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THE DAILY PERIODICITY OF TRANSPIRATION IN THE TULIP POPLAR LIRIODENDRON TULIPIFERA L.*.

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Although a large number of papers have been published describing investigations upon the daily periodicity of transpiration in herbaceous plants very little information appears to be available upon this subject for ligneous species. There are almost no critical data of this sort for the important tree species of the deciduous forests of eastern North America. In this investigation the daily transpiration periodicity was studied in young tulip poplars (*Liriodendron tulipifera* L.). This species plays an ecologically important role over large portions of the eastern deciduous forest area. It is an important timber tree throughout much of its natural range, and has many advantages as a species for reforestation projects in suitable habitats. Hence studies on the fundamental physiology of this species appear to be desirable. A knowledge of transpiration rates and periodicity are necessary as integral parts of any study of the water relations and requirements of this or any other species.

A review of the more recent literature on transpiration reveals a few papers which have a direct bearing on this general problem. Dole (1924) determined the daily periodicity of transpiration in the white pine (*Pinus strobus* L.). In this investigation potted plants growing in a well watered soil were used. When grown in an uncontrolled atmospheric environment such plants showed a regular cyclical periodicity of transpiration with the maximum at about 1 P. M. and a very low rate during the hours of darkness. The effects of differences in the water content of the soil, temperature, and relative humidity upon the rate of transpiration were also investigated.

Wilson (1924) determined the daily periodicity in transpiration rates for a large number of Australian xerophytes, including a number of ligneous species. He also used potted plants growing in well watered soils. The peak of the transpiration

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curve for the ligneous species, almost without exception, was found to occur in the middle part of the day, that is, between the hours of 11 A. M. and 3 P. M. In most of the species studied the night rates of transpiration were very low. These results are in general accord with published records of transpiration periodicity in herbaceous species.

Several field studies of the transpiration periodicities in ligneous species have been made by means of one from or other of the hygrometric paper method. Cribbs (1919, 1921) studied the daily march of "transpiring power" in the basswood (*Tilia americana* L.) by such a method. The results for trees growing in a number of different habitats were compared and considerable attention was paid to the effects of various environmental factors. The maximum rate of water loss was found to occur at different times of the day depending upon the habitat of the trees, and the diurnal march of atmospheric factors. In general, however, a cyclical diurnal variation in the rates of water loss was found for this species.

Meyer (1927) determined the transpiration periodicity for six species of Ohio trees and shrubs *in situ* by a modified form of the hygrometric paper method. In all of these species the maximum rate of water vapor loss as indicated by this method was found to occur relatively early in the day, usually between the hours of 8 and 10 A. M.

Blaydes (1928), using the same method as Meyer, studied the daily periodicity of transpiration in a number of species of plants native to Ohio, including several trees and shrubs. His results also show that the maximum rate of water vapor loss usually was attained during the mid-morning hours.

The hygrometric paper method, as commonly employed, does not measure transpiration in the usual sense of the word, but merely the ease with which the leaves of plants will lose water vapor to a standardized environment. The effects of diurnal variations in the atmospheric factors are largely or almost entirely eliminated. Because of its obvious advantages in the field this method has been widely used, but its limitations should be clearly realized. Apparently the general type of curve obtained by the hygrometric paper method differs somewhat from the general type obtained when the method of weighing potted plants is used. The latter method almost always indicates a transpiration peak in the middle part of the day, while the former more often indicates a peak in the curve during the morning hours. It is clear, on theoretical grounds, that this difference is in part due to inherent differences in these two methods of measuring transpiration. However, it also seems almost certain that there are also real differences between the transpiration periodicities of plants growing under certain field conditions, and those growing in watered pots. A careful analysis of the exact methods used and the conditions under which the plants were growing is obviously necessary in evaluating results of this kind. A discussion of some of the limitations of the hygrometric paper method will be found in a previous paper by the author (1927).

The purpose of the present investigation was to study the daily periodicity of transpiration in the tulip poplar, and to obtain some approximate data, at least, on the magnitude of the daily transpiration loss from this species under the conditions of a fairly "typical" central Ohio summer day. The method chosen for the measurement of transpiration was that of weighing potted plants, which appears to be the most satisfactory method which is readily available for the determination of the daily periodicity in transpiration rates. The water content of the soil in the pots was maintained at approximately the moisture equivalent percentage. The results of the investigation represent, therefore, the daily periodicity curve for transpiration in young tulip poplars on a representative summer's day under conditions in which soil moisture deficiency, in itself, was probably not a limiting factor.

METHODS.

The tulip poplars used were grown especially for this investigation. Seeds of the 1928 crop were stratified over winter and sown in flats the following spring. About twenty-five of the resulting seedlings were later selected and each transplanted into a weighed earthenware pot 10 cm. in top diameter, and of known weight. Each of the pots was provided with 500 gm. of air dry loam soil which had a moisture equivalent value of 22.

After the transplanting of the seedlings was completed the pots were sunk for about one-third of their height in sand in a frame which was located out-of-doors. The sand matrix in which the pots were imbedded was watered from time to time during the growing seasons but otherwise the plants were exposed to the normal environmental conditions. The plants remained in this location from early in the summer of 1929 until August 10, 1930. They had therefore completed practically two growing seasons before they were used in the present investigation.

For the specific purposes of this investigation seven plants were selected from the group, all closely similar in height and general appearance. These plants had stems about 15 cm. high and total leaf areas of between 2 and 3 square decimeters.

At about 7:00 P. M. on August 10 these pots were removed to an indoor bench, carefully brushed free from sand and allowed to stand until their outer surface had dried. Each pot was then fitted into a weighed metal shell and this set-up in turn weighed. A simple calculation then made it possible to add to each pot just sufficient water to bring the water content of the soil in that pot up to its moisture equivalent percentage.

This calculation was made possible by the fact that the weights of the shell, pot, and dry soil were known. The weight of the plant and the weight of the water held in the walls of the pot when in equilibrium with the same type of soil at its moisture equivalent were also known quite accurately from determinations on similar plants and pots.

As soon as the added water had been absorbed by the soil its surface was covered with a disk of cardboard, so cut that it fitted the inside walls of the pot snugly. This disk was cut radially to a central aperture through which the stem of the plant passed; a second aperture was provided through which a glass watering tube was inserted into the soil. This tube was provided with a rubber stopper. The stem of the plant was wrapped with cotton at the point where it protruded above the cardboard and this in turn covered with grafting wax. The entire soil surface as well as the gap between the rim of the pot and the rim of the metal shell was then sealed over with a layer of plastic clay. Finally the top of the pot was covered with a tinned metal disk which was radially cut to a central aperture to provide for the stem of the plant and was also supplied with an aperture through which passed the glass watering tube.

As soon as each pot was completely assembled it was weighed. Just before the experiment began each pot was reweighed and any loss of water which had occurred between the two weighings was restored.

At 10:00 P. M. on the evening of August 10 the seven potted plants were moved out into an open spot in the Botanical

Garden of the Ohio State University and supported on an especially built frame so that the metal shells would be shielded from any direct sunlight, without interfering in any way with the exposure of the plants. The next weighing of the pots was not made until 4 A. M. on the morning of August 11; weighings then followed at two hour intervals until 12 P. M. on this latter date. After each weighing any water which had been lost by transpiration was restored to the pot in units of 1 ml. The pots were always replaced in the frame so that the orientation of the leaves with respect to the environment remained unchanged throughout the 24-hour period.

A parallel series of determinations was made of wet and dry bulb thermometer readings, soil temperatures, light intensity, and wind velocity. The wet and dry bulb readings were obtained with a sling pyschrometer in the standard way. Soil temperatures were measured by thermometers set in the soil of two of the pots. The average reading of the two was recorded. These thermometers were calibrated against each other and with the psychrometer thermometers just before the series of determinations began.

Relative light intensity measurements were made with Eder-Hecht "Graukeil" photometers using Solio paper. It is recognized of course, that this method of photometry is subject to all the errors of any method in which sensitized paper is used and in which the surface exposed to the light is flat and horizontally placed. In spite of the known limitations of this method it gives, under the conditions under which it was used in this investigation, a fairly reliable indication of relative light intensities. The numerical values obtained with the instrument as used are of relative significance only. The photometers were exposed for full two hour periods, so that each value represents an integration of the light intensities for a two-hour period.

The wind velocity was measured by means of a wind meter which was oriented in the direction of the maximum wind velocity for 5-minute intervals once every two hours. The prevailing winds during the course of the experiment were from the north and northwest.

In general the day chosen for the determinations was a "typical" Ohio summer day except that the temperature was not quite as high as usual at this season. The day was clear, except for a very high thin film of cloud which passed across a portion of the sky between the hours of 1:30 and 4:30 P. M. During a portion of this period this thin cloud was across the line of direct sunlight. According to the photometer readings, however, this cloud was too insubstantial to have any appreciable effect on the relative light intensity falling on the earth's surface.

At the conclusion of the experiment, determinations were made of the total leaf blade area for each plant, and also of the fresh weight and dry weight of the leaf blades for each plant. The main stem and petioles were both disregarded as transpiring surfaces in the final calculations, preliminary experiments with plants which had had the leaf blades stripped from them having shown that the magnitude of the transpiration from surfaces other than the leaf blades was less than the experimental errors in the method used.

DISCUSSION.

Table I presents in detail the data obtained concerning transpiration rates. These data are based on measurements made, except during a part of the first night, at two-hour intervals. They have been computed upon four different bases: grams of water transpired per plant, per square decimeter of leaf surface, per gram of fresh weight of the leaves, and per gram of dry weight of the leaves. The mean two-hourly value for the seven plants has been computed and also the total daily transpiration for each plant, as well as the mean for the total transpiration.

The figures presented in this table give a fairly definite conception of the quantitative values for the amounts of water transpired by young tulip poplars under what for the lack of any more precise term are here called "typical" Ohio mid-summer meteorological conditions. The figures as given on the basis of transpiration per plant are probably of greatest significance from the ecological standpoint. Although the variability in transpiration rates for these apparently similar plants, all growing under the same set of external conditions is striking and the number of plants used is insufficient to permit of statistical treatment, nevertheless the results would appear to be quite indicative of the amounts of water transpired by young trees of this species. The average total transpiration per plant was found to be 25.4 grams per day. Since soil water conditions were favorable this does not represent a minimum transpiration rate for this species, but probably does represent the approximate transpiration rate under conditions suitable for growth.

TABLE I.

DAILY VARIATIONS IN THE TRANSPIRATION RATES OF TWO-YEAR OLD TULIP POPLARS.

Plant		AUGUST 11, 1930					NOON							TOTAL
		12-2	2-4	4-6	6-8	8-10	10-12	12-2	2-4	4-6	6-8	8-10	10-12	
		GRAMS WATER LOST PER PLANT												
1		0.1	0.1	0.2	0.9	5.0	6.1	5.2	3.9	4.1	2.7	0.3	0.2	28.8
2		0.2	0.2	0.3	1.0	3.5	4.2	3.7	3.6	3.6	2.5	0.3	0.2	23.3
3		0.3	0.3	0.3	1.5	3.9	4.6	4.1	3.0	2.8	1.9	0.4	0.3	23.4
4		0.2	0.2	0.2	1.4	4.2	4.4	4.0	3.6	3.6	2.0	0.3	0.3	24.4
5		0.2	0.2	0.3	1.6	3.9	3.8	3.7	3.0	3.2	1.6	0.3	0.2	22.0
6		0.3	0.3	0.5	2.0	5.2	6.7	6.4	5.2	4.8	2.1	0.7	0.2	34.4
7		0.3	0.2	0.2	1.6	4.1	3.5	3.5	3.2	3.1	1.6	0.3	0.1	21.8
Mean		0.2	0.2	0.3	1.4	4.3	4.8	4.3	3.6	3.6	2.1	0.4	0.2	25.4
	Leaf Area Dm^2	GRAMS WATER LOST PER DM^2 OF LEAF SURFACE												
1	2.73	.04	.04	.07	.33	1.80	2.23	1.90	1.43	1.50	.99	.11	.07	10.51
2	2.08	.10	.10	.14	.48	1.68	2.02	1.78	1.73	1.73	1.20	.14	.10	11.20
3	2.61	.11	.11	.11	.57	1.49	1.76	1.57	1.15	1.07	.73	.15	.11	8.93
4	2.58	.08	.08	.08	.54	1.63	1.70	1.55	1.39	1.39	.78	.12	.12	9.46
5	2.79	.07	.07	.11	.57	1.39	1.36	1.33	1.08	1.14	.57	.11	.07	7.87
6	2.57	.12	.12	.19	.78	2.02	2.61	2.49	2.02	1.87	.81	.27	.08	14.38
7	2.57	.12	.12	.08	.62	1.59	1.36	1.36	1.24	1.20	.62	.12	.04	8.47
Mean	2.56	.09	.09	.11	.55	1.66	1.86	1.70	1.42	1.41	.81	.17	.08	10.11
	Fresh Weight Leaves	GRAMS WATER LOST PER GRAM OF FRESH WEIGHT												
1	3.52	.03	.03	.06	.26	1.42	1.73	1.48	1.11	1.16	.77	.08	.03	8.16
2	2.67	.07	.07	.11	.37	1.31	1.57	1.39	1.35	1.35	.94	.11	.07	8.71
3	3.18	.09	.09	.09	.47	1.23	1.45	1.29	.94	.88	.59	.13	.09	7.34
4	3.03	.07	.07	.07	.46	1.38	1.45	1.32	1.19	1.19	.66	.10	.10	8.06
5	3.42	.06	.06	.09	.47	1.14	1.11	1.08	.88	.93	.47	.09	.06	6.44
6	3.32	.09	.09	.15	.60	1.57	2.02	1.93	1.57	1.44	.63	.22	.06	10.37
7	3.27	.09	.09	.06	.49	1.25	1.07	1.07	.98	.95	.49	.09	.03	6.66
Mean	3.20	.07	.07	.09	.44	1.33	1.49	1.36	1.12	1.13	.65	.12	.06	7.96
	Dry Weight Leaves	GRAMS WATER LOST PER GRAM OF DRY WEIGHT												
1	0.78	.13	.13	.26	1.15	6.41	7.82	6.66	5.00	5.26	3.46	.38	.26	36.92
2	0.60	.33	.33	.50	1.67	5.83	7.00	6.16	6.00	6.00	4.16	.50	.33	38.81
3	0.67	.45	.45	.45	2.24	5.82	6.86	6.12	4.47	4.18	2.83	.60	.45	34.92
4	0.57	.35	.35	.35	2.45	7.37	7.71	7.02	6.31	6.31	3.51	.53	.53	42.79
5	0.81	.25	.25	.37	1.98	4.81	4.69	4.56	3.70	3.95	1.98	.37	.25	27.16
6	0.71	.42	.42	.70	2.82	7.32	9.43	9.01	7.32	6.76	2.96	.99	.28	48.43
7	0.67	.45	.45	.30	2.36	6.12	5.22	5.22	4.77	4.62	2.39	.45	.15	32.50
Mean	0.69	.34	.34	.42	21.0	6.24	6.96	6.35	5.37	5.30	3.04	.53	.32	37.36

The diurnal periodicity of transpiration for this species is shown by the curve in Text Fig. 1. This curve is based on the mean two-hourly transpiration based on the square decimeter basis. Exactly the same type of curve would of course result if any of the other bases for transpiration were used.

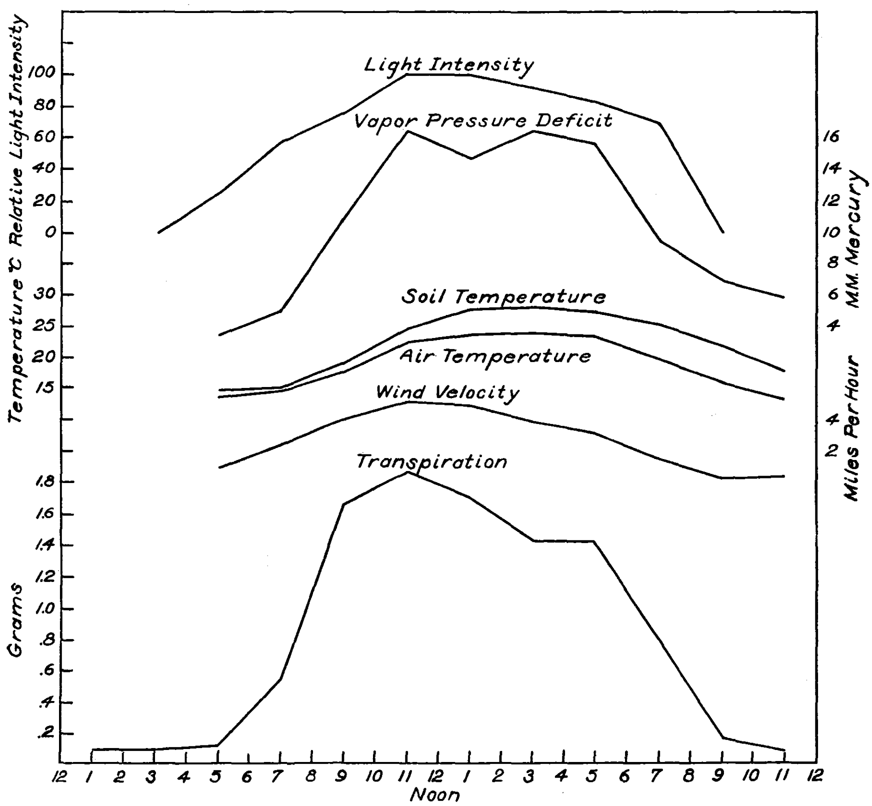

FIGURE 1. Diurnal variations in tulip poplar transpiration and in environmental factors.

Curves are also included in Text Fig. 1 for the daily periodic variation in the vapor pressure deficit, relative light intensity, soil and air temperature, and wind velocity. The vapor pressure deficit data were calculated from the wet and dry bulb thermometer readings.

A detailed discussion of the results does not appear to be necessary. In general the curve for the rate of transpiration is symmetrical, although it shows a slightly skewing towards the morning hours, and there is a tendency for the curve to flatten out for a period during late afternoon. Transpiration during the hours of darkness is almost negligible and may be assumed to be entirely cuticular. The rate begins to rise between the hours of 5 and 6 in the morning, rises very rapidly between the hours of 7 and 9, reaches a peak about 11, declines slowly but mostly consistently until 5 P. M. after which the decline in rate is very rapid until the practically stable night rate is attained, apparently some time between the hours cf 8 and 10 P. M.

This transpiration periodicity curve resembles very clcsely those obtained for various species of herbaceous plants by Briggs and Shantz (1916), Sayre (1919), and others, all of whom used methods very similar to those employed in the present investigation. It seems probable that the diurnal transpiration periodicity in woody plants is, in general, similar to that found in herbaceous plants growing in similar habitats.

The data on environmental factors are plotted graphically, not primarily in an attempt to explain the transpiration periodicity in this species, but rather to define in quantitative terms the environmental conditions to which the plants were subjected during the course of the experiment. Attempts to trace a causal relationship between the daily periodicity of transpiration and the daily periodicity of certain environmental factors have been made by a number of investigators, including some of those previously mentioned (Briggs and Shantz, 1916, and Sayre, 1919). A detailed analysis of the cause of transpiration periodicity is beyond the scope of this paper. The most definite correlations in these experiments are between transpiration periodicity and the daily periodicity of light intensity and to a somewhat less degree the daily periodicity in the vapor pressure deficit. This result would be anticipated on theoretical grounds. Light is the primary factor concerned in the opening and closing of the stomata. The vapor pressure deficit theoretically comes the closest of any readily determined environmental measure of indicating the steepnees of the diffusion gradient through the stomata.

Most of the recorded investigations of the daily periodicity in the transpiration rate in plants have been conducted with potted plants. Although this method offers many advantages from the experimental standpoint it is extremely doubtful if the results obtained always indicate the usual transpiration rates as they occur in plants growing under field conditions. The customary procedure, which has been the one followed in the present investigation, has been to provide the plants with favorable soil water conditions, and usually to maintain at least an approximately constant percentage of water in the soil during the course of the experimentation. Such soil water conditions are not always present under field conditions. The available soil water is very apt to be deficient, and is probably often a limiting factor in transpiration. Daily variations in the amount of water present may also occur in natural soils. It seems certain, therefore, that because of these rather fundamental differences in soil water supply, that the daily periodicity curve for plants rooted in a natural soil will often differ from that obtained with potted plants in which the pots are well supplied with water. A difference in magnitude of the transpiration rates is certain, and differences in the trends of the curves might also occur. Of course, when a natural soil is supplied with water to approximately its moisture equivalent percentage there is every reason to believe that the transpiration curves for the plants growing in that soil and the curves for plants grown in pots containing the same soil and under the same soil water conditions would be essentially the same.

SUMMARY.

This paper reports the results of a study of the daily periodicity of transpiration in young tulip poplar trees on a "typical" Ohio summer's day. Transpiration was measured by the method of weighing potted plants. The soil in the pots was maintained at approximately the moisture equivalent percentage. Transpiration rates were calculated on four bases: per plant, per square decimeter of leaf surface, per gram of fresh weight and per gram of dry weight. All data are the averages for seven different plants. The results indicate that tulip poplar trees at the end of their second season of growth transpire about 25 grams of water per day per plant under such conditions as those chosen for this experiment. The peak of the transpiration curve was found to occur a little before mid-day. The maximum rate of transpiration recorded was 4.8 gms. per plant for the two-hour period between 10:00 A. M. and 12:00 M. Transpiration during hours of darkness was low and can be assumed to be entirely cuticular. In general, the transpiration periodicity for this species is similar to that

which has previously been described for a number of other species, mostly herbaceous. Measurements were also made of the daily march of soil and air temperatures, light intensity, wind velocity, and vapor pressure deficit. Of the environmental factors only the light intensity and vapor pressure deficit periodicity showed close correlation with transpiration periodicity.

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Are Healthy People Interested in Health?

It would be simple enough to sell ideas of health to the inmates of a hospital or sanitarium, but to do the same to a group of college students who, as a rule, have plenty of health, is a different task and requires a super sales talk. It is of primary importance, however, that this very group of healthy youngsters become interested in preserving that which they already have.

In their recent book, "Fundamentals of Health," Kirkpatric and Huettner have attempted to utilize those phases of biology which their experience has shown them to be of most interest to their students. Capitalizing upon this interest they have made use of it as a basis for presenting their "fundamentals" for health.

For the most part the book is very well done. The opening chapter on the "Evolution of Man" is the weakest. The attempt to develope an evolutionary background is often teleological and unsound. But the book contains much of value upon foods, embryology and reproduction, immunity and immunology, public health relations, etc. The matter of sex is especially well treated in a frank and open manner as it should be.

Diagrams, cuts and tables are profusely used to advantage. There is an excellent list of references for further reading with each chapter and a glossary of terms which should be useful to the student.

Fundamentals of Health, by KIRKPATRIC AND HUETTNER, 8 vo.: VII, 576 pp., Ginn and Company, 1931.