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VARIATION OF THE TRANSPIRING POWER OF LEAVES AS RELATED TO THE WILTING OF PLANTS[1]

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I. INTRODUCTION

Since LIVINGSTON (15) made it possible, to find out the index of the transpiring power of the leaf surface by measuring the relative transpirational water loss from leaf surface as compared with the water loss from some standared evaporating surface, our knowledge of the transpirational phenomenon of the leaf has made a great advance, especially in regard to its variation as influenced by the internal and external conditions of plants. On the other hand, our knowledge concerning the behavior of wilting plants and its relation to the environment has been recently enlarged by a great number of studies. As a matter of course the variation of the foliar transpiring power of wilting plants, which is dealt with in this paper, has already been studied by some investigators. Among others, BAKKE's works (2, 3) are valuable contributions. When he studied in *Helianthus annus* the variation of the foliar transpiring power as related to the wilting, he was able to discover a critical state of wilting, where this power shows very little fluctuation. He saw also a remarkable phenomenon in the uprooted specimens, namely that the transpiring power of leaves, which decreases with the progress of wilting, increases again somewhat at a

[1] Contributions from the Botanical Laboratory, Kyushu Imperial University No. 12.

point, where the plant is probably fallen into the critical state of wilting. This critical state of wilting he ascertained to be approximately the same as the point of so-called permanent wilting (5, 6, 7, 9, 20).

Thus the studies on the variation of the transpiring power of leaves relating to the wilting of plants have become very interesting, especially as we hope further to discover what relation exists between this phenomenon of plants and the nature of soils. The present paper is to deal with this phase of the question and is based on the results of work, which was done during 1919-1920 in the Plant Physiological Laboratory of Johns Hopkins University. The writer desires here to express his gratitude to the director of the laboratory, Professor B. E. LIVINGSTON, for his kindness in permitting the writer to use the facilities and equipment of the laboratory so freely, and for the many helpful suggestions given thruout the progress of this work.

II. MATERIAL AND METHOD

The plants used in this work were *Coleus* (*C. blumei*), wheat (*Triticum vulgare*), and soy-bean (*Glycine Soja*). The *Coleus* plants were transplanted from the culture pots, where they had been raised from cuttings, to unglased pots, 9 cm. in diameter, which contained the various kinds of soil used. After they had become well rooted, they were used for experimentation. The wheat and soy-bean plants were grown from seeds in similar experimental pots.

Three kinds of soil were used: sand, loam and humus; and nine mixtures were made by using two soils in each mixture, in the volumetric proportions of 1:3, 2:2 and 3:1. Thus including the three constituent soils, there were twelve kinds of soil for the experiments.

The water holding capacity of each soil was then determined, the method of HILGARD (11) being used, by means of a pan 1 cm. high and of 100 c.c. capacity. Two parallel determinations were made on each kind of soil, and the resultant average value was adopted. Determined in this way the water holding capacity was given in percentages on the basis of the oven-dry volume, as well as on the basis of the oven dry weight (Tab. 1). The soils and the plants planted therein were numbered according to the value of the water holding capacity on the former basis.

All plants were cultivated in the green house, and watered every morning, the pots containing the plants being placed in wooden boxes filled with wet sand. When it was desired that the plants should wilt for the experiment, they were transfered into another box filled with dry sand, the greater part of each pot being buried in sand for the purpose of protecting the plants from too rapid progress of wilting. The plants were also protected from direct sunlight for the same reason.

Tab. 1. Water holding capacity of the soil and its moisture residue at the critical point of wilting of plants rooted therein

Soil number	Constitution of soils	Water hold. capacity Volumetric	Water hold. capacity Gravimetric	Soil moisture residue Volumetric *Coleus*	Soil moisture residue Volumetric Wheat	Soil moisture residue Gravimetric *Coleus*	Soil moisture residue Gravimetric Wheat
1	S	40.7	28.9	2.3	1.6	1.4	1.0
2	S3 L1	43.0	32.8	2.5	2.5	1.7	1.7
3	S2-L2	45.8	37.0	6.1	5.0	4.9	3.7
4	S1-L3	50.7	43.6	8.9	6.2	7.3	4.7
5	S3-H1	55.7	43.9	11.8	7.6	8.0	5.1
6	L	57.1	56.8	13.1	9.3	10.4	7.4
7	L3-H1	67.5	70.3	18.5	16.7	17.6	15.5
8	S2-H2	71.1	64.4	22.9	17.5	10.9	13.9
9	L2 H2	79.5	90.6	26.7	23.2	28.2	24.7
10	S1-H3	81.4	91.0	30.2	28.7	32.1	28.0
11	L1 H3	86.5	114.0	33.2	32.9	40.1	39.7
12	H	103.1	140.5	48.8	46.2	70.7	58.1

S-Sand, L-Loam, H Humus.

Plants thus treated usually wilted rather slowly. If it was necessary, however, to hasten the wilting process of the plants, the larger part of the surface of the pots was left uncovered and exposed to the air. If some retardation of the wilting process seemed to be necessary, the plants were surrounded with a tall paper cylinder. By such methods, the writer was able to have plants wilted to an approximately equal degree for testing, at a definite hour each day. No means of preventing the evaporation of moisture from the surface of the pots and soils were tried in these experiments.

For the determination of the foliar transpiring power, LIVINGSTON's method of studying the relative transpiring power of leaves by means of standardized hygrometric paper (15, 1) was adopted; but the improved method of LIVINGSTON and SHREVE (16) was generally employed. The time-period required for the color change of hygrometric papers not only upon the leaf surface but also upon the standared evaporating surface at any given temperature was reduced as a rule to the theoretically required time at 20°C. In this case the table given in the page 305 of LIVINGSTON and SHREVE's paper (16) was used for the calculation of the time required. The reduced time-period for each hygrometric paper slip both upon the standard evaporating surface T and upon the leaf surface t being thus calculated, the index of the relative transpiring power for each leaf test upon a given leaf was easily to be found from the ratio T/t.

In order to study the behavior of wilting plant, it is first necessary to know that of healthy plants. Therefore the writer examined the transpiring power of leaves in healthy state for each material used, and then that during the wilting process.

The variation of the foliar transpiring power of plants during the process of wilting was considered from the two points of view, namely the variation of the transpiring power itself, and the variation of the amplitude of the daily fluctuation or the "day-night ratio" of this power. But in the large parts of the experiments, the behavior of the plants at or near the time of permanent wilting was given primary consideration.

The permanent wilting of the plants was determined by applying the BRIGGS and SHANTZ's method modified by SHIVE and LIVINGSTON (20). Many preliminary experiments were undertaken to become familiar with the critical state of wilting in the plants. Thus the writer was able to judge the time of permanent wilting for each plant with few mistakes. When a plant tested at a supposedly critical degree of wilting recovered its turgidity in the moist chamber for test, further tests were performed.

The water content of the soils at the point of permanent wilting of the plant rooted therein was also determined for the purpose of judging the water relation between the soil and plant at the critical point.

III. EXPERIMENTS

1. *Coleus*, rooted

The *Coleus* plants used in this experiment were a type of Mendelian hybrid, which had pale yellow leaves. Each plant had 6 or 7 pairs of leaves. Twelve plants were used for experiment, each of which was cultivated in a different soil. As is known, the foliar transpiring power of plants usually shows a considerable fluctuation during the day. As to the *Coleus* plants it was ascertained by the writer (13), that the variation of transpiration on the healthy leaves is caused principally by the function of stomata and the age of leaves. In this connection the leaf tests were done only upon the leaves, which were completely or nearly completely developed, their under surface, on which many stomata are situated, alone being tested.

After the preliminary work the highest value of the foliar transpiring power of *Coleus* plants, which was determined on the under surface of leaves, was found at afternoon and the lowest at the night. Therefore the leaf tests were tried two times a day, namely first during the period 15:30-16:30 and second during 22-23, for the purpose to know the amplitude of variation of the transpiring power.

Three leaves arranged in succession in different nodes were tested in each plant, one test being made on each leaf at each period. The plants were watered abundantly on the morning of the day they were tested. The average value of the indices of the foliar transpiring power found by three tests at each test period and the ratios between them were calculated (Tab. 2). This ratio or "day-night ratio" is nothing else than the value, which indicates the degree of the fluctuation of the transpiring power.

Thus a relatively high value of transpiring power in the day-time was found in the plants cultivated in the soils with lower water holding capacity, while the value found in the plants planted in the soils with higher water holding power was much lower. On the other hand, the transpiring power at night proved to be less variable in the different plants. Another point of interest was that the "day-night ratio" for the plants of the former group was higher than the unity as the matter of course, but the ratio for the latter was usually less than the unity. We may say, therefore, that the *Coleus* plants supplied with too much water in the soil with high water holding capacity, have less transpirational activity at day-time and show an unusual character in fluctuation. As a causal factor for this phenomenon we may perhaps point out the lesser aeration in the soil.

Consideration must next be given to the behavior of the plants on the day before the day of permanent wilting. In this case two leaves in each plant were tested. The leaf tests were performed in the day preceding the one, on which the tested plants were supposed to become permanently wilted. If a plant did not come to the state of permanent wilting on the next day, the leaf tests were continued on successive days, until the critical day arrived.

On the next day, on which the plants fell into the state of permanent wilting, the leaf tests for the day-time were made, and then a sample of soil (about 5 c.c.) was taken from each pot by means of corkborer, for the purpose of determining the water content of the soil. A glass tube, which was just large enough to fit the hole left by the withdrawal of the sample, was placed in the hole to prevent the drying of the soil. Then the plants were put into a moist chamber for 24 hours. All the plants did not recover their turgidity as was expected.

From the indices found on two successive days, namely on the critical day and the day previous, the writer could see the facts, that the value itself of the indices for the wilted plants came generally much lower than that of the turgid plants, and that it decreased progressively until it reached its minimal value at the critical state of wilting. The daily fluctuation of the transpiring power became less in the wilting plants, the "day-night ratio" coming near to unity (Tab. 2).

On the other hand, it was remarkable, that the minimal value found in each plant at the critical state of wilting came very similar to every other. The variation of these critical values was namely from 0.0140 to 0.0291, average value being 0.0197.

2. *Coleus*, rooted

In this series of experiment a variety of *Coleus* plants, which has pale yellow leaves with a purple colored central portion, was employed. In this case eleven plants were used, each of which was cultivated in a different soil, excepting the loam 2 – humus 2 mixture, in which the plant died.

Experiments were done in each plant at three different states of wilting, i.e. when slightly wilted, at the state of permanent wilting, and when completely wilted. The tests of the third state of wilting were made on the day following the one, during which the plants were enclosed in the moist chamber for determining the permanent wilting. For each plant three leaves arranged in successive nodes of the stem were tested on their under surface only, twice a day 15:30-16:30 and 22-23.

Considering first the "day-night ratio" of the indices, it was seen, that the ratios found on the day on which permanent wilting occurred and on the day following were in most cases very near to unity. Hence we may say that the fluctuation of the foliar transpiring power of this plant at or near the state of permanent wilting is less variable than that of the healthy or slightly wilted plants (Tab. 3).

Tab. 2. Indices of the foliar transpiring power of healthy and wilted *Coleus* plants

Number of plants and soils	Indices for healthy plants at			Indices for plants at the day before the day of permanent wilting at			Indices for plants at the day of permanent wilting at			Critical indices	Relative value of the critical indices
	15:30-16:30	22-23	*Ratio*	15:30-16:30	22-23	*Ratio*	15:30-16:30	22-23	*Ratio*		
1	.1314	.0633	*2.08*	.0352	**.0291**	*1.21*	.0329	(.0336)	*0.98*	.0291	1.48
2	.1340	.0635	*2.11*	.0279	.0255	*1.09*	**.0176**	(.0330)	*0.53*	.0176	0.89
3	.2243	.0945	*2.37*	.0314	.0241	*1.30*	**.0179**	(.0299)	*0.60*	.0179	0.91
4	.1559	.0830	*1.88*	.0227	**.0169**	*1.34*	.0213	(.0186)	*1.15*	.0169	0.86
5	.1761	.0802	*2.20*	.0300	.0294	*1.02*	**.0156**	(.0223)	*0.70*	.0156	0.79
6	.1470	.0803	*1.83*	.0257	**.0243**	*1.06*	.0348	(.0423)	*0.82*	.0243	1.23
7	.0590	.0918	*0.64*	.0289	**.0265**	*1.09*	.0099*	(.0280)	*0.35*	.0265	1.35
8	.1244	.0884	*1.41*	.0184*	.0231	*0.80*	**.0216**	(.0192)	*1.13*	.0216	1.10
9	.0435	.0646	*0.67*	.0101*	.0243	*0.42*	**.0140**	(.0129)	*1.09*	.0140	0.71
10	.0887	.0924	*0.96*	.0123*	.0269	0.46	**.0172**	(.0131)	*1.31*	.0172	0.87
11	.0384	.0398	*0.96*	.0252	.0240	*1.05*	**.0157**	(.0321)	*0.49*	.0157	0.80
12	.0482	.0581	*0.83*	.0287	.0273	*1.05*	**.0199**	(.0188)	*1.06*	.0199	1.01
Average	.1142	.0750	*1.52*	.0247	.0251	*0.98*	.0199	(.0253)	*0.79*	**.0197**	—

The indices at the test period 22-23 of the day of permanent wilting do not come into consideration, because the test material at this time was injured by the withdrawal of the soil sample for the determination of the water residue in the soil.

* Questionable values: In the case, where the indices indicated by an asterisk in the table were obtained, the air temperature of the green house was unusually high. The temperature in the green-house during the course of the experiment ranged from 11°C to 22°C, but in this case the air temperature was 27-29°C. All the day-time indices found in this case were unexpectedly very low. Therefore those indices are left as doubtful results, because the writer questions whether the procedure used for calculating the value of indices may be applied without correction in a case, where the extremely wilted leaves were tested in such high air temperature.

Tab. 3 Variation of the indices of the foliar transpiring power of *[illegible]* plants during the process of wilting

Number of plants and soils	Indices for slightly wilted plants at			Indices for plants at the permanent wilting at			Indices for plants after the day of permanent wilting at			Critical indices	Relative value of the critical indices
	15:30-16:30	22-23	*Ratio*	15:30-16:30	22-23	*Ratio*	15:30-16:30	22-23	*Ratio*		
1	.0319	.0326	*0.98*	**.0273**	.0303	*0.90*	.0278	.0263	*1.06*	.0273	1.22
2	.0408	.0316	*1.29*	.0296	**.0269**	*1.10*	.0328	.0317	*1.03*	.0269	1.20
3	.0284	.0255	*1.11*	**.0253**	.0275	*0.92*	.0351	.0309	*1.14*	.0253	1.13
4	.0283	.0241	*1.17*	**.0206**	.0291	*0.71*	.0259	.0269	*0.96*	.0206	0.92
5	.0466	.0392	*1.19*	.0323	**.0283**	*1.14*	.0288	.0297	*0.97*	.0283	1.26
6	.0281	.0194	*1.45*	.0261	**.0211**	*1.24*	.0297	.0313	*0.95*	.0211	0.94
7	.0462	.0389	*1.19*	.0423	.0415	*1.02*	**.0163**	.0199	*0.82*	.0163	0.73
8	.0505	.0409	*1.23*	.0293	.0279	*1.05*	**.0163**	.0204	*0.80*	.0163	0.73
9	—	—	—	—	—	—	—	—	—	—	—
10	.0468	.0386	*1.21*	**.0219**	.0298	*0.73*	.0226	.0210	*1.08*	.0219	0.98
11	.0322	.0213	*1.51*	.0091*	.0191	*0.48*	**.0185**	.0209	*0.89*	.0185	0.83
12	.0461	.0362	*1.27*	.0283	**.0243**	*1.16*	.0379	.0333	*1.14*	.0243	1.08
Average	.0387	.0317	*1.22*	.0266	.0278	*0.96*	.0265	.0266	*1.00*	**.0224**	—

* Questionable values (see table 2).

As regards the variation of the indices themselves, the fact was here again to be seen, that the values in question become generally smallest at or near the point of permanent wilting. We may say, therefore, that the indices become progressively smaller as wilting proceeds, and after their value reached the critical point, once more higher though but slightly.

The critical index found in each plant came again very similar to the average, as was the case in the preceeding experiment.

3. Wheat, rooted

Wheat plants 5-7 weeks old were used in this experiment series. In this case four stages of plants were studied, namely the stage of healthy state, slightly wilted, of permanent wilting and over-wilted. After the leaf tests were performed on the day of permanent wilting, the water residue in the soil, in which each plant was rooted, was determined by the same procedure as in the case of the experiment series 1. Then the plants were enclosed in a moist chamber for 24 hours for the test of permanent wilting. On the next day, the leaf tests were again tried for the plants, which were now in the state of over-wilting.

Twelve plants cultivated in different soils were tested in the state of permanent wilting, but in the other three states only 6 plants, which were grown in the sand, loam, humus and mixtures composed of equal parts of each of two of these soils.

There were three plants in each pot, but only one of them was tested and on its two most highly developed leaves. The leaf tests were made on their upper surface only, because it had been shown by a preliminary experiment, that the daily fluctuation of the foliar transpiring power of wheat is much higher on the upper surface of the leaves than on the lower (Tab. 4).

Tab. 4 Daily fluctuation of the foliar transpiring power of wheat in the healthy state

	Observed values				Values, when the minimal taken as the unity			
Test periods:	10-11	13-14	16-17	22-23	10-11	13-14	16-17	22-23
Indices for upper surface:	1,187	2,922	1.217	0,788	1,51	**3.71**	1.54	1.00
Indices for lower surface:	0.538	1,070	0.557	0.596	1.00	**1.99**	1.04	1.11
Average:	0.863	1.996	0.887	0.692	1.25	**2.88**	1.28	1.00

According to this preliminary research the highest value of indices was found at the period 13-14 and the lowest at 22-23. Therefore these two periods were adopted as the test time for the subsequent experiments.

The wheat plants grew very well, when they were cultivated in humus, sand-humus and loam-humus mixtures, while those in sand, loam and sand-loam mixtures showed less growth. Whether this fact is due to physical of nutritive properties of the soil is an unsolved question But there was no noticeable difference in the transpirational action on all tested plants, when the soils were abundantly watered. Namely in the healthy state all of six plants showed high value of index and also wide amplitude of its fluctuation; only the plant grown in loam showing somewhat lower value (Tab. 5).

The transpiring power became, however, progressively lower, as the plants fell into the state of wilting and showed a tendency to increase somewhat, after it had reached its minimal value at the time of permanent wilting. The indices found on the day of over-wilting were generally much lower than that of the day of permanent wilting as a matter of course, because the leaves tested in this state were already in drying phase.

Taking this minimal value as the index of the critical state of wilting, it was seen, that all plants tested had very similar transpiring power at this point, the index varying from 0 0100 to 0 0195 and average value being 0.0130 (Tab. 5). As regards the "day night ratio" it became much smaller in the wilting plants than in the healty. But it came generally under unity on the phase of permanent wilting or over-wilted, since the night-index became higher than the day-index.

4. Soy-bean, rooted

A variety of soy bean named "Wilson" was used for this experiment series The tested plants were about seven weeks old. The soy bean did not seem to be well adapted to the loam and loam-mixtures, because the growth of plants in such soils were highly retarded. Therefore five plants only were tested, namely those cultivated in sand, humus and in three mixtures made from them. The leaves of the soy bean have their stomata in greater number on the under surface. Some preliminary tests showed, that the transpiring power was much higher on that surface. Hence the leaf tests were done on the lower surface only, each test being made on the middle and one side leaflet

Tab. 5. Variation of the indices of the transpiring power of wheat plants during the process of wilting

Number of plants and soils	Indices for healthy plants at			Indices for slightly wilted plants at			Indices for plants at the permanent wilting at			Indices for over-wilted plants at			Critical indices	Relative value of critical indices
	13-14	22-23	*Ratio*	13-14	22-23	*Ratio*	13-14	22-24	*Ratio*	13-14	22-23	*Ratio*		
1	.3365	.0955	*3.52*	.1134	.0737	*1.54*	**.0126**	.0145	*0.87*	.0089	.0208	*0.43*	.0126	0.97
2	—	—	—	—	—	—	**.0108**	.0244	*0.44*	—	—	—	.0108	0.83
3	.2260	.0630	*3.59*	.1060	.0726	*1.46*	**.0100**	.0185	*0.54*	.0092	.0235	*0.39*	0100	0.77
4	—	—	—	—	—	—	**.0120**	.0223	*0.54*	—	—	—	.0120	0.92
5	—	—	—	—	—	—	.0157	**.0154**	*1.02*	—	—	—	.0154	1.18
6	.4173	.1031	*4.05*	.0886	.0753	*1.18*	**.0112**	.0258	*0.43*	.0253	.0232	*1.09*	.0112	0.86
7	—	—	—	—	—	—	.0185	**.0145**	*1.28*	—	—	—	.0145	1.12
8	.2335	.0670	*3.45*	.0570	.0564	*1.01*	**.0105**	.0196	*0.54*	.0108	.0253	*0.43*	.0105	0.81
9	.1054	.0546	*1.93*	0684	.0599	*1.14*	**.0112**	.0186	*0.60*	.0109	.0253	*0.43*	.0112	0.86
10	—	—	—	—	—	—	**.0148**	.0174	*0.85*	—	—	—	.0148	1.14
11	—	—	—	—	—	—	**.0130**	.0254	*0.51*	—	—	—	.0130	1.00
12	.3315	.0868	*3.82*	.0723	.0631	*1.15*	**0195**	.0222	*0.88*	.0107	.0255	*0.42*	.0195	1.50
Average	.2750	.0784	*3.51*	.0843	.0668	*1.26*	.0133	.0199	*0.67*	.0126	.0239	*0.53*	**.0130**	—

of a compound leaf in full development, on each plant. The average value of the indices of these two tests came into consideration.

Watering the plants well in the morning, the writer tried the leaf tests at four periods in the day in the usual manner. The foliar transpiring power itself and the manner of its daily fluctuation were similar in all tested plants. The maximal index was found in all cases in the period 10-11. The average values of indices for all plants obtained in the four test periods 10-11, 13-14, 16-17 and 22-23 were 0.1749, 0.1452, 0.0876 and 0.0849 respectively.

After the healthy plants well watered were tested, the pots with the plants were replaced in a box filled with dry sand, the greater part of the pots being buried in the sand. Thereafter the pots were never touched, and no more water was given to either plants or soils. Letting the plants wilt gradually in this manner, the writer tried the leaf tests once a day during the period 10:30-11:30 on successive days, until it became impossible to continue the tests, because of the drying and crumpling of the leaves.

The foliar transpiring power of all tested plants became, as the results of this experiment showed, gradually smaller in the wilting phase of plants, and reached its minimal value on the sixth day, showing a tendency to become a little higher again, before the leaves went into the drying phase. The minimal indices found in all plants had almost equal value, which fluctuated from 0.0191 to 0.0206, with the average value of 0.0196 (Tab. 6). Those minimal values might be the critical ones at the time of permanent wilting.

Tab. 6. Variation of the indices of the foliar transpiring power of soy bean during the process of wilting

Number of plants and soils	1	5	8	10	12	Average
March 3.	.1540	.2148	.1513	.1692	.1850	.1749
„ 4.	.1952	.2890	.2900	.2420	.3070	.2646
„ 5.	.1154	.2960	.1970	.1646	.2120	.1970
„ 6.	.1023	.0557	.0511	.0485	.0930	.0701
„ 7.	.0926	.0824	.0518	.0482	.0782	.0706
„ 8.	.0312	.0236	.0227	.0253	.0327	.0271
„ 9.	**.0191**	**.0194**	**.0206**	**.0191**	**.0200**	**.0196**
„ 10.	dry up	.0284	dry up	.0225	.0327	.0279
„ 11.	—	dry up	—	dry up	dry up	—
Relative value of critical index	0.97	0.99	1.05	0.97	1.02	—

It may be remarked here as a fact of interest, that the indices of the foliar transpiring power found in the plants well watered were much lower in all cases, than those found on the next day. And this fact was more marked in the plants planted in the soils with high water holding capacity. This fact means perhaps that too much water or insufficient aeration in the soil acts on the transpiring power of soy bean as a depressive factor.

5. *Coleus*, wheat and soy bean, uprooted

In this series of experiment was studied the variation of the foliar transpiring power of uprooted plants. Two *Coleus* plants (the same variety as used in the experiment series 2), two wheat plants and one soy bean plant were employed as the test material.

The *Coleus* plants were cultivated in pots filled with common garden soil. After the first leaf tests were made at 9:30, the plants were uprooted at ten o'clock, care being taken to avoid injuring the root systen as much as possible, and they were allowed to wilt in the air of the green house. The second tests were made at 10:30, and at one hour intervals thereafter. The indices were obtained in this case from the test results on the lower side of two middle aged leaves.

The experiments in wheat and soy bean followed the same procedure. The wheat plants were planted in sand (plant a) and in humus (plant b); they were about four weeks old. The leaf tests were made on the upper surface of two leaves. The soy bean plant, about six weeks old, was cultivated in sand. The leaf tests were performed on the under surface of the two leaflets of a compound leaf.

The results of these experiments are brought together in table 7. In all cases studied, the character of the variation of the foliar transpiring power was similar to that found in the experiment series 4. The critical index in question was found in the *Coleus* plants at 14:30, in the wheat plants at 12:30 and in the soy bean plant at 13:30; its value being 0.0191, 0.0226 and 0.0211, respectively. It is worth while to point out that the values found in these uprooted plants were very near to those obtained in the potted plants. The average values of the latter were, namely, 0.0197 for a variety of *Coleus*, 0.0224 for another variety of *Coleus*, 0.0130 for the wheat plant and 0.0196 for the soy bean plant, as seen in the tables 2, 3, 5 and 6.

It is remarkable, that the critical value in question in these different cases is approximately the same for any kind of plants and we may consider that this critical point must have an important meaning in the physiology of wilted plants. Another suggestive fact is that the values found in different kinds of plants are also very similar to each other. The variations of the foliar transpiring power were also similar in the three species.

Tab. 7. Variation of the indices of the foliar transpiring power of up-rooted plants

Hour of test	*Coleus* a	*Coleus* b	*Coleus* Average	Wheat a	Wheat b	Wheat Average	Soy bean a
9:30	.1605	.1360	.1483	.3710	.3600	.3660	.2096
10:30	.0887	.1215	.1051	.0534	.0569	.0552	.0644
11:30	.0788	.0893	.0841	.0278	.0299	.0289	.0304
12:30	.0298	.0437	.0368	**.0201**	**.0250**	**.0226**	.0236
13:30	.0285	.0251	.0268	.0215	.0274	.0245	**.0211**
14:30	**.0187**	**.0194**	**.0191**	.0253	.0316	.0285	.0216
15:30	.0219	.0218	.0219	.0347	.0479	.0413	.0269
16:30	.0237	.0263	.0250	.0419	.0477	.0448	.0160
17:30	.0173	.0231	.0202	.0459	.0555	.0507	dry up

6. Determination of the water residue in the soil at the critical point of wilting of *Coleus* and wheat

The water residue in the soil at the time of permanent wilting of the plant and its relation to the soil have been studied hitherto by many investigators (5, 6, 7, 9, 17, 20). Some believed that the water content at this time is constant in a given soil, while others said that the moisture residue in question varies according to the kind of plant used as an indicator (7). On the other hand, it was pointed out by other writers (8, 20), that it is affected by the atmospheric evaporating power, regardless of the plant used as an indicator.

The writer's experiments were performed in the air conditions of the green house, and no special consideration was given to the atmospheric factors. The soil moisture was determined by the manner described by SHIVE and LIVINGSTON (20). The water content was calculated as the percentage on the basis of the volume and weight of the over-dry soil. Two series of determination were made; one series with *Coleus* plants and the other with wheat, which were the test material for the experiment series 1 and 3.

The results obtained are shown in table 1. In both series, the value of the water residue and its ratio to the value of the water holding capacity in any soil, rise generally as this capacity increases. In other words, the percentage of the available water for *Coleus* and wheat on the basis of the amount of water held in the soil become higher as the water holding capacity of the soil is smaller.

The results of the determination in both series were similar to each other for a given kind of soil. However, without exception, the value found in the wheat series was somewhat smaller than the corresponding value in the *Coleus* series. This fact might have an important meaning in proving that the water residue at the critical state of wilting of the plant is not of a constant nature for a given soil, but that it may be affected more or less by the character of plants.

IV. GENERAL CONCLUSIONS

Upon examination of the data in the various series of experiments described above, some further discussion of the results is necessary. As far as the daily variation of the foliar transpiring power of a plant is concerned, its character seems, to a certain extent, peculiar to any particular species of plants, as is usually believed. Generally speaking, the highest value of the indices was found for the *Coleus* plants in the test period 16-17, for wheat plants in the period 13-14 and for the soy bean plants in the period 10-11, while the value found in the period 22-23 was minimal in almost all cases (13). However this progress of the transpiring power may be affected by the external conditions. For example, the daily progress in the *Coleus* plants, which were cultivated in soil with a high water holding capacity, was usually very different from the average progress, the night index of this power being relatively high. Therefore the point of the highest and the lowest value of the indices may not be definite for a kind of plants, but may be affected by external conditions.

The ratio between the highest and the lowest value of the indices or the "maxinum-minimum ratio" of the transpiring power, which was suggested by BAKKE (3), is nothing else than an index showing the degree of daily fluctuation of this process. But the procedure to find out this ratio every day in each plant is very troublesome for the reason above-mentioned. For the sake of convenience, the writer adopted, therefore, the "day-night ratio" of the transpiring power, which means the ratio of the index at a definite time of the day, on which the highest value of the day-time indices was most often found, to the index at the night time 22-23, on which the transpiring power was generally low, for studying the degree of the daily fluctuation of the transpiring power.

During the progress of wilting, this "day-night ratio" of a plant generally comes progressively nearer to unity. But on or after the day of permanent wilting, it tends in many cases to become less than unity, because the night index becomes somewhat higher than the day index. In this connection we may say that the wilting process of the plants goes hand in hand with the diminution of the fluctuation of the foliar transpiring power, until the "day-night ratio" becomes unity for a while at the time of permanent wilting.

On the other hand, the indices of the transpiring power itself become lower and lower during the progress of wilting. At the time of permanent wilting the value of the indices reaches its minimum, from this point it again rises a little, and at last the leaf goes into the phase of drying up.

The minimal value of the indices in question found at the critical state of wilting was varied little for a given plant species. It seems, therefore, that this critical index is approximately constant for any given kind of plants. Whether this critical value is affected by external factors or not, however, remains a question, but examining the results of our experiments in detail, it is highly probable, that this may be affected by the soil conditions, even if slightly. However our data are for the present insufficient for solution of this fundamental question.

The critical values found in the three different kinds of plants are also similar to each other, the average value obtained in two different varieties of *Coleus*, wheat and soy bean being 0.0224, 0.0197, 0.0130 and 0.0196 respectively. That is to say, the three plants have a similar transpiring power at the critical state of wilting.

On the other hand, comparing the values obtained in the *Coleus*- and wheat-experiment series, which were performed in the same manner, we see that the values in the wheat series are generally lower than those in the *Coleus* series. This fact may have some meaning when considered by itself. Although the value in question found in these three mesophytic plants was not noticeably different from each other, yet it may probably be, that it would be affected considerably by the nature of the plants, when they are widely different in their manner of living.

The uprooted plants show a similar variation of the transpiring power and a similar value of the critical index, to that found in the wilting process of rooted plants. This fact shows, no doubt, that a leaf in the process of wilting passes through the same physiological processes, regardless of whether it is attached to a plant rooted in the soil or not.

We have to consider next the nature of the critical point in question. When BAKKE (2) observed a similar point in the uprooted specimen of *Helianthus*, he thought that this point of wilting was nothing else than the point of permanent wilting, and the secondary rise of the transpiring power after that point was due to the decrease in the water retaining property of the leaf tissue, which is caused by the breaking of the water columns in the vessels. Of course, this thought has for its basis the cohesion hypothesis of water movement in the plant body (18, 19, 4).

On the other hand, CALDWELL (9) considered the permanent wilting to be a condition of general plasmolysis (but not of death) in all the tissues of the plant accompanying the cessation of certain protoplasmic activities. But this question must remain unsolved for this study. Whether the temporary opening of the stomata in the leaves during the process of wilting, which was described by some writers (10, 14), is related to our problem or not must similarly remain an open question.

We may, however, say with certainty that a plant in the progress of wilting reaches a point, where its resistance against the filtration of water vapor becomes highest, and then decreases again for some reason. This point of the maximal resistance, or the minimal transpiring power, must be the critical point itself, with which we are concerned. Consequently, the study of this point will possibly throw light upon the problem of the comparative xerophytism of plants, its value being applied as a measure of that chracteristic.

The fact that the "day-night ratio" of the transpiring power in a plant approaches unity at or near the time of permanent wilting, might go to show the weaker regulative action of the physiological process. BAKKE (3) paid much attention to this equilibrium phase and suggested that the duration of this phase gives a measure of the comparative drought resistance of different plants. The writer, however, supposes that this duration may be more affected by the external condition than is our critical value index itself. The latter seems, therefore, to be more essential for such a purpose.

Another point of interest in this critical point is the fact that it was usually found on the day of permanent wilting according to BRIGGS and SHANTZ's procedure. This fact indicates that a plant in this critical state can scarcely recover its turgidity without the addition of water to the soil. In this connection, this point for any plant may be the standard indicator for the determination of the critical moisture residue of the soil, in which this plant is rooted, although use of this for such a purpose is practically too troublesome (12).

Thus our results of determination of the soil moisture residue at the time of permanent wilting of *Coleus* and wheat must be related to the critical state as is here considered. The fact that the water residue of the soil found in the determination for the wheat series was, as a rule, somewhat smaller than that in the case of *Coleus*, must mean that different kinds of plants have unequal water absorbing power at the critical point of wilting. This may also be a measure of the xerophytism of plants.

Here we may call attention to a interesting parallelism between the critical transpiring power of the plant and the critical water residue in the soil, which was found both in *Coleus* plants and in wheat. Both critical values found in the wheat series were generally smaller than those found in the *Coleus* series. These two kinds of critical value must, therefore, be in intimate relation, and according to those two measures of xerophytism, wheat plants might be said to be more xereophytic than *Coleus* plants.

V. SUMMARY

1. The variation of the foliar transpiring power of plants was studied by means of standardized hygrometric paper in *Coleus*, wheat and soy bean plants.

2. The ratio of the index of the foliar transpiring power at a difinite time of the day, at which the highest value of day-time indices is most often found, to the index at night, when the transpiring power is generally low, was named "day-night ratio." This ratio was used for judging the degree of the daily fluctuation of the transpiring power of plants.

3 This "day night ratio" of the plant approaches in the wilting process nearer and nearer to unity, as wilting progresses, that is, there an equilibrium phase, in which the foliar transpiring power shows little variation is attained. But after that time it tends in many cases to

become less than unity, because the night index becomes higher than the day index.

4. During the process of wilting, the index of the transpiring power itself decreases progessively, until it reaches its minimal value at the critical point of wilting, corresponding to the time of permanent wilting. After that time, it begins again to rise more or less, and then the plant falls into the drying phase of low transpiration or evaporation. The same phenomenon can be seen in the uprooted plants.

5. The value of the critical index in question seems to be practically constant for a given plant species, regardless of plants rooted or uprooted. However, it may be probably more or less affected by the external factors, for instance by the nature of the soil.

6. The critical indices found in the three mesophytic plant species used appeared to be approximately alike. But, although the difference between them was rather slight, it was suggested that the critical index in question is characteristic for each kind of plants.

7. The soil moisture residue at the time of critical state of wilting seems not to be constant for a given soil, but affected more or less by the nature of plants.

8. The index of the foliar transpiring power of a plant and the soil moisture residue at the time of the critical state of wilting may be applied as the measure of the comparative xerophytism of plants, in both the lower value showing the greater drought resistance.

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