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THE LEAF ORGANIZATION OF *HEDERA HELIX*

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Hedera helix L. is commonly grown in our area as an indoor ornamental plant and in milder climates it thrives outdoors. Its capacity to endure difficult conditions is well known and quite naturally it has been used extensively in teaching and research. Several studies have related to its leaf form and size under various conditions. Ursprung and Blum explored its osmotic values and their work was later summarized by Ursrung (1929). Watson's recent papers (1942 a, 1942 b) discussed certain aspects of its leaf tissues. The present paper deals with general foliar organization of this plant in comparison with mesomorphic leaves.

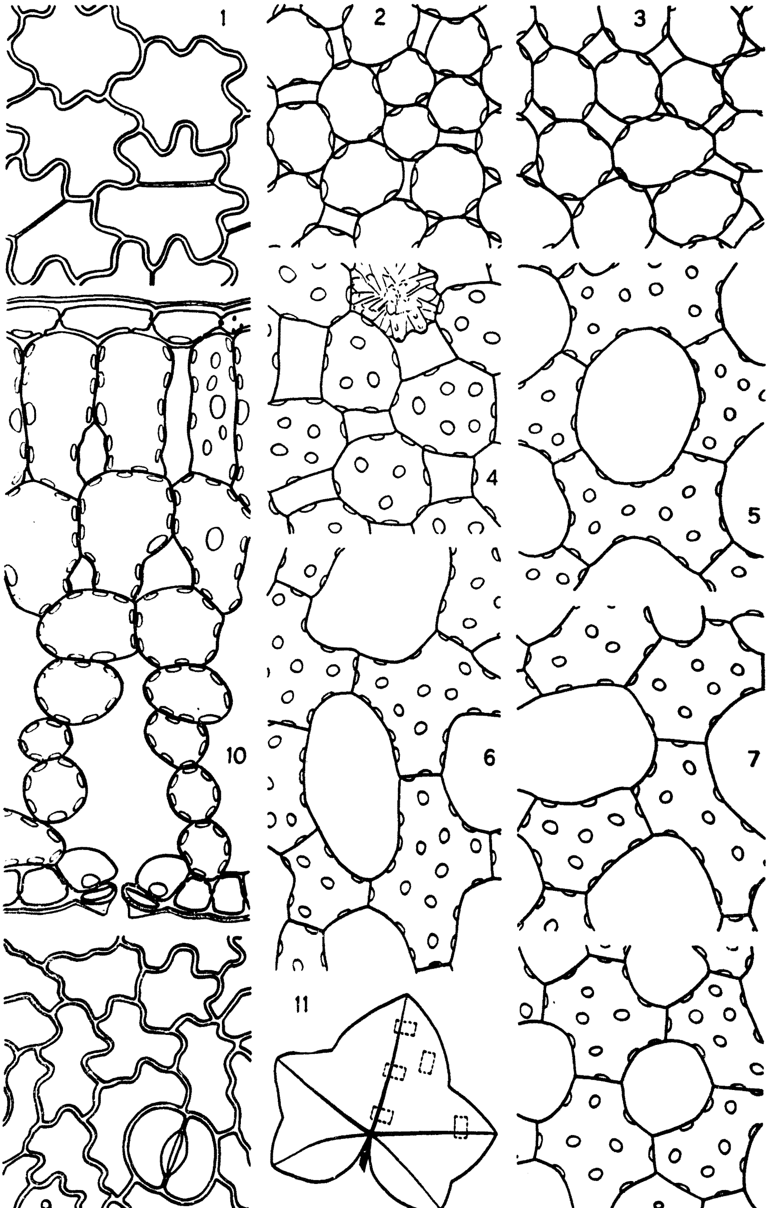
Since *Hedera helix* is very generally grown under conditions of diminished light and low humidity the chief material for this study was taken from a vine growing near the east window of a small office in the Pharmacy-Botany Building at the State University of Iowa. This room was heated by steam and lacked both humidifying and special ventilating devices, consequently the plant, especially during the winter months, experienced wide fluctuations in temperature and humidity. The vine, which was about 10 feet long, was draped about a window aperture only a few inches from the edge of the glass so received fair light part of the day but experienced both low and high temperatures at various times. This particular plant was started from a cutting in 1939 and during the long summer vacations had been kept in the plant house on top of this building.

The leaves surveyed were taken from a region about twenty inches from the base of the main stem; these were still green and vigorous though about three years old. The leaf used for cell measurments was 5.8 cm. long; sample areas for study were taken at five stations from a lateral half of the blade; three were nearer the middle and two towards the outer margin (fig. 11). The tissues were killed in F.A.A. and subsequently sectioned 12 μ thick in both transverse and paradermal planes. Portions of leaves were cleared in lactic acid for general study and free hand sections were useful for comparison of leaves from different plants and for chemical tests.

It is fully realized that with so plastic a form as *Hedera helix* no one plant would reveal the possible range in size, form and structure shown by the foliage of this species. However, the aim of this paper has been an analysis of the general foliar organization and further work deals with the modifications of its leaves under different conditions.

The leaf blade of this variety is entire, slightly lobed, with digitate arrangement of primary veins. Because of the thickness of the blade all veins are imbedded and only the primary and secondary veins form ridges on the surface. Smaller major veins lie within the mesophyll and the entire minor venation is inclosed by the spongy mesophyll. There were no vein-extensions from these veins such as are so con-

 , 11 figs



DESCRIPTION OF FIGURES

Figs. 1-9. Samplings of the nine layers of this leaf, drawn from paradermal sections cut parallel to the plane of the blade.—Fig. 1. Upper epidermis.—Fig. 2. Upper palisade layer.—Fig. 3. Lower palisade.—Fig. 4. Transition layer.—Figs. 5-8. Four layers of spongy mesophyll, in sequence from above downward.—Fig. 9 Lower epidermis.—Fig. 10. Cross section of blade.—Fig. 11. Outline of a leaf. Figs. 1-10 are drawn to a common scale (x361).

spicuous in mesomorphic leaves where they aid both in support and in supply to the epidermal layers (Wylie, 1943). The minor venation was much branched with twigs ending freely in the mesophyll. All lesser veins had each a well developed border parenchyma and a similar layer invested the smaller major veins.

The venation of this leaf is marked by a wide separation of its members and this is associated with a low vein length per unit area of blade. The vein length per sq. cm. for the five stations averaged 35.7 cm. and ranged from 32.4 to 40.8 cm. per sq. cm. It was greatest i· the outer part, least nearer the base of the blade and both marginal stations were higher than the other median one.

The intervascular-interval for this leaf (average of the five stations) was 298 μ. The veins were closest together in the apical area and most widely separated nearer the base, with intermediate separation at other stations. Ten representative Iowa mesomorphic leaves under survey by the writer had an average distance of 99 μ between veins, measured from xylem to xylem. A factor in the wide spacing of veins in *Hedera helix* is the amount and nature of the spongy mesophyll.

The major veins, which occupied 4.8% of the total leaf area, all interrupted the mesophyll in considerable degree and the larger displaced this tissue entirely. The minor veins, completely imbedded in the mesophyll, were without vein-extensions and so did not interfere with the palisade but displaced their volume of sponge. In representative mesophytes the veins displaced about 25% of the mesophyll (Plymale and Wylie, 1944).

The uniseriate epidermal layers have relatively small cells which are also shallow in depth (fig. 10). The upper epidermis was only 12.2 μ thick and slightly thinner than the lower which was 13 μ in thickness. Together they made up only 10% of the blade's thickness. In a recent study of leaf epidermis the writer (Wylie, 1943) reported that for 46 spp/. of Iowa plants with mesomorphic leaves the epidermal layers together averaged 32.5 μ, made up over 20% of the blade thickness, and, due to spaces in the mesophyll, included about 30% of the tissue between veins. For reasons outlined later in this paper it seems probable that the epidermal layers on leaves of *Hedera helix* have a somewhat restricted rôle.

The walls of these epidermal cells were thickened, averaging 3 μ, and all contact walls were freely pitted. The lateral walls were somewhat thinner in the areas of cell contact and with certain exceptions were sinuous especially in the under side of the leaf (figs. 1, 9). The epidermal walls in this species have recently been studied by Watson (1941 b). His work included careful chemical tests and his explanation for the sinuousity of vertical walls is based upon local differences in the composition of the cuticle during leaf development. A feature not mentioned by him in this article is the common occurrence of straight partitions in many upper epidermal cells of our variety. These cross-walls are usually thinner, as if formed later in leaf development. The mature leaf, from which our measurements were taken, had developed such cross-walls in about 60% of the upper epidermal cells (fig. 1) but they were lacking in the lower epidermis. A study of various ages and sizes showed that these cross-walls were lacking in leaves less than 3 cm. long but were always present in the larger leaves examined. These straight cross-walls were more abundant in the thickened areas of blade near larger veins than in the general spread of the lamina.

The cuticle on these ivy leaves was well developed for an indoor plant; on the upper epidermis this layer averaged 1.5 μ and on the lower 1.0 μ. These values were higher than for the average cuticle on outdoor mesophytic leaves of this region (Wylie, 1943). Stomata were limited to the lower epidermis and their number per unit area was greatest in the apical region (223 per sq. mm.), least near the lower margin (180 per sq. mm.) and intermediate in the central area of the blade (184 per sq. mm.). The average for the five stations was 194 per sq. mm.

Over half of the entire lamina was made up of 9 layers of cells but, since the thickness of the blade increased in regions along all major veins, there were areas that had from 10 to 14 cell layers in cross section. Nearer the margins, outside the submarginal veins, this was reduced to seven layers. Using data obtained from many cross sections a chart was prepared and measured giving the distribution of thickness for a mature leaf. Both prepared slides and freehand sections were used and the samplings covered the general area of the blade as well as regions adjacent to major veins of various sizes. The blade surveyed had an area of 24.92 sq. cm. which included the 4.8% dominated by the major veins. Of this total leaf area 0.4% had 14 cell layers (averaging 360 μ thick); 2.4%, 13 layers (315 μ); 3.9%, 12 layers (284 μ); 8.6%, 11 layers (272 μ); 21%, 10 layers (262 μ); 55.0%, 9 layers (239 μ); 2.2%, 8 layers (221 μ); and 1.7%, 7 layers (183 μ). There was thus a range of nearly 100% in total blade thickness for various parts (183μ to 360) and the figures also revealed that about 75% of the blade had either 9 or 10 layers and over half of its area had 9 layers.

The width of thickened areas along larger veins varied in different leaves and also with vein-rank and region of blade. In the central area the zone of thickening averaged about 4.2 mm. wide on either side of the midvein. These strips were wider nearer the base and narrowed towards the apex and along smaller major veins they were narrower and somewhat thinner. In all cases the added thickness was due to extra layers of spongy mesophyll.

In all areas of thickened blade the palisade gradually diminished in thickness and that of the sponge increased with approach towards larger veins. The vertical depth of the upper palisade decreased from 52 μ to 35 μ near the midvein in the central area of the blade and its cells took on the appearance of the normal transition layer, having short, rounded cells with reduced lateral contact. Across this thickened area toward the vein the spongy mesophyll increased from 123 μ to 275 μ in thickness.

The organization of the mesophyll was studied in regions of blade having nine cell layers (fig. 10). Of these the two uppermost layers of mesophyll were palisade, the third was a transition layer with rounded cells (fig. 4) while the remaining four layers were spongy mesophyll (figs. 2-8). The lowest of these cell layers, next to the lower epidermis, was least specialized and should be considered here, and elsewhere generally, as a distinct layer (fig. 8). Walls of all mesophyll cells averaged over 1 μ in thickness which is considerably more than in most mesomorphic leaves of this climate.

The outer palisade (fig. 2) had much longer cells than the inner (fig. 3) and there was contact between adjacent cells. However, they were separated at the corners by spaces which extended the full length of these cells and contacted the upper epidermis. The cells of this outer palisade layer had about 1.57 sq. cm. of lateral contact per sq. cm. of blade, yet they exposed 3.87 sq. cm. of their surface to these intercellular spaces. Their contact surface was considerably greater along walls parallel to a near-by major vein than for walls at right angles to such vein.

The inner layer of palisade had shorter cells with wider spaces so that lateral contact area was reduced to 0.57 sq. cm. per sq. cm. of leaf area and the proportion exposed to spaces greatly increased. Some cells of this zone were not even joined laterally to others of the same layer. The transition layer, between palisade and sponge, was made up of globular cells having constricted connections which further reduced their contact with each other and left a still greater proportion of surface exposed to adjoining space (fig. 4).

The cells of the spongy mesophyll layers were drawn out in the plane of the blade into contact-arms (figs. 5-8). These joined adjacent cells around large spaces which extended from the lower epidermis through the spongy mesophyll and ramified through the palisade zone. There was noted a definite tendency to have the cells of all layers of the sponge superimposed, so that they formed vertical curbs around the well-like intercellular spaces (fig. 10). This arrangement, also gave added firmness to the blade and favored conduction upward and downward from the midplane of the leaf. It was found from cross sections that the average width of cell-contact between adjacent layers of sponge was 10.2 μ. The total length of cell-contact between two adjacent sponge layers per unit area was measured from paradermal sections; after deductions due to tapering arms, the average for fifteen sample areas was 230.5 cm. per sq. cm. of blade. From these figures it was apparent that the area of vertical contact between two layers of sponge cells was about 0.24 sq. cm. per sq. cm. of blade.

Small as this area seems it is nearly twice the average amount of lateral contact between the cells of a given layer of spongy mesophyll for equal area of blade. Such figures reveal the marked porosity of this zone of the leaf, and show that most of the surface of the spongy mesophyll cells borders upon intercellular space.

The individual sponge cells had considerably greater spread in the plane of the blade than those of any other layer. The lateral extent of cells for typical sponge averaged 46.4 μ while the epidermal layers averaged but 33.1 μ and the palisade only 26.5 μ in diameter. The average cell volume for each of the three main zones of the blade could be approximated by means of measurements made from transverse and paradermal sections. These volumes showed less disparity than the above figures on cell diameter suggested because the spongy mesophyll cells are drawn out into contact-arms. Comparing upper epidermal, upper palisade and median sponge cells, their volumes were respectively, as 13, 28.5, and 28.

The total area of lateral contact between cells of the upper epidermal layer was 0.8 sq. cm. per sq. cm. of blade. About 7% of the inner wall of this layer bordered upon the spaces extending upward between palisade cells. For the corresponding surface of the lower epidermis about 56.0% of its inner wall met the spaces between cells of the lowermost layer of spongy mesophyll. Disregarding stomatal openings the percentage of epidermis exposed upon interior spaces of this leaf is greater than casual study suggested.

Attempts were made, without success, to demonstrate conduction from larger veins into the epidermal layers of these leaves. The tests involved leaves differing both in size and age and from different plants. The writer (1943) recently described results of such tests with mesormorphic leaves, using potassium ferrocyanide checked by ferric chloride. This tracer reagent moved quickly from minor veins of those leaves through vein-extensions and into both epidermal layers. In *Hedera helix* there was no evidence of any movement of this reagent into either epidermal layer, nor was its presence demonstrated in any chlorophyll bearing cell. There was prompt conduction of the potassium ferrocyanide solution throughout the vein system but its presence could not be established even in the cells of the epidermal layers over or under major veins. Since this leaf lacks vein-extensions there were no special paths of transfer to the epidermis from the minor venation. In the case of experimental leaves of this species which had been left to absorb the potassium ferrocyanide solution for an hour or more it could be established that the reagent had moved upward in the walls of mesophyll cells located over minor veins and had entered locally into the walls of upper epidermal cells. These experiments confirm findings based upon the study of sections and reveal the peculiar isolation of the epidermal layers from the vascular system. It seems probable that both palisade and epidermis derive their chief water supply from the adjacent minor venation.

DISCUSSION

The leaf *Hedera helix* combines structural adaptibility with a marked capacity for water conservation but lacks strongly xeromorphic structures. It tends towards succulence and probably has pronounced capacity for holding water by adsorption. Its ability to thrive under reduced illumination is also an important factor in the adaptability of this plant.

Morphologically the outstanding feature of this leaf is the spongy mesophyll. This zone included 4 to 10 cell layers in the leaves surveyed and involved 51% to 76% of the blade thickness. Compared with other tissues the spongy mesophyll made up the major portion of blade volume between veins, had the highest percentage of intercellular space, had the greatest cell width (in the plane of the blade), exposed the greatest surface to intercellular space and had the lowest percentage of lateral cell contact. Watson (1942 a) reported that some shade leaves of this species showed no palisade and had only spongy mesophyll.

The unusually wide separation of veins in this leaf is probably made possible by the amount and nature of the spongy mesophyll which has its cells outstretched between minor veins in the plane of the blade. In a recent paper (1939) the writer showed that for nearly 50 species of mesomorphic leaves there was a fairly close correlation between vein separation and the combined amount of sponge and epidermis compared with the amount of palisade. With greater proportions of palisade the veins were closer together while increased amounts of tissues having cells elongated in the plane of the blade permitted wider separation of vascular strands. The application of this principle to *Hedera helix* suggests that lateral conduction through the spongy mesophyll is primarily responsible for the wide separation of veins since the epidermal layers are thin and seem, like the palisade, to depend primarily upon the subjacent mesophyll for water supply.

Ursprung (1929) supported the view that upper layers of this leaf secured water laterally from the larger veins. He found that in the leaves of *Hedera helix* the osmotic values increased markedly from spongy mesophyll to palisade but declined sharply in passing to the contiguous upper epidermis. Because of this relation he questioned the importance of water transfer from mesophyll to epidermis. He noted also that the osmotic values for cells of the upper palisade increased laterally with remoteness from larger veins and reached their maximum in areas midway between major veins. He noted further that these values were depressed slightly over lesser veins imbedded in the spongy mesophyll. This distribution doubtless led to his suggestion that both the epidermis and palisade layers of this leaf derived their "main supply" of water from the "principal" veins (transmitted laterally through these cell layers) and secured an "accessory supply" from the "small veins below."

Since the intervals between principal veins average probably 7500 μ

one wonders why Ursprung did not stress more strongly the possibilities of water supply to the upper part of the blade by way of the underlying minor venation. The osmotic gradient among palisade cells across the areas between major veins would apply helpfully to water movement by either route, whether horizontally from a remote major vein or vertically from a nearby minor veinlet. Practically all lesser veins contact the transition layer below the palisade and no minor vein is separated from the palisade by more than three cell layers. The intervals between minor veins are spanned by the spongy mesophyll which distributes water throughout the central zone of the leaf. While the upper palisade of this leaf, because of its compactness, is well fitted for lateral movement of water there are areas of this tissue that are 2 to 5 mm. from any larger vein, and to reach the centers of these areas water would have to move through 80 to 200 cells. Meanwhile all the underlying lesser veins are within 65 μ of this layer. Another problem relates to the diminished contact between palisade and major veins. The palisade, as noted above, diminished in thickness near larger veins and in these regions its cells are more rounded and so have diminished lateral contact.

As for the upper epidermis it is more nearly cut off laterally from vascular supply than is the palisade and its isolation is increased by whatever of osmotic barrier exists between mesophyll and epidermis. Our experiments with living leaves failed to demonstrate conduction of potassium ferrocyanide from major veins into either epidermal layer and direct movement from underlying minor veins is not possible since there are no vein-extensions in this leaf joining the epidermal layers with the minor venation system, such as are common in mesomorphic leaves. The only important source of water for the epidermis seems to be from the palisade, and Watson's (1942a) recent experiments seemed to show that the upper epidermis not only takes water from the mesophyll but in emergency may take so much as to kill the upper palisade layer.

SUMMARY

Leaf thickness in *Hedera helix* varies greatly in different parts of the blade. Distal and lateral regions are thinner than the median-basal area, and the major veins are bordered by thickened zones which range from 2 to 5 mm. wide on each side of the veins and may be as many as 14 layers of cells thick while the main body of the leaf has only 9 cell-layers. The normal blade thickness thus ranged from 240 μ to 360 μ, with a narrow peripheral strip that was only 183 μ thick.

Under moderate illumination there were two layers of differentiated palisade cells but this zone varies widely under different conditions and may be lacking in shaded plants. The palisade layer in the leaves studied had diminished depth in the thickened areas of blade near major veins, while in the same regions the spongy mesophyll was greatly thickened, increasing from the normal 4 layers to as many as 10 layers of cells.

All lesser veins are imbedded in the spongy mesophyll and the average distance between minor veins was 298 μ. Total vein length and stomatal count were greatest in the outer part of the blade. The epidermal layers are thin, have small cells with thickened walls, and, since there are no vein-extensions from the minor veins to the epidermis in this leaf, the covering layers are peculiarly isolated from vascular supply. Experiments using potassium ferrocyanide did not confirm any conduction of this reagent from the major veins directly into either of the epidermal layers.

The spongy mesophyll makes up the main body of this leaf and its outstretched cells are joined around large spaces. This zone of tissue appears to be primarily responsible for conduction between veins. Cells of the several layers of sponge are usually superimposed thus offering mechanical advantage, and the considerable contact area between cells of adjacent layers of sponge favors conduction upward or downward from the plane of the minor venation. In spite of a tendency towards succulence the leaves of *Hedera helix* have an extensive intercellular space system which reaches every cell of the blade between veins.

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