[Proceedings of the Iowa Academy of Science](https://scholarworks.uni.edu/pias)

Volume 56 | Annual Issue | Article 27

1949

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Differences in Foliar Organization Among Leaves from Four Locations in the Crown of an Isolated Tree (*Acer platanoides*)

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Structural differences among the leaves of a single tree are well known and the literature on this subject is extensive. In most of these papers the tissue study was limited to transverse sections of the blade. Some of them included more or less critical analysis of various environmental factors. A limited number gave some measurements of venation but relatively little attention has been given to the inter-relations of the blade tissues, viewed as working unit. Reference is here limited to a few papers that are of interest in this connection and each of them carries a bibliography of related titles.

Hanson (1) has given a general picture of the varying conditions normally present in the crown of a single tree. He reported in detail on ten species of mesomorphic deciduous trees growing in the North Central states. His analysis of environment included the effects of light, humidity, wind and temperature at different locations in the crown. Structural differences among these leaves are well illustrated. He showed also that on trees normally developing both earlier and later leaves the summer crop was definitely more xeromorphic than that of early spring.

Schuster (4) studied the sun-shade leaves of about twenty-five species of woody plants and dealt both with their tissue differentiation and their vascularization. He found the vein length per unit area was greater in blades having better illumination.

Schramm (3) gave primary attention to the leaf structure of seedlings grown under various light conditions. He included, however, for each species, the sun-shade structure of its adult leaves. Records included structural differences, stomatal counts, as well as data on vascularization. He also tabulated for each species the ratio between its volumes of palisade and spongy mesophyll. This paper has received less recognition than it merits.

Thompson (5) in a preliminary paper described experiments involving the shading one bud each of opposite pairs on the branches of *Cornus florids rubra* and *Acer platanoides*. She used four degrees of shading with one set of buds, leaving the others of the experimental pairs to develop normally. Because representatives of both grew at the same node, automatic controls were established.

Results were recorded on differences in blade size, tissue development and cell dimensions. The author noted that the number of cell layers in the lamina remained constant for each species, regardless of the degree of shading, but that the degree of cell enlargement at right angles to the plane of the blade was much greater in well illuminated leaves. Other results of these experiments are taken up in a second paper by this author (Isanogle [2]).

Watson (6) studied critically the effects of controlled environment on mature and developing leaves of *Hedera helix*. The results of his experiments showed the effects of humidity as well as light upon the development and modification of palisade.

The present writer has given some attention to foliar organization and in this connection three papers are noted. One (7) discussed the role of the epidermis in foliage leaves and stressed its functional importance in addition to serving as a platform or support for the cuticle. Another (8) dealt particularly with the relations of the mesophyll-ratio to vascularization for 90 species of dicotyledon leaves, collected near Miami, Florida. A later paper (9) reviewed the problems of translocation in foliage leaves and discussed the frequency, and possible importance, of vein-extensions in translocation.

The present paper examines the foliar organization of leaves from four locations in the crown of an isolated tree (*Acer platanoides*). No attempt was made to evaluate the surrounding of these leaves because a primary objective was an examination of criteria which may be helpful in the comparative study of leaves. This particular species was chosen partly because of its dense crown and also because of the peculiar compactness of its sun leaf.

The material was taken from a vigorous tree near the south end of the west slope on Old Capitol Campus at the State University of Iowa. It was about twenty feet in height, with rather low branches, and was exposed to full sunlight most of the day. The collections included leaves from four stations: A, south periphery, at a height of 14 feet; B, north side, at a height of 12 feet; C, low interior, above lowest branches; D, deep interior, NNE of the center of the crown and about 10 feet from the ground. While the collections included several leaves from each location, special study was limited to one representative leaf from each station. A portion of each was excised from midway in the favorable spread of the blade and these were cut into small rectangles, killed in FAA, imbedded and sectioned 12 μ thick in both transverse and paradermal planes. As usual, a few sections were cut somewhat thicker for

Table 1

Organization of Sun-shade Leaves on a Single Tree (*Acer platanoides*)
(Measurements are in microns)

Leaf Location	Blade Thickness	Upper Epidermis	Total Epidermis	Spongy Mesophyll	Palisade Meso.	Tissue Ratio SEE/P	Vein Spacing IVI	Vein-Ext Spacing VEI	Ratio of VEI/IVI
South	198	22.7	33.5	57.3	106.6	0.85	129	172	1.2+
North	148	22.0	31.3	44.5	72.6	1.04	158	204	1.3
Lower Int.	91	23.6	33.2	26.1	35.4	1.67	183	226	1.2+
Deep Int.	77	23.2	34.2	23.9	22.4	2.57	227	300	1.3

study of tissue relations. The stains used were Rapid Safranin in combination with Delafield's Haematoxylin or Fast Green.

Results

The leaves from north and south periphery averaged nearly the same size but those at interior stations were much smaller, one third to one fourth the area of the outside leaves. Tissue measurements of these several leaves were made as tabulated in Table I. It may be noted that columns 1-6 are factual, while 7-9 include derived values brought out by comparisons among the measurements. Blade thickness ranged from 198 μ for the sun leaf to 77 μ for deep interior, which of course modified the volume of interior tissues.

While the total epidermal thickness was nearly uniform at all stations, there were marked differences between the upper and lower layers. The former averaged about 23 μ in thickness while the latter was only 10 μ. Cells of the lower layer which carried all the stomata were flattened while those of the upper were rounded in cross section and had broad areas of lateral contact between. This layer usually showed evidence of slime content. Of special interest was the relatively thick epidermis on interior leaves.

The mesophyll varied markedly in volume and expression through the series. Typically there are four layers of cells in this zone though modified locally and especially influenced by proximity to larger veins. The peripheral leaves were conspicuously compact while those of the interior were very porous.

The palisade of the sun leaf was marked by extreme elongation of its cells, often over 100 μ in length. A unique feature of this tissue is its compactness, though this is not fully apparent in cross sections. But paradermal sections showed that its angled cells were closely fitted together throughout most of their length. Under dry lenses of compound microscope few intercellular spaces can be seen but under 90x objective many tiny spaces are evident though they occupy a relatively small proportion of the area. Examination of paradermal sections from about 100 species of dicotyledon leaves from scattered geographical areas did not reveal another with like compactness of the palisade.

Palisade cells of the north periphery averaged about 72 μ in length, with spaces well distributed among them. At both interior stations this tissue was greatly reduced and had tapering cells surrounded by air spaces. In the upper interior leaf the palisade cells, 22 μ in length, were slightly shorter than the depth of its upper epidermis.

The lower portion of the mesophyll in peripheral leaves, as seen in cross sections, is distinctly different from the palisade but lacks individuality. There was a marked transition through the series but only the interior leaves possessed typical spongy mesophyll. These differences were even more marked in paradermal sections and it was only by means of these that the agreements among them could be identified. While this tissue decreased greatly in volume through the series, with the thinning of the blade, its percentage of the total thickness was nearly constant (20-30%), and it typically included three layers of cells.

Cells in the uppermost layer of this zone are enlarged, about three times as long, as wide, and oriented nearly vertically. They are closely united laterally but paradermal sections show some spacing between their cells which are partly grouped around openings; this, however, does not interfere with their lateral continuity. This layer lies in the plane of the xylem strands and is a connective between veins and the lower ends of the long palisade cells. In the leaf from north periphery cells of this layer are rounded but united laterally while in the interior leaves the corresponding layer has cells elongated in the plane of the blade.

The two lower layers of the spongy mesophyll have cells somewhat elongated parallel to the epidermis and are definitely united into meshes around larger openings. One reason for the compact appearance of these layers is the small size of the substomital chambers. Interior leaves have a normal "sponge" with the three layers of cells much alike. Paradermal sections show their meshed arrangement with the cells closely united both vertically and laterally, thus favoring movement of materials through this tissue in any direction.

For a number of years this writer has used vein-spacing as an index to the vascularization of foliage leaves (7, 8), and results seem to justify continuation of this plan. For each leaf an attempt is made to determine the mean separation of its minor veins, which usually have a fairly uniform distribution in a given blade, and are most closely associated with the mesophyll. Numerous precautions must be observed in using this method but a careful worker soon gets consistent results. Numerous (20-50) measurements yield a mean which is appropriately called the intervascular-interval. For the leaves here under study the mean spacings were: sun leaf, 129 μ; north periphery, 158 μ; low interior, 183 μ, and deep interior, 227 μ.

In each leaf blade the tissues are organized somewhat in relation to the problems of translocation, particularly in the plane of the blade. For many dicotyledon leaves the combined volumes of epidermis and spongy mesophyll, if divided by the volume of the palisade, yields a quotient (ratio) which is significantly correlated with the vascularization of that leaf (7, 8). These ratios were determined for the members of this series but further statistical analysis was not justified because of the limited sampling. They will be used in a more extensive survey now in progress. Since these tissue relations of the four leaves are of some interest in themselves, they are included in Table I.

Cross sections of most mesomorphic leaves show sheets or columns of colorless tissue, here called vein-extensions, extending from veins to epidermal layers. In such leaves, when associated with smaller veins, they are usually but one or two layers of cells in thickness, seen in transverse section, but show as sheets of cells when the cut lies along and through the vein (figs. 1-3). Their cells have diminished chloroplast content, are enlarged and flattened in the plane of the layer and marginal ones often contain crystals. In *Acer platanoides* they have thin walls, few or no associated mechanical cells, and are closely fitted together. In the sun leaves of this species these vein-extensions are very conspicuous because of the great depth of the palisade zone.

When seen in paradermal sections through the palisade they show a pattern similar to that of the venation below, except that certain minor veins are not represented, since these intrusive veins are invested only by the border parenchyma. From such sections the mean separation of these vein-extensions may be measured in the same manner as the intervals between veins, as given above. For the leaves from the four locations, beginning with south periphery, the spacings of their vein-extensions were: 172, 204, 226 and 300 μ respectively. Some significance may be associated with the fact that the ratio between vein-extension and vein spacing at each station was approximately 1.3 (table I).

Discussion

Differences among foliage leaves are greater than studies reveal. Added sampling, especially from the top of the tree, would extend the range and more precise methods of tissue evaluation would contribute to better understanding of their relations. There is a strong probability that the leaves of a given deciduous tree are never quite adjusted to their own shade. This type of leaf is an organ of limited growth and there can be little change except in cell content after maturity. Watson (6) found some modification of the palisade in mature leaves of *Hedera helix* when exposed to brighter light and drier air but this leaf is very different from that of our deciduous trees. It seems doubtful whether their foliage can be fully adapted to its shadows because two variables are involved, one of which necessarily precedes the other, and maturity quickly follows the period of blade expansion. Only by experiment may their capacity for adjustment be determined.

Other factors favor working out tolerable relations among leaves of a tree top. Leaf development, fortunately, is a matter of weeks rather than days. This tends to level out the effects of variable weather during the growing period. The earlier epoch in leaf development, characterized by cell divisions and the beginnings of organs, while carried out with fairly uniform illumination of all buds, is less modified by light differences. Isanogle (2, 5) found that in all experimental leaves of a species had the same number of cell layers in the blade. But during the later epoch she noted that cell elongation at right angles to the blade was markedly influenced by differences in illumination. This, of course, favored the sunshade differentiations as did also numerous other associated changes in environment. Her experiments, using one bud of a pair and leaving the other as control, indicated also that the major differences in leaf expression are not predetermined by the environment of the bud during its formation the preceding season.

Because tree leaves are extremely conservative organs their elaborate vein-extension development argues for its functional importance. The palisade of such leaves usually involves translocation problems and the upper epidermis adds to this tissue-mass somewhat removed from vascular connections. Repeated experiments with living leaves by various workers in this laboratory show that dilute dye solutions move rapidly from veins, into the border parenchyma and up through the vein-extensions to the upper epidermis. It seems probable that these sheets of living cells aid in translocation to or through nonvascular tissues of the blade. A recent paper by the writer (9) presented preliminary evidence that vein-extensions, a conspicuous feature of most deciduous leaves of our latitude, are much farther apart or lacking in many dicotyledons of warmer areas. Scattered samplings from southern states, tropical and subtropical regions showed a lower proportion of species with these structures.

There seems a need for added designations to cover the varied expressions of the mesophyll even for leaves of one tree. The terms palisade and spongy mesophyll, even with supplementary adjectives, cannot express the transitions involved. Such problems disturb the few, however, rather than the many who look at leaves. Popularly the palisade is readily identified in cross sections of the blade as having elongated cells vertically arranged. If there is any mesophyll remaining it is, of course, the "sponge." Granted that this lower tissue always lacks coherence and individuality in transections, yet negative characteristics are feebly descriptive. However, viewed in paradermal sections, it is revealed as a unified tissue with distinctive specializations, and supposed palisade sometimes turns out to be something else. Spongy mesophyll is usually characterized by having much intercellular space, cells closely jointed laterally and usually elongated and meshed in the plane of the blade. Each of these characters is a variable, and not all may be well developed in a given leaf. For instance in the sun leaf of *Acer platanoides* paradermal sections show that this puzzling lower mesophyll has much intercellular space and that cells of all its layers are meshed in some degree and somewhat elongated, but those of the uppermost layer are vertical in arrangement while in the interior leaves of the same tree they are elongated horizontally, like the other layers. This suggests that direction of elongation need not be diagnostic, otherwise mesophyll of many deciduous trees would all be palisade. One object of this study of sun-shade leaves was to determine the usefulness of the range in expression of a given tissue in identifying its category. If the same layer is vertical in one leaf and horizontal in another does it shift its group or its expression in that group? Even though they do not cover degrees of transition, the terms palisade and spongy mesophyll are full of meaning and much more precise information about them, rather than new words, is the greater need at this time.

Summary

This paper summarizes differences noted among leaves from four locations on one tree. Blade thickness, and that of both palisade and spongy mesophyll, decreased with shading, but the epidermal

Description of Figures

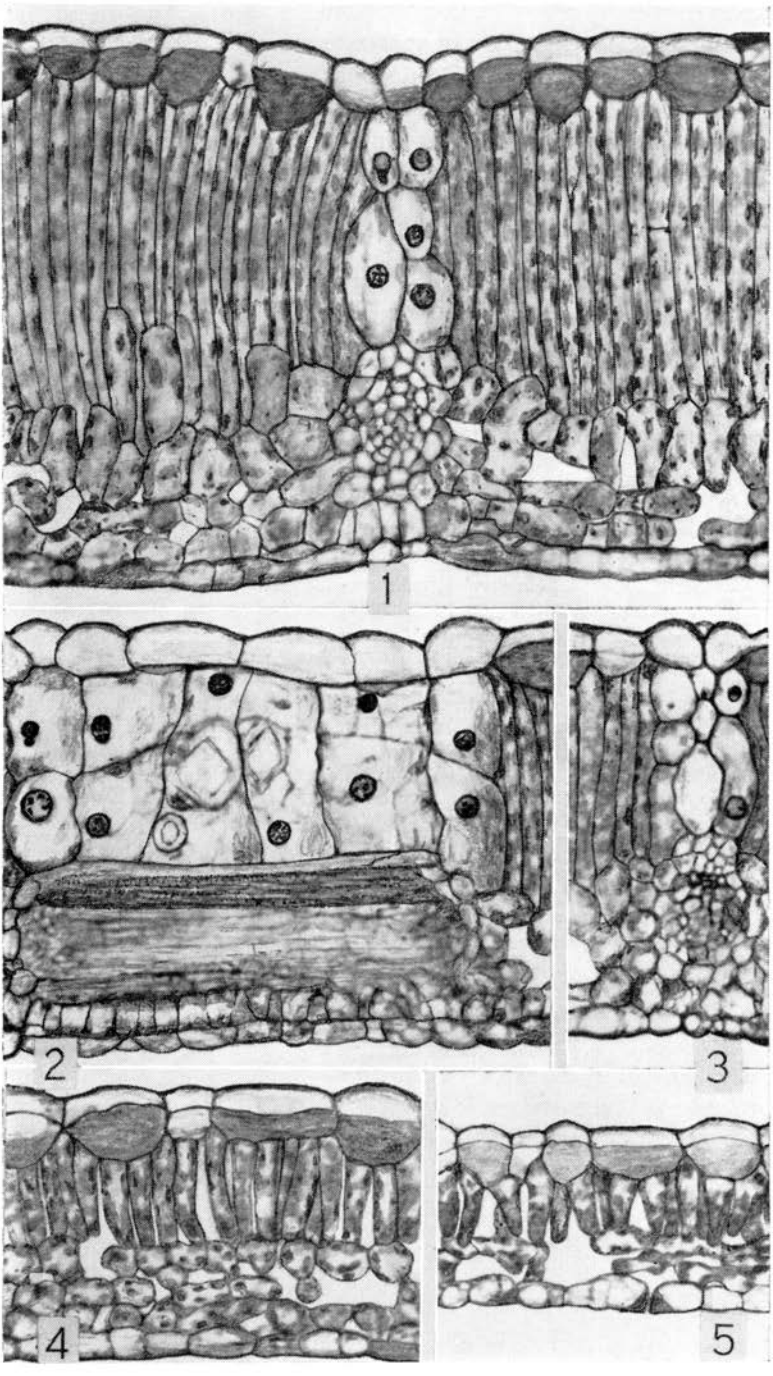
Figs. 1-5. Cross sections of representative leaf blades from four locations in the crown of a tree (*Acer platanoides*). These photomicrographs were all taken with the same scale of enlargement.

Fig. 1. Sun leaf, with long palisade cells.

Figs. 2, 3. North periphery of crown and showing both transverse and longitudinal aspects of the vein-extensions.

Fig. 4. Leaf from low interior.

Fig. 5. From deep interior of crown.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layers were of nearly uniform thickness at all stations. Vein-spacing and the separation of vein-extensions increased with shading, and their ratio at each location was about 1.3. The tissue ratio (combined volumes of epidermis and spongy mesophyll divided by palisade-volume) increased threefold, comparing the sun leaf and that of deep interior. Peripheral leaves were much more compact, with longer palisade cells and less distinctive spongy mesophyll. Interior leaves had typical spongy mesophyll and greatly increased intercellular space. The volume of tissue per unit area of blade was about four times as great in the sun leaf as in deep shade. The vein-extensions were conspicuous in peripheral leaves and doubtless function in translocation. Transitions in both palisade and spongy mesophyll suggest that the study of such series for a given species may aid in the identification and interpretation of its tissues.

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