TRANSPIRATION RATES UNDER CONTROLLED ENVIRONMENT: SPECIES, HUMIDITY, AND AVAILABLE WATER AS VARIABLES*

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There is little agreement in the rates of transpiration reported for common species of plants. Some of the discrepancies are due to methods of measurement which influence the rate of transpiration. Much of the confusion is undoubtedly due to the lack of adequate controls in many of the experiments which have been performed.

On the basis of available data it would appear that the following factors significantly affect transpiration rates: species, light, temperature, humidity, availability of water, stage of development of plants, root aeration, wind velocity, cutinization, and size, number, and distribution of stomata. These factors must be considered in any experiment designed to determine transpiration rates.

The most variable factors influencing transpiration rates are rapid fluctuations in the environment. The development of growth chambers in recent years has made possible the control of light, temperature, humidity, and wind velocity. The use of these chambers greatly increases reliability of results within the range of conditions available. Because of present limitations, specifically in simulation of natural light intensity, it is not possible to equate results from growth chamber studies with those for plants growing under natural conditions.

The method of measurement must not detract from the reliability gained by the use of controlled environment. The hygrometric paper and calcium-chloride-cup methods have been discounted by Bailey et al. (1952) as they interfere with air movement and the gradient into low vapor pressure chemicals gives highly distorted values. Potometer methods, using only portions of plants, have only relative value as it is recognized that intact root systems may actually slow absorption and/or transpiration (Kramer, 1945). Potometers employing whole plants (Wallace, 1943) overcome the above objection, but do not allow the availability of water to be varied.

The theoretical importance of the vapor production method, first introduced by Guettard in 1748 (Maximov, 1929), has caused repeated attempts to improve it as a research method. Investigation in this laboratory showed calcium chloride drying tubes to be unreliable at high humidities and the high rates of flow necessary to keep the water vapor concentration approximately constant within the chamber. Recent interest has centered around improved hygrometers for rapid detection of humidity changes (Anderson et al., 1954), (Decker and Wetzel, 1957). The nature of the equipment required has limited its use to samples of less than significant size.

The gravimetric method has been in general use at least since the time of Stephen Hales in 1769 (Crafts, 1961). The main difficulty with this method is the separation of loss of water vapor from the plants from loss of water vapor from the containers. Attempts to remedy this have led to various sealing systems which in turn have required elaborate aeration and rewatering techniques. For several years a check pot method has been employed in this laboratory. The use of duplicate pots without the plants allows determination of evaporation rates and correction of the apparent transpiration for a potted plant without sealing.

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Large numbers of plants and check pots are easily handled with corresponding increase in reliability.

Transpiration rates are sometimes expressed on an average plant basis. The expected rate method is a modification of the above in which a norm is established prior to introduction of a variable. (Southwick and Childers, 1941), (Wright and Barton, 1955). Evaporation is usually ignored or considered as a constant. Failure to determine evaporation limits the method thus far to comparison of relative rates of transpiration for the same group of plants under conditions which affect only loss of water vapor from the plants.

Attempts to quantify transpiration usually consist of expressing the water vapor lost in grams per square decimeter of transpiring surface per hour. Traditionally the transpiring surface has become identified with the plane area of the leaf surfaces containing stomata. Leaf areas are determined by planimetering with mechanical or photoelectric devices. Stem surfaces are usually omitted. Cuticular transpiration is commonly ignored.

Considerable controversy exists as to the effects of the number, distribution, size, and degree of opening of the stomata upon the rate of transpiration. Earlier literature considered the stomata as the main controlling factor in transpiration, but the recent trend has been to minimize their importance.

METHOD

The experiment was designed to determine the transpiration rate at different humidities for two species of plants. The effects of different availability of water was sought by not adding water during the experimental run, and performing the experiment in duplicate using sand culture for one set of plants and a clay loam soil for the other. Species effects were determined by employing coleus, *Coleus blumei* Benth, the clone which was used containing stomata only on the lower surface, and geranium, *Pelargonium zonale* Ait., which had stomata on both leaf surfaces.

The experiment was conducted in the 1100 ft^3 controlled environment room in the Botany Department at Ohio University. Temperature was maintained at 71° F plus or minus 1° F for all runs. A constant air flow was established below that affecting transpiration (Wooley, 1961). Relative humidities at four levels, 35 percent, 46 percent, 58 percent, and 70 percent, were maintained to within plus or minus 2 percent for the different runs. Light was supplied continuously by a ceiling bank of 26 forty watt G.E. fluorescent tubes. An adjustable steel rack supported the plants at three non-overlapping levels receiving approximately 300, 200, and 100 ft-c at mid-plant height as measured by a Weston Master light meter. The three levels were employed to determine the effect of illumination upon transpiration and was found to be not significant at these light intensities.

Clonal cuttings of geranium and coleus were employed to eliminate variations due to genetic or age differences (Martin, 1935). The cuttings were rooted in the greenhouse, then twelve plants of each species were selected on the basis of similar appearance and root development (Parker, 1949). The plants were potted and placed in the environment chamber for two weeks prior to testing to overcome any reactions due to change in environment.

Thirty-six new clay pots, 3-in. size selected for uniformity, were covered with aluminum foil except for the drain hole. One half of these were filled with 200 g air-dried clay loam soil of known composition, the other half with 300 g of washed, air-dried, coarse quartz sand. These media filled the pots to within approximately 0.5 in. of the top and supplied approximately the same water retaining capacity when saturated. The pots containing soil were watered with tap water, and the pots containing sand with Meyer's modification of Shive's solution (Meyer and Anderson, 1941).

Potted plants and check pot duplicates were spaced uniformly throughout the rack. All pots were watered to capacity as indicated by dripping. The pots were then allowed to stand for 10 hr to overcome flooding effects (Kramer, 1951). Weights were obtained to 0.1 g on a Torsion balance at intervals of 4 hr for the first 24-hr period, and at intervals of 12 hr up to at least 60 hr. No water was added during the run. When continued up to 120 hr there was no evidence of permanent wilting.

The loss in weight of the check pots was due to evaporation. The loss in weight of the pots containing plants was caused by evaporation and transpiration, other factors, under conditions of the experiment, not being significant. The difference between loss in weight by the potted plants and the check pots was due to transpiration.

Leaf areas were determined with a simplified, collimated lens, photoelectric planimeter developed in this laboratory and based upon the general principles of those described by Frear, (1935), and Kramer, (1937). Calibration for leaves of the species used showed the error to be less than 1 percent.

Stomatal dimensions were determined with an ocular micrometer with the leaves attached to the plant.

RESULTS AND DISCUSSION

The average transpiration rate in grams per square decimeter of stomatal-bearing leaf surface per hour for the first and second 24-hr periods is presented in table 1. This includes data for both species of plants in both soil and sand culture and at all four humidity levels. The vapor pressure of the leaves which were assumed to be saturated, the vapor pressure of the atmosphere during the experimental run, and the vapor pressure deficit of the atmosphere are included for reference.

During the first 24-hr period both species in soil transpired directly proportional to the vapor pressure deficit of the atmosphere, the positive correlation coefficient exceeded 0.94 in both cases. Coleus consistently transpired at a significantly higher rate than geranium.

During the second 24-hr period in soil coleus again transpired at a higher rate than geranium except at 35 percent relative humidity when geranium transpired at a significantly greater rate than coleus. No correlation between rate of transpiration and vapor pressure deficit was evident.

The transpiration rates for both coleus and geranium in sand culture did not correlate with the vapor pressure deficit of the atmosphere during either period. Rates were generally erratic, and differences between species not significant.

Except for the run at 70 percent relative humidity, both kinds of plants transpired at a significantly higher rate in soil than in sand culture. Absorption would be expected to be higher from the sand culture where a greater proportion of the moisture is capillary water, but this is not shown by the data.

Table 2 shows the total loss or evapotranspiration and the transpiration per average plant in grams of water lost for both species in soil for four humidity levels during five consecutive 12-hr periods. The experimental runs were terminated at 60 hr at which time the readily available water had become exhausted for the lowest humidity checked. The evaporation per average check pot for corresponding periods is included for reference.

There was no significant decrease in rate of evaporation from the check pots during any 60-hr period at any of the four humidity levels. The maximum standard deviation occurred during the 35 percent relative humidity run. However as each individual pot maintained a consistently higher or lower rate than the average, it was assumed that these deviations reflected slight fluctuations in the environment known to occur within the chamber. These variations should be compensated for as the potted plants were distributed throughout the chamber in a similar pattern to the check pots. The positive correlation coefficient between

TABLE 1

Average transpiration rates for coleus and geranium in g per dm² per hr of stomatal-bearing surface for two 24-hr periods in sand and soil at four relative humidities

Relative humidity (%)	Atmospheric vapor pressure (mm Hg)	Vapor pressure of plant (mm Hg)	Vapor pressure deficit (mm Hg)	Transpiration first 24 hr				Transpiration second 24 hr			
				soil		sand		soil		sand	
				coleus	geranium	coleus	geranium	coleus	geranium	coleus	geranium
35	6.9	19.8	12.9	0.140	0.085	0.079	0.067	0.077	0.091	0.037	0.041
46	9.1	19.8	10.7	0.135	0.072	0.004	0.007	0.086	0.063	0.025	0.003
58	11.1	19.8	8.7	0.087	0.044	0.025	0.011	0.095	0.071	0.032	0.003
70	13.9	19.8	5.9	0.076	0.044	0.089	0.083	0.072	0.051	0.094	0.600

TABLE 2

Average transpiration and evapotranspiration per 12-hr period, totals for 60 hr, for coleus and geranium in soil. Evaporation from check pots for reference.

Rel. hum.	Period	Coleus						Geranium						Check pots					
		1	2	3	4	5	Total	1	2	3	4	5	Total	1	2	3	4	5	Total
35	evapo-transp.	13.9	15.2	11.9	9.9	5.7	56.5	9.8	15.5	13.9	11.6	7.6	59.5	6.5	7.7	7.0	6.7	7.0	34.9
	transp.	7.3	7.5	4.9	3.2	1.3	21.6	3.3	7.8	6.9	4.9	0.6	23.5						
46	evapo-transp.	13.0	13.0	13.3	8.2	6.4	53.9	10.8	10.3	12.3	8.4	8.7	50.5	5.7	6.0	6.7	5.7	6.0	30.1
	transp.	7.3	7.0	6.6	2.5	0.4	23.8	5.1	4.3	5.6	2.7	2.7	20.4						
58	evapo-transp.	9.3	10.2	8.9	10.5	8.0	46.9	7.8	8.2	8.3	10.3	8.1	42.8	5.0	5.3	4.2	5.1	4.4	24.0
	transp.	4.3	4.9	4.7	5.4	3.6	22.9	2.8	3.0	4.1	5.2	3.7	18.8						
70	evapo-transp.	7.0	8.1	8.3	7.4	5.2	36.0	6.4	7.4	7.5	7.2	5.4	33.9	3.8	4.2	4.1	3.9	3.5	19.5
	transp.	3.2	3.9	4.2	3.5	1.7	16.5	2.6	3.2	3.4	3.3	1.9	14.4						

TABLE 3

Average transpiration and evapotranspiration per 12-hr period, totals for 60 hr, for coleus and geranium in sand culture. Evaporation from check pots for reference.

Rel. hum.	Period	Coleus						Geranium						Check pots					
		1	2	3	4	5	Total	1	2	3	4	5	Total	1	2	3	4	5	Total
35	evapo-transp.	11.7	13.3	10.9	9.8	6.4	52.1	8.8	9.8	9.1	8.8	6.9	43.4	8.0	8.8	8.3	8.5	7.4	41.0
	transp.	3.7	4.5	2.6	1.3	-1.0	11.1	0.8	1.0	0.8	0.3	-0.5	2.4						
46	evapo-transp.	9.2	7.1	10.2	7.6	9.7	43.8	7.4	7.6	8.5	6.6	7.2	37.3	7.3	7.5	8.5	6.7	7.5	37.5
	transp.	0.9	-0.4	1.7	0.9	2.2	5.3	0.1	0.1	0.0	-0.1	-0.3	-0.2						
58	evapo-transp.	6.3	6.4	5.9	6.6	5.8	31.0	5.2	5.2	4.8	5.5	4.8	25.5	4.9	5.2	4.7	5.5	5.1	25.4
	transp.	1.4	1.2	1.2	1.1	0.7	5.6	0.3	0.0	0.1	0.0	-0.3	0.1						
70	evapo-transp.	8.6	10.6	9.5	10.3	6.8	45.8	5.4	6.5	5.9	5.8	4.8	28.4	4.5	5.2	4.9	5.2	4.3	24.1
	transp.	4.1	5.4	4.6	5.1	2.5	21.7	0.9	1.3	1.0	0.6	0.5	4.3						

the average total water loss from the check pots and the vapor pressure deficit of the atmosphere exceeds 0.97 for all four humidities.

The total evapotranspiration for each humidity level for both coleus and geranium was quite similar at the end of the 60-hr period, although the average stomatal-bearing leaf surface for coleus was 4.40 dm^2 which was significantly less than the 5.40 dm^2 area of geranium. The total evapotranspiration for both kinds of plants is closely correlated with the vapor pressure deficit of the atmosphere.

The transpirational loss in grams per average plant for each 12-hr period for each of the four humidity levels is depicted graphically in fig. 1. In general the transpiration rate increased after the first 12-hr period, reached a maximum, and then gradually decreased. The period in which the highest transpiration rate was attained was usually later as the humidity of the atmosphere increased.

The amount of transpiration, as determined by this method, became very low for both kinds of plants during the final 12-hr period at 35 percent relative humidity. The value for coleus, which appears to be statistically significant and negative, is an artifact caused by the greater total loss by the potted plants than by the check pots. Runs with the check pots beyond the 60-hr period showed that evaporation remained constant until approximately 50 g of water had been lost, then the rate of evaporation dropped rapidly. As a result transpiration rates cannot be considered reliable for low humidities during the final 12-hr period.

Evapotranspiration and transpiration in grams per average plant for both species in sand culture at four humidity levels per 12-hr period together with evaporation in grams from the check pots and totals at the end of 60 hr are presented in table 3.

The evaporation in grams from the check pots was slightly higher than from the corresponding series of soil check pots, showed little standard deviation, correlated highly with the vapor pressure deficit of the atmosphere, and remained constant up to a total loss of 43 g.

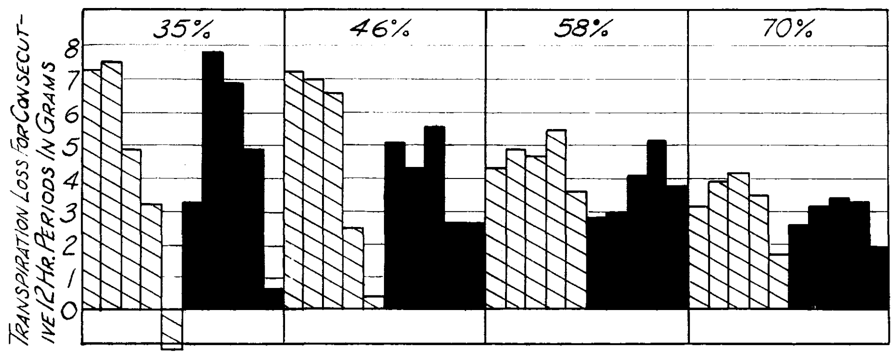
The coleus plants in sand culture with an average leaf area of 4.30 dm^2, when compared with the similar group in soil having an average leaf area of 4.40 dm^2, lost significantly less by evapotranspiration except at 70 percent relative humidity. The geranium plants lost leaves until their average leaf area was only 1.14 dm^2. Consequently no attempt was made to compare data for the two media.

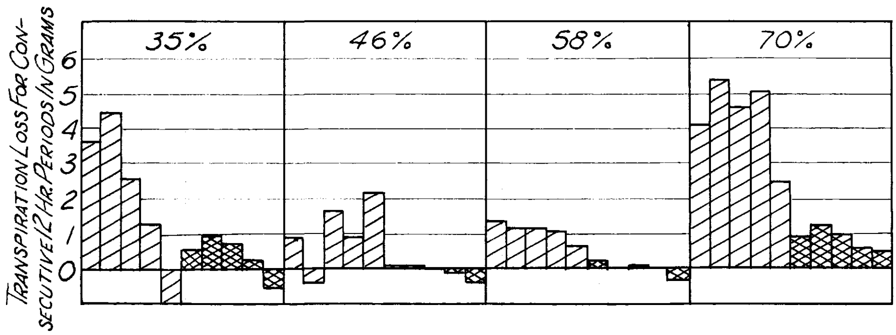
The transpiration in grams per average plant for each 12-hr period for each of the four humidity levels is depicted in graphic form in fig. 2. It will be noted that the coleus plants in sand culture transpired at a significantly lower rate than the similar group of plants in soil except at 70 percent relative humidity.

The plane surface of the soil or sand in the check pots was calculated to be 0.46 dm^2. The loss by evaporation from the soil surface varied from a low of 42.4 g per dm^2 in 60 hr at 70 percent relative humidity to a high of 75.9 g per dm^2 in 60 hr at 35 percent relative humidity. On a per hour basis these are rates of 0.66 g up to 1.4 g per dm^2. Values obtained similarly for sand culture are 52.4 g and 89.1 g per dm^2 for 60 hr, or 0.87 g up to 1.5 g per dm^2 per hr. The lowest of these rates is at least six times the maximum rate of transpiration attained by the plants at the identical humidity levels.

The total water vapor loss per plant and container, the evapotranspiration, for all runs as shown in table 2 and table 3 for 60 hr was divided by the total plant and soil or sand surface area to determine the evapotranspiration rate. In fig. 3 the total height of the bar graphs depict the evapotranspiration rate. For comparison the transpiration rate of the same average plant is shown as the clear area at the base of the bar.

The evapotranspiration rate for both species of plants in soil decreases in approximately a straight line relationship with increase in humidity. The evapotranspiration rate for both kinds of plants in sand culture follows the above pattern except for an unexplained rise at the highest humidity level.





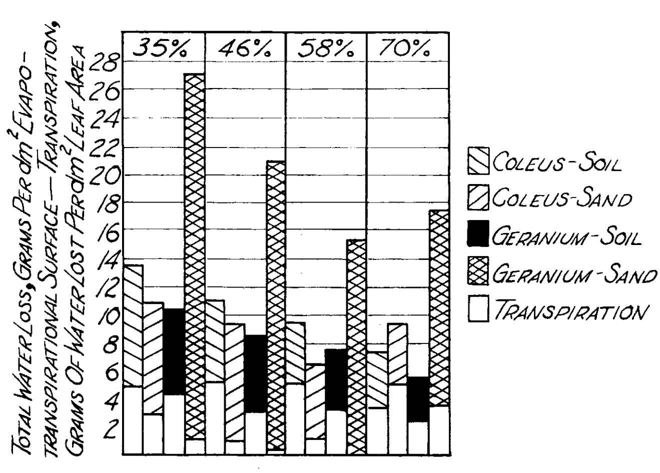


FIGURE 1. (Upper) Transpirational loss per average plant for 12-hr periods for each humidity level in soil media.

FIGURE 2. (Center) Transpirational loss per average plant for 12-hr periods for each humidity level in sand media.

FIGURE 3. (Lower) Total water loss (evapotranspiration) and transpiration loss for each species in two media at each humidity level.

The average transpiration rate over the 60-hr period gives some indication of the relative ability of the kinds of plants used to absorb and transpire as the available water in the medium decreases. Coleus consistently transpired at a higher rate than geranium in both media and at all humidity levels tested, although the differences in rate between the two kinds of plants are not significant at 35 percent relative humidity.

The consistency of the evapotranspiration rates emphasizes the fluctuations in the transpiration rates at 60 hr. Competition between transpiration and evaporation is indicated. It appears that if water is absorbed rapidly and transpired, the rate of evaporation is reduced. The possibility that the plants caused reduction of evaporation by shading was investigated. Artificial shading equivalent to the plant area did not significantly reduce evaporation under conditions of the experiment.

The average stomatal opening for geranium had diameters of 19 and 4 μ and for coleus was 12 and 3 μ. Apparently under the conditions of the experiment the stomata were not fully open (Eckerson, 1908). Using the data from Eckerson (1908) the number of stomata per average plant were calculated for the soil series in which both kinds of plants transpired similar total amounts at all humidity levels. The average coleus plant had approximately three times the total number of stomata present in geranium. No correlation was evident between amount of transpiration and numbers of stomata.

Calculation of the area of the stomatal openings showed coleus to have approximately twice that of geranium. No correlation was evident between amount of transpiration and stomatal area.

The total perimeters of stomatal openings were almost identical for the two species of plants. There is a close correlation between the amount of transpiration and the total perimeters of the stomatal openings of these plants.

CONCLUSIONS

1. The check pot method of measuring transpiration is reliable up to a critical value, depending upon the medium, after which the rate of evaporation decreases.
2. During the first 24-hr period when water was readily available, except at the 46 percent relative humidity level, coleus transpired at a significantly higher rate per square decimeter per hour than geranium in both soil and sand culture.
3. When water is readily available both species in soil transpired at rates which correlated highly with the vapor pressure deficit of the atmosphere.
4. Lack of readily available water limits transpiration rates when the medium is above permanent wilting percentage.
5. Evaporation from the sand or soil in the pots occurred at a greater rate than transpiration.

SUMMARY

Transpiration rates were determined under a controlled environment for coleus, having stomata only on the lower leaf surface, and geranium, having stomata on both leaf surfaces. A modification of the gravimetric method in which check pots were used as controls was employed. The experiment was performed in duplicate with sand and soil as the media. Light intensity, wind velocity, and temperature were kept constant, while humidity and water availability were varied.

In general, coleus transpired at a significantly higher rate than geranium. Both kinds of plants transpired at rates which highly correlated with the vapor pressure deficit of the atmosphere, as long as water was readily available. Transpiration rates remained fairly constant during the early periods of any one run

while water was abundant, then dropped sharply while the media was well above permanent wilting percentage.

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