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BULLETIN No. 341

A COMPARISON OF THE TRANSPIRATION
RATES OF TWENTY-ONE DECIDUOUS
FRUIT SPECIES

By VICTOR W. KELLEY

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A COMPARISON OF THE TRANSPIRATION RATES OF TWENTY-ONE DECIDUOUS FRUIT SPECIES

BY VICTOR W. KELLEY, Associate in Pomology*

The loss of water thru transpiration has long been a question of great interest to plant scientists. There are perhaps few physiological problems which have been investigated so much, yet about which so little really is known. Most writers regard transpiration as a function of plants, but less than two decades ago a prominent botany text^{3*} called it a "menace to plant growth," an "unavoidable danger."

The object of this experiment was not to investigate the mechanics of transpiration, or to determine whether it is a plant function or a plant hazard, but rather to find out how much difference exists in the rates of transpiration in some of the economic deciduous fruit species and to determine whether such knowledge might be useful in explaining some of the differences in adaptability and response to cultural conditions.

REVIEW OF LITERATURE

There is much divergence of opinion as to what differences in rate of transpiration really signify, or to what factors differences in rate may be attributed. Those opinions which are related to the problem under investigation are here presented briefly.

Drouth Resistance

Some investigators have concluded that transpiration is a measure of water economy; that a plant which transpires relatively small quantities of water may be considered as drouth resistant. Others think that transpiration is not a measure of drouth resistance.

Iljin^{17*} reported that it was not yet possible from a study of transpiration rate alone to ascertain the degree of protection enjoyed by types biologically different. In 1916 this same author, as a result of his study of the relation of transpiration to assimilation in steppe plants, concluded that we may expect to find in drouth-resistant plants an economical evaporation of water.

Dosdall^{9*} employed transpiration as the basis for classifying *Equisitum fluviatile* as a hydrophyte in relation to mesophytes and xerophytes with which it was compared. Gavarra and Espino^{11*} con-

*Grateful acknowledgment is made to Dr. W. A. Ruth, Chief in Pomological Physiology, for assistance in planning the experiment and designing the apparatus.

cluded that transpiring power, determined experimentally, and drouth resistance are correlated with varieties of abaca (*Musa textilis*).

Koketsu^{24*} concluded that with *Coleus blumei*, *Triticum vulgare*, and *Glycine soja* the index of foliar transpiring power and the soil moisture residue at time of wilting may be applied as the measure of comparative xerophytism of plants. On the other hand, Maximow,^{30*} working with the sunflower, buckwheat, and other plants, stated that the rate of transpiration under conditions of normal water absorption from the soil cannot be used for judging the drouth resistance of a plant; he considered xerophytism to be the ability to resist prolonged wilting.

Pool,^{35*} using the cobalt chlorid method, which, however, he did not regard as satisfactory, found little correlation between habitat xerophytism, leaf anatomy, and transpiring power among about forty species which were included in his experiments.

Miller and Coffman^{31*} found the rate of transpiration per unit area of leaf surface lower for corn than for sorghums. Kiesselbach,^{21*} as a result of his studies with many varieties of corn and sorghums, concluded that drouth-resistant qualities must lie elsewhere than in a low water requirement per pound of dry matter.

Haines^{12, 13*} regarded actual or relative transpiration as not necessarily an index of drouth resistance. He has evolved a method for determining "drouth resistivity" which consists of finding the relationship between transpiration rate, "pressure deficit," and evaporation as measured by an atmometer, according to a somewhat complicated formula.

Transpiration and Growth

As in the case of drouth resistance, considerable difference of opinion exists among investigators in regard to the relation of transpiration to growth.

Livingston^{25*} regarded transpiration to be as good a criterion for comparing the relative growth of wheat as the weight of the plants. Cole and Matthews,^{2*} working with spring wheat, found a high correlation between the total amount of water consumed by the crop and the yield. Dastur^{8*} found that in different leaves of the same plant a high rate of assimilation accompanied a low water content of foliage; and a low rate of assimilation a high water content. Bews and Aitken,^{1*} working with *Bidens pilosa*, found the actual amounts of water lost by transpiration to be more or less proportional to the weights of the plants.

On the other hand, Dachnowoski^{5*} found no direct relation between growth, green and dry weight, and transpiration. Cullinan^{4*} concluded that neither relative nor total transpiration was a reliable index to growth activity in the apple.

Transpiration and Water Content of Foliage

More unanimity of opinion is found in the literature dealing with the relation of transpiration to water content of foliage.

Knight^{22*} stated that the water content of the leaf played an important part in the control of transpiration. Livingston and Brown^{26*} recognized that the water content of leaves under conditions of rapid evaporation varied at different times in the day, and that such a reduction acted as a check upon transpiration.

Lloyd^{28*} found that with ocotillo the rates of intake and outgo of water were not a constant, but that the outgo during the day was greater than the intake, the reverse being true at night. Because the decrease in water content occurred during the opening of the stomata, Lloyd concluded that these organs were not closely regulatory of the loss of water by transpiration.

Knight^{23*} found the diurnal change in leaf water content of plants in southeastern England to be less than 2 percent. He also found that wilting really commenced and could be predicted from a flaccid condition of the foliage before it was possible to determine experimentally a definite decrease in water content. As much as 2 percent variation in the water content of leaves similar in external appearance was noted in several species.

Maximow^{30*} corroborated much of Knight's work. While studying the relation of wilting to drouth resistance, he found that xerophytic types at wilting had a much greater water deficit than did mesophytic types. In fact, with shade mesophytes, visible loss of turgidity appeared when the decrease in water content was so insignificant that it could be ascertained analytically only with difficulty; while under conditions of prolonged wilting, xerophytic plants were capable of losing one-half of their water without apparent harm. He concluded that one of the principal features of drouth-resisting plants is their capacity for enduring a considerable loss of water without permanent injury.

Inamdar^{19*} made a study of the hourly variations in water content of leaves of jasmine under conditions of rapid transpiration, and found that the water content varied in an inverse direction to the amount of the transpiration. Bews and Aitken^{1*} found that leaves of the common natal weed transpired in proportion to their water content, those leaves having the highest percentage transpiring most rapidly.

Transpiration and Number and Size of Stomata

Investigators are agreed that stomata exert an influence on the regulation of transpiration, but to what extent they control water loss is still in dispute.

Yost^{38*} and Palladin^{34*} both stated that the transpiration rate is in proportion to the number of stomata. Lloyd^{27*} was perhaps the first to question the completeness of stomatal control of transpiration. Eckerson^{10*} determined the number and size of stomata for 37 different plants. She found marked variations occurring in number and size of stomata, not only in different varieties, but in the same varieties grown under different external conditions. The variation seemed greater in number than in size. In general, she reported an inverse proportion between number and size of stomata.

Muencher^{32*} found no correlation between either the length of the pore or the number of stomata per unit area of leaf surface and transpiration. He concluded that the amount of transpiration is probably not governed by the number and size of the stomata but by a complex of several factors. Kiesselbach^{21*} found no apparent relation between stomatal number and transpiration in corn and sorghums.

Wilson^{37*} found that the so-called xerophytic plants of Australia were provided with a high average number of stomata, and concluded that this enabled these plants to regulate the transpiration rate under rapid variations in temperature and water supply.

Coulter, Barnes, and Cowles^{3*} quoted the results of a transpiration test for ten species of plants varying in rate from 2.81 to 16.4 grams per 100 square centimeters for 24 hours. Eckerson,^{10*} who counted the number of stomata on eight of these species, found a range of 49 to 500 stomata per square millimeter of leaf surface. By using the data from these two sources, it was possible to make a study of the relation of stomatal number to rate of transpiration. This comparison showed that there was no correlation between the number of stomata per unit of leaf area and the transpiration rate. With such a wide range in stomatal number, as well as transpiration rate, it would seem that if there were a correlation between these two factors, it would be evident in these species where the extremes are so great.

Briefly summarized, the literature shows that investigators are perhaps about equally divided on the relation between transpiration and drouth resistance and transpiration and growth. This would indicate either that these relationships vary with different species or that we must wait for further research for a definite answer as to the nature or extent of this relationship. Workers in this field agree that the water content of foliage fluctuates daily under different environmental conditions, and that this variation influences the transpiration rate. The results to date show that stomata are to some degree regulatory of the water loss thru transpiration. The older idea, perhaps largely theoretical, that the rate of transpiration is in proportion to the number of stomata, is being replaced gradually by later research, which is almost unanimous in concluding that there is no correlation between transpiration rate and stomatal number.

METHODS OF EXPERIMENTATION

Plant Materials

Twenty-one species of deciduous fruits available on the horticultural grounds of the University of Illinois were used in the experiments. They included the common fruit trees, a number of nut species, and several small fruits. In some cases several varieties of a species were used.

The fruit species included in this study differ widely in many characteristics. In form and size they vary from the recumbent strawberry, thru the bush fruits and brambles, to trees of different sizes and shapes. Each species has a wood structure peculiar to itself. Leaf characters vary from simple to compound, from long, narrow leaves to those broader in proportion to length. In some species the leaf surface is glabrous, in others varying amounts of pubescence occur. The depth and extent of the root system of each is peculiar to itself. While the native home of many of these species is in dispute, we may be sure that they have come from several continents and from regions widely different in soil and climate. In resistance to cold, drouth, and heat, and general tolerance or intolerance to unfavorable conditions great differences exist.

FIG. 1.—POTOMETER USED IN EXPERIMENTS

A is an ordinary burette; B is a glass cylinder (specimen jar) fitted with a three-hole rubber stopper; C is a glass tube, the purpose of which is to equalize the atmospheric pressure. The cutting is sealed air-tight with plastoline. The difference between two successive readings is the amount of water taken up by the cutting.

In selecting the material for study from so many different types, only cuttings of the current season's growth were employed. Care was exercised to choose terminal shoots of average vigor which were comparable in rate of growth, age, size of leaf, and as free from disease and insect injury as possible. In the fruits, the trees from which the

cuttings were taken were about the same age, the range being from six to eight years. The nut trees were slightly younger, and the small fruit plants were all of bearing age. More shoots than really were needed were always cut, so that it would be possible to make a second selection for uniformity in the laboratory. The shoots were placed in water in the field and then immediately taken to the laboratory where, after cutting under water, they were connected to the potometers. A minimum of two shoots from each species was used in each series.

Measurement of Transpiration

The potometers used in these experiments were constructed so that it was possible to read the water transpired directly on a burette (Fig. 1). Specimen just about $1\frac{1}{2}$ inches in diameter and 12 inches high were fitted with rubber corks in which there were three holes.

FIG. 2.—THE LABORATORY IN WHICH THE EXPERIMENTAL WORK WAS DONE

In one opening was inserted a short bent glass tube which was connected to the burette by a rubber tube. A long, straight glass tube extended from the bottom of the jar to a point several inches above the top. This tube was for the purpose of keeping the water in the jar under the same atmospheric pressure as that in the burette. In the third opening the shoot was sealed air-tight with plasticine. In order to lessen evaporation, the tops of the burettes were closed with corks fitted with capillary tubes to admit air. Before adjusting the shoot in place, the jar, burette, and connections were filled with water, from which all air bubbles had been driven out. The shoot was then sealed air-tight. When taking readings, the burette was raised or lowered so that the water level in the long, straight glass tube was at a definite point near the top of the jar. The difference between two suc-

cessive readings is the amount of water absorbed by the cutting. The water taken up by the plant is called water of transpiration in these experiments.

The leaf area was determined with a planimeter, tracings being made on paper and the measurements subsequently made from the tracings.

Environmental Conditions

The experiments were conducted in a large, well-ventilated laboratory (Fig. 2) in which the light, temperature, and air circulation were quite uniform for all the shoots in any series. No attempt was made to control temperature or humidity, but records of these variables were kept and will be used in evaluating the data. In some of the series hygro-thermograph records were kept, while in others this instrument was not available, and temperature and humidity records were made only at the time burette readings were taken.

EXPERIMENTAL DATA

A transpiration experiment involving a comparison of twenty species of plants presents a number of difficulties. Ideally, all the species should be compared directly in all the series, but when one realizes the variation in individual shoots which always occurs, it is desirable to have as large a population as possible in order to reduce to a minimum the error due to variation. This could be accomplished only by reducing the number of species for comparison in any single time. For this reason the selection of the species for the different series was purposely varied in order to make as many direct comparisons as possible. Because of this variation of the species in the different series and the varying conditions of humidity and temperature encountered, it was not possible to present the data adequately in a summary table. On the other hand, it would not be feasible to publish the data for all the series separately. Hence it seemed advisable to present sufficient detailed data of those series which show the maximum number of direct comparisons, and then follow this with a table giving a summary of all the series. Reference to Table A, which gives this summary, will show that nine series were run. Only four of these, however, will be given in detail. For convenience of presentation and discussion, each series will be considered as a unit.

Series 1. The data in this series (Table 1) represent a comparison of the relative rates of transpiration of eight species of tree fruits and one small fruit, belonging in all to three genera. The genus *Pyrus* is represented by two species, *Prunus* by six, and *Eubus* by one. Since climatic conditions greatly affect transpiration, it is important to note these factors. This series was started on July 15,

TABLE 1.—SERIES 1: COMPARISON OF TRANSPARATION RATES OF EIGHT SPECIES OF TREES FRUITS AND ONE SMALL FRUIT STARTED JULY 15, 1927
The climatic conditions were described as "clear and hot."

Species	Variety	Number of shoots	Average transpiration rate in cubic centimeters per square inch per hour			Ratio of night rate to day rate	Average rate compared with the apple
			Night 7:15 p.m. to 5:00 a.m.	Day 5 a.m. to 7 p.m.	Average day and night		
<i>Prunus armeniaca</i>	Harris	2	.0096	.0128	.0115	per cent. 75	38
<i>Prunus avium</i>	Governor Wood	2	.0100	.0150	.0129	87	42
<i>Prunus cerasus</i>	Montmorency	2	.0081	.0183	.0141	44	46
<i>Prunus munsoniana</i>	Wild Goose	2	.0052	.0070	.0063	67	20
<i>Prunus persica</i>	Elberta	4	.0042	.0048	.0045	87	15
<i>Prunus persica</i> (nectarine)	Elberta	2	.0057	.0076	.0068	75	22
<i>Pyrus communis</i>	Kieffer	3	.0066	.0320	.0217	20	71
<i>Pyrus malus</i>	Grimes	3	.0256	.0341	.0300	75	100
<i>Rubus nigrobaccatus</i>		2	.0175	.0208	.0195	84	64

when it was clear and hot. Clear weather is generally accompanied by relatively low humidity, which favors rapid transpiration. A high temperature also facilitates water loss from the leaves. The conditions, therefore, at the time this series was run were favorable for a rapid rate of transpiration.

A study of these data shows that on the basis of transpiration rate these plants may be grouped into three classes. The peach, nectarine, and plum, all belonging to the genus *Prunus*, have a very low rate; the apple, pear, and blackberry form a group with the highest rate; and the sour cherry, sweet cherry, and apricot, also from the genus *Prunus*, are in an intermediate group. The most striking difference is that of the peach, plum, and nectarine, which have an average rate in this series of less than 20 percent of that of the apple.

The night rate in every instance is lower than the day rate, but there is considerable variation in this relationship with the different species. Climatic conditions at night generally favor a decrease in transpiration in comparison to the day rate because of a lower temperature and higher relative humidity. The maximum closure of the stomata at night, however, is perhaps the greatest factor in the reduction of water loss during darkness. The very low night rate recorded for the pear in this series is not usual for this species, as will be seen by comparing subsequent series.

Series 3. Even a wider range of individuality is encountered among the plants in this group (Table 2) than was found in Series 1. Eleven species representing seven genera are compared, the group comprising three tree fruits, four nut species, and four small fruits.

On the basis of their relative rates of transpiration, this series may likewise be divided into three groups. The blackberry, currant, filbert, raspberry, and quince, in the order named, have a high transpiration rate; the gooseberry and sour cherry, a medium rate; and the peach, almond, black walnut, and pecan, a very low rate. The sour cherry and the peach are the only species included in both Series 1 and 3; hence these may be used to compare the relative rates of the species in the two series. On this basis the high transpiration group in Series 3 is somewhat higher in rate than that group in Series 1, all of the species ranking higher than the apple, which ranked first in Series 1. The Taylor blackberry seems to have a higher rate than the unknown variety included in Series 1. As was true in Series 1, the most striking difference is in the low transpiration group, it being in general less than one-half that of the sour cherry and only about one-fifth as great as the group with a high transpiration rate.

The effect of climatic differences on transpiration is shown by a comparison of Series 1 and 3. The records indicate that the temperature was somewhat lower, with perhaps not much difference in the relative humidity. The average transpiration rates for the peach and

TABLE 3. Comparison of the average rate of the reaction between the reaction rate and the reaction rate.

The above data were taken from the laboratory July 28, 1917. The reaction rate was calculated as follows:

Reaction	Amount	Number of atoms	Average reaction rate in cubic centimeters per square inch per hour			Ratio of rate to rate rate	Average rate with the rate
			Day 7.30 a.m. to 4.45 p.m.	Night 7.30 p.m. to 11.45 p.m.	Average rate rate		
Wettest	Wettest	1	0.001	0.001	0.001	1.00	1.00
Wettest	Wettest	2	0.017	0.017	0.017	0.017	0.017
Wettest	Wettest	3	0.030	0.030	0.030	0.030	0.030
Wettest	Wettest	4	0.037	0.037	0.037	0.037	0.037
Wettest	Wettest	5	0.039	0.039	0.039	0.039	0.039
Wettest	Wettest	6	0.048	0.048	0.048	0.048	0.048
Wettest	Wettest	7	0.053	0.053	0.053	0.053	0.053
Wettest	Wettest	8	0.101	0.101	0.101	0.101	0.101
Wettest	Wettest	9	0.152	0.152	0.152	0.152	0.152
Wettest	Wettest	10	0.151	0.151	0.151	0.151	0.151
Wettest	Wettest	11	0.151	0.151	0.151	0.151	0.151
Wettest	Wettest	12	0.151	0.151	0.151	0.151	0.151
Wettest	Wettest	13	0.151	0.151	0.151	0.151	0.151
Wettest	Wettest	14	0.151	0.151	0.151	0.151	0.151
Wettest	Wettest	15	0.151	0.151	0.151	0.151	0.151
Wettest	Wettest	16	0.151	0.151	0.151	0.151	0.151
Wettest	Wettest	17	0.151	0.151	0.151	0.151	0.151
Wettest	Wettest	18	0.151	0.151	0.151	0.151	0.151
Wettest	Wettest	19	0.151	0.151	0.151	0.151	0.151
Wettest	Wettest	20	0.151	0.151	0.151	0.151	0.151
Wettest	Wettest	21	0.151	0.151	0.151	0.151	0.151
Wettest	Wettest	22	0.151	0.151	0.151	0.151	0.151
Wettest	Wettest	23	0.151	0.151	0.151	0.151	0.151
Wettest	Wettest	24	0.151	0.151	0.151	0.151	0.151
Wettest	Wettest	25	0.151	0.151	0.151	0.151	0.151
Wettest	Wettest	26	0.151	0.151	0.151	0.151	0.151
Wettest	Wettest	27	0.151	0.151	0.151	0.151	0.151
Wettest	Wettest	28	0.151	0.151	0.151	0.151	0.151
Wettest	Wettest	29	0.151	0.151	0.151	0.151	0.151
Wettest	Wettest	30	0.151	0.151	0.151	0.151	0.151

sour cherry, the only species common to both series, are lower in Series 3 than in Series 1. The ratio of night rate to day rate is also lower than in Series 1. This is due primarily to the fact that Series 1 was started so that the night reading came first, while in Series 3 the day reading was taken before the night record. As will be shown more definitely in another series, the rate of transpiration of cuttings gradually declines as the period of their separation from the plant increases.

Series 6. The preceding series have been comparisons of transpiration rates in midsummer. Series 6 (Table 3) provides an opportunity to study the relative rates of five tree fruits and one grape species in the autumn under conditions of high relative humidity, as it was raining during most of the period that the shoots were in the potometer.

In spite of the high relative humidity and the moderate autumn temperature, the transpiration rate in each case is high in comparison with previous series which were run during midsummer. This may be accounted for by the fact that the leaves were older at this time of year, as it has been demonstrated by the author²² with the apple, as well as by other investigators with other plants, that older leaves transpire more rapidly than do younger leaves.

In this series the relative humidity was the same during the first afternoon and the night following, and it was raining all the time. The temperature range was only 1 degree Fahrenheit lower at night than in the day time. Hence this series gives a good opportunity to compare the day and night rates with the environmental conditions almost identical. Reference to Table 3, eighth column, "Ratio of night rate to day rate," shows that there were wide differences in the day and night rates in spite of the fact that the environmental conditions were quite similar. The writer²² has shown that the stomata of the apple are more nearly closed at night. Hemmickson²³ found this to be true with several species of *Prunus* also. The most plausible explanation is that this difference is due to stomatal influence, the stomata being more nearly closed at night, thus reducing the water loss. The peach seems to reduce its water loss at night much more than the other species in this series. Further evidence of the lower rate at night is shown by the fact that in all the species the second day rate was higher than the preceding night rate.

The reduction in the transpiration of cuttings which occurs as the time of their separation from the plant increases is indicated by the data in the column headed "Ratio of second day rate to first day rate." The rate on the second day is only two-thirds as high as that on the first day in spite of a lower relative humidity. This probably is due to the fact that in cuttings the soluble carbohydrates are gradually diminished by respiration, and this would no doubt influence

TABLE 3.—SERIES 6: STUDY OF FIVE SPECIES OF TREE FRUITS AND ONE SMALL FRUIT UNDER CONDITIONS OF HIGH RELATIVE HUMIDITY

The shoots were cut on October 5, 1926. The temperature range was 61° to 69° F., and it was raining during most of the period that the shoots were in the potometers.

Species	Variety	Num- ber of shoots	Average transpiration rate in cubic centimeters per square inch per hour				Ratio of night rate to day rate	Ratio of second day rate to first day rate	Average rate com- pared with the apple
			Day period 10:30 a.m. to 6:00 p.m. R. H. 67-75% Temp. 65° - 69° F.	Night period 6:00 p.m. to 6:00 a.m. R. H. 68-75% Temp. 61° - 65° F.	Day period 6:00 a.m. to 1:00 p.m. R. H. 58-68% Temp. 61° - 67° F.	Average rate first 19½ hours			
<i>Prunus cerasus</i>	Early Richmond	2	.0557	.0355	.0384	.0434	perct. 64	perct. 69	perct. 80
<i>Prunus munsoniana</i>	Wild Goose	2	.0213	.0115	.0150	.0153	54	71	28
<i>Prunus persica</i>	Elberta	2	.0214	.0070	.0200	.0125	33	94	23
<i>Pyrus communis</i>	Kieffer	2	.0594	.0356	.0437	.0448	60	73	82
<i>Pyrus malus</i>	Grimes	2	.0690	.0420	.0500	.0544	61	73	100
<i>Vitis labrusca</i>		1	.0357	.0223	.0248	.0274	62	70	50

TABLE 4.—SERIES 8: COMPARISON OF TRANSPIRATION RATES OF TEN SPECIES OF TREE FRUITS UNDER CONDITIONS OF LOW RELATIVE HUMIDITY AND MODERATE AUTUMN TEMPERATURE

The shoots were cut on October 7, 1926. General weather conditions were recorded as "clear."

Species	Variety	Number of shoots	Average transpiration rate in cubic centimeters per square inch per hour			Ratio of night rate to day rate	Average rate compared with the apple
			Day, 2:00 p.m. to 6:30 p.m. R.H. 46-57% Temp. 68°-72° F.	Night 6:30 p.m. to 6:00 a.m. R.H. 55-57% Temp. 69°-72° F.	Average rate day and night		
<i>Prunus armeniaca</i>	Harris.....	2	.0286	.0210	.0231	percd. 73	percd. 70
<i>Prunus avium</i>	Governor Wood...	2	.0246	.0141	.0170	51	51
<i>Prunus cerasus</i>	Early Richmond...	2	.0562	.0328	.0394	58	120
<i>Prunus cerasus</i> X <i>Prunus avium</i> ..	Late Duke.....	2	.0357	.0225	.0263	63	80
<i>Prunus munsoniana</i>	Wild Goose.....	2	.0074	.0070	.0071	95	21
<i>Prunus persica</i>	Elberta.....	2	.0114	.0098	.0103	86	31
<i>Prunus persica</i> (nectarine).....	Elruge.....	2	.0094	.0074	.0080	78	24
<i>Prunus salicina</i>	Burbank.....	2	.0211	.0139	.0160	66	48
<i>Pyrus communis</i>	Kieffer.....	2	.0329	.0236	.0262	72	80
<i>Pyrus malus</i>	Delicious.....	2	.0440	.0288	.0330	65	100

the rate of transpiration thru a lowering in the water content which would partially close the stomata. A partial clogging of the vessels at the base of the cuttings might also be a contributing factor. It is interesting to note that the rate for the peach was not materially reduced during the second day.

As in the two preceding series, the peach and the plum represent a group with a low transpiration rate, the rate being only one-fourth as great as the apple. The pear and the sour cherry have a rate about four-fifths of the apple, and the grape transpires just one-half as rapidly per unit area of leaf surface as the apple.

Series 8. Series 6 was a study of the comparative rates of transpiration in the autumn at a time when the relative humidity was high. This series records the transpiration data for ten species of tree fruits under conditions of low relative humidity with a moderate autumn temperature. Practically the only difference in environmental conditions between this series and Series 6 is a considerably lower relative humidity and a slightly higher temperature.

As in Series 6, all the species show a reduction in transpiration rate during the night. It is notable, however, that the peach, Wild Goose plum, and nectarine do not show so great a decrease at night under the humidity conditions prevailing in this series. It will be remembered from the discussion of Series 6 that the night rate of the peach, under conditions of high relative humidity, was reduced to only about one-third of the day rate. Another striking fact to be noted in this series is the wide difference in the rates between the two species of plums included in this series, the rate of the Wild Goose variety being only about one-half that of the Burbank.

Under these environmental conditions the peach, Wild Goose plum, and nectarine again show a very low transpiration rate, a rate only one-fourth as great as the apple. The Burbank plum and sweet cherry have a rate equal to one-half that of the apple. The pear, Duke cherry, and apricot, show still greater transpiration. The apple and sour cherry show the highest rate.

For some reason, which is not apparent, the rates in every case of the same species are higher in Series 6 (Table 3) than in Series 8 (Table 4), in spite of the fact that the relative humidity was higher and the temperature slightly lower in Series 6.

Different Series Compared

A summary of the average transpiration rates for all the series is given in Table 5. The purpose of such a summary is twofold: (1) to present the data for each of the nine series for examination and comparison; and (2) to place the species in groups on the basis of their relative transpiration rate, as shown in the following classification.

High transpiration rate. *Ribes vulgare* (Perfection), *Corylus maxima* (Daviana), *Rubus nigrobaccatus* (Taylor), *Cydonia oblonga* (Champion), *Rubus*

TABLE 5.—SUMMARY OF DATA FOR ALL NINE SERIES OF TRANSPIRATION TESTS
(Average transpiration rate given in cubic centimeters per square inch per hour)

Date.....	July 15, 1927	July 23, 1927	July 25, 1927	October 5, 6, 1926	October 6, 7, 1926	October 7, 8, 1926	October 8, 9, 1926	September 20, 1926	September 22, 1926
Series No.....	1	2	3	6	7	8	9	4	5
Relative humidity (%)	Clear	Clear 45-65	Clear	Rainfall most of the time	Clear 46-58	Clear 46-62	Clear 60-62	Clear 76-78	Rainfall 80-91
Temperature.....	Hot	68-75°	Moderate to hot	61-69°	61-68°	68-75°	70-75°	69-74°	72-75°
<i>Corylus pecan</i>		Warwick .0066	Warwick .0049						
<i>Corylus americana</i>		Owensia .0275	Owensia .0267						
<i>Cydonia oblonga</i>		Champion .0242	Champion .0306						
<i>Prunella chinensis</i>			Forbes .0130						
<i>Juglans nigra</i>		Ten Eyck .0052							
<i>Juglans regia</i>			Mayeda .0036						
<i>Prunus amygdalus</i>		Hard Shell .0043	Hard Shell .0102						
<i>Prunus americana</i>	Harris .0115				Harris .0201	Harris .0231	Harris .0168		
<i>Prunus avium</i>	.0120								
<i>Prunus cerasus</i>	Monte- mancy .0141	Early Rich- mond .0110	Monte- mancy .0164	Early Rich- mond .0034		Early Rich- mond .0070		Early Rich- mond .0277	Early Rich- mond .0168
<i>Prunus cerasus</i> & <i>Prunus avium</i>					Late Duke .0262	Late Duke .0263	Late Duke .0191		

(Table is continued on next page)

accidentalis (Quillen). *Prunus nana* (Jonathan). *Crataegus velutina*. *Prunus americana* (Lefler). *Prunus serotina* (Ledy Richmond). *Monticola*.

Medium transpiration rate. *Fraxino salicifolia* (Parker). *Prunus americana* (Burtis). *Prunus virginiana* (Governeur Wood). *Prunus pennsylvanica* (Late Ohio). *Prunus domestica* (Imperial Sage). *Prunus virginiana* (Burtis). *Ribes prunifera* (Purman). *Tilia americana*.

Low transpiration rate. *Corylus pennsylvanica* (Watters). *Lupinus albus* (Tex. Exptl.). *Lupinus albus* (Mayotte). *Prunus virginiana* (Earl Hall). *Prunus americana* (Wild Goose). *Prunus pennsylvanica* (Liberty and Kings).

No attempt has been made to rank the species within the above groups with the exception of the high-transpiration group, where no significance is to be attributed to the order in which the species are named. In the high-transpiration group there is considerable range in the rates, and an attempt has been made to indicate the order in a general way at least. There is perhaps considerable range within the other groups, but because all the species were not included in any one series and environmental conditions in the different series were so variable, slight differences in rate cannot be evaluated accurately.

DISCUSSION

No very satisfactory method of measuring growth resistance in plants having been devised, knowledge of this characteristic based on experimental work is very meager. In the absence of experimental evidence the consensus of opinion of close-observing individuals who are well acquainted with the plants may have some value. An attempt has been made to gather together the opinions of horticultural writers concerning the growth resistance of the species studied in this investigation to see if there is any correlation between these opinions as to growth resistance and transpiration rate. Table 4 represents the data secured in this study of the literature.

The ranking of the species according to transpiration rate is determined by this investigation, is given in the first column; the summated number for those species for which this information was available in the second column; while columns 3 and 4 indicate the opinions of horticultural writers at various periods. Not every reference cited deals with a plain statement concerning growth resistance, but in a few cases inferences that seem reasonable are drawn from statements about soil preferences, inches of rainfall best for the species, or general statements about resistance to unfavorable conditions. The agreement among these writers is rather remarkable when it is considered that the statements are the opinions of horticulturists widely separated in time and place.

Those species which have a high rate of transpiration, it will be seen from this table, are not considered growth resistant. The sour cherry is the only exception. In the transpiration studies the sour

TABLE 6.—RELATION OF TRANSPIRATION RATE TO STOMATAL NUMBER AND DROUTH RESISTANCE

Species and ranking according to data obtained in present study	Stomatal number per square millimeter ¹	Considered drouth resistant ²	Considered not drouth resistant ²
1. High rate			
<i>Ribes vulgare</i>	145		I(918) II(263, 265) VI(529) VII(124)
<i>Corylus maxima</i>	...		I(511) II(107) III(152) VI(505)
<i>Rubus nigrobacchus</i>	...		IV(652) VI(389)
<i>Cydonia oblonga</i>	...		II(42) III(152) VI(517)
<i>Rubus occidentalis</i>	...		I(313)
<i>Pyrus malus</i>	246		I(2506) VI(372)
<i>Pyrus communis</i>	253		
<i>Prunus cerasus</i>	297	IV(246) VI(411)	
2. Medium rate			
<i>Fragaria chiloensis</i>	...		I(3260) III(152) V(13) VI(564)
<i>Prunus armeniaca</i>	228		I(333)
<i>Prunus avium</i>	...		I(741) III(152) VI(411)
<i>Prunus avium</i> X <i>Prunus cerasus</i>	...		
<i>Prunus domestica</i>	253		I(2716) VI(457) XI(52)
<i>Prunus salicina</i>	...	VI(457)	
<i>Ribes grossularia</i>	...		I(1358) II(288) IV(295) VI(529)
<i>Vitis labrusca</i>	...	IV(300) VI(475) IX(25)	
3. Low rate			
<i>Carya pecan</i>	...	XIII(6-8)	
<i>Juglans nigra</i>	461	I(3505) XII(232)	
<i>Juglans regia</i>	299	III(150)	I(3501)
<i>Prunus amygdalus</i>	...	I(250) III(152) XII(232)	
<i>Prunus munsoniana</i>	...	VI(457) XI(52)	
<i>Prunus persica</i>	186	I(2495) X(6, 142)	
<i>Prunus persica</i> (nectarine)..	...	I(2116) VIII(118)	

I. Bailey, *Encyclopedia of Horticulture*.II. Card, *Bush Fruits*.III. Chandler, *Fruit Growing*.IV. Downing, *Fruits and Fruit Trees of America*.V. Fletcher, *Strawberry Growing*.VI. Fraser, *American Fruits*.VII. Fuller, *Nut Culturist*.VIII. Hedrick, *Encyclopedia of Hardy Fruits*.IX. Hedrick, *Manual of Grape Growing*.X. Hedrick, *Peaches of New York*.XI. Hedrick, *Plums of New York*.XII. Morris, *Nut Growing*.XIII. Stuckey and Kyle, *Pecan Growing*.¹Taken from Eckerson (1908) and Weiss (1865-1866).²Citations to opinions concerning drouth resistance.

cherry is a species which was on the border line and difficult to classify and, for that reason, was placed at the bottom of the high-transpiration group. While there is disagreement between two writers as to the drouth resistance of one of the low-transpiring group (*Juglans regia*), this group as a whole is considered very markedly drouth resistant. The species with the medium transpiration rate seem to be considered partly drouth resistant, but most plants in this group are not considered resistant to drouth.

The grape and strawberry, it should be stated, are classified on what perhaps is insufficient evidence. Cuttings from these plants wilted repeatedly and it was very difficult, for some reason, to keep them turgid long enough to secure reliable information concerning their transpiration.

There is no correlation between stomatal number (shown in the second column of Table 6) and transpiration rate, the species with the lowest number being in the high-transpiration group and the one with the highest number being in the low-rate class.

Next to temperature, water is perhaps the chief factor concerned in the distribution of plants. Deficient or excessive seasonal moisture conditions also play a tremendous role in limiting production with all kinds of crops. Any information relating to the tolerance or intolerance of a species or variety to unfavorable conditions is useful in determining the regions where they should be grown commercially, as well as the particular sites for planting within the region.

Drouth resistance may depend upon several characteristics. Unquestionably transpiration is a factor in conserving or exhausting the supply of soil moisture. The plant which transpires very rapidly will reduce the available soil water faster than one with a lower rate of transpiration. Another factor that determines a plant's ability to resist drouth is the extent and depth of its root system. Annual plants, because of their shallower root systems, are generally less able to endure, without serious injury, protracted seasons of deficient soil moisture, than perennials, especially trees. The inability of the strawberry to withstand drouth may be due as much to its shallow root system as to its medium rate of transpiration.

Most of the species studied in this investigation, because of the depth and extent of their root systems, are generally considered resistant to drouths of ordinary duration. Protracted drouths, however, often take a heavy toll in the production of plants with deep and extensive root systems. It is well known that the peach will thrive in regions and on sites where the apple will not develop satisfactorily or where corn will scarcely grow at all. It is not primarily because of a difference in the nutrient requirements of these species, for the peach responds to good care and fertilization more than most of our fruit crops. It is very probable that this difference in adaptability

is due to different moisture relationships. The transpiration rate may therefore be looked upon as having an important bearing upon the adaptability of the different fruit species where soil moisture is likely to be a limiting factor.

CONCLUSIONS

1. Wide variations in rate of transpiration exist in the 21 species of deciduous fruits included in these tests.

2. On the basis of transpiration rate, the series may be arranged in three groups, as follows:

(1) **High transpiration rate.** *Ribes vulgare* (Perfection), *Corylus maxima* (Daviana), *Rubus nigrobacchus* (Taylor), *Cydonia oblonga* (Champion), *Rubus occidentalis* (Quillen), *Pyrus Malus* (Jonathan, Grimes, Delicious), *Pyrus communis* (Kieffer), *Prunus cerasus* (Early Richmond, Montmorency).

(2) **Medium transpiration rate.** *Fragaria chiloensis* (Parker), *Prunus armeniaca* (Harris), *Prunus avium* (Governor Wood), *Prunus avium* X *Prunus cerasus* (Late Duke), *Prunus domestica* (Imperial Gage), *Prunus salicina* (Burbank), *Ribes grossularia* (Poorman), *Vitis labrusca*.

(3) **Low transpiration rate.** *Carya pecan* (Warrick), *Juglans nigra* (Ten Eyck), *Juglans regia* (Mayette), *Prunus amygdalus* (Hard Shell), *Prunus munsoniana* (Wild Goose), *Prunus persica* (Elberta and Elruge).

3. Very great differences in rate of transpiration exist among the above groups. Some of the species in the medium-rate group transpire only about one-half as rapidly as those in the high-rate class; and certain species in the low-rate group consistently transpire only from one-third to one-fifth as much water per unit area of leaf surface as those species having the highest rate. Considerable variation in rate of transpiration also occurs among species in the same group.

4. There is no correlation between stomatal number per unit area of leaf surface and transpiration rate. The species with the highest number of stomata is in the low-rate group, while the one with the lowest number is in the high-rate group.

5. All species studied usually transpire more rapidly during the day than at night. This is in accord with the results of other investigators working with other plants. Closure of the stomata, lower temperature, and higher humidity are factors in the reduction of transpiration during darkness.

6. The transpiration rate of cuttings decreases as the period of their separation from the plant increases. A reduction of the supply of soluble carbohydrates by respiration, which lowers the water content of the leaf, thus causing a partial closure of the stomata, is probably the chief factor in the reduced rate of transpiration. A partial clogging of the vessels at the base of the cuttings may also be a contributing factor.

7. Transpiration rate and drouth resistance are correlated with these fruits. Those species which in this investigation have been found

to transpire very slowly are considered drouth resistant by close-observing horticulturists, while those which have a high rate are said to be non-resistant to drouth. This fact has some significance in horticultural practice and should be kept in mind in a broad way in making recommendations involving locality, site, and cultural operations.

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