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SUBMARGINAL VENATION OF FOLIAGE LEAVES

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An earlier paper* gave a brief account of experiments dealing with the conductive efficiency of certain types of vein systems in foliage leaves. By cutting the blade in various ways it was possible to show some of the advantages and also the disadvantages of different types of venation. The results indicated that larger veins, while highly efficient for conduction along their length, may constitute real barriers to movement across them, especially when interrupted by breaks in the veins, which cuts doubtless lead to leakage. On the other hand, regions free from larger veins showed marked capacity for conduction in all directions. The relatively small veins constituting the islet-borders were found to be capable not only of ready conduction in any direction in the blade but were demonstrably capable of carrying a very great overload.

By isolating peninsulas of blade with narrow isthmus at the base one could readily show that the ability of the minor venation to supply water to areas is far in excess of what would be ordinarily required in the normal leaf. Such results revealed the importance of islet-borders both for conduction and for mechanical support. The submarginal regions, relatively free from larger veins, function not only for general conduction but may provide for increased or even reversed flow of materials. This part of the leaf is thus peculiarly fitted to deal with serious wounds or breaks, and also to adapt the leaf to the shifting demands of transpiration as different parts of the blade may through external influences vary in their water loss.

Monocotyledons with their parallel venation and marginal vein present relatively uniform conditions throughout the area of the leaf. Dicotyledons on the other hand generally show marked differences in various parts of the blade due to the tree-like arrangement of the principal veins with its larger branches and smaller twigs. In such leaves there is reduction in size of veins with remoteness from midrib and the submarginal region of the blade becomes the portion of greater vascular uniformity. In

* Wylie, Robert B., concerning the capacity of foliage leaves to withstand wounding. Iowa Acad. Sci., Vol. XXVIII, pp. 293-304; 1922.

many leaves of this group there is a more or less pronounced tendency to combine branches in the peripheral region into a submarginal path for conduction. The outer portion of the leaf has, therefore, a greater freedom of conduction, especially as regards the direction of flow, and probably acts as a general equalizing system between the various parts of the lamina.

With the great diversity in form and structure of Dicotyledon leaf it is not surprising to find that even those possessing similar outline have marked differences in their venation and consequent variety in the submarginal zone. While no attempt is made at this time to present a detailed discussion of these differences, a few examples may suggest the range of differentiation. Towards one extreme of the series is the situation represented by *Ulmus fulva,* or *Betula nigra* in which the major laterals run almost to the edge of the leaf and so break up the submarginal strip. It should be noted, however, that even in such leaves the outer portion of the blade is the part most nearly free from obstructions.

Less strict are the conditions in such leaf as that of *Catalpa bignonioides* where the major laterals are widely separated and stop short of the margin leaving a peripheral plexus consisting chiefly of islet borders with occasional larger connectives. Throughout a large part of this leaf there are seen only the versatile islet-borders of proven efficiency for varied conduction.

In Lilac one finds the slanting major laterals connecting nearer the margin with a peripheral meshwork of veins that are intermediate in size. These anastomotic veins stretch around the outer part of the leaf and penetrate with larger meshes back between the chief lateral veins. Filling the entire area of the blade are, of course, the islet-borders. Lilac thus presents a triple vascular system but avoids large cross veins and never approaches the rectangular type seen in Tilia (l. c., p. 303). The graduated submarginal plexus favors distribution around the circumference and also radially between the larger veins.

Asclepias syriaca possesses a sharply defined submarginal strand located about one-eighth of the distance from the edge of the leaf to midrib. The chief laterals run out nearly at right angles to the central vein. Without giving off important branches these laterals are joined in the submarginal region by heavy outcurving connectives thus building a prominent sinuous vein parallel to the edge of the leaf. Still nearer the margin the minor veins also unite to form a smaller strand roughly parallel to the leaf margin, but much less conspicuous than the principal submarginal vein just mentioned.

In the earlier paper (l. c., p. 301) the writer noted the striking inability of *Aslcepias syriaca* to meet demands resulting from wounds. Excepting in the marginal areas the blades quite uniformly failed to meet critical tests. Slashed longitudinally the strips usually died almost to the base with the exception, of course, of the zone along the midrib and the lateral zones watered by the submarginal strands. In these earlier experiments the outside edge of the leaves was not disturbed and since this limited water loss in the outer zones to one edge, the observed results might have been due in part, at least, to the diminished loss through evaporation from but one margin in these outer strips.

During the summer of 1921 wound experiments were carried on at the Iowa Lakeside Laboratory on various leaves including those of *Asclepias syriaca* and Lilac. Conditions in the marginal strips were made then equally difficult with those of the interior zones by removing first from the outer edge of the leaves a narrow strip of tissue parallel to the margin. The leaves were then slashed longitudinally into roughly parallel zones (fig. 1). Under the circumstances of the experiment each strip should suffer approximately equal traumatic water loss.

Two leaves of *Asclepias syriaca,* exhibiting typical results, are shown in the accompanying plate (fig. 1, d.e.). It will be noted that the middle and marginal strips suffered no death of tissue while all other zones died throughout most of their length. The central zone was, of course, taken care of by the midvein, while the outer strips were obviously well supplied by the submarginal veins.

The marked inefficiency of the intermediate strips deserves attention since they show so little adaptability to the altered demands forced by the conditions of the experiment. Though supplied with water from both the inner and outer ends, and apparently with equal liberty from both ends, these strips seemed unable to conduct water through any considerable distance. Reasons for this failure must be attributed primarily to the rectangular system of major veins in this leaf. The major laterals are nearly parallel while right and left the midvein and submarginal veins fence off the leaf blade into a series of closed rectangles bordered by large strands. However efficient this plan may be in the uninjured leaf, wounds of the type described, forcing conduction across larger veins show that they always, under such circumstances, act as barriers. *Asclepias syriaca* seems then to possess right-angle efficiency but is relatively inefficient in other directions.

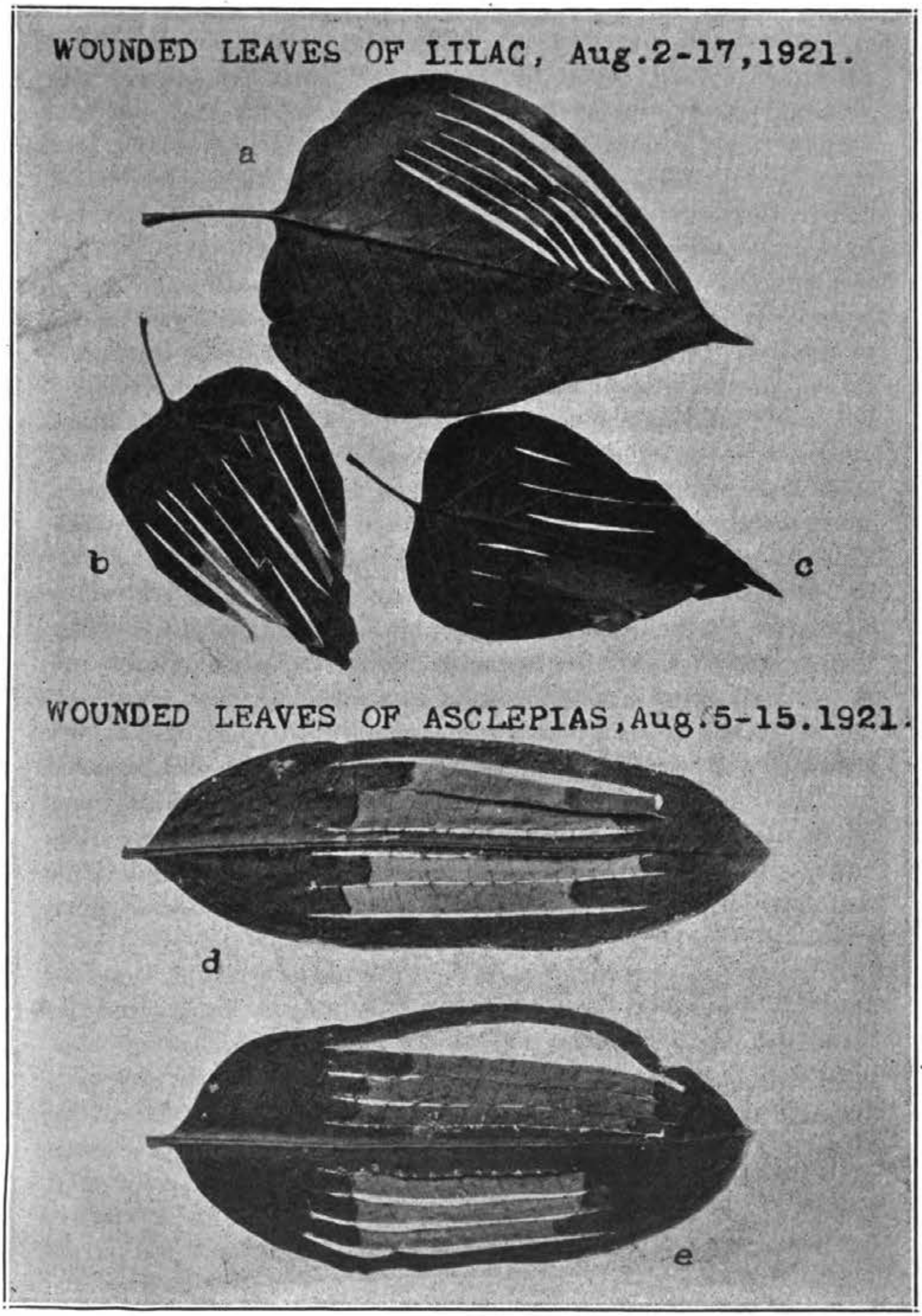

FIGURE 1.

In marked contrast to Asclepias were the results obtained with Lilac. Figure 1 shows a larger partly shaded leaf, (a), and two smaller sun leaves (b c). In all three of these the outer margin was removed with scissors before the leaf was slashed longitudinally with razor, so as to equalize water loss for all strips. Recalling the marked efficiency shown by the leaf of Lilac in earlier experiments (l. c., p. 301) conditions for these sun leaves were made doubly difficult by continuing the slashes through the end of the leaf thus reducing the blade to a series of strips with connection only at the base. The shade leaf (fig. 1, a) suffered no loss of tissue though the slits were long and the strips of tissue quite narrow. Of the sun leaves the one with broader strips (c) suffered no loss of tissue and the other (b) with much narrower zones lost only a little in three or four places.

Comparisons are difficult in the absence of precise environmental data together with facts relative to amount of water loss, etc. But assuming, roughly, proportional loss from wounds and transpiration and like efficiency of stem for raising water, etc., the type of venation seems to be an important factor in wound tolerance.

The development of a submarginal system, unless this is interrupted, adds greatly to the leaf's conductive efficiency. In *Asclepias syriaca* there is an evident transverse-longitudinal organization, the latter represented by the midvein and lateral submarginals. Wounding experiments indicate that this plan is inelastic though doubtless efficient in the normal leaf. In Lilac the oblique laterals, in combination with a marginal plexus of smaller veins, seem to constitute a versatile arrangement very useful in meeting conditions demanding modified flow of materials. It would appear that in the outer part of the leaf a plexus of connecting veins offers advantage over a definite, single submarginal vein.

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