that devised by Livingston (**11**). The apparatus for the standard evaporating surface was that already described. The paper used (treated with a 3 per cent. solution of cobalt chloride) was also that used by Livingston, the "Scott tissue towel." In later work I have made use of a thin filter paper (J. H. Munktel's "Unrivalled Swedish," no. 00), which has proved more satisfactory than the

"towel" in several ways. An acetylene bicycle lamp was used to dry the hygrometric paper slips, as well as to furnish light for night observations. The clips were the same as those of Livingston, as above described. In these experiments the best results in all cases were obtained by employing the end point when the hygrometric paper had first attained its complete colour change.

In order to ascertain the extent of the variation, or "experimental error," that might be expected in determining the time of the colour change in the same and in different pieces of the paper, ten determinations were made over the standard evaporating surface, with each of five different squares of paper. The results are shown in Table I. The stock of slips (10 mm. square) were placed in a glass dish and five slips were taken indiscriminately for the tests. The paper was blue even before heating (because of the low air humidity) but each slip was dried as usual, by holding the square, with light forceps, over the lighted lamp. The time was noted by means of a stop watch. The temperature remained very close to 38° C. during the series.

TABLE I

Time, in seconds, required for complete colour change in five slips of hygrometric paper, each slip tested ten times

No. of slip	1	2	3	4	5
No. of test					
1	11.4	11.4	11.1	11.1	11.0
2	11.3	11.0	11.0	11.4	11.1
3	12.3	11.0	11.0	11.0	11.0
4	12.1	12.1	11.2	11.0	11.0
5	12.2	11.2	12.0	11.1	11.0
6	12.3	12.0	11.1	11.0	11.0
7	12.1	12.1	11.1	11.0	11.1
8	11.1	11.2	11.1	11.0	11.2
9	11.3	11.2	11.1	11.2	11.0
10	12.2	11.2	11.3	11.3	11.0
Average	11.8	11.4	11.2	11.1	11.0

From Table I it will be noted that there is comparatively little variation in the time required for the different slips and still less in that for different tests with the same slip. The general average time coefficient (average of averages) is 11.3.

The only variable condition, external to the leaf, which may be effective to modify the time required for the colour change in the hygrometric paper (assuming that the paper itself does not vary and that the influence of air humidity, wind and solar insolation are removed by the glass plate and by shading), is the temperature; with higher temperature the vapour tension of the leaf surface must increase, which should result in a shortening of the time in question. If, however, as was indicated by Livingston, the standard evaporating surface (saturated blotting paper) and the millimetre air layer above it have the same temperature as the leaf, for any test, it then follows that temperature is eliminated as a factor

in determining the ratio employed as index of transpiring power, and this ratio must be a function only of internal conditions within the leaf. Though the evaporating surfaces of leaves are probably never at exactly the same temperature as that of the surrounding air (being usually somewhat cooler) the author of the method of standardized hygrometric paper tacitly assumes that the difference between these two temperatures is negligible, recommending that the standard evaporating surface be kept covered and shaded and thus at approximately air temperature. It appears that this assumption is practically legitimate, at least in most cases, and it has been adhered to in the present work. With changes in temperature the critical time period over both leaf and standard surface must vary and the variation in both surfaces should occur in the same proportion; thus,

FIG. 22. Graph showing the relation of air temperature to the time required for complete colour change of hygrometric paper over the standard evaporating surface. Abscissas are degrees C. and are indicated below; ordinates are seconds and their values are placed upon the graph.

if higher air temperature decrease the time over the standard surface to one-half what it has been, that over the leaf surface should be similarly decreased, leaving the index of transpiring power the same as before.

It was thus suggested that the constant employment of the standard evaporation surface might possibly be dispensed with, if the relation of the time required for the colour change over this surface to temperature were known. This relation was roughly approximated by making a number of determinations with the standard evaporation surface for each of several different air temperatures. The average of 20 different determinations for each air temperature is shown on the graph of

Fig. 22, which thus presents the empirically determined relation between air temperature and the time coefficient as obtained with the standard surface.

Although the experimental data shown in Fig. 22 exhibit comparatively slight unexplained fluctuations, it is clear that a simple general relation holds between the two variables here dealt with. It seems fair to conclude that a linear function practically represents the relation sought, for the range of temperature from 25° to 35° C. For higher temperatures the straight line of the idealized graph (shown by a broken line in Fig. 22) becomes concave upward and seems to tend to become asymptotic with the horizontal axis. On theoretical grounds it is to be expected that the relation here brought out is simply the well-known relation which holds between temperature and the vapour pressure of water. As Livingston and Livingston (13) have pointed out, for ordinary temperatures this relation is almost the same as the logarithmic one stated in the law of the influence of temperature on chemical reaction velocity; the vapour tension is about doubled for each rise of 10° C. Although it thus seems quite possible to standardize the hygrometric paper once for all and then to dispense with actual tests with the standard surface, making corrections of the given time coefficient according to the air temperature, yet this has not been the procedure of the experimentation dealt with below. Before such procedure is adopted a more thorough-going test of the temperature relation will be requisite.

2. Daily march of foliar transpiring power

A somewhat detailed study of the daily march of the foliar transpiring power, similar to the studies made by Livingston (11) on *Datura* and *Physalis*, was carried out on *Quamoclidion multiflorum* Torr., the plants growing in the open soil, but partly shaded by being within a lath shelter of similar form to that employed by Brown (1), by Caldwell (3), and by Shive and Livingston (16). The leaves of this plant are very uniform, a feature which makes it less requisite to have many simultaneous observations in such a study as this than would otherwise be the case. The series of observations began with the 21st hour of July 8, 1913, and was continued, at varying intervals, to end with the 15th hour of the following day. Five determinations of the time coefficient were made for the standard water surface at each time of observation, and two determinations were similarly made for each of the two leaf surfaces. Neither very old nor very young leaves were employed. The data obtained are presented in Table II, where the hours are simply designated by their serial number within the day. It is understood, of course, that the tests were actually made within the stated hour, usually within the first 30 minutes of that hour. The temperatures given were taken from a thermometer suspended near the plant, at the beginning of the hour indicated. The individual time coefficients for the standard evaporating surface are not given, being very nearly of the same magnitude in every case; only the averages of the sets of five numbers are presented. The two individual time coefficients for the leaf tests and the corresponding individual indices of transpiring power (derived by dividing the average time coefficient for the standard surface by the coefficient for the leaf surface in each case) are presented, as are also the

respective averages for the different pairs (the latter in full face type). The data of the last column represent the entire leaf, being derived by averaging the proper numbers for the two foliar surfaces.

TABLE II

Data of foliar transpiring power for the upper and lower foliar surfaces of Quamoclidion multiflorum Torr., and for the entire leaf surface, determined at intervals throughout the day

Hour of observation ¹	Air temperature ° C.	Time coefficient in seconds			Index of transpiring power of leaf surface		
		For standard water surface ²	For leaf		Upper	Lower	Entire
			Upper surface	Lower surface			
July 8			{ 295·0 203·6		0·070	0·101	0·086
			{ 288·4 209·0		0·072	0·100	0·086
21	36·5	20·64	{ Av. 291·1 206·3		0·071	0·101	0·086
			{ 347·0 230·0		0·064	0·094	0·080
			{ 350·0 245·0		0·063	0·090	0·077
22	35·0	22·15	{ Av. 348·5 237·5		0·063	0·092	0·078
			{ 280·0 275·0		0·082	0·084	0·083
			{ 295·0 280·0		0·078	0·082	0·080
23	33·0	23·04	{ Av. 287·5 278·0		0·080	0·083	0·082
July 9			{ 420·0 315·0		0·066	0·088	0·077
			{ 435·0 323·0		0·064	0·086	0·075
1	32·0	27·84	{ Av. 427·5 319·0		0·065	0·087	0·076
			{ 464·0 363·0		0·074	0·094	0·084
			{ 464·0 363·0		0·074	0·094	0·084
4	31·0	34·28	{ Av. 464·0 363·0		0·074	0·094	0·084
			{ 505·0 385·0		0·069	0·091	0·080
			{ 495·0 385·0		0·071	0·091	0·081
5	28·5	35·08	{ Av. 500·0 385·0		0·070	0·091	0·081
			{ 93·0 86·4		0·290	0·312	0·301
			{ 93·0 87·6		0·290	0·308	0·299
10	33·5	27·00	{ Av. 93·0 87·0		0·290	0·310	0·300
			{ 57·0 55·0		0·355	0·368	0·362
			{ 60·0 60·0		0·338	0·338	0·338
11	35·0	20·28	{ Av. 58·5 57·5		0·347	0·353	0·350
			{ 50·0 50·0		0·322	0·322	0·322
			{ 47·0 50·0		0·343	0·322	0·333
12	38·0	16·12	{ Av. 48·5 50·0		0·333	0·322	0·328
			{ 46·0 45·0		0·224	0·229	0·227
			{ 46·0 45·0		0·224	0·229	0·227
13	39·5	10·32	{ Av. 46·0 45·0		0·224	0·229	0·227
			{ 39·6 40·6		0·293	0·278	0·286
			{ 37·0 39·6		0·301	0·293	0·297
14	40·0	11·32	{ Av. 38·3 40·1		0·297	0·286	0·292
			{ 46·0 41·0		0·245	0·275	0·260
			{ 45·0 38·0		0·250	0·247	0·248
16	39·5	11·28	{ Av. 45·5 39·5		0·248	0·261	0·254

¹ Hours are simply numbered consecutively in the day; the 21st hour is from 8 to 9 p.m., etc.

² Average of five determinations.

The average transpiring powers given in Table II are presented graphically in Fig. 23, which brings out the fact that for the night period (from hour 21 to hour 5) the foliar transpiring power is uniformly low, the highest average value obtained for the entire leaf during this period being only 0.0856. Between the 5th and the 10th hour this average value rises markedly, to a magnitude of 0.300 and has, in the 11th hour, a value of 0.350, which is its maximum for the day. It is thus apparent that the leaves of this plant increased in transpiring power for several hours after sunrise, but that the transpiring power begins to decrease long before the occurrence of the temperature maximum. This is in perfect agreement with the observations of Livingston (7) and of E. B. Shreve (17), that the value of the ratio of relative transpiration (which must be an index of transpiring power) reaches its maximum and begins to decrease several hours before the occurrence of the maximum of absolute transpiration or that of the evaporating power of the air. There seems to be no reason to doubt that the early fall in foliar transpiring power, while the air temperature—and presumably the leaf temperature—are still rising, is largely or wholly due to the phenomenon of incipient drying of Livingston and Brown (12). The last named writers invoked this phenomenon as the cause of the apparently premature maximum in the ratio of relative transpiration. There was no wilting in the plants of the present study and there is no reason to suppose any marked closure of stomata so early as the 11th hour, although, if such closure occurs, it must of course have the same effect as has pronounced incipient drying. No explanation is apparent for the anomalous, but only temporary, depression indicated for the 13th hour.

FIG. 23. Graphs showing the daily march of the foliar transpiring power of *Quamoclidion multiflorum* Torr., as determined by the method of standardized cobalt chloride paper, the plants growing in open soil but under a lath shelter.

The graphs here presented suggest fully as good if not better agreement between the ratio of relative transpiration and the hygrometric paper index of foliar transpiring power than that actually brought out by Livingston (11). No relative transpiration ratios were obtained in the present study, but the graph of Fig. 23 has all the characteristics of the typical graphs of relative transpiration so far published (7, 8, 17).

3. Relation of position upon the plant and age of leaves to their transpiring power

That the younger leaves of plants exhibit greater transpiring power than do the older ones is generally known. Also, it seemed highly probable that different types of leaves on the same plant might show variations in transpiring power, in those forms where the leaves vary in size, shape, etc., with their position on the plant or with the stage of the plant's development at which they were formed. Several very vigorous plants of *Verbascum thapsus* L., growing in open soil, within the lath shelter mentioned above, furnished opportunity for a comparison of the transpiring power of leaves on the same stem but at different heights above the ground. The plants were in bloom when these tests were made, July 22 for the day tests and July 24 for the night determinations. The tests of the different leaves were unfortunately not made simultaneously, either for the day or for the night, but the several leaves were tested in several groups, those of each group being studied within the same hour. Thus the results are not strictly comparable throughout the entire series, but only within their respective groups. The first group included leaves of the first, second and fifth rows from the ground for the day tests, and those of the first and second rows for the night test; these were studied early in the 11th hour, July 22, and in the 22nd hour, July 24, respectively. The second group included leaves of the sixth and eighth rows for the day study, made in the 11th hour, and comprised those of the fifth, sixth, eighth and tenth rows for the night test, made in the 23rd hour. The third group consisted of leaves of the tenth and eleventh rows for the day, tested in the 12th hour, and included a leaf of the eleventh row and a small leaf about 60 cm. from the tip of the shoot for the night test, made in the 24th hour. In the day test the small leaf 60 cm. from the tip was dealt with alone, in the 13th hour. Table III gives representative results of this study. The final averages are given in full face type.

TABLE III

Data of foliar transpiring power for the upper and lower surfaces and for the entire leaf surface, of leaves in various positions upon the stem of Verbascum thapsus L. The upper division of the table represents diurnal, the lower division, nocturnal conditions

Position of leaf on stem, number of row from base	Day and hour of observation	Time coefficient in seconds			Index of transpiring power of leaf surface		
		For standard water surface	For leaf		Upper	Lower	Entire
			Upper surface	Lower surface			
	July 22						
1	10	19.2	237	35	0.0817	0.5485	0.3151
			275	60	0.0713	0.3200	0.1966
					Av. 0.0744	0.4343	0.2559
2	10	19.2	235	30	0.0817	0.6400	0.3609
			215	25	0.0892	0.7680	0.4286
					Av. 0.0855	0.7040	0.3948

TABLE III (continued)

Position of leaf on stem, number of row from base	Day and hour of observation	Time coefficient in seconds			Index of transpiring power of leaf surface		
		For standard water surface	For leaf				
			Upper surface	Lower surface	Upper	Lower	Entire
	July 22						
			{ 205 24		0·0937	0·8000	0·4469
			{ 198 27		0·0969	0·7111	0·4040
					Av. 0·0953	0·7556	0·4255
5	10	19·2	{				
			{ 141 18		0·1171	0·9111	0·5141
			{ 175 19		0·0937	0·8525	0·4731
6	11	16·4	{		Av. 0·1054	0·8818	0·4936
			{ 55 19		0·2981	0·8631	0·5806
			{ 62 17		0·2645	0·9647	0·6146
8	11	16·4	{		Av. 0·2813	0·9139	0·5976
			{ 42 16		0·2611	0·6875	0·4743
			{ 38 16		0·2894	0·6875	0·4885
10	12	11·0	{		Av. 0·2753	0·6875	0·4814
			{ 90 16		0·1222	0·6875	0·4049
			{ 92 15		0·1541	0·7333	8·4437
11	12	11·0	{		Av. 0·1384	0·7104	0·4243
			{ 100 14		0·1111	0·7857	0·4484
(60 cm. from tip)			{ 80 16		0·1375	0·6875	0·4125
	13	11·0	{		Av. 0·1243	0·7366	0·4305
	July 24						
			{ 640 435		0·0441	0·0646	0·0521
			{ 670 455		0·0421	0·0620	0·0544
1	22	28·2	{		Av. 0·0431	0·0633	0·0532
			{ 765 740		0·0369	0·0441	0·0405
			{ 677 583		0·0417	0·0484	0·0541
2	22	28·2	{		Av. 0·0393	0·0463	0·0428
			{ 650 360		0·0462	0·0833	0·0648
			{ 375 335		0·0800	0·0894	0·0847
5	23	30·0	{		Av. 0·0631	0·0864	0·0748
			{ 441 350		0·0676	0·0857	0·0767
			{ 567 470		0·0529	0·0638	0·0583
6	23	30·0	{		Av. 0·0603	0·0704	0·0675
			{ 420 255		0·0714	0·1174	0·0944
			{ 500 230		0·0600	0·1304	0·0952
8	23	30·0	{		Av. 0·0657	0·1239	0·0948
			{ 405 265		0·0619	0·1132	0·0876
			{ 440 270		0·0618	0·1111	0·0865
10	23	30·0	{		Av. 0·0619	0·1122	0·0871
			{ 442 312		0·0864	0·1224	0·1044
			{ 400 270		0·0956	0·1415	0·1186
11	24	33·2	{		Av. 0·0910	0·1320	0·1115
			{ 375 242		0·1019	8·1579	0·1299
(60 cm. from tip)			{ 330 262		0·1157	8·1458	0·1308
	24	32·0	{		Av. 0·1088	0·1519	0·1304

In examining the data for the day tests of Table III, it is at once clear that the lowest two rows of leaves on the stem have low transpiring power (both 0.256), as compared with that of the fifth row (0.426), that the sixth row has a transpiring power (0.494) markedly lower than that of the eighth row (0.598), and that the transpiring power of the tenth row (0.481) is somewhat, but not considerably, greater than that of the eleventh row (0.424). The night test shows, as is usual for ordinary plants, a very markedly decreased transpiring power for all leaves, as compared with their power in the day. Although the night tests were not timed to bring out clearly the relations between the different rows of leaves, yet (since the transpiring power of leaves usually remains low during the whole night and may be supposed to vary but little during the hours at which these determinations were made) it is strongly suggested that there is a pronounced general increase in the magnitude of the night index as the position of the leaves is farther from the ground.

In general, the leaves of *Verbascum* may be said to have a day index (for the entire leaf surface) of from about 0.400 to about 0.600. With the exception of the two lowest rows (as here indicated), the transpiring power of all the leaves appears to be about four or five times as great for the lower surface as it is for the upper.

4. The relation of diurnal to nocturnal foliar transpiring power

To obtain a preliminary and merely general idea of what may be expected as to the relative magnitudes of the indices of transpiring power for day and night, three day and three night determinations were made on apparently representative leaves of each of ten plant forms. These plants were growing in the open or in the lath shelter at the experiment grounds of the Desert Laboratory. The plant names, the times of observation and the numerical data are given in Table IV, where the time coefficients for the two leaf surfaces are omitted. These may be calculated from the data given if they be desired. Although the number of observations in each case is far too small to allow reliable generalization, yet the averages may indicate, in an approximate way, what sort of daily variation is to be expected in such plants as these. The day-night ratios, derived by dividing the day average by the night average, are given in full face type. The plants are arranged in the numerical order of these ratio values.

The results presented in Table IV show a broad range in the value of the general day-night ratio of transpiring power, from 0.135 in *Cissus* to 5.99 in *Kalstroemia*. In general, those plants which exhibit low average values of this ratio also show a low value for each of the leaf surfaces considered separately. It appears, however, that the serial order would be slightly altered if the lower leaf surface alone were considered.

The actual magnitudes of the day-night ratios are especially instructive when we regard the *direction* of the day-night variation in transpiring power. For the first two plants all the ratios are less than unity, which means simply that the transpiring power (of both leaf surfaces and of the leaf as a whole) is greater by night than by day. The two cases with *Prunus* agree in showing the upper leaf

TABLE IV

Data regarding diurnal and nocturnal transpiring power for representative leaves of ten different plants growing in the open soil, three tests being made in each case

Serial No.	Name of plant	Time of observation	No. of test	Index of transpiring power of leaf surface				
				Upper	Lower	Entire		
1	<i>Cissus macrocarpa</i> Rose	July 29 12.15 p.m.	1	0.0141	0.0232	0.0187		
			2	0.0154	0.0269	0.0212		
			3	0.0149	0.0229	0.0189		
			Av.	0.0148	0.0243	0.0196		
		10.45 p.m.	1	0.0683	0.1295	0.0989		
			2	0.1021	0.1419	0.1220		
			3	0.2591	0.1674	0.2133		
			Av.	0.1431	0.1463	0.1447		
		Day-night ratio			0.10	0.17	0.135	
		2	<i>Parthenocissus dumetorum</i> Rehder	10.30 a.m.	1	0.0246	0.0877	0.0562
					2	0.0277	0.1121	0.0610
					3	0.0208	0.0840	0.0524
					Av.	0.0244	0.0946	0.0565
Aug. 2 10.15 p.m.	1			0.0666	0.0847	0.0757		
	2			0.0710	0.1211	0.0961		
	3			0.1795	0.1125	0.1460		
	Av.			0.1057	0.1061	0.1059		
Day-night ratio				0.23	0.89	0.53		
<i>Prunus persica</i> Stokes (1)	Aug. 4 11.00 a.m.			1	0.0345	0.1628	0.0987	
				2	0.0345	0.2151	0.1248	
				3	0.0786	0.3800	0.2293	
		Av.	0.0492	0.2526	0.1509			
	Aug. 5 12.15 a.m.	1	0.1786	0.1317	0.1552			
		2	0.1632	0.1607	0.1620			
		3	0.2255	0.2300	0.2278			
		Av.	0.1741	0.1741	0.1816			
	Day-night ratio			0.28	1.45	0.82		
	4	<i>Prunus persica</i> Stokes (2)	Aug. 4 10.45 a.m.	1	0.0460	0.1652	0.1056	
				2	0.0489	0.2151	0.1320	
				3	0.0792	0.2923	0.1858	
Av.				0.0514	0.2242	0.1411		
Aug. 5 11.45 p.m.			1	0.1044	0.1516	0.1280		
			2	0.1224	0.1574	0.1399		
			3	0.1382	0.2077	0.1730		
			Av.	0.1213	0.1789	0.1469		
Day-night ratio			0.42	1.25	0.95			

TABLE IV (continued)

Serial No.	Name of Plant	Time of observation	No. of test	Index of transpiring power of leaf surfaces				
				Upper	Lower	Entire		
5	<i>Fragaria californica</i> Newberry	July 28 12.00 noon	1	0.0937	0.2303	0.1620		
			2	0.0875	0.2000	0.1438		
			3	0.0957	0.2310	0.1634		
			Av.	0.0923	0.2204	0.1564		
		10.30 p.m.	1	0.0698	0.2293	0.1496		
			2	0.0683	0.2143	0.1413		
			3	0.0656	0.2234	0.1445		
			Av.	0.0679	0.2223	0.1451		
		Day-night ratio			1.36	0.99	1.13	
		6	<i>Phytolacca decandra</i> L.	July 28 11.00 a.m.	1	0.0767	0.1434	0.1102
					2	0.0963	0.2491	0.1727
					3	0.1178	0.2808	0.1993
					Av.	0.0969	0.2044	0.1607
9.15 p.m.	1			0.0575	0.0686	0.0631		
	2			0.0639	0.0758	0.0699		
	3			0.0709	0.1234	0.1972		
	Av.			0.0641	0.0893	0.0767		
Day-night ratio				1.51	2.51	2.09		
7	<i>Oenothera hookeri</i> Torr. and Gray			July 25 11.00 a.m.	1	0.2700	0.1500	0.2100
					2	0.1028	0.0765	0.0897
					3	0.0792	0.0935	0.0864
		Av.	0.1307		0.1067	0.1287		
		9.15 p.m.	1	0.0783	0.0417	0.0600		
			2	0.0830	0.0421	0.0626		
			3	0.0630	0.0501	0.0566		
			Av.	0.0748	0.0446	0.0597		
		Day-night ratio			1.75	2.39	2.15	
		8	<i>Solanum rostratum</i> Dun	July 30 9.20 a.m.	1	0.8143	0.3454	0.5789
					2	0.6333	0.4222	0.5273
					3	0.7125	0.4560	0.5843
Av.	0.7200				0.4079	0.5638		
Aug. 2 12.15 p.m.	1			0.1755	0.1858	0.1807		
	2			0.1153	0.0929	0.1041		
	3			0.2548	0.1556	0.2052		
	Av.			0.1819	0.1447	0.1666		
Day-night ratio				3.96	2.81	3.38		
9	<i>Datura stramonium</i> L.			July 25 10.15 a.m.	1	0.1600	0.1167	0.1394
					2	0.1963	0.1500	0.1732
					3	0.6323	0.5268	0.5769
		Av.	0.3295		0.2651	0.2965		

TABLE IV (*continued*)

Serial No.	Name of Plant	Time of observation	No. of test	Index of transpiring power of leaf surface		
				Upper	Lower	Entire
9	<i>Datura stramonium</i> L.	July 25 11.00 p.m.	1	0.0731	0.0640	0.0586
			2	0.0548	0.0484	0.0516
			3	0.0544	0.0431	0.0488
			Av.	0.0608	0.0518	0.0563
			Day-night ratio	3.10	5.12	5.30
10	<i>Kalstroemia grandiflora</i> Torr.	July 30 9.25 a.m.	1	0.4956	0.3454	0.4205
			2	0.4560	0.3800	0.4180
			3	0.4750	0.3562	0.4156
			Av.	0.4755	0.3605	0.4180
			Day-night ratio	7.68	4.65	5.99
		Aug. 3 9.44 p.m.	1	0.0511	0.0840	8.0676
			2	0.0613	0.0764	0.0689
			3	0.0729	0.0722	0.0726
			Av.	0.0618	0.0775	0.0697
			Day-night ratio	7.68	4.65	5.99

surface to have a higher index by day than by night, while the lower leaf surface exhibits the reverse of this relation. For the entire leaf surface the day index is somewhat less than the night one. With *Fragaria* the day index is higher for the upper surface, the night and day indices are equal for the lower surface, and the day index is somewhat higher than the night one for the leaf as a whole. The remaining cases recorded all agree in showing a higher transpiring power by day than by night, when either leaf surface is considered separately as well as with regard to the entire surface. A general survey of the whole series suggests that the more xerophilous forms may possess lower diurnal than nocturnal transpiring power and that the more mesophilous plants may be characterized by greater diurnal than nocturnal power to give off water. Whether this condition of affairs may be related to less marked stomatal movements, to more pronounced diurnal incipient drying in the first group, or to some other undiscovered internal condition, cannot now be surmised.

5. Transpiring power as an index of xerophytism or of mesophytism

As has been suggested by Livingston (11), as far as the aerial water relation is concerned, the foliar transpiring power should be a more or less definite quantitative index of the position of any plant, among others, in a scale of power to withhold water against its loss by transpiration. Also, since most of the water absorbed by ordinary plants is almost immediately lost by transpiration, it follows that transpiring power should be an approximate measure of the relative amounts necessarily absorbed by different plants in order that they may thrive under any given complex of atmospheric conditions. The Warming classification of plants, on the basis of their so-called water-requirements, though never yet placed upon any dynamically quantitative basis, obviously rests upon this necessary rate of

water absorption. It thus appears that the method of standardized hygrometric paper should furnish comparative data by the use of which a scale of relative xerophytism or mesophytism might be elaborated. The position of any given plant in such a scale might thus be determined simply by the magnitude of its index of transpiring power.

The only methods thus far suggested, by which the transpiring power of plants may be approximated, are (1) those by which the rate of transpirational water loss from the plant (or from a portion of it) is determined under known conditions, the plant being enclosed in a chamber of some sort, the temperature and humidity of which are known or at least uniform for different tests; (2) that of the ratio of relative transpiration, involving the weighing of potted plants and the operation of an atmometer; and (3) the method by which a standardized water-absorbing surface is applied directly to the leaves. Various workers¹ have employed the closed chamber method, usually, however, with the idea that measurements comparable to those of transpiration in the open were being obtained thereby, whereas, as Livingston and E. B. Shreve have emphasized, transpiration is dependent upon various external conditions as well as upon the transpiring power of the plant surfaces, which alone may be determined by such methods. The relative transpiration ratio has been used for studying transpiring power by its author (Livingston, **7**, **11**), but is not at all suited, as he has noted, for determinations involving plants growing in the open. The application of water-absorbing surfaces to the leaves is exemplified in Darwin's method of the horn hygroscope (**5**) and by Livingston's method of standardized hygrometric paper, with the latter of which the present studies have to deal.

The methods employing closed chambers give, of course, the average transpiring power of the whole plant, while the method of hygrometric paper or horn gives for each test no information excepting for the small sample surface to which the absorbent material is actually applied. In order satisfactorily to approach an approximation for the entire plant it is necessary to take as large a number of samples as possible, performing as many tests. Since, however, the transpiring power of the whole plant is usually practically controlled by that of the leaves, and since relatively few well-chosen leaves may give a fair approximation as to the average index for the whole leaf surface, it should not require a very large number of observations to give an average index nearly enough equal to that of the entire plant for present purposes.

In the tests here presented in this connection, three apparently representative leaves were tested, in the day, for a number of different plants. These were growing healthily under irrigated conditions at the University of Arizona, where the privilege of making use of these plants was very kindly extended to me by Professor Geo. F. Freeman, Plant Breeder of the Arizona Experiment Station. The results of the tests are shown in Table V, where the notation is the same as in the preceding table.

¹ For earlier references see Burgerstein (**2**). Cannon (**4**) employed an ingenious hygrometer method, which does not seem to have been adopted by others. Very recently Edith B. Shreve (**17**) has employed the closed chamber and dew-point apparatus. Especially has Freeman (**6**) used the method of the closed chamber and an absorber for water, with very valuable results.

TABLE V

*Data of diurnal foliar transpiring for various plants growing in the open,
with irrigation, at Tucson*

Serial No.	Name of Plant	Time of test	Foliar index of transpiring power for		
			upper surface	lower surface	entire surface
1	<i>Dahlia variabilis</i> Desq.	Aug. 12 10.00 a.m.	0.7039	0.9231	0.8130
			0.9863	1.0000	0.9934
			0.9600	1.0000	0.9800
			Av. 0.8834	0.9744	0.9288
2	<i>Verbesina encelioides</i> Benth. and Hook.	Aug. 13 10.45 a.m.	0.6921	0.9777	0.8349
			0.7847	0.9058	0.8458
			0.8381	1.0352	0.9347
			Av. 0.7716	0.9729	0.8723
3	<i>Verbena hybrida</i> Hort.	Aug. 12 10.15 a.m.	0.7164	1.0285	0.8725
			0.5454	0.8944	0.7195
			0.9000	1.0000	0.9500
			Av. 0.7206	0.9743	0.8473
4	<i>Arundo Donax</i> L.	Aug. 19 12.00	0.8105	0.7857	0.7981
			0.8462	0.7700	0.8081
			0.7264	0.8370	0.7817
			Av. 0.7944	0.7976	0.7960
5	<i>Rudbeckia laciniata</i> L.	Aug. 12 10.45 a.m.	0.3031	0.8780	0.5906
			0.5878	0.9863	0.7871
			0.9290	1.0511	0.9901
			Av. 0.6063	0.9718	0.7893
6	<i>Medicago sativa</i> L.	Aug. 8 11.00 a.m.	0.7488	0.7817	0.7603
			0.6880	0.8958	0.7919
			0.8113	0.7963	0.8038
			Av. 0.7494	0.8246	0.7853
7	<i>Zinnia elegans</i> Facq.	Aug. 11 3.45 p.m.	0.5251	0.3322	0.4287
			0.9244	0.6038	0.7641
			1.2721	1.0319	1.1520
			Av. 0.9072	0.6559	0.7849
8	<i>Mirabilis jalapa</i> L.	Aug. 15 10.45 a.m.	0.4951	0.9438	0.7195
			0.6205	0.8312	0.7254
			0.6613	0.9848	0.8231
			Av. 0.5923	0.9199	0.7580
9	<i>Ricinus communis</i> L.	Aug. 11 1.45 p.m.	0.4797	0.5221	0.5009
			0.8875	0.9441	0.9158
			0.5547	0.7651	0.6599
			Av. 0.6406	0.7438	0.6922

TABLE V (continued)

Serial No.	Name of Plant	Time of test	Foliar index of transpiring power for		
			upper surface	lower surface	entire surface
10	<i>Washingtonia filifera</i> Wendl.	Aug. 21 10.45 a.m.	0.4603	0.7104	0.5854
			0.6290	0.7847	0.7018
			0.5530	0.7423	0.6477
			Av. 0.5474	0.7458	0.6450
11	<i>Helianthus annuus</i> L.	Aug. 19 10.30 a.m.	0.3730	0.4591	0.4161
			0.6130	0.8100	0.7115
			0.7085	0.7821	0.7453
			Av. 0.5648	0.6837	0.6243
12	<i>Parthenium argentatum</i> A. Gray	Aug. 13 11.15 a.m.	0.9621	0.5340	0.7482
			0.7521	0.4092	0.5807
			0.7120	0.3560	0.5340
			Av. 0.8087	0.4330	0.6210
13	<i>Prosopis velutina</i> Wooten	Aug. 18 10.15 a.m.	0.6280	0.5179	0.5739
			0.7647	0.4815	0.6231
			0.8333	0.4422	0.6373
			Av. 0.7420	0.4805	0.6114
14	<i>Tropaeolum majus</i> L.	Aug. 11 3.00 p.m.	0.3400	0.6037	0.4719
			0.3715	0.9647	0.6681
			0.4242	0.6827	0.5535
			Av. 0.3786	0.7504	0.5978
15	<i>Petunia hybrida</i> Hort.	Aug. 14 2.00 p.m.	0.3386	0.5246	0.4316
			0.4923	0.5517	0.5220
			0.5470	0.7529	0.6495
			Av. 0.4593	0.6097	0.5345
16	<i>Schinus molle</i> L.	Aug. 16 9.45 a.m.	0.6548	0.2368	0.4458
			0.6810	0.2868	0.4839
			0.7484	0.4191	0.5838
			Av. 0.6947	0.3142	0.5045
17	<i>Jatropha cardiophylla</i> Muell. Aig.	Aug. 21 11.30 a.m.	0.2426	0.4990	0.3708
			0.4517	0.6238	0.5378
			0.4637	0.5402	0.5020
			Av. 0.3860	0.5543	0.4702
18	<i>Phoenix dactylifera</i> L.	Aug. 21 11.00 a.m.	0.3476	0.4175	0.3826
			0.4175	0.4378	0.4277
			0.6000	0.5625	0.5813
			Av. 0.4550	0.4726	0.4639
19	<i>Populus fremonti</i> S. Wats.	Aug. 13 12.00 p.m.	0.3232	0.3808	0.3520
			0.3665	0.4787	0.4226
			0.4171	0.4252	0.4212
			Av. 0.3689	0.4282	0.3986

TABLE V (*continued*)

Serial No.	Name of Plant	Time of test	Foliar index of transpiring power for		
			upper surface	lower surface	entire surface
20	<i>Viola odorata</i> L.	Aug. 14 4.00 p.m.	0.2835	0.8416	0.5626
			0.3793	0.9287	0.6540
			0.4060	0.9853	0.6957
			Av. 0.3563	0.9185	0.3674
21	<i>Panicum sanguinale</i> Dulac.	Aug. 20 10.45 a.m.	0.1707	0.4497	0.3102
			0.1813	0.5095	0.3454
			0.1898	0.6907	0.4403
			Av. 0.1806	0.5499	0.3653
22	<i>Antirrhinum majus</i> L.	Aug. 11 3.15 p.m.	0.2773	0.3070	0.2922
			0.2164	0.2773	0.2469
			0.4931	0.5444	0.5188
			Av. 0.3289	0.3762	0.3526
23	<i>Sorghum halepense</i> Pers.	Aug. 21 10.30 a.m.	0.1814	0.4521	0.3181
			0.1622	0.5618	0.3620
			0.1588	0.5877	0.3733
			Av. 0.1675	0.5339	0.3511
24	<i>Punica granatum</i> L.	Aug. 16 11.15 a.m.	0.0608	0.5586	0.3047
			0.0457	0.6480	0.3469
			0.0627	0.6703	0.3665
			Av. 0.0564	0.6256	0.3394
25	<i>Vitex agnus-castus</i> L.	Aug. 16 10.45 a.m.	0.0428	0.5623	0.3026
			0.0452	0.6292	0.3372
			0.0645	0.6560	0.3603
			Av. 0.0508	0.6158	0.3333
26	<i>Chloris elegans</i> H. B. and K.	Aug. 21 11.00 a.m.	0.2285	0.4570	0.3428
			0.2004	0.3152	0.2578
			0.1705	0.5077	0.3391
			Av. 0.1995	0.4299	0.3132
27	<i>Melia azedarach</i> L.	Aug. 18 11.00 a.m.	0.0551	0.5400	0.2976
			0.0556	0.7589	0.4073
			0.0520	0.3815	0.2163
			Av. 0.0542	0.5601	0.3072
28	<i>Pittosporum tobira</i> Ait.	Aug. 19 11.00 a.m.	0.0442	0.4067	0.2255
			0.0460	0.6892	0.3676
			0.0447	0.5782	0.3115
			Av. 0.0449	0.5580	0.3015
29	<i>Atriplex canescens</i> James	Aug. 15 11.30 a.m.	0.1851	0.3627	0.2739
			0.2370	0.4301	0.3336
			0.1491	0.2963	0.2227
			Av. 0.1904	0.3630	0.2767

TABLE V (continued)

Serial No.	Name of Plant	Time of test	Foliar index of transpiring power for		
			upper surface	lower surface	entire surface
30	<i>Amaranthus paniculatus</i> L.	Aug. 19 11.30 a.m.	0·1119	0·2830	0·1975
			0·1376	0·4613	0·2995
			0·1146	0·4671	0·2909
		Av.	0·1214	0·4038	0·2627
31	<i>Dasyllirion wheeleri</i> S. Wats.	Aug. 18 3.00 p.m.	0·2879	0·2379	0·2629
			0·3147	0·1829	0·2488
			0·2653	0·2234	0·2444
		Av.	0·2893	0·2147	0·2520
32	<i>Olea europea</i> L.	Aug. 14 3.15 p.m.	0·0083	0·3894	0·1988
			0·0132	0·4903	0·2518
			0·0154	0·4384	0·2269
		Av.	0·0123	0·4394	0·2258
33	<i>Ficus carica</i> L.	Aug. 20 10.15 a.m.	0·1048	0·2586	0·1817
			0·0744	0·3221	0·1983
			0·0680	0·4167	0·2424
		Av.	0·0824	0·3325	0·2075
34	<i>Rosa lamarque</i>	Aug. 15 10.15 a.m.	0·0318	0·3146	0·1732
			0·0360	0·3595	0·1982
			0·0398	0·3839	0·2118
		Av.	0·0359	0·3527	0·1944
35	<i>Pelargonium zonale</i> L'Herit.	Aug. 15 10.00 a.m.	0·1013	0·2416	0·1715
			0·1006	0·2626	0·1816
			0·1065	0·2461	0·1763
		Av.	0·1028	0·2501	0·1761
36	<i>Nerium oleander</i> L.	Aug. 15 11.30 a.m.	0·0237	0·3764	0·2001
			0·0180	0·2397	0·1289
			0·0233	0·3244	0·1739
		Av.	0·0217	0·3135	0·1676
37	<i>Chrysanthemum indicum</i> L.	Aug. 18 11.30 a.m.	0·0939	0·0520	0·0730
			0·3649	0·0717	0·2182
			0·2135	0·1399	0·1767
		Av.	0·2241	0·0879	0·1560
38	<i>Canna indica</i> L.	Aug. 18 12.00	0·0379	0·0482	0·0431
			0·0246	0·2704	0·1475
			0·0314	0·3380	0·1847
		Av.	0·0313	0·2189	0·1251
39	<i>Atriplex wrightii</i> S. Wats.	Aug. 15 12.00 a.m.	0·0867	0·1534	0·1201
			0·0652	0·0912	0·0782
			0·0858	0·1154	0·1006
		Av.	0·0792	0·1200	0·0996

TABLE V (*continued*)

Serial No.	Name of Plant	Time of test	Foliar index of transpiring power for		
			upper surface	lower surface	entire surface
40	<i>Grabowskia glauca</i> Schlecht.	Aug. 20 11.15 a.m.	0.0296	0.1012	0.0654
			0.0319	0.1280	0.0800
			0.0374	0.0861	0.0618
		Av.	0.0330	0.1051	0.0691
41	<i>Chenopodium incanum</i> Heller	Aug. 18 1.45 p.m.	0.0708	0.0456	0.0582
			0.0565	0.0463	0.0513
			0.0854	0.0573	0.0714
		Av.	0.0709	0.0497	0.0603
42	<i>Eriogonum aberteanum</i> Torr.	Aug. 15 2.00 p.m.	0.0089	0.0048	0.0069
			0.0081	0.0037	0.0059
			0.0095	0.0049	0.0072
		Av.	0.0088	0.0045	0.0066
43	<i>Atriplex elegans</i> Dietr.	Aug. 15 2.00 p.m.	0.0009	0.0009	0.0009
			0.0049	0.0010	0.0030
			0.0066	0.0009	0.0037
		Av.	0.0041	0.0009	0.0025

According to the average indices for the entire leaf surfaces, as given in Table V, *Dahlia variabilis* has the greatest diurnal foliar transpiring power (0.9288) and *Atriplex elegans* has the lowest (0.0025). There will probably be no dissent from the proposition that *Dahlia* is typically mesophytic and that this *Atriplex* is typically or even extremely xerophytic. No plants of extreme mesophytic leaf structure were included in the series; most such plants would hardly be expected to thrive in the open during the Tucson summer. It may therefore be expected that many plants will be found under less arid atmospheric conditions than those here dealt with, which will be characterized by markedly higher indices than those of Table V. If the list of Table V might be extended towards higher indices than that of *Dahlia* it might soon include plants that can grow only in deep shade, even in the humid regions. It is also possible, since the nature of the leaf structures and their water content may be as much dependent upon the water-extracting power of the air as upon the water-supplying power of the soil¹, that many of the same species here considered (*Dahlia* included) may be found to exhibit higher foliar indices than are here recorded, when they come to be studied under less arid atmospheric conditions. In the present tests, it is to be remembered, the soil moisture content was rather high.

There will probably be no serious objection raised by students of ecology to the further propositions, that *Ricinus* is a mesophyte, being no. 9 in Table V, and that all the plants preceding it belong to the same general class. Likewise, it may

¹ In this connection see Livingston's note on the growth of mesophytes with plentiful soil moisture but with high evaporating power of the air (9 and 10—the former paper includes practically all that is in the other).

be safely assumed that *Atriplex wrightii* is undoubtedly xerophytic in leaf character, and that all the plants following it in the list are xerophytes. From these propositions it is seen that all the forms listed with indices above 0.69 are surely mesophytes and all with indices below 0.28 are as surely xerophytes, in the vague sense of these terms as heretofore employed by ecologists. The intermediate numbers of the list, between these two groups, include plants of more or less questionable nature as far as this ecological classification is concerned. Some of them can live in comparatively dry conditions of both soil and air but do not grow markedly during periods so characterized (*Prosopis*, *Parthenium*) and some grow well with moist soil and dry air (*Helianthus*, *Schinus*, *Phoenix*, *Populus*, etc.). It is therefore practically impossible to apply the terms xerophyte and mesophyte in this portion of the list, at least until such time as these terms are made susceptible of quantitative definition. As a result of this preliminary study, it may be suggested that plants exhibiting a diurnal foliar transpiring power of less than 0.30 may be regarded as xerophytes, while those exhibiting indices above 0.70 may be considered mesophytes. Whether there may be any advantage in erecting an intermediate critical point (as at the value of the index 0.50) by which mesophytes and xerophytes may be distinguished, is to be found out only through much fuller study.

If these conclusions be expressed in ordinary terms, instead of in those here adopted, it may be stated that those plants are surely mesophytes whose average leaf surface is capable of giving off water in the daytime seven-tenths as rapidly as does a saturated blotting paper surface blanketed by a millimeter of air (under the same temperature conditions as the leaves). Also, plants thus capable of giving off water less than three-tenths as fast as the standard blotting paper surface are unquestionably xerophytes. This is as far as it is possible to go at present, but an important constructive problem appears to be here opened, and its study should do much to put at least one phase of ecology upon a quantitative basis.

6. Transpiring power of floral parts

Little if anything is thus far known quantitatively of the transpiring power of floral parts, and the adaptability of the method of standardized cobalt chloride paper to a study of this, together with the availability of a number of kinds of flowers in apparently healthy condition at the time of these studies, led the writer to undertake some preliminary tests in this connection. For comparison, similar tests were carried out on the leaf surfaces of the same plants. The data of these tests are given in Table VI, for the petals and leaves of six different species. Only day observations were made. The plants are listed in the order of their average floral indices.

As might be expected the different flowers here considered show great differences, not only in their general transpiring power, but also in the relation shown between the transpiring power of their upper and lower surfaces. The data at hand are not adequate for useful generalization, but it may be noted that the order of magnitude of the general floral indices among these six plants appears to be about the same as is that of the corresponding average foliar indices.

TABLE VI

Indices of diurnal transpiring power of floral and foliar surfaces in the same plant

Name of plant	Time of observation	Index of transpiring power					
		For floral surface			For foliar surface		
		Upper	Lower	Entire	Upper	Lower	Entire
<i>Verbesina encelioides</i> Benth. and Hook.	Aug. 13 11.00 a.m.	0.5176	0.6222	0.5699	0.7716	0.9729	0.8723
<i>Rudbeckia laciniata</i> L.	Aug. 12 11.00 a.m.	0.4376	0.4881	0.4629	0.6063	0.9718	0.7893
<i>Zinnia elegans</i> Facq.	Aug. 12 11.00 a.m.	0.4487	0.2488	0.3488	0.9072	0.6559	0.7816
<i>Petunia hybrida</i> Hort.	Aug. 13 2.15 p.m.	0.2341	0.3832	0.3087	0.4593	0.6097	0.5345
<i>Solanum rostratum</i> Dun.	July 30 9.30 a.m.	0.0760	0.0844	0.0802	0.7200	0.4079	0.5640
<i>Kalstroemia grandiflora</i> Torr.	July 30 9.30 a.m.	0.0251	0.0407	0.0329	0.4755	0.3605	0.4180

7. Relation of foliar transpiring power to the phenomenon of wilting

It was the writer's good fortune to be able to have the kind cooperation of Mr John W. Shive, of the Johns Hopkins University, which cooperation made possible the comparison of the foliar transpiring powers of leaves of potted plants of *Phaseolus vulgaris* L. before and after wilting. The plants were some of those employed by Shive and Livingston (16) in their studies on the relation of atmospheric conditions to the soil moisture residue at permanent wilting. As these authors have stated, their plants were sealed in water-proof containers and exposed to different atmospheric conditions until permanent wilting ensued. The hygrometric paper tests were performed upon some of these plants when in the turgid condition and the tests were repeated after wilting had occurred. Two examples of a number of experiments—all giving similar results—may here suffice.

Experiment 1. In the first experiment three plants were exposed in the cheesecloth chamber in the lath shelter, as described by Shive and Livingston. Two tests were made on each plant in the turgid condition, Aug. 26, 11 to 11.30 a.m. After about 29 hours, on Aug. 27, 3.45 to 4 p.m., these tests were repeated, the plants being then in the wilted condition. The averages of the two indices for the upper, lower and entire leaf surface, resulting from each test, are presented in Table VII, which also gives the ratio of the first to the second general index for each plant.

The change in transpiring power is very marked, the index for the entire leaf surface being only about eighteen-hundredths as great at the last test as at the first. It is seen that the indices for the separate leaf surfaces both alter markedly, that for the lower about twice as much, however, as that for the upper.

TABLE VII

Average indices of foliar transpiring power (each from two tests) for three Phaseolus plants in the turgid and wilted conditions. Experiment 1, exposure between tests 29 hours, in cheesecloth chamber in lath shelter

Plant No.	Average index for leaves						Ratio of second to first index, entire leaf
	In turgid condition			In wilted condition			
	Upper surface	Lower surface	Entire leaf	Upper surface	Lower surface	Entire leaf	
1	0.1040	0.5226	0.3133	0.0319	0.0886	0.0603	0.19
2	0.1719	0.6011	0.3865	0.0634	0.0938	0.0786	0.20
3	0.1810	0.6114	0.3962	0.0480	0.0596	0.0538	0.14
Aver.	0.1523	0.5784	0.3653	0.0478	0.0807	0.0642	0.18

Experiment 2. The three plants were allowed to wilt in the glass box described by Shive and Livingston and by Caldwell. In this box the air humidity was kept high and there was no wind nor direct sunshine, though strong diffuse light was allowed to enter. The study began Aug. 26, 12.30 p.m. and continued about 50 hours till Aug. 28, 3 p.m. Determinations were made at four times in this experiment, once at the beginning, once after fourteen hours (when wilting was already evident), again after forty-eight hours, and still again after fifty hours, at the end of the experiment. Table VIII gives the average indices.

TABLE VIII

Average indices of foliar transpiring power (each from two tests) for three Phaseolus plants, in the turgid condition, and after 14, 48, and 50 hours exposure in a moist chamber

Plant No.	1	2	3	Average
1st determination, turgid condition				
Upper leaf surface	0.3005	0.2713	0.3813	0.3177
Lower leaf surface	0.6235	0.6409	0.3423	0.5356
Entire leaf surface	0.4620	0.4561	0.3618	0.4266
2nd determination, after 14 hours wilted condition				
Upper leaf surface	0.0759	0.0566	0.0733	0.0686
Lower leaf surface	0.0712	0.0815	0.0621	0.0716
Entire leaf surface	0.0736	0.0691	0.0682	0.0703
3rd determination, after 48 hours				
Upper leaf surface	0.0289	0.0383	0.0388	0.0353
Lower leaf surface	0.1050	0.0736	0.1246	0.1011
Entire leaf surface	0.0670	0.0561	0.0792	0.0674
4th determination, after 50 hours				
Upper leaf surface	0.0198	0.0229	0.0262	0.0230
Lower leaf surface	0.1169	0.0618	0.0287	0.0681
Entire leaf surface	0.0684	0.0424	0.0275	0.0461
Ratio of 4th to 1st index, entire leaf surface	0.15	0.09	0.08	0.10

The averages of Table VIII show the same phenomenon of markedly reduced indices of general foliar transpiring power, accompanying the wilting of the plant, as has been brought out above. Here it is evident that most of the alteration in the value of the index for the entire leaf surface took place in the first 14 hours during which this value changed from 0.43 to 0.07. Further decrease was less pronounced and the final index appears as 0.05. In these tests the transpiring power of the lower leaf surface again altered only about one-half as much as did the upper. Under these moist conditions it is notable that the time required for wilting was much longer than in cases with higher evaporation rates, but that the degree of reduction of transpiring power was greater in the present instance.

Results. From the two experiments just presented and from other similar ones, it is clear that the wilting of the plant is accompanied by a marked fall in foliar transpiring power, as was to be expected from the studies of F. Darwin, Lloyd, and others on stomatal movement, as well as from the general nature of the wilting process which is simply a highly developed stage of incipient drying. The data at hand are not sufficient to warrant any further attempt at generalization, but it is clear that the method here employed is eminently suited for the investigation of this whole matter.

8. Transpiring power as an index of drought resistance

If the relative transpiring power of foliar surfaces furnishes a criterion by which plants may be arranged in a scale of xerophytism, as has been shown above to be the case, it logically follows that this same index must furnish a criterion for the comparison of different forms of agricultural plants with regard to drought resistance, at least as far as the foliage is concerned in the determination of this character. To test this proposition by means of the standardized hygrometric paper, two very different varieties of alfalfa (*Medicago sativa* L.) and two varieties of *Sorghum halepense* (L.) Pers. were employed.

Alfalfa. The alfalfa plants were growing healthily in the grounds of the Arizona Experiment Station; it was again through the courtesy of Professor Geo. F. Freeman of that station that I was enabled to make use of them.

The two forms studied are designated by Professor Freeman as no. 17 and no. 112, in his series of new varieties of alfalfa. No. 17 is characterized in Professor Freeman's description as having "stems large, light green and somewhat succulent; leaves large, abundant, light green, thin, elongated, smooth." No. 112 is characterized as having "stems exceedingly large and stiff, purplish; plants tall, leaves abundant, large, very narrow." Of the plants used in these tests, a difference in the size, colour and stiffness of the leaves was apparent, as well as some difference in stems. Comparing the two, no. 17 had somewhat less woody stems and larger, lighter coloured, more flexible leaves; no. 112 appeared more xerophilous, in general.

Five determinations of the transpiring power of upper, lower and entire leaf surfaces (for apparently representative leaves, in the day) were made, on Aug. 4, 8 and 25. Corresponding night determinations were made only on the first date.

The individuals tested were growing side by side. The resulting averages, together with the maximum and minimum of each series, are given in Table IX.

TABLE IX

Data of foliar transpiring power, each from five approximately simultaneous tests, on two varieties of Medicago sativa L., growing side by side, irrigated

Approximate time of ob- servation		No. 17			No. 112		
		Upper surface	Lower surface	Entire surface	Entire surface	Lower surface	Upper surface
<i>Day</i>	Min.	0·8769	1·1400	1·0085	0·6966	0·6333	0·7600
Aug. 4	Max.	1·0364	1·6286	1·2307	1·1880	1·4250	0·9500
11 a.m.	Av.	1·0857	1·1916	1·1287	0·9409	1·0224	0·8594
<i>Night</i>							
Aug. 4	Min.	0·2057	0·2594	0·2326	0·1903	0·1504	0·2256
9 to	Max.	0·4316	0·6277	0·5297	0·2691	0·2457	0·3633
11 p.m.	Av.	0·3777	0·4054	0·3916	0·2398	0·1880	0·2945
<i>Day</i>	Min.	0·8804	0·9456	0·9130	0·7653	0·7817	0·7488
Aug. 8	Max.	0·9575	1·1889	1·0732	0·8252	0·8958	0·8686
11 a.m.	Av.	0·9436	0·9848	0·9642	0·8004	0·8089	0·7918
<i>Day</i>	Min.	0·6071	0·7954	0·7013	0·5111	0·6718	0·3503
Aug. 25	Max.	0·8479	0·8622	0·8552	0·7053	0·8157	0·5948
3 p.m.	Av.	0·7301	0·8246	0·7774	0·6219	0·7188	0·5247

From the results given in Table IX it becomes apparent that in every case but one the final average index is considerably greater for no. 17 than for no. 112. The exception occurs with the lower leaf surface in the first day determination, where no. 17 has an index (0·99) about the same as that of no. 112 (1·02). It thus appears, in general, that the foliar transpiring power of no. 17 is clearly greater than that of no. 112.

Another interesting point brought out by these determinations is this, that the index of foliar transpiring power decreases throughout the time period from Aug. 4 to Aug. 25, a phenomenon that may be due to the maturing of the plant; no attempt was here made to enquire into the causal conditions determining such changes, however. Since this alteration in the index value is observed, it is obviously impossible to use the general average index for any one time of determination as a criterion of drought resistance. It is possible, however, to average these general indices for the three day determinations, thus getting a single number to represent the diurnal foliar transpiring power of each plant. If this is done, we have for no. 17 the average of 1·13, 0·96 and 0·78, which is 0·96; similarly, for no. 112, we have the average of 0·94, 0·80 and 0·62, which is 0·79. If these results represent the truth, it may be said that the degrees of drought resistance possessed by these two plants, under the given conditions of growth and as far as diurnal foliar transpiring power is concerned, are in about the ratio of 8 to 9. Not enough data are at hand for a corresponding attempt to derive similar indices of drought resistance for the night, though it is clearly apparent

from the results given that there occurs a marked difference between the two plants in this respect and that this difference likewise points to the conclusion that no. 112 is considerably more drought resistant than no. 17.

In connection with these studies on *Medicago* it is pertinent to point out the interesting fact that the index of diurnal foliar transpiring power of this plant, as determined on Aug. 4, attains the value somewhat above unity for the upper (1.09) and for the entire leaf surface (1.13) in the case of no. 17, and for the lower leaf surface (1.02) in that of no. 112. The generalization is thus warranted, that we may expect to find plants with power to give off moisture to the standard paper more rapidly than does the standard saturated blotting-paper surface blanketed by a millimeter layer of air.

Johnson grass and Soudan grass. A study similar to that made upon alfalfa was carried out with Johnson grass and Soudan grass, growing side by side in the same irrigated bed at the experimental grounds of the Desert Laboratory. The seed of Johnson grass was obtained in the local Tucson market; that of the other variety was kindly furnished by Professor Charles V. Piper, of the Bureau of Plant Industry, U. S. Dept. of Agriculture. Soudan grass has been lately introduced into Arizona and in it some of the features of Johnson grass objectionable to stockmen seem to be eliminated. In these tests the grasses were both six weeks old, from the seed, and were producing heads. The data of these determinations are given in Table X, where the calculations and arrangement are the same as in Table IX.

TABLE X

Data on foliar transpiring power, each from three approximately simultaneous tests, on Johnson grass and Soudan grass (Sorghum halepense L.), growing side by side

Approximate time of ob- servation		Johnson grass			Soudan grass		
		Upper surface	Lower surface	Entire surface	Entire surface	Lower surface	Upper surface
<i>Day</i>	Max.	0.0441	0.0630	0.0535	0.2629	0.2459	0.2800
Aug. 28	Min.	0.0424	0.0520	0.0481	0.1319	0.1414	0.1224
4 p.m.	Av.	0.0435	0.0587	0.0511	0.2067	0.2077	0.2055
<i>Night</i>	Max.	0.4540	0.2982	0.3761	0.4052	0.5751	0.3982
Aug. 29	Min.	0.4313	0.2302	0.3273	0.2561	0.2469	0.2353
9.30 p.m.	Av.	0.4365	0.2695	0.3530	0.3313	0.3629	0.2996

These tests of Johnson and Soudan grass indicate clearly enough that the specimens of Soudan grass here dealt with possessed a very much higher transpiring power, for both upper and lower leaf surfaces and for the entire leaf, than did the plants of Johnson grass tested. For the entire leaf surface the index for Soudan grass is about four times as great as for Johnson grass. Whether such a relation may always hold between these forms is, of course, an open question, but the evidence points definitely to the conclusion that Johnson grass is very much more drought resistant, at least under the conditions of these tests, and as far as foliar transpiring power is concerned, than is Soudan grass.

An interesting feature of Table X lies in the relation which seems to prevail between the diurnal and nocturnal transpiring powers of these grasses. In every case the former is smaller than the latter, in the case of Johnson grass this difference being very pronounced and in the other case considerable.

III. GENERAL CONCLUSIONS.

The results obtained in this investigation demonstrate plainly enough a number of ways in which the method of standardized cobalt chloride paper is suitable for physiological and ecological enquiries. The method is well suited to studying the daily march of foliar transpiring power; the data here presented for *Quamoclidion* are as clear and definite as those obtained in the same way for *Datura* and *Physalis* by Livingston. In so far as the tests of *Verbascum* bear on this question their results are in general agreement with those for the other three plants hitherto studied in this way. The magnitude of the index of foliar transpiring power remains approximately constant and at a low value, throughout the night hours, but suddenly increases at about sunrise. It attains a maximum for the day some time before the occurrence of the daily maximum of temperature or of evaporation, and then falls to the night value. How far stomatal movements may be involved in these changes cannot be determined till the condition of stomata is studied in connection with transpiring power. Without entering into this discussion it may be noted that F. Darwin (5) seems to regard most of the diurnal variation in transpiration rate as due to stomatal movement, while Lloyd (14)¹ concluded that, in some plants at least, stomatal movement is not the controlling condition.

The studies upon *Verbascum*, as presented in this paper, show that the transpiring power of younger and older leaves is not to be considered the same, a proposition probably generally accepted. They suggest also that, apart from age, the position of a leaf upon the stem and the variations in structure related to correlations, may influence its transpiring power.

Various plants growing under more and under less arid conditions of the soil and air gave differences in transpiring power which suggest that the same species may possess quite different indices when grown under moist conditions, from those exhibited by individuals grown under dry conditions. Opportunity was not offered for a definite study of this relation, but it appears that the magnitude of the foliar transpiring power is probably a physiological character that will be found to vary for each species, within somewhat distant limits, just as do the cruder morphological characters employed by plant taxonomists, such as leaf size, shape, hairiness, etc.

The relation between diurnal and nocturnal transpiring power can be studied advantageously by the means of the method of standardized hygrometric paper, in the same way as this method is available for the study of the daily march already mentioned.

Perhaps the most important outcome of these studies is the conclusion that the method here employed offers an apparently adequate and somewhat simple means for classifying plant forms in a scale of xerophytism or of mesophytism. Of

¹ See this paper and that of Darwin (5) for the literature of this subject.

course a classification on this basis is quite without reference to the relative water-absorbing powers of roots or the relative conducting powers of stems, which will need to be quantitatively considered before a satisfactory scale of relative water requirements may be attained, but a classification based on leaf transpiring power should be vastly more satisfactory in use than is the vague ecological classification usually employed, based, as it is, on the appearance of the plant and the judgment of the observer. From the tests here recorded it is suggested that the term mesophyte as now used may be quantitatively defined as referring to plants with average index of foliar transpiring power between 0.70 and 1.00 or higher, while the term xerophyte may be considered as connoting plants with an index below 0.30. Plants with indices between 0.30 and 0.70 thus lie in the intermediate group of xero-mesophytes or meso-xerophytes. With further researches it may emerge that the limits just mentioned need modification, and perhaps a range may be established for the foliar transpiring power of hydrophytes, but the indications are clear enough that the method employing hygrometric paper and the standard evaporating surface will prove very valuable in this descriptive or classificational portion of ecological science.

The ecological classification just referred to is a classification according to water-need, as far as this depends upon foliar transpiring power, and the agricultural problem of determining the relative drought resistance of different crops or different varieties should be approachable by means of such studies as are here reported. The tests recorded for *Medicago* and *Sorghum* point promisingly in this direction. The full diurnal march of foliar transpiring power should probably be employed, however, rather than merely a few day and night determinations. Of course a comparatively large number of individual tests will be requisite, more of these with some plant forms than with others, but the method here employed appears to be by far the most satisfactory yet suggested.

Studies on the transpiring power of potted *Phaseolus* plants before and after wilting agree in general with the conclusions of F. Darwin, that resistance to transpiration increases at wilting, and with those of Livingston and Brown, that incipient drying may produce such an increased resistance before wilting occurs. No attempt is here made to deal with the question regarding the causal conditions determining the fall, as wilting occurs, in the values of the indices here used. It is suggested, however, that foliar transpiring power may be a characteristic of plants, the magnitude of which may prove valuable in predicting the need of irrigation long before the occurrence of any wilting.

IOWA STATE COLLEGE,
AMES, IOWA.

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