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CONDUCTION IN DICOTYLEDON LEAVES

ROBERT B. WYLIE

This paper outlines briefly certain aspects of foliage leaves that are related to the form and distinctive functions of these organs. Conclusions from earlier papers on conduction problems of leaves are noted in connection with a preliminary report on the patterns of the minor venation in dicotyledon leaves. In most of these studies on leaves it has been necessary to use serial sections cut both transversely and in the plane of the blade. The latter, or paradermal sections, are favorable for the study of all tissues, seen, as if looking through the blade. They are especially helpful in the interpretation of mesophyll organization and for the measurement of vein spacing. These sections have been cut uniformly 12μ in thickness; a few additional slides with sections cut somewhat thicker and lightly stained are often helpful in the study of tissue relations.

The foilage leaf because of its flattened form and distinctive functions, encounters numerous problems including those related to material transport in the blade. As the plant's most exposed organ, the leaf encounters the full impact of external forces, both physical and biotic, yet is denied the major protective structures found on other plant parts. For all leaves there are the dangers related to wind and hail, sudden temperature changes, water supply, abrupt transpiration demands and the continuous pressure of pathogens and destructive animals. In addition to the functional adjustments to diurnal changes there are seasonal extremes for evergreens and the annual refoliation for deciduous plants.

A prescribed economy of tissue is also imposed upon dicotyledon leaves excepting certain highly specialized types. The normal leaf has definitely limited growth and restricted mass. No opaque coverings are permitted, because of the light relation; for many Iowa leaves the cuticle is so thin that its accurate measurement is difficult. The general flattening of the blade as well as the mesophyll organization are dominated by the demands of photosynthesis; broad leaves intercept more light per mass and the differentiated mesophyll makes the most of a given degree of illumination. Thin leaves conserve weight but at the expense of all storage tissues. Gaseous exchange calls for the exposure of a vast spread of internal surface which in turn involves an appalling waste of water. Stomata are necessary but may admit pathogens. The entire arrangement of parts and tissues necessary for photosynthesis automatically forces excessive transpiration which at best can only be retarded but never stopped. Cork, bark, pith, wood, special storage tissues and various mechanical structures are freely used by stems and roots but are denied to the foliage leaf.

Both because of these restrictions and its expanded surface the leaf requires an elaborate conductive system. The photosynthate, manufactured exclusively by the leaves, must be exported promptly;

this rhythmic activity seems to be carried out in orderly manner and here fluctuations are probably downward rather than upward. But maintenance of the water supply is more critical; while there is a normal expectancy, transpiration demands may increase abruptly and remain at high level as during a succession of hot dry days. The lack of any adequate provision for water storage in the blade calls for a conductive system having a wide margin of safety in order to deal with sudden transpiration emergencies.

The venation is much more elaborate than casual study suggests, partly because attention is naturally centered upon the larger veins. Plymale (2) has surveyed the major veins of a number of Iowa leaves, both with respect to their extent and tissue organization. He found that the major veins system, which includes three (sometimes four) categories of diminishing size, made up only five per cent of the total vein length in these blades. The tissues of larger veins are essentially stem like and while they carry the main conductive channels they have little direct contact with the mesophyll. The major veins also have most of the mechanical tissue and are primarily responsible for the support of the blade.

The minor venation, making up 95 per cent of the total vein length, constitutes the real distributive system. These lesser veins, lacking secondary growth and having greatly reduced xylem, are each invested by a specialized border parenchyma which functions as an intermediary between vascular and nonvascular tissue. Armacost (1) has recently analyzed the extent and importance of this sheath in dicotyledon leaves; it adds greatly to the volume of the vein and increases proportionately the area for contact with the mesophyll cells.

The flattened form of the leaf, in contrast to the radial pattern of root and stem, complicates the conductive system for this organ and involves greatly increased vascularization. The shift from radial to planar organization for an organ of given volume, compels increases in venation as may be illustrated by the following measurements.

The mean thickness for leaves of twenty-two Iowa woody plants was 152μ (4). A blade of this thickness, three inches wide, would have a breadth nearly 500 times its thickness. If now this blade volume, including epidermis, mesophyll intercellular spaces and imbedded veins, were reshaped into a circular cylinder, its greatest diameter would be about one-ninth of an inch, tapering to a point at the outer end. Plymale (2) carried out volumetric measurements for a few Iowa species and found that the imbedded veins and associated tissues, excluding all protruding parts of larger veins, occupied about one-fourth of the blade volume between the epidermal layers. If now the included veins of our hypothetical leaf should all be segregated without change of volume into a single strand it would occupy the central half of the cylinder's diameter, leaving an outer shell of chlorenchyma only one thirty-sixth of an inch in radial thickness. Because the perimeter of this transformed leaf would be only one-

third of an inch the external surface of our compact leaf, if four inches in length, would be less than one square inch, whereas the original blade, counting both sides, had an exposed area of at least 12 square inches. No radial branches would be necessary; this central strand would be its only vein.

In contrast to this situation it might be noted that an average leaf of an American elm had a total vein length 670 times the length of its midrib and for a *Liriodendron* leaf the corresponding ratio was 970. Such figures reveal some of the corollaries involved in the development of broad foliage leaves. If taking such liberties with an ordinary dicotyledon leaf converts it into something suggesting the axis of ancient Psilophytales, it might be recalled that the leaf of *Pinus monophylla* is in size, form and distribution of tissues quite like the hypothetical leaf just described.

The rapid transport of liquids through the venation of a dicotyledon leaf can be readily demonstrated by the use of dye solutions which may color an entire blade in two or three seconds. The writer (3) recently described simple experiments which showed the marked overload that can be carried by even the smallest of minor veins. Mature lilac leaves after being cut across near the base leaving only a slender margin of blade on either side remained alive for months. In these cases sections subsequently cut through the marginal strips showed that they might be only one millimeter wide and carry but a few tiny minor veins, yet they supplied water to an entire blade for the remainder of the summer. Plymale (2) has shown that a single lateral major vein, with all other veins and tissues of the blade transected near its base, could sustain a leaf with little or no death of tissue unless other major veins block the lateral spread of water. While such experiments reveal that the carrying capacity of a major or a few minor veins may be adequate to supply an entire leaf, attention should be called to the fact that once the water was brought into the blade the entire venation system was ready to provide for its distribution through the lamina. Naturally all such experiments lead some to the assumption that the dicotyledon leaf is greatly overvascularized but the writer does not concur in that view, because other factors must be considered, as noted below.

In a preliminary paper (4) he outlined the results of an attempt to find an explanation for the variations in vein spacing among dicotyledon leaves. In the first place it was assumed that a degree of proximity between conductive strands in the blade was necessary because of the slow diffusion through living cells spread out between veins. Liquids move rapidly in the xylem and seemingly with little resistance but this mass movement ceases when materials leave vascular channels. Diffusion through the living cells is relatively slow and the distance between veins must be adjusted to the rate of this extra-vascular transfer in amount sufficient for normal as well as emergency requirements. In the absence of information as to the rate of movement through living tissues in leaves it was further assumed

that the size, shape and trend of living cells between veins might influence the rate of such intervascular movement.

Accordingly, the nonvascular tissues of the blade were measured and divided into two groups; one category included the epidermal layers, the sponge and any other tissues with cells closely united in the plane of the blade. The other category was made up of the palisade together with any other tissues having cells loosely united laterally. Tissues of the former group might favor the transfer of materials between veins; the latter, obviously, would retard such transfer of materials between veins; the latter, obviously, would retard such transport. The ratio between the total volumes of tissue in these two categories for a given blade was found to have a significant correlation with the vein spacing, when averaged for a group of species. For 22 Iowa woody plants the coefficient of correlation between tissue organization and vein distribution was found to be 0.735 ± 06 and for 24 Iowa herbaceous dicotyledons the corresponding value was $0.648 \pm .08$. During the present year a similar analysis of blade tissues for nearly a hundred species of Florida dicotyledons gave a somewhat higher degree of correlation. Such results seem to confirm the judgment that the spacing of strands in the blade is influenced in appreciable degree by the nature of living tissues between veins. In other words, the total capacity of veins for conduction does not alone determine their separation, but the possibilities of that leaf for intervascular transfer must also be taken into account. If this is true the leaves studied yielded no evidence of overvascularization.

The disposition of the larger veins in the blade presents few alternatives; their chief branches are pinnate, palmate or in a few instances "parallel", but the minor venation offers a wide range of patterns. Study of a few leaves may suggest distinctive types but a wider survey shows that they constitute an intergrading series, influenced in some degree by climatic conditions. A majority of Iowa woody plants, and many herbaceous forms as well, have areas of mesophyll which are more or less completely bordered by connected minor veins. Examination of sections shows that almost all of these recognizable boundaries are veins having special tissues, both above and below, which usually contact both epidermal layers. These are of course obvious in any transverse section but in general have attracted little attention. Armacost (1) in his recent paper on the border parenchyma referred to these structures as "vein-ribs", noted also their close association with the border parenchyma and found that they conducted colored solutions upward or downward from the vein. The writer (5) has discussed their relations to the epidermal layers and suggested that when these structures, which he termed "vein-extensions", were close together the epidermis might share in some degree with the conduction of water to meet its transpiration losses. In any event these vein-extensions, when present, offer a degree of mechanical support to the covering layers and may aid in water supply. Whatever their functions they have an important relation to the vein pattern as far as the minor venation is concerned.

In some of our deciduous leaves, and in a lesser proportion of subtropical species, minor veins having these vein extensions form boundaries around limited areas of mesophyll. In *Tilia americana*, (fig. 1) these units may have only the border veins but other areas have been invaded by intrusive veins, branching inward from one or more of the lateral boundaries. Among the oaks, example, *Quercus macrocarpa*, (fig. 2), the bordered areas are larger, the intrusive veins are more numerous, often branched, mutually adjusted one to another and are obviously making an important contribution to the distributive system. In the American elm, *Ulmus americana*, (fig. 3) the pattern is more intricate, with intrusive veins spreading out freely within boundaries that are still fairly definite. Among others, native of other climates, but growing freely in this region, the intrusive veins largely dominate the plan as the unit boundaries become remote and indistinct. This situation is well illustrated by *Morus alba* (fig 4). The vein-extensions of this species are very widely separated and the well organized intrusive vein system is elaborately branched. *Ricinus communis*, (fig. 5), a native of warmer climates, grown here as an herbaceous annual, has large leaves with very wide spacing of the vein-extensions. Its intrusives have spread through the mesophyll in wide stretches of blade, often thousands of microns across. They have established frequent anastomoses in various vein categories and consequently present to the casual observer many aspects similar to those with the simpler venation patterns noted above. In a large proportion of the dicotyledons of southern Florida vein-extensions are completely lacking and the alternative system, now dendroid in type, includes veins of all categories. Of considerable interest is the fact that in all leaves with remote vein-extensions the epidermis is spread out over great areas of blade without contacts other than with the underlying mesophyll; its only service seems to be the secretion of the protective cuticle.

The following table summarizes briefly the chief points relating the venation of these five species:

Names of Species	Figure Number	Vein Spac'g	Spacing of Vein-Extensions	Venation Pattern
<i>Tilia americana</i>	1	124 μ	199 μ	—Polygons, some with simple intrusive veins.
<i>Quercus macrocarpa</i>	2	103 μ	225 μ	—Larger polygons, each with branched intrusive veins.
<i>Ulmus americana</i>	3	76 μ	248 μ	—Polygons dominated by much branched intrusive veins.
<i>Morus alba</i>	4	89 μ	378 μ	—Polygons much larger and each with extensively branched intrusive veins.
<i>Ricinus communis</i>	5	85 μ	1581 μ	—The venation between widely spaced vein-extensions is of an elaborate dendroid type.

Brief reference might be made to the word "islet" which is frequently used, even in publications, in description of dicot leaf vena-

tion. In a general way the term has been applied to areas of blade which are more or less completely surrounded by veins. It has also been applied to polygons having intrusive vein patterns of varying degrees of complexity. Since the term is difficult of definition, except in its simplest expression (areas of mesophyll without intrusive-veins that are bordered by connected minor veins having vein-extensions), its usefulness is limited, and unfortunately, few examples can be found that fit the definition. For these reasons the "islet" concept is not useful in the interpretation or description of vascularization. For such purposes the measurement of total vein length per unit area is fully acceptable; this method has been used by many critical workers and, with certain restrictions, gives significant results. The word "islet" however as a descriptive term should be discontinued or limited to the one type of vein arrangement.

The writer, on the basis of principles discussed above, has attempted to use vein-spacing as a measure of vascularization. Working with paradermal sections the intervals or spaces between veins may be readily measured. Of greater significance in this connection is the spacing of minor veins since these are differentiated late in ontogeny and are in some degree adjusted to the mesophyll pattern of that particular blade. Studies now in progress seem to further validate this method when used with leaves having both sponge and palisade well differentiated.

SUMMARY

This paper outlines certain problems of the foliage leaf that seem related to the distinctive form and functions of these organs, with illustrations from published papers and work in progress.

The flattened form of the blade, compared with a radial organ of like mass, calls for an extended conductive system. Transpiration losses are greatly increased while the porous mesophyll has diminished contact between cells.

Experiments are cited which reveal, for both major and minor veins, a capacity for conductive overload. This has suggested to some that foliage leaves have overvascularization.

Evidence is also recalled that the spacing of veins is restricted to the capacity of intervening living tissues for transfer of materials to and from the veins. This argues against overvascularization.

Measurements of nonvascular tissue for a considerable number of species indicate that the size, form and arrangement of living cells may further or retard the intervascular movement of materials in the blade and thus indirectly influence vein spacing.

In the large it seems clear that the venation of leaves is not governed by their total carrying capacity so much as by the necessity for an elaborate distributive system for servicing the living tissues.

The minor venation of dicotyledon leaves presents a wide range of intergrading patterns. It is shown that proximity and arrangement of veins carrying vein-extensions greatly influence the general disposition of the lesser veins.

For many Iowa leaves (and a smaller proportion of southern types) veins having vein-extensions more or less completely surround small areas of mesophyll. Others have intrusive veins, of varying degrees of complexity, within these areas. The term "islet" has been loosely applied to all types of this series.

Many subtropical dicotyledons have few veins with vein-extensions; these are often far apart, with elaborate venation between. Others have no veins with vein-extensions and the entire venation system is dendroid in pattern, with frequent anastomoses among veins of all categories which insure rapid transfer in any direction in the plane of the blade.

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LITERATURE

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DESCRIPTION OF FIGURES

Drawings of minor venation patterns, made from paradermal sections, at a magnification of 125 diameters; plate was reduced from 14 inches to 4 inches in width for reproduction.

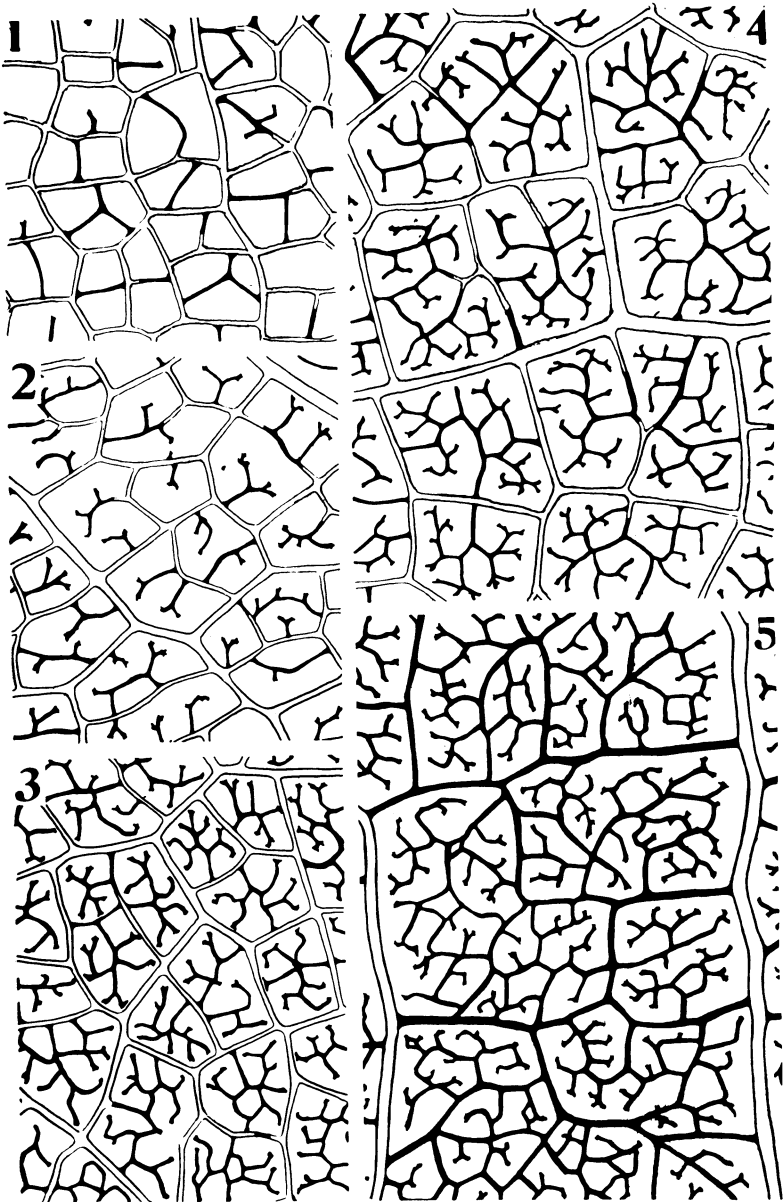


Fig. 1. *Tilia americana*. Fig. 2. *Quercus macrocarpa*. Fig. 3. *Ulmus americana*. Fig. 4. *Morus alba*. Fig. 5. *Ricinus communis*. Veins bordered by lines carried vein-extensions both above and below. Veins drawn in solid black are without vein-extensions.