LEAF-STRUCTURE AS RELATED TO ENVIRONMENT

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Introduction

This investigation was begun during the summer of 1915 and carried on for about a year. Preliminary observation showed that the leaves growing in the sun at the south periphery were thicker than the leaves growing in the shade at the center of the same tree. The purpose of the investigation was to find out the exact differences in the structure of the leaves from the two positions, and to compare by measurements of the factors the environments in which the leaves were growing. The factors measured were light, evaporating power of the air, temperature, humidity and wind. A study of transpiration was also made during the summer of 1916.

Historical

The relation of leaf structure to factors of the environment has been studied by numerous investigators. Although very few works give factor measurements, some of the more recent investigations on leaf structure are here reviewed. One of the most detailed works is by Mrs. Clements (12), which shows the differences in the structure of numerous hydrophytic, mesophytic and xerophytic leaves, and of sun and shade leaves on different plants of the same species. The physical factors, light, water-content of the soil, humidity and temperature, were measured for most of the habitats in which the plants studied were growing. Good reviews of earlier articles on leaf structure, and of explanations concerning the structure and formation of palisade cells, are given by Mrs. Clements.

Experiments performed by Eberhardt (14) showed that humid air caused an increase in the size of the leaf, in the amount of chlorophyll and in root development; while dry air caused an increase in the thickness of the cuticle, in the number of stomata, and in the amount of sclerenchyma, woody tissue and palisade.

Brenner's (9) experiments on various succulent plants are interesting and important. Plants grown in moist air showed the following changes as compared with plants growing in the normal environment: storage tissue, the fibro-vascular bundles, air-spaces, dry weight, ash and acid content of the leaves all decrease; chlorophyll tissue increases; chlorophyll cells become more isodiametric; walls of epidermal cells become wavy; number of stomata per leaf increases, although the number for a unit area may be the same; and epinasty replaces hyponasty, so that the leaves grow at right angles to the stem. He believed the air factors, not the soil factors, determined these changes, but that physical explanations do not always seem adequate to account for the changes.

Brenner (10) concludes from his anatomical and experimental study on Quercus leaves that modifications caused by the environment are hereditary and may develop into new species.

Bonnier (7) selected about fifty species of perennial plants at Fontainebleau. Each plant experimented upon was split, one part planted at Fontainebleau, the other at Toulon. The plants set out at Toulon became like the wild plants surrounding Toulon in leaf and and wood structure and in external characters.

Hansgirg (18) gives descriptions in detail of more than fifty types of leaves, with a discussion of their ecological advantages.

Chrysler (11) compared the leaf structure of nine strand plants from the Atlantic coast near Wood's Hole, Massachusetts, and from the vicinity of Chicago. The leaves of the maritime plants were from less than once to a trifle over twice as thick as the inland plants. The increase in thickness was mostly due to increased palisade development. Greater compactness in tissue and increased thickness of the outer epidermal wall were found in certain plants. The amount of salt in the soil is given as the probable cause for the variations.

Boodle (8) in his experimental study on the leaves of *Pteris aquilina* Linn. found that leaves grown in dry and exposed situations had a xerophytic structure while those grown in sheltered positions were more mesophytic. The former leaves possessed hypoderm, the latter had none and the palisade was poorly developed, or entirely missing. The same differences were found on leaves of the same plant, or on different parts of the same leaf. A plant that had been producing shade leaves in a moist greenhouse, produced sun leaves when placed in a garden. The mature structure of the leaf is not determined at an early stage in the leaf's growth.

Copeland (13) found great variations in the shape and thickness of leaves on the same branches of various plants.

Hesselman (23) brought out many important facts in his very detailed and quantitative work. Leaves formed in the stronger light of the forest in the spring developed more palisade than leaves that developed later in the weaker light. The trees that had high light requirements, Betula, Fraxinus, produced sun-leaves, while the trees of low light requirements, Quercus, Corylus, produced both sun and shade leaves. The trees in the first group produced starch in all the leaves, while those in the latter group produced no starch in the innermost leaves. Shade leaves make more starch than sun leaves of the same species when the light is equal. The production of starch decreases from spring to summer in the forest more in sun plants than in shade plants. The respiration of sun plants is far greater than of shade plants. If the leaf surface is equal, transpiration increases with the amount of palisade. Sun plants in the sun transpire much more than shade plants in the shade. The work also contains good representations of ecological structures of plants.

Bergen (4) compared the transpiration, color, size and the general structure of sun and shade leaves of the same individuals of the following: *Olea europea sativa, Pistacia, Lentiscus, Quercus, Ilex, Rhamnus Alaternus.* He found the ratio in thickness of sun leaves to shade leaves to be 1.5–3.7 to 1. The sun leaves had thicker cuticle, more palisade, smaller air spaces, greater bundle development, 15 percent more stomata as determined by two observations, greater scaliness, darker color and smaller area. The greater transpiration in the sun leaves was due to their greater activity, because their larger stems and bundles transfer the water more quickly, and because the greater thickness of the leaves afforded a larger interior evaporating surface. In another article (5) Bergen compares the thickness and transpiration of new and old leaves. From the result of another study (6) he states that "it is undoubtedly a fact that the great majority of woody dicotyledons have leaves which when freely exposed to the sun are concave on the upper surface and that this concavity usually lessens or disappears in the case of much shaded leaves on the same plant."

Oltmans (26) noted that the leaflets growing on the south periphery of *Robinia Pseudo-Acacia* trees were concave, while those on the north periphery were flat. Wiesner (32) also observed that while the upper surface of peripheral leaves was concave, the leaves in the shade of the same tree were usually flat.

Herriott (22) gives the frequency and violence of the wind and the peaty soil as causes for the xerophytic leaf structure of some New Zealand plants.

Raunkiaer (27) found that palisade tissue was equally well developed in the leaves of certain plants above the water and to a depth of twenty centimeters. Below this the length of the palisade cells gradually decreases. No palisade tissue was distinguished in shade plants under water, nor above, to a height of about thirty centimeters. His discussion of the causes of palisade development and the orientation of the palisade cells is valuable.

Lubimenko (25) determined that the chloroplasts of certain ombrophilous plants, as Tilia and Abies, were greater in size and in sensitivity than the chloroplasts of ombrophobous plants, as Pinus and Betula. The pigment was more concentrated in the former group.

Baumert's (3) work contains a good review on the literature of structures protecting leaves from light. From his own experiments he found that a thick white coating of hairs as in *Centaurea candidissima* reduced the heat in the leaf 37.5 percent, shininess reduces the heat 30 percent, and a wax coating up to 13.6 percent. Wiegand's (31) experiments show the efficiency of hairy and cutinized coverings in reducing the water loss by transpiration.

Areschoug (2) maintains that well-developed, compact palisade tissue reduces transpiration, despite Hesselman's experiments to the contrary.

Ewart (15) experimenting upon *Tilia europaea* found that mature leaves do not increase in size when most of the leaves are removed from the tree. The increased size of the new leaves which replace those defoliated is due to the increase in the number of cells.

Sampson and Allen (29) found that the sun leaf transpired from two to four times as much as the shade leaf of the same species whether the leaves were placed in the sun or shade. This was explained by the greater number (20 percent–60 percent) of stomata in the sun leaf.

Harshberger (20, 19) investigated the leaf structure of strand plants in New Jersey, and sand dune plants in Bermuda. He states that the xerophytic structures are due to intense light, strong winds, and in rare cases to salt spray. The unequal illumination of the two sides of the leaf causes the formation of palisade and sponge tissues.

Renner (28), in discussing the relation of wind to transpiration, says that the transpiration of small mature leaves is increased to a far greater extent by the wind than that of large leaves. This is explained by the vapor cap which is thicker about the larger leaves. If the air were absolutely quiet Renner believed the thickness of the vapor cap would vary with the diameter of the leaves.

Adamson (1) found the xerophytic structures in leaves of certain species of Veronica to consist in reduced leaf surfaces, reduction in intercellular spaces, and an increase in the thickness of the cuticle.

Livingston and Brown (24) in their study of the daily march of transpiration showed that the water content of leaves falls during the day and rises during the night.

Starr (30) compared the structures of stems and leaves of plants on dunes and on flood plains. She discusses the ecological factors of the dunes, but no measurements are given. The leaves of the dune plants owe their greater thickness to increased palisade tissue chiefly.

Ganong (16) states that one of his students found that the petioles from the exposed part of a tree were larger than those from more sheltered positions.

Haberlandt (17) says that a comparison of the vigorously transpiring sun leaves and the feebly transpiring shade leaves of the same plant shows an increase in the linear dimensions of the vascular system in the sun leaves.

Hasselbring (21), working on tobacco plants growing in the sun and in the shade, showed that the proportions of dry matter, and the production of plant substance for equal areas of leaf surface were greater in the sun plants. The shade plants transpired 186.99 cc. of water in producing one gram of plant substance, while the sun plants transpired 241.72 cc. He found the water content of leaves from sun plants to be 81.39 percent and of leaves from shade plants to be 83.68 percent. The sun plants transpired .412 cc. while the shade plants transpired .224 cc. per square decimeter of leaf surface per hour.

Methods

The readings of the environmental factors were made in the sun among the leaves on the south periphery of untrimmed isolated trees and at the apex of trees growing in the forest. At a height corresponding to the sun readings on isolated trees, readings were taken in representative positions within the crowns; and for the forest trees readings were taken among the lowest leaves. For a given species the readings were taken upon the same individual in the forest or in isolated positions. Care was taken so that the various factors were measured in the same positions in the crown or at the south periphery of each tree. Cytological material was collected from leaves growing in these positions respectively. Pieces from about twenty leaves from each position were killed in chromo-acetic acid and in Juel's killing solutions. The material from Juel's solution gave the best specimens for study. The ordinary paraffine method was used in preparing the material.

The response of the leaves to the environmental factors was shown in transpiration; in the green and dry weights and water content of given leaf areas; in the thickness of the leaf and its parts, palisade, sponge, upper and lower epidermis and the cuticle; in the compactness of the tissues; in the structure of individual cells; and in the macroscopic characters, as area and lobing.

The Physical Factors

1. *Light*

The light was measured by means of the Clements' photometer between 11 A.M. and 2 P.M. in August, 1915. Four readings were taken within the crown of isolated trees and among the lowest leaves of the forest trees for four or five individuals of ten species. From these 16 to 20 readings for each species the light values, as arranged in the following table, were averaged.

Table 1

Showing the Light Values in the Crown of Isolated Trees and at the Base of Forest Trees

Species	Position of Trees*	Light Value in Crown or at Base
Acer saccharum Marsh.	Isolated	0.0175—crown
	Forest	0.0076—base
Tilia americana L.	Isolated	0.0688—crown
	Isolated (L.)	0.1000—crown
	Forest	0.0086—base
Quercus macrocarpa Michx.	Isolated	0.1132—crown
	Forest	0.0754—base
Quercus rubra L.	Forest	0.0425—base
Quercus alba L.	Forest	0.0100—base
Acer saccharinum L.	Isolated	0.0406—crown
	Isolated (L.)	0.0380—crown
Acer negundo L.	Isolated	0.0979—crown
Ulmus americana L.	Isolated	0.0770—crown
Fraxinus pennsylvanica Marsh.	Isolated	0.0497—crown
Celtis occidentalis L.	Isolated (L.)	0.0591—crown

* Trees marked (L.) in Lincoln, all others in Minneapolis.

The order of the light values in isolated trees, beginning with the lowest, is seen to be *Acer saccharum*, *Acer saccharinum*, *Fraxinus pennsylvanica*, *Celtis occidentalis*, *Tilia americana*, *Ulmus americana*, *Acer negundo*, and *Quercus macrocarpa*. In the forest the order is *Acer saccharum*, *Tilia americana*, *Quercus alba*, *Quercus rubra*, and *Quercus macrocarpa*. Comparing the isolated and forest individuals of the same species it may be noted that the trees in the forest have the lower light intensity.

2. *Evaporating Power of the Air*

Livingston's standardized porous cups were used for measuring the evaporating power of the air. The cups were placed in the trees between 8 and 10 A.M. and taken down about 5 P.M. The ratios of the amounts of water evaporated from the crown to that from the south periphery in isolated trees, or from the base to the apex of the crowns of forest trees were lowest in isolated trees of *Ulmus americana* and *Acer negundo* (1 : 1.44, 1 : 1.48) and greatest in isolated *Acer saccharinum* and *Tilia americana* (1:2.3, 1:2.2). The ratios of five other species ranged between these. The ratios in the isolated trees were always less than the ratios in forest trees of the same species, for example, in the isolated tree of *Quercus macrocarpa* the ratio was 1 : 1.3, while in the forest tree it was 1 : 2.2. This is due to the greater humidity at the base of the forest tree as compared with the humidity within the crown of the isolated tree.

The temperature and humidity data indicate that the differences in the amounts evaporated in the sun and in the shade positions cannot be explained by these two factors alone. The movement of the air seems to be the controlling factor. As the water evaporates from the cups in the exposed situations it is rapidly carried away from the vicinity of the cups by air currents. As the wind data show, there is much less air movement within the crown than at the south periphery, so it is very probable that a vapor blanket is formed about the cups within the crown. This blanket would very likely be formed also about each leaf. Renner (28) concluded that the thickness of the vapor blanket varies with the leaf size. In this way the saturation deficit would be decreased, and evaporation and transpiration lowered. Radiant energy may also play an important rôle in causing the differences, because it is greater in the exposed than in the sheltered positions. As the readings were not taken upon all of the trees at the same time, comparisons between species cannot be made except in a very general way.

3. *Temperature*

Numerous simultaneous readings of temperature were made in the shade within the crown and in the sun at the south periphery upon several isolated trees of *Acer saccharum*, *A. saccharinum*, *Tilia americana* and *Fraxinus pennsylvanica*. The greatest differences between the two positions were 2.8° C. at 2:50 P.M. on *Acer saccharum* and 1.8° C. at 1:00 P.M. on *Tilia americana*. Usually the difference was about 1° C. This difference was caused by the stronger light at the south periphery.

4. *Humidity*

Humidity readings were made with cog psychrometers simultaneously within the crown and at the south periphery of the same trees that were used for temperature readings. The greatest differences were found on *Acer saccharum*, 16 percent, at noon. The greatest difference in the case of *Tilia americana* was 9 percent at 2 P.M. The usual differences in the humidity of the two positions was from 1 percent to 2 percent. The greatest factor in causing these differences was the movement of the air. Dense crowns impeded the free movement of the air far more than open crowns, so that trees with dense crowns, as *Acer saccharum*, showed greater differences than trees of open crowns. The greatest saturation deficits were always found on the exposed parts of trees from 1 P.M. to 3 P.M.

5. *Wind*

Numerous readings of wind velocity were taken by hand anemometers, operated simultaneously in the two positions. The ratios of the velocity within the crown to that at the periphery have been determined from several readings on each tree. In *Acer saccharum* the ratio was 1:2.2; in *A. saccharinum*, 1:2.1; in *Quercus macrocarpa*, 1:2.0; in *Ulmus americana*, 1:1.6; in *Tilia americana*, 1:1.4; in *Fraxinus pennsylvanica*, 1:1.4; in *Acer negundo*, 1:1.3.

The amount of air movement within the crown depends upon the openness of the crown. The two extremes in crown density in the above series were *Acer saccharum* and *Acer negundo*. As seen from the figures the least air movement within the crown in comparison to that at the south periphery was found in the former, and the greatest in the latter. When the wind velocity was high or if it came in gusts there was less difference in the air movement within the crown and at the south periphery than when the velocity was low. This is explained by the fact that the leaves and branches were more effective in keeping the wind out of the crown when the wind velocity was low than when it was high. As the wind velocity was not the same when all the readings were made, the ratios of the various trees cannot be directly compared with each other. It is highly probable that if readings were taken on *Acer negundo* under the same velocity as on *Acer saccharum*, *i. e.*, 68.9 meters per minute instead of 58.6, the ratio of wind in the crown to that of the south periphery would be less than 1 : 1.3. In the case of *Acer saccharum* as high a ratio of crown to south periphery as 1: 8.1 was found when the wind velocity was regular and fairly low.

Readings were taken with two cup anemometers on a *Fraxinus pennsylvanica* near Lincoln. The readings were made every half hour from 9:45 A.M. to 3:45 P.M. As the wind came from the northwest, readings were made at the northwest periphery and within the crown. The wind velocity within the crown was found to vary from 32 percent to 52 percent of that at the northwest periphery. At 9:45 A.M. the velocity within the crown was 3.7 kilometers per hour and at the northwest periphery 11.6. At 3:45 P.M. the velocity within the crown was 6.6 km., and at the periphery 12.7 km.

Effects of the Physical Factors

1. *Transpiration*

Method

Branches from the center of the crown and from the south periphery, bearing numerous leaves, were cut under water. These branches were securely fastened by rubber tubing to the base of burette tubes graduated to tenths of cubic centimeters. The amount of water in each tube was about equal throughout the experiment, so that there would be no error due to unequal heads of pressure. The tubes, with the branches attached so as to be upright, were fastened in representative situations in the center or at the south periphery. Readings were usually taken simultaneously in both situations every 15 minutes. The leaf area was measured from prints on Kresko paper by means of the planimeter.

Results

On July 11, 1916, four sets of branches were arranged on a *Fraxinus pennsylvanica* growing isolated in a pasture. The tree had a well-shaped, fairly dense crown. One potometer containing south periphery leaves and one containing center leaves were placed among the leaves at the south periphery about 10 feet above the ground. Two more potometers, one containing south periphery leaves, the other center leaves, were placed within the crown at about the same height as the other two potometers. There was very little wind and the sky was very hazy. The transpirations for periods of 15 minutes and for a total of three hours are given in the following table:

TABLE 2

Transpiration of Fraxinus Pennsylvanica on July 11, 1916

	Time P.M.	Total Loss in Cc.	Loss per Sq. Dcm. in Cc.		Time P.M.	Total Loss in Cc.	Loss per Sq. Dcm. in Cc.
Leaves from south periphery placed at south periphery	1:08			Leaves from center of crown placed at south periphery	1:23		
	1:23	0.5	0.0212		1:38	0.10	0.0054
	1:38	0.9	.0383		1:53	.20	.0110
	1:53	1.2	.0512		2:08	.20	.0110
	2:08	1.3	.0554		2:23	.35	.0194
	2:23	1.45	.0617		2:38	.35	.0194
	2:38	1.45	.0617		2:53	.35	.0194
	2:53	1.4	.0596		3:08	.30	.0166
	3:08	1.45	.0617		3:23	.35	.0194
	3:23	1.45	.0617		3:38	.55	.0304
	3:38	1.35	.0574		3:53	.45	.0248
	3:53	1.3	.0554		4.08	.35	.0194
	4:08	1.15	.0488				
Total	3 hrs	14.90	.634		2 ¾ hr	3.55	0.1962
Leaves from south periphery placed at center of crown	1.08			Leaves from center of crown placed at center			
	1:23	.45	0.0175		1:23		
	1:38	.55	.0216		1:38	0.20	0.0087
	1:53	.65	.0254		1:53	.25	.0110
	2:08	.75	.0293		2:08	.25	.0110
	2:23	.80	.0313		2:23	.35	.0155
	2:38	.90	.0352		2:38	.30	.0132
	2:53	.95	.0372		2:53	.40	.0177
	3:08	1.00	.0392		3.08	.40	.0177
	3:23	1.05	.0411		3:23	.40	.0177
	3:38	1.10	.0431		3:38	.40	.0177
	3:53	0.90	.0352		3:53	.35	.0155
	4:08	0.90	.0352		4:08	.35	.0155
Total	3 hrs	10.00	.3913		2¾ hr	3.65	.1612

The losses of the south periphery leaves were from 3 to 6 times as great as those from the center leaves when placed in their native situations. It is interesting to note that the south periphery branch in the center of the crown lost more water than the center branch at the south periphery. This may be due to several causes; probably the stomata in the leaves of the center branch closed when exposed to the sun (but other experiments indicate that this was not the case), or the center leaf may have been transpiring up to its full capacity. The south periphery leaf had greater capacity for transpiration than the center leaf, because of its greater amount of solid matter and chloroplasts. Graphs for the two potometers of center leaves give evidence by their parallelism for this view, indicating that the center leaves placed in the center are transpiring at almost full capacity. Sampson and Allen (29) account for the greater transpiration of the sun leaves, because they have from 20 to 60 percent more stomata. Hesselman (23) accounts for the increase in transpiration in his statement that the leaf surface being equal, plants transpire more as they have greater development of palisade. Bergen (4) explains the greater transpiration in the sun leaves by their greater activity, by their greater thickness affording a larger interior evaporating surface, and by their larger bundles and stems which would transfer the water more quickly. These graphs also show by their abrupt changes that the center leaves are more responsive to the environmental factors than the south periphery leaves. This is explained by the greater amount of protective material, as thicker cuticle, greater thickness of the leaf and more solid material in the south periphery leaves.

On July 22, 1916, a clear, hot day, with a light south breeze, three sets of branches were used in an experiment on an isolated *Ulmus fulva* Mich. Each set contained one potometer of a south periphery branch placed at the south periphery, and one potometer of a center branch placed at the center. The sets were run from 1¼ hours to 2¼ hours, readings being taken every 15 minutes. The greatest differences in the water loss between the south periphery and center leaves occurred in the first set where in 1½ hours the south periphery leaves lost 1.956 cc. per square decimeter, while the center leaves lost 0.1614 cc. per square decimeter, a ratio of about 12 : 1. The least differences were in the third set, where the south periphery leaves in 2¼ hours lost 3.10 cc. per square decimeter, while the center leaves lost 0.638 cc.

per square decimeter, a ratio of about 5 : 1. As the readings for the third set were made in the morning and those of the first set in the afternoon, the difference in the ratios of the two sets are most likely due to the lower humidity, higher temperature and stronger light, causing greater differences between the center and south periphery during the first experiment.

The differences in the transpiration of *Ulmus fulva* leaves is about twice as great as the differences in *Fraxinus pennsylvanica* leaves of July 11. This greater ratio between the exposed and sheltered leaves in Ulmus is partly due to weather conditions. On July 11 the temperature was lower, the humidity higher, and the sunlight was less bright than on July 22. The physical factors in the center and at the south periphery were therefore more alike.

On June 23, 1916, a cloudless, warm day with a light breeze, an experiment was performed on a well-formed isolated *Acer saccharinum*. Two potometers of south periphery leaves were prepared, one was placed at the south periphery, the other at the center. A potometer of center leaves, also, was placed at the south periphery. At the end of 50 minutes readings were made and the positions of all potometers were changed from south periphery to center or vice versa, and allowed to run 50 minutes after about 5 minutes for adjustment had been allowed.

The potometers, containing south periphery leaves, placed at the south periphery, lost 10.5 cc. and 11.95 cc. When these were moved to the center of the tree the losses were 3.95 cc. and 2.85 cc., respectively. The center leaves lost 5.4 cc. at the south periphery and 1.2 cc. in the center. The temperature at the periphery of the tree was practically the same during the 105 minutes. The evaporation from Livingston's porous cups was 4.6 cc. in 50 minutes at the south periphery and 3.4 cc. in the center.

The amount of water lost by transpiration is increased from about 3 to over 4 times when the potometer is changed from center to the south periphery. The small differences in temperature and evaporation in the two positions compared to the great differences in transpiration show that plants, compared with mechanical apparatus, are more sensitive to environmental factors. Comparison cannot be made between the three potometers in this experiment as the leaf area was not measured. Comparison can be made only between the positions of the same potometer.

2. *Surface Area and Lobing*

In nearly all cases the leaves from the center or from the base of the crown were larger than those from the south periphery or apex. The greatest differences were found in the second crop of leaves during the season on forest forms of *Tilia americana*, in the first crop leaves of isolated *Fraxinus pennsylvanica* and in the first and second crops of leaves of isolated and forest individuals of *Quercus macrocarpa*. The production of a second crop of leaves was due to the warm weather in June following a cold spring. The least differences in surface extent were found in the isolated *Tilia americana* and *Acer saccharum*. Usually the leaves from the exposed positions were more deeply and narrowly lobed, and more prominently toothed than the leaves from the protected positions. The lobing of the south periphery and the apex leaves of *Acer saccharum* was less deep than in the center or base leaves.

3. *Green and Dry Weights: Water Content*

Two methods were employed in determining the green and dry weights and the areas of the leaves weighed; one by means of the Ganong leaf area cutter, the other by weighing entire leaves and then determining their area by means of the proportional weights, using solio paper for the leaf prints. Sufficient material was used in each method so as to render the error negligible. The leaves were always collected late in the afternoon. The green and dry weights per square decimeter of leaf surface and the water content are given in the following table:

In every case the green and dry weights were lower, and the water content higher, in the shaded than in the sunny positions. The ratio between the weights is greater in the dry weights than in the green weights, showing that more solid material was laid down in the leaves where the light and other factors were more intense. The highest water content was found in the shade leaves of *Acer saccharum*, *A. saccharinum* and *Fraxinus*, while the lowest was in *Quercus alba* and *Q. rubra*. The greatest differences in water content between the sun and shade leaves were found in *Fraxinus* and *Acer saccharum*, while the smallest occurred in *Quercus rubra* and *Q. alba*. According to the amount of dry material in the leaves at the south periphery or apex the trees fall into the following order: *Fraxinus* 1.639 g., *Q. macrocarpa* 1.272 g., *Q. rubra* 1.190 g., *Q. alba* 1.173 g., *Tilia americana*

TABLE 3

Green Weight, Dry Weight and Water Content of Leaves from the Center and South Periphery of Isolated Trees, and from the Base and Apex of Forest Trees

	Position of Tree	Green Weight		Dry Weight		Water Content		
		Grams per Sq. Dcm.	%	Grams per Sq. Dcm.	%	Grams per Sq. Dcm.	% of Green Wt.	% of Dry Wt.
Acer saccharum (isolated)....	Center..	0.835	46	0.354	38	0.481	74.6	135.9
	So. Per..	1.760	100	0.937	100	0.823	52.1	87.9
Acer saccharum (forest)......	Base....	0.878	47	0.361	35	0.517	58.8	143.2
	Apex...	1.882	100	1.029	100	0.853	45.4	82.9
Tilia americana (isolated)...	Center..	1.078	58	0.038	51	0.698	64.8	183.7
	So. Per..	1.861	100	0.745	100	1.116	59.9	149.8
* *Tilia americana* (forest)....	Base....	0.745	29	0.223	20	0.522	70.1	234.1
	Apex...	2.589	100	1.114	100	1.475	56.9	132.4
Quercus alba (forest)........	Base....	1.354	74	0.817	70	0.537	39.7	65.7
	Apex...	1.825	100	1.173	100	0.652	35.7	55.6
* *Quercus alba* (forest)......	Base....	1.276	58	0.467	47	0.809	63.4	173.2
	Apex...	2.186	100	0.997	100	1.189	54.4	119.2
Quercus rubra (forest).......	Base....	1.458	63	0.699	58	0.759	52.1	108.5
	Apex...	2.331	100	1.190	100	1.141	48.9	95.9
Quercus macrocarpa	Center..	1.469	66	0.579	46	0.890	60.7	153.8
(isolated)..............	So. Per..	2.227	100	1.272	100	0.955	42.9	75.1
Ulmus americana (isolated)..	Center..	0.906	71	0.309	55	0.597	65.9	193.2
	So. Per..	1.274	100	0.560	100	0.714	56.0	127.5
Fraxinus pennsylvanica	Center..	1.428	59	0.467	29	0.961	67.3	205.8
(isolated).............	So. Per..	2.440	100	1.639	100	0.801	32.8	48.8
Acer saccharinum (isolated)..	Center..	0.723	60	0.229	42	0.494	68.3	215.9
	So. Per..	1.211	100	0.546	100	0.665	54.9	121.8

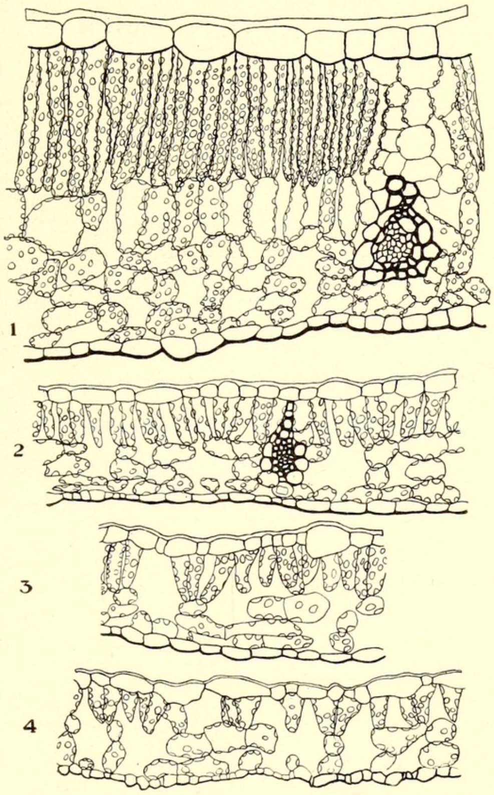
* Second growth leaves of the season.

1.114 g., *A. saccharum* 1.029 g., *Ulmus americana* 0.560 g., *A. saccharinum* 0.546 g. The relation of this sequence to tolerance is noteworthy. The green weights of the leaves from the same position do not show so much relationship, but *Fraxinus*, *Q. rubra* and *Q. macrocarpa* weighed most, while *Ulmus* and *A. saccharinum* weighed least.

Two crops of leaves were produced by many trees during the growing season of 1915. The first crop appeared under cold and humid conditions. The second crop developed about June 25 when the warmer and drier summer weather had arrived. In the latter part of August the first crop of leaves showed a much lower water content than the second crop. The total green weight of the base leaves of the second crop was less and of the apex leaves greater than that of the first crop. The explanation of this probably is that the new base leaves were developed under lower light intensity caused by the shade of the first leaves; while the new apex leaves appeared when the light intensity and the evaporating power of the air were greater than when the first crop developed. In the former case less solid material, and in the latter, more solid material would form in the leaf cells.

4. *Comparison of Leaf Structure*

The detailed microscopical study and measurements of the leaf structure of various trees are summarized in the following observations for each species. This detailed study was made upon cross sections of from five to ten representative leaves from each position of the trees.



All figures are made from photographs of camera lucida drawings of sections of leaves. The leaves were taken from the various positions indicated below. Except as indicated, all material was from the vicinity of Minneapolis, Minn.

Figs. 1–4. *Acer saccharum.* Fig. 1, Isolated tree. Leaves from south periphery. Fig. 2, Isolated tree. Leaves from center of crown. Fig. 3, Forest tree. Leaves from base. Fig. 4, Forest, seven-year-old tree. Leaves from base.

The trees were selected carefully so as to secure specimens typical of the species. Permanent mounts of these sections were made by the paraffin process. Care was taken so that the sections were cut from the same part of leaves of like age and that the measurements were made in typical parts of the sections so that no error would be caused by the thickening due to fibro-vascular bundles.

Acer saccharum.—The study of an isolated tree showed that the center leaves were on an average 38 percent as thick as the south periphery leaves. This increase was caused mostly by the great palisade development, the thickness of the palisade tissue in the center leaves being about 25 percent that of the south periphery leaves. In the center leaves the palisade made up 38 percent of the total thickness, while in the south periphery leaves it made up 58 percent. The thickness of the sponge tissue and upper epidermis was about one half as great, and the lower epidermis three fourths as great in the center leaves as in the south periphery leaves.

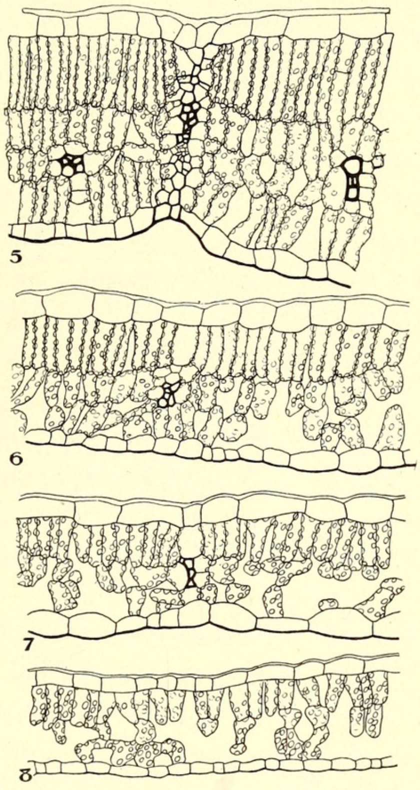
Great differences in structure were found in the leaves from the two positions. The south periphery leaves had two layers of palisade and these layers were far more compact than the single layer in the center leaves. The sponge tissue was more compact, the bundles and water storage tissue more abundant, the cells in the upper and lower epidermis more regular, and the number of crystals greater in the south periphery leaves than in the center leaves.

The weight of the green leaves per given area and the weight of the water-free leaves in the center were 46 percent and 38 percent of the weights at the south periphery. The water content based on green weight of the center leaves was 75 percent, and of the south periphery leaves 52 percent.

Factor measurements showed that the amount of evaporation and the rate of the wind in the center of the tree were respectively 67 percent and 28 percent of the amounts at the south periphery. The light within the crown was 0.0086, while at the south periphery it was 1.00.

Less pronounced differences were found in the leaf-structure of trees growing in the forest. The thickness of the leaves growing at the base of the trees were 44 percent the thickness of the leaves at the apex. The apex leaves were 77 percent the thickness of the south periphery leaves of the isolated tree and the base leaves 92 percent the thickness of the center leaves. The weight of the green leaves and the weight of the water-free leaves of the base leaves were 47 percent and 35 percent the weights of the apex leaves. The light intensity of the base leaves was 0.0076. Leaves were found growing in a light intensity of 0.0024, fifteen centimeters above the ground. The thickness of these leaves was 30 percent the thickness of the south periphery leaves of the isolated tree. The palisade and sponge tissue were very loose.

Tilia americana.—The total thickness of the center leaves of isolated *Tilia americana* in Minneapolis was 52 percent the thickness of the south periphery leaves. This difference was caused chiefly by



Figs. 5–8. *Tilia americana.* Fig. 5, Isolated tree. Leaves from south periphery. Fig. 6, Isolated tree. Leaves from center of crown (Lincoln). Fig. 7, Isolated tree. Leaves from center of crown. Fig. 8, Forest tree. Leaves from base.

the great increase of palisade tissue, the center leaves having only 22 percent as much palisade as the south periphery leaves. The palisade tissue composed 34 percent of the thickness of the center leaves, and 81 percent of the other. The sponge tissue is changed to palisade in the south periphery leaves. There are four layers, usually, of palisade in the latter leaves and only one in the former. The cells in the center leaves are larger, more irregular, more often funnel-shaped, the air-spaces are larger and more numerous, the bundles and water storage cells are more poorly developed, the crystals are less numerous, and the side walls of the epidermal cells are more wavy. The weight of the green leaves from the center was 58 percent the weight of the south periphery leaves, the weight of the water free leaves from the center 51 percent. The water content of the center leaves was 65 percent, of the south periphery leaves 60 percent.

The amount of evaporation and the wind in the center were 77 percent and 65 percent of the amounts at the south periphery. The light intensity in the center was 0.0353.

The center leaves of an isolated tree examined in Lincoln had thicker leaves than the isolated tree in Minneapolis, although the south periphery leaves were thinner. As the light intensity in the center was 0.115, and the evaporation 59 percent that of the south periphery; it seems probable that the increase in light intensity accounts for the increase in the leaf thickness.

As in *Acer saccharum* the leaves on forest individuals of this species are thinner than on isolated individuals. The apex leaves of forest trees are about the same thickness as the south periphery leaves of isolated trees, while the base leaves of the forest trees are 69 percent the thickness of the center leaves of isolated trees. The decrease in thickness may be accounted for by the increased humidity and the lower light intensity, 0.00865, in the forest, as compared with the isolated tree.

The second crop leaves from the base of the forest individuals were thicker (31 percent) than the first crop while the apex leaves were thinner (17 percent). The weight of the green leaves and the weight of the air-dried leaves at the base were 29 percent and 20 percent that of the apex leaves per given area. Although the difference in the thickness of the first and second crop apex leaves was only 17 percent, the structure of the second crop leaves was far more mesophytic as seen in the amount of air space, number of bundles, and water storage cells.

Quercus macrocarpa.—The center leaves of a well-formed, typical isolated tree were 61 percent of the thickness of the south periphery leaves. The increase in thickness was due chiefly to the increased development of palisade tissue. The amount of palisade in the center leaves was 37 percent of that in the south periphery leaves. The amount of sponge in the center leaves was over twice as great as in the south periphery leaves, showing that most of the sponge tissue had become palisade. In the center leaves the palisade made up 46 percent of the total thickness; the sponge, 34 percent; the upper epidermis 13 percent; the lower epidermis 7 percent. In the south periphery leaves the palisade made up 75.8 percent of the total thickness; the

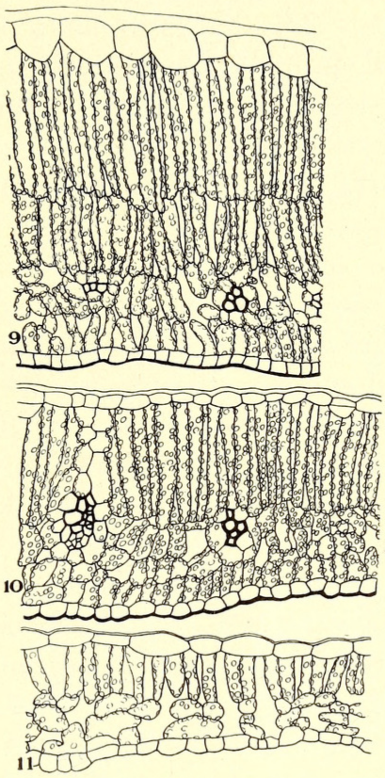


Fig. 9. *Quercus macrocarpa.* Isolated tree. Second growth leaves from south periphery.

Figs. 10–11. *Acer saccharinum.* Fig. 10, Isolated tree. Leaves from south periphery (Lincoln). Fig. 11, Isolated tree. Leaves from center of crown.

sponge 7.8 percent; the upper epidermis 10.6 percent; the lower epidermis 5.8 percent. The weight of the green leaves and the weight of the water-free leaves in the center were 66 percent and 46 percent of those at the south periphery. The water content of the former leaves was 61 percent, of the latter leaves 43 percent.

The amount of evaporation and the rate of the wind in the center were 75 percent and 50 percent of the amounts at the south periphery. The light intensity at the center was 0.148. Another isolated tree, having a more open crown, showed an increase in the south periphery leaves of about 3 percent and in the center leaves of about 12 percent.

Both the south periphery (22 percent) and center (13 percent) second crop leaves of this tree were thicker than the first crop leaves. The increase in the compactness of the palisade tissue in the south periphery leaves was especially noticeable.

The base leaves of forest individuals were thinner than the center leaves of isolated trees. The light intensity in which these leaves grew was 0.075 and the amount of evaporation 46 percent of that at the apex. The apex leaves were slightly thicker than the south periphery leaves of isolated trees. The thickness of the base leaves was 47 percent that of the apex leaves and the thickness of the palisade in the former was 30 percent that of the latter.

Quercus rubra.—An individual of *Quercus rubra* growing in an *Acer saccharum* and *Tilia americana* forest was studied. The lowest leaves, 7.3 m. high, were 67 percent the thickness of the apex leaves, 12.8 m. high. The difference in the amount of palisade in the leaves from the two positions was not so great as in the trees so far noted. The thickness of the palisade in the base leaves was 57 percent that of the apex leaves. In the base leaves the palisade made up 44 percent; the sponge, 30 percent; the upper epidermis, 16 percent; the lower epidermis, 10 percent of the total thickness. In the apex leaves the palisade made up 52 percent; the sponge, 26 percent; the upper epidermis, 15 percent; the lower epidermis 7 percent.

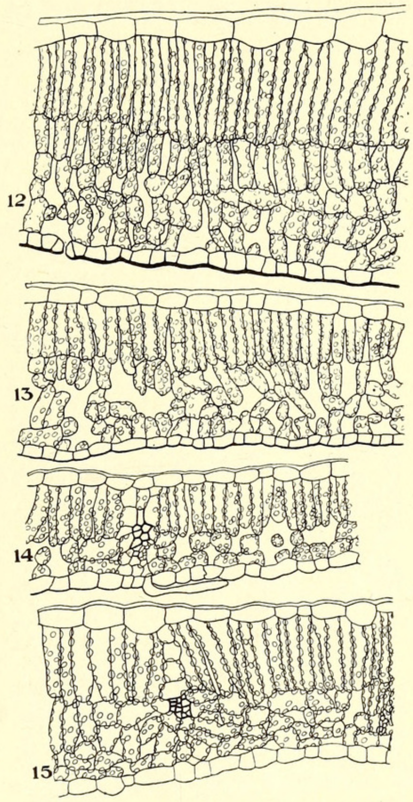
The chief differences in structure were that the apex leaves often had three layers of palisade cells, while the base leaves had two; the palisade was more compact and composed of longer cells, and there was a decrease in the air-space and an increase in the water storage cells and fibro-vascular bundles in the apex leaves.

The weight of the green leaves at the base was 63 percent that of the apex leaves, the weight of the water-free leaves 58 percent. The water content of the former was 52 percent, of the latter 49 percent.

The amount of evaporation at the base was 58 percent that of the apex, and the light intensity at the base was 0.0425.

Quercus alba.—The *Quercus alba* studied grew in the forest very near the *Quercus rubra.* The base leaves, 3 5 m. high, were 64 percent the thickness of the apex leaves 9.2 m. high. The thickness of the palisade in the base leaves was 38 percent that of the apex leaves. The thickness of the sponge and the lower epidermis was less in the latter than in the former. In the base leaves the palisade made up 33 percent; the sponge, 41 percent; the upper epidermis, 15 percent;

the lower epidermis, 11 percent of the total thickness. In the apex leaves, the palisade made up 57 percent; the sponge, 25 percent; the upper epidermis, 12 percent; the lower epidermis, 6 percent of the total thickness.



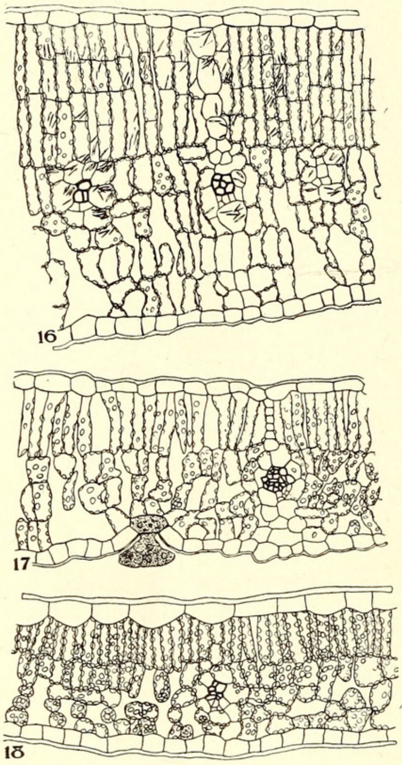
Figs. 12–13. *Quercus macrocarpa*. Fig. 12, Isolated tree. First growth leaves from south periphery. Fig. 13, Figure represents first and second growth leaves from isolated tree, center of crown; and forest tree, base of crown.

Figs. 14–15. *Acer saccharinum*. Fig. 14, Isolated tree. Leaves from center of crown (Lincoln). Fig. 15, Isolated tree. Leaves from south periphery.

As in the leaves already studied the chief differences in structure consisted in the increase in palisade tissue and the greater compactness of the tissue in the apex leaves. From two to four layers of palisade were found in the apex leaves, while only one was found in the base leaves. The cells in the former leaves were more prolate in shape than those in the latter. The apex leaves had greater bundle development than the base leaves. The weight of the base green leaves was 58 percent, the weight of the water-free leaves 47 percent the weights of the corresponding apex leaves. The water content of the former leaves was 63 percent, of the latter 54 percent.

The amount of evaporation at the base was 57 percent that of the apex, and the light intensity at the base was 0.010.

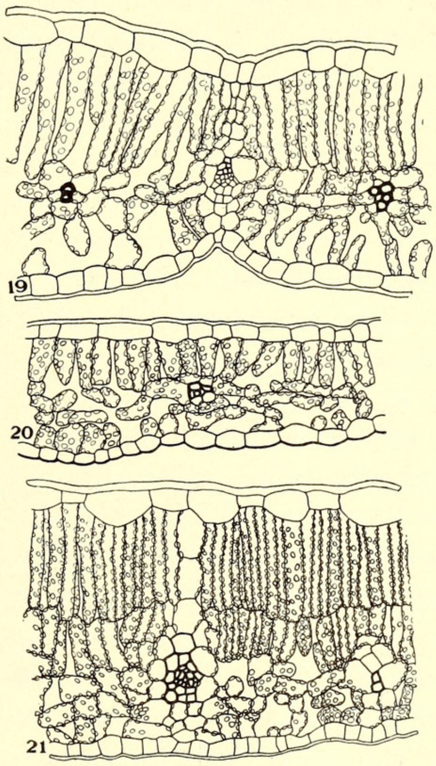
Acer saccharinum.—Isolated individuals of *Acer saccharinum* were studied in Minneapolis and Lincoln. The center leaves of the tree in the former place were 66 percent the thickness of the south periphery



Figs. 16–17. *Fraxinus pennsylvanica.* Fig. 16, Isolated tree. Leaves from south periphery. Fig. 17, Isolated tree. Leaves from center of crown. Fig. 18. *Quercus rubra.* Forest tree. Leaves from base.

leaves. Most of this increase was caused by the palisade as the thickness of the palisade in the former was but 48 percent that of the latter. In the center leaves the palisade made up 39 percent; the sponge, 32 percent; the upper epidermis, 16 percent; the lower epidermis, 13 percent of the total thickness. In the south periphery leaves the palisade made up 53 percent; the sponge, 26 percent; the upper epidermis, 11 percent; the lower epidermis, 9 percent of the total thickness.

The center leaves had one layer of loose palisade while the south periphery leaves had one or two layers composed of larger and more compactly arranged cells. The entire structure of the south periphery leaves was more compact and there was greater development of bundles and water storage cells. The weight of the green center leaves was 60 percent the weight of the south periphery leaves, the weight of the water-free center leaves 42 percent. The water content of the center leaves was 68 percent, of the south periphery leaves 55 percent.



Figs. 19–20. *Platanus occidentalis.* Fig. 19, Isolated tree. Leaves from south periphery (Lincoln). Fig. 20, Isolated tree. Leaves from center of crown (Lincoln).
Fig. 21. *Quercus rubra.* Forest tree. Leaves from apex of crown.

The evaporation at the center was 65 percent that at the south periphery, and the light intensity .038.

The studies of several trees at Lincoln showed that the south periphery leaves of these trees were from 13 percent to 42 percent thicker than the south periphery leaves of Minneapolis trees. The increase was due to the increase of palisade chiefly. The structure of the south periphery leaves from Lincoln was more xerophytic. The center leaves were about the same in both places.

Acer negundo.—The thickness of the center leaves of an isolated *Acer negundo* tree at Minneapolis were 79 percent that of the south periphery leaves. Most of this increase was due to the palisade as it more than doubled in thickness. In the center leaves the palisade made up 33 percent; the sponge, 45 percent; the upper epidermis, 12 percent; the lower epidermis, 10 percent the total thickness. In the south periphery leaves the palisade made up 57 percent; the sponge, 24 percent; the upper epidermis, 11 percent; the lower epidermis, 8 percent of the total thickness. The south periphery leaves had two layers of compact palisade, the center leaves one layer. The amount of evaporation at the center was 67 percent that at the south periphery, and the light was 0.082.

Ulmus americana.—The thickness of the center leaves of an isolated *Ulmus americana* was 64 percent the thickness of the south periphery leaves. The palisade in the former was 45 percent the thickness of that in the latter. In the center leaves the palisade made up 35 percent of the total thickness, the sponge 38 percent, the upper epidermis 16 percent, the lower epidermis 11 percent. In the south periphery leaves the palisade made made up 50 percent of the total thickness, the sponge 26 percent, the upper epidermis 15 percent, the lower epidermis 9 percent.

The south periphery leaves were more compact in structure, the cells were narrower and longer, the upper epidermis more regular, and two layers of palisade were developed as compared with one in the center leaves. The weight of the green center leaves was 71 percent that of the south periphery leaves; the water-free leaves, 55 percent. The water content of the center leaves was 66 percent, of the south periphery leaves 56 percent.

The amount of evaporation at the center was 69 percent; the wind 57 percent the amounts at the periphery. The light intensity at the center was 0.084.

Fraxinus pennsylvanica.—The thickness of the center leaves of an isolated *Fraxinus pennsylvanica* was 63 percent that of the south periphery leaves. The palisade in the former was 38 percent the thickness in the latter. In the center leaves the palisade made up 35 percent the total thickness, the sponge 50 percent, the upper epidermis 8 percent, the lower epidermis 7 percent. In the south periphery leaves the palisade made up 58 percent the total thickness, the sponge 30 percent, the upper epidermis 6.4 percent, the lower epidermis 5.6 percent.

The south periphery leaves were frequently entirely palisaded;

the upper part consisting of three or four layers of very compact cells, the lower part of four or five layers of irregular cells; while in the center leaves there was usually but one layer of palisade. The bundles and water-storage cells, and the crystals were more numerous in the former also.

The weight of the center green leaves was 58 percent that of the south periphery leaves, the weight of the water-free leaves 28 percent. The water content of the former leaves was 67 percent; of the latter, 33 percent.

The amount of evaporation at the center was 53 percent that at the south periphery; the wind, 65 percent. The light at the center was 0.015.

Celtis occidentalis L.—The thickness of the center leaves of an isolated *Celtis occidentalis* at Lincoln was 63 percent the thickness of the south periphery leaves. All of the sponge tissue in the center leaves was palisaded in the south periphery leaves, so the palisade in the former is only 31 percent that in the latter. The differences in structure were again found in the compactness of the cells, the shape of the cells, and the cystolithic cells were more abundant in the south periphery leaves. The light in the center was 0.059.

Platanus occidentalis L.—The thickness of the center leaves of an isolated *Platanus occidentalis* at Lincoln was 61 percent the thickness of the south periphery leaves. The palisade tissue in the center leaves was 46 percent that of the latter. The palisade made up 32 percent the thickness of the center leaves, the sponge 38 percent, the upper epidermis 17 percent, the lower epidermis 13 percent. The palisade made up 42 percent the thickness of the south periphery leaves; the sponge 38 percent, the upper epidermis 12 percent, the lower epidermis 8 percent. The south periphery leaves had more compact tissue, the cells were more prolate, although there was but one layer as in the center leaves. The scalloped appearance of the cross section of the south periphery leaves was caused by the greater bundle and water storage tissue development as compared with the center leaves.

Summary

1. The light intensity, as measured by the Clements photometer, within the crown of 10 common broad-leaved trees was found in August to vary from .0076 of full sunlight in *Acer saccharum* to .1132 in *Quercus macrocarpa.*

2. The evaporation, measured by the Livingston porous cup atmometers, was found to be from $1\frac{1}{2}$ to $2\frac{1}{3}$ times as great at the south periphery as within the crown.

3. The temperature at the south periphery was usually but one or two degrees higher than within the crown.

4. The humidity, measured by cog-psychrometers, was usually from 1 percent to 6 percent higher within the crown.

5. A wind of low velocity caused greater differences in the air movement between the center and the periphery of the crown than a strong wind. The wind was found to be from $1\frac{1}{3}$ to 8 times as strong at the periphery as within the crown.

6. Transpiration experiments showed that the south periphery leaves lose more water per unit area than the center leaves. In *Fraxinus pennsylvanica* the south periphery leaves lost from 3 to 6 times as much as the center leaves; in *Ulmus americana* about 12 times as much. Even when the potometer containing south periphery leaves is placed under similar conditions with the potometer containing center leaves it will lose more water per unit area.

7. The leaves from the periphery of the tree were usually more deeply lobed, more prominently toothed, and smaller than the leaves from the center of the same tree.

8. The water content of the leaves from the center of the tree was always higher than that of the leaves from the south periphery. The amount of dry material per unit area in the exposed leaves bears a relation to tolerance. The dry weight of the leaves of the most tolerant trees is less per unit area than the dry weight of the leaves of the least tolerant trees, as, leaves from *Acer saccharum* contain 1.029 gr. of dry matter per unit area, while leaves from *Quercus macrocarpa* contain 1.272 gr.

9. *The differences in the total thickness between the south periphery and the center leaves on the same tree are usually greater than the differences heretofore reported from leaves of mesophytic and xerophytic forms of the same species.* The leaves from the south periphery have more palisade tissue, greater compactness of structure, thicker epidermis and cuticle than the leaves from within the crown.

This subject, the structural response of leaves of the same plant to measured environmental factors, is so large that this paper can only be considered as an opening wedge into further investigation. Detailed studies are needed on specific aspects, as transpiration, water content, etc.

In conclusion I wish to acknowledge my indebtedness to Dr. J. E. Weaver, who suggested this investigation and assisted in securing a part of the data obtained during the summers of 1915 and 1916. I also wish to express my appreciation of the encouragement offered by Dr. Raymond J. Pool and of the facilities afforded by the department of botany at the University of Nebraska.

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