TRANSPIRATION IN AMERICAN HOLLY IN RELATION TO LEAF STRUCTURE

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Although the structural leaf type represented by that of American holly (*Ilex opaca* Ait.) is often regarded as an adaptation to xeric conditions, this species of holly, throughout its native range, occurs most frequently in swamps, stream banks, moist woods, and other similarly mesic to hydro-mesic habitats. It appears that American holly, despite its heavily cuticled and coriaceous leaf, is not a drought-enduring species.

Preliminary experiments made by the writer a number of years ago on potted holly plants are also indicative of a low degree of drought-endurance in this species. When drought conditions were simulated in a green house by not adding water to the soil, the holly leaves soon died, becoming brittle-dry. It was noted that the ordinary yellow coleus, with its thin, parenchymatous leaves, would often survive a considerably longer period of soil desiccation than holly.

Interest was therefore aroused in studying further the water relations of American holly under carefully controlled conditions. Since relatively little experimental work has been done on the influence of structural differences in leaves on transpiration rates, the present investigation has been concerned mainly with this phase of the problem.

MATERIALS AND METHODS

Three series of experiments were carried out, involving different comparative materials and methods.

SERIES I. Potted plants of American holly (*Ilex opaca*) and tobacco (*Nicotiana tabacum* var. White Burley), 15–20 inches and 9–12 inches high respectively, were used in this series of experiments. Comparative records of water-loss in these species were obtained on an automatic transpirometer described by Transeau (1911), and the results calculated in terms of grams of water lost per square decimeter of lower leaf surface. The apparatus and plants were mounted on a slowly rotating table which completed one revolution in about two minutes. The pots were sealed in metal jackets, and provided with stoppered tubes for periodic watering and aeration of the soil.

SERIES II. American holly and yellow coleus (*Coleus blumeii*) were compared in this series. By potting the plants in known weights of soil of known moisture content (30% saturation), and periodically restoring to original weight, a more precise control over the factor of soil water content was effected. The method of experimentation was otherwise essentially the same as in Series I, except that only the cumulative water-loss per day was determined.

SERIES III. In order to eliminate the effect of stem and root conducting systems on the rate of water-loss, the experiments of Series I and II were supplemented by a number of studies using single leaves or small shoots, the cut ends being immersed in water, and necessary precautions taken to safeguard against evaporation from the free water surfaces. The plant parts were cut under water, placed in the containers, and allowed to stand for several hours under a bell-jar, in order to insure an equilibrated internal water balance before making the initial weighing. To maintain uniform environmental conditions, the cuttings were mounted on a slowly rotating table during the course of each experiment in the greenhouse. By this method, the observed water-loss is more nearly a function of leaf structure.

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RESULTS AND DISCUSSION

Data are tabulated in Table I to show the comparative leaf structure of holly, coleus, and tobacco. The value R is the ratio of internal to external exposed surface of the leaves, and was calculated by Turrell's method (1936). In Table II the data of experiments in Series I and II, are summarized and the average rates of water-loss expressed in terms of per cent relative to holly. The variability of data obtained in Series III precludes a concise summation of the results, but data for three representative experiments are given in Table III.

It is evident from the data in Table II that the rate of water-loss in American holly was on the average higher than in either yellow coleus or tobacco. These

TABLE I

COMPARATIVE LEAF STRUCTURE

Species	Total Thickness of Leaf	Stomates / sq. mm.		Thickness of Cuticle	R
		Upper	Lower		
Am. Holly	375 μ	0	220	7–10 μ	12.9
Tobacco	182 μ	90	190	1 μ	7.1
Yellow Coleus	155 μ	0	150	1 μ	4.6

TABLE II

RELATIVE TRANSPIRATION RATES BETWEEN SPECIES

Series	Expt.	Species Compared	Average Relative Transpiration	Duration of Experiment
I	1	holly : tobacco	100 : 91	11 hrs.
	2	holly : tobacco	100 : 87	24
	3	holly : tobacco	100 : 95	32
	4	holly : tobacco	100 : 97	6
II	1	holly : coleus	100 : 67	5 hrs.
	2	holly : coleus	100 :104	12
	3	holly : coleus	100 : 88	12

results agree with those of Bergen (1904), Maximov (1929), and others, who have shown that the rate of transpiration in xeromorphic species is often higher than in mesomorphic species.

Turrell (1936) showed that a xeromorphic leaf is characterized by a higher ratio of exposed mesophyll to epidermal surface than a mesomorphic leaf, and suggested that the greater rate of transpiration demonstrated in many xeromorphic species may probably be accounted for in these terms. For *Citrus limonia* and *C. grandis*, Turrell was able to demonstrate a remarkably close correlation. The internal-external surface ratio for *C. limonia* is 1.29 times that of *C. grandis*, and the corresponding ratio of water-loss in rooted cuttings of these species, as calculated from the data of Haas and Halma (1932) was 1.20. This close correlation, however, does not hold for the species used in this investigation; thus, the mesophyll surface exposed per unit external surface in the holly leaves was about 2.8 times as great as that exposed in the coleus leaves, but the average transpiration rate in holly was only 1.2 times as great. Indeed, no close correlation is to be expected, for too many other variables are always present. The greater transpiration rate in *C. limonia*, for example, may have been due in part to a greater root area relative to the transpiring surface. According to Haas and Halma (1932), *C. limonia* produces more roots per cutting than *C. grandis*.

In order to eliminate such variables as the root/shoot ratio, experiments were carried out using single detached leaves, or small cuttings, as described in the methods. Seventeen experiments comprised this series, the results of which were quite variable. Individual variations within the same species may have been due to differences in stomatal behavior. Marked differences in the percentage of stomates open on different leaves of the same corn plant have been observed by Sayre (1939). Unfortunately, time did not permit an evaluation of this factor in the present experiments.

TABLE III

Relative Transpiration Rates of Single Detached Leaves

Expt.	Species	Leaf	Water-loss in grams / sq. dm.	Average per sq. dm.	Time
1	Holly	1 2 3 4 5	1.40 1.14 1.46 1.32 1.70	1.4	4–7 p. m.
	Coleus	1 2 3 4 5	0.75 0.43 0.92 1.32	0.9	
2	Holly	1 2 3	1.43 1.28 1.98	1.6	2–5 p. m.
	Lilac	1 2 3	1.86 0.56 0.55	1.0	Bright sun Temp. 35° C.
3	Holly	1 2 3	0.84 1.70 1.00	1.5	11 a. m.–7 p. m.
	Lilac	1 2 3	3.10 3.20 3.50	3.3	Dull, cloudy Temp. 32° C.

Evidence for a differential behavior in leaves of different species to varying conditions of light is also indicated. Thus under conditions of high light intensity, holly transpired more rapidly than lilac (*Syringa vulgaris*), but under conditions of lower light intensity (as on cloudy days), less rapidly. This difference probably results from differences in stomatal behavior under the two sets of conditions.

A similar effect of variation in light intensity on the transpiration ratio of *Melissa officinalis* is shown by the experiments of Mittmeyer (1931). Mittmeyer found that in *Asarum* the stomates closed at high light intensities, but remained open in *Melissa*. Under these conditions, the rate of transpiration in *Melissa* exceeded that in *Asarum*, but when the stomates were open in both plants, *Asarum* exceeded *Melissa*.

It seems evident from these experiments and from those of Blaydes (1935) and others, that differences in leaf structure are of little ecological significance in determining differences in transpirational water loss among species. As Shaffner (1928) has pointed out, "the same evolutionary progressions take place whether a group is moving into the water or remaining in the aerial environment." Accordingly, species with thick cuticles, sunken stomates, epidermal hairs, cell mucilages, or a protoplasmic structure capable of enduring desiccation, may be expected to occur in habitats of diverse water relations. From this viewpoint, any correspondence between xeromorphy in plants and drought-endurance would be merely a coincidence.

SUMMARY

The relative rates of transpiration in American holly, tobacco and yellow coleus were determined. Under the same conditions of soil and atmosphere, the holly leaf with its very thick cuticle had an average rate of transpiration which exceeded that of either tobacco or yellow coleus, both with thin cuticles.

The stomatal frequency, when averaged for both upper and lower surfaces, is highest in tobacco, and least in coleus. The internal leaf surfaces of holly, tobacco, and coleus are in the proportion of 12.9, 7.1, and 4.6. No close correlation between relative transpiration rates and the internal surface ratio is evident in these species.

From studies on excised leaves supplied with water, it appears that the relative importance of different leaf structures in affecting the rate of foliar water-loss in different species varies with qualitative and quantitative differences in the environmental conditions to which the leaves are subjected.

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LITERATURE CITED

Bergen, J. Y. 1904. Transpiration of sun and shade leaves of *Olea Europaea* and other broad-leaved evergreens. Bot. Gaz. 38: 285–296.
Blaydes, G. W. 1935. Water-vapor loss from plants growing in various habitats. Ohio Jour. Sci. 35: 112–130.
Haas, A. R. C., and **F. F. Halma.** 1932. Relative transpiration rates in *Citrus* leaves. Bot. Gaz. 93: 466–473.
Maximov, N. A. 1929. The plant in relation to water. George Allen & Unwin, Ltd., London.
Mittmeyer, G. 1932. Studien uber die Abhangigkeit der Transpiration verschiedener Blattypen vom Licht and Sattigungsdefizit der Luft. Jahrb. Wiss. Bot. 74: 364–428.
Sayre, J. D. 1939. Corn stomata. Paper presented before the Plant Institute of the Ohio State University, February 5.
Shaffner, J. H. 1928. Principles of plant taxonomy V. Ohio Jour. Sci. 28: 69–85.
Transeau, E. N. 1911. Apparatus for the study of comparative transpiration. Bot. Gaz. 52: 54–60.
Turrell, F. M. 1936. The area of the internal exposed surface of dicotyledon leaves. Amer. Jour. Bot. 23: 255–263.