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The Structure and Function of the Border Parenchyma and Vein-Ribs of Certain Dicotylendon Leaves

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THE STRUCTURE AND FUNCTION OF THE BORDER PARENCHYMA AND VEIN-RIBS OF CERTAIN DICOTYLEDON LEAVES[1]

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The border parenchyma has long been recognized as a structural constant in the many kinds of angiosperm leaves. As an unbroken sheath it invests all minor veins and is an intermediary between the conductive channels and the mesophyll. Though the presence of the border parenchyma has long been known, references to it have been casual and its significance has not been adequately appreciated. The uniform presence of this sheath in an organ marked by economy of tissue has invited this attempt to evaluate its place in the foliage leaf as a whole.

Schubert (24) discussed the structure of the border parenchyma in various plant families and recognized two classes of "starch sheaths": those in which there was "nerve parenchyma" associated with the sheath, and others in which it was lacking. The former refers undoubtedly to the vein-ribs described later in the present paper while the latter is the border parenchyma proper. The "nerve parenchyma", he said, was generally present in large leaves and absent in small ones. This generalization was found to be incorect for the sixty species studied in this research. Schubert was more accurate in his suggestion that "it is possible that the nerve tissue assists in the transport of assimilate."

Wylie (29), in describing experiments on the conductive capacity of minor veins, stated that the border parenchyma shares with the veins the transfer of materials. In a second paper (30) he discloses a significant correlation between mesophyll organization and vein distribution. He points out that "increased amounts of palisade tend to force veins nearer together while larger proportions of spongy mesophyll favor their wider separation." He suggests that problems of transfer from cell to cell restrict mesophyll to proximity to vascular supply, and "all tissue arrangements that further or retard conduction between living cells and veins become factors in vein separation." Wylie, in a third paper, (31) disclosed that 58 per cent of the total vein length of ten species carried dorsi-ventral extensions which were conductive.

Sachs (22) discussed the vein system of dicotyledon leaves, mentioned a multi-layered investment around the larger veins, and said erroneously that "the finer veins consisted of bundles which disappear in the mesophyll." DeVries (28), working with sugar beet leaves, noted incidentally that the border parenchyma consisted of a single layer of cells without intercellular spaces, and stated that it was an interconnected system. Haberlandt in three of his publications (13, 14, 15) recognized a "starch sheath" in dicotyledon leaves. He de-

[1]The writer wishes to express appreciation to Dr. R. B. Wylie, Iowa City, Iowa, under whose direction this research was done.

scribed it, but failed to limit it properly though he ascribed to it the function of conduction. DeBary (2) noted that the ultimate vein endings in leaves often bordered on parenchyma which in form approached that of the tracheae on one hand and the typical parenchyma on the other. Stevens (25) stressed the relation of the border parenchyma to the distribution of water and translocation within the leaf. Foster (10) referred to the border parenchyma as a "mestome sheath which transports photosynthate directly to the vascular system."

The leaves studied in this research included sixty species of dicotyledons representing four groups of plants from three decidedly different regions. These groups were: (1) Iowa woody, (2) Iowa herbaceous, (3) California woody, (4) New Zealand woody. The Iowa leaves, which were mesophytic and deciduous, were collected in southeastern Iowa. New Zealand leaves were mostly evergreen and came from North Island, New Zealand. The California species were also mainly evergreen and were collected from the coastal region of California in the vicinity of Los Angeles. Some slides of Iowa leaves and all those of New Zealand and California leaves were loaned by Professor R. B. Wylie, The State University of Iowa, Iowa City.

In collecting material, only mature sun leaves were taken. Portions of leaves were cut into small rectangles and killed in Nawaschin's solution, made up as follows: Solution A, Chromic acid 1.5 grams, glacial acetic acid 10 c.c., distilled water 90 c.c.; Solution B, Formalin 40 c.c., distilled water 60 c.c. Ethyl-butyl was used in dehydration before embedding in paraffin. Both cross and paradermal sections, of each leaf studied, were cut 10 microns thick and stained with Delafield's haematoxylin and safranin.

ANALYSIS OF VEIN CATEGORIES AND GENERAL DESCRIPTION OF THE BORDER PARENCHYMA

A preliminary phase of this study involved an analysis and definition of vein categories in the sixty leaves used. For convenience, leaves were divided into the following categories: (1) major (2) intermediate, and (3) minor. The first category consists of the midrib and its main lateral branches. The second category, intermediate veins, was divided into two groups, the primary and secondary intermediates. The primary intermediates included those veins which in most species act as cross ties between the major laterals. The secondary intermediates comprise the veins which anastomose between the primary intermediates and the minor venation. The minor veins constitute the ultimate divisions of the vein system of a leaf.

Since the relative extent of veins belonging to each category is important, a preliminary study was made of two mesophytic types, *Cercis canadensis* and *Ulmus americana*, to determine the proportion of their veins in each of the vein groups previously defined. The *Cercis* leaf, approximately 132 sq. cm. in area, had about 4 feet of majors; about 13 feet of intermediates; and about 776 feet of minor veins. A leaf of *Ulmus americana*, approximately 111 sq. cm. in area,

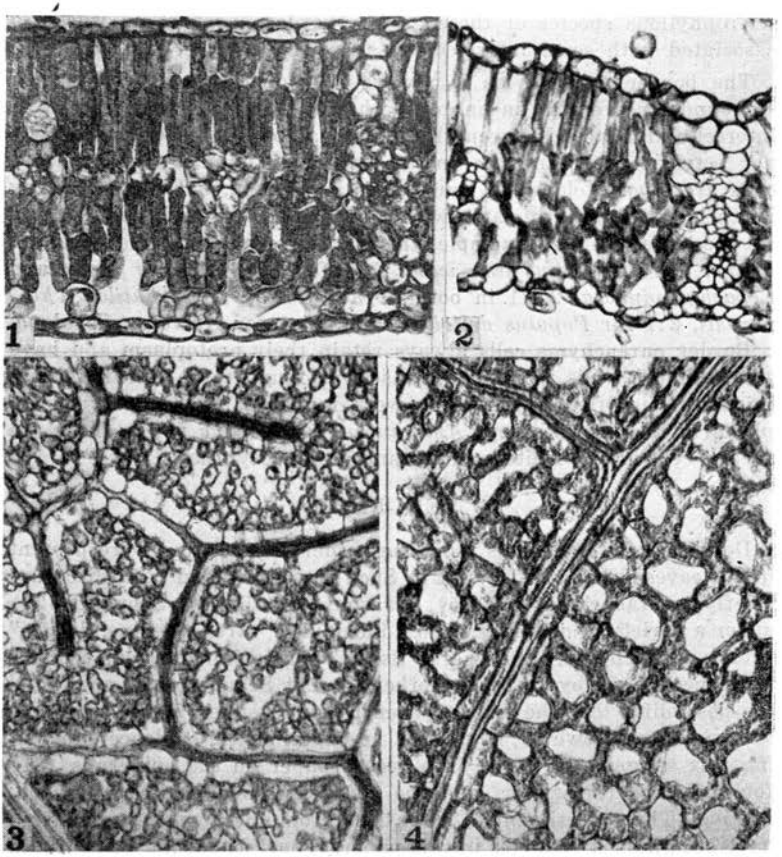

Fig. 1. Cross section of *Populus deltoides* showing one vein-rib which extends to the epidermis and one which ends in the mesophyll.

Fig. 2. Cross section of *Solidago rigida* with vein-rib.

Fig. 3. Paradermal section of *Helianthus grosseserratus* showing the border parenchyma around minor veins and their endings.

Fig. 4. Paradermal section of *Cornus florida* with border parenchyma and large mesophyll spaces in evidence.

had about 4½ feet of majors; about 10½ feet of intermediates; and about 721 feet of minor veins. Since the border parenchyma is associated with all minor veins and some intermediates, the surveyed species showed that the sheath is involved in about 99 per cent of their total vein length.

The border parenchyma invested all minor veins in every leaf studied. In Iowa leaves it was also associated with most secondary intermediate veins, and in a few species with primary intermediates. The broad-leaved evergreens of New Zealand and California usually had border parenchyma around the minor veins only, but in the less

sclerophyllous species of these groups, border parenchyma was also associated with some intermediates.

The border parenchyma is always a single layer of cells which surrounds the vein as an unbroken sheath (Figs. 1-4). There are no intercellular spaces between the individual border parenchyma cells nor between them and the enclosed vascular bundle. These sheath cells are always elongated parallel with the vein, but differ greatly in their length/width ratio within a single leaf and vary widely between species. For example, this ratio averaged 6:1 for *Arctium minus*, 4:1 for *Ulmus americana*, 3:1 for both *Juglans nigra* and *Lepachys pinnata*, 2.5:1 in both *Cornus florida* and *Abutilon Theophrasti*, 2:1 for *Populus deltoides*, and 1.5:1 for *Acerates floridana*.

Border parenchyma cells always retain their protoplasm and have thin cellulose walls which in no case was found to be cutinized, suberized, or lignified. These cells were found to contain few chloroplasts in all species except *Amaranthus retroflexus* where the large sheath cells are definitely important in photosynthesis.

VEIN-RIBS

Dorsi-ventral extensions from the border parenchyma were present in all leaves studied (Figs. 1, 2). Such structures had been discussed briefly by Haberlandt (14, 15), Strasburger (26) and Schubert (24) under a variety of different names, including: "strengthening sheath," "nerve parenchyma," and "nerve tissue." Their function was thought to be mechanical by all these workers except Schubert who suggested the possibility that the "nerve parenchyma" assisted in the transport of assimilate. However, he offered no experimental evidence supporting this suggestion. Wylie in a recent paper on the epidermis (31) found, as did the writer, that the vein-extensions studied were conductive. These dorsi-ventral extensions from the border parenchyma have been named vein-ribs in this paper. They should not be confused with the more massive investments built up around all major veins and also around some intermediates. Such massed tissues are primarily mechanical and consequently not directly comparable to either vein-ribs or border parenchyma.

A vein-rib is one or more cells wide and runs the full length of a given vein segment. Cross sections of leaves showed that in some species these ribs extended to both epidermal layers, but in others to one only, either upper or lower. In several instances they ended in the mesophyll. A vein-rib is always made up of living cells which are without chloroplasts. In general, their walls were thin when an extension was developed from the border parenchyma investing a minor vein. However, the ribs associated with intermediate veins were made up of cells which were usually slightly thickened at the corners. These resembled the collenchyma of the major vein investments, though their walls were not so thick. There were, of course, varying degrees of wall thickening in these cells. In no case was there evidence of suberization, cutinization, or lignification of vein-rib cell walls. These dorsi-ventral extensions then are similar to the border parenchyma

with which they are so closely associated structurally and functionally.

In Iowa leaves vein-ribs usually extended from all veins invested by border parenchyma, except the small intrusive minors. *Baptisia leucantha* and *Populus deltoides* both had well developed ribs extending from intermediate as well as minor veins. In a few herbaceous species, such as *Amaranthus retroflexus*, *Chenopodium album*, and *Lepachys pinnata*, ribs were developed only with the intermediate veins. In the thick New Zealand and California broad-leaved evergreens, vein-ribs were usually associated only with the minor veins. However, in some of the less sclerophyllous species vein-ribs were found with intermediates as well as minors.

COMPARATIVE QUANTITATIVE STUDY

A comparative study of Iowa woody, Iowa herbaceous, California woody, and New Zealand leaves was made (Tables I, II, III, IV). Measurements included: (1) leaf thickness (2) radial border parenchyma thickness (3) vein diameter (4) intervascular interval. Though not given in the tables, the palisade, sponge, upper and lower epidermis were measured for all of the New Zealand and California leaves and for most of the Iowa leaves listed. Each number in the columns of the tables represents a mean of ten to twenty measurements.

TABLE I. IOWA WOODY DECIDUOUS LEAVES
(Data in microns)

	Total thickness	Vein interval	Vein diam.	Border parenchyma thickness
Catalpa speciosa Warder	252.3	107.7	10.1	19.0
Populus deltoides Marsh	220.8	65.4	9.2	17.7
Syringa vulgaris L.	237.5	91.9	15.8	15.4
Prunus Persica (L.) Stokes	131.2	87.5	18.5	15.3
Sambucus canadensis L.	141.9	174.0	12.6	14.6
Cornus florida L.	131.8	175.1	21.0	13.4
Cercis canadensis L.	109.9	129.0	17.8	13.2
Pyrus ioensis (Wood) Bailey	154.4	102.5	11.3	13.1
Prunus Cerasus L.	199.0	104.5	15.5	13.0
Tilia americana L.	138.3	171.0	14.0	12.2
Ulmus americana L.	152.3	102.0	8.1	12.0
Corylus americana Walt.	108.1	142.6	10.5	11.3
Juglans nigra L.	95.8	143.8	10.8	11.0
Quercus alba L.	152.6	95.1	11.2	10.5
Platanus occidentalis L.	136.8	78.6	13.4	10.0
Acer saccharinum L.	99.2	142.8	13.6	9.8
Populus grandidentata Michx.	130.9	111.0	8.6	9.8
Ailanthus glandulosa Desf.	173.4	89.0	9.0	9.7
Cretaegus sp.	125.0	98.0	9.8	8.8
Morus alba L.	144.7	75.6	7.2	8.6
Average	152.7	111.1	12.4	12.4

TABLE II. IOWA HERBACEOUS DECIDUOUS LEAVES
(Data in microns)

	Total thickness	Vein interval	Vein diam.	Border parenchyma thickness
Silphium integrifolium Michx.	343.0	108.0	16.0	25.3
Baptisia leucantha T. & C.	318.8	109.5	16.7	23.7
Silene stellata (L.) Ait. f.	144.0	188.4	20.3	22.4
Lepachys pinnata (Vent.) T. & C.	223.3	140.9	14.3	20.6
Xanthium commune Britton	201.7	138.0	15.0	20.2
Helianthus grosseserratus Martens	274.1	111.1	14.5	19.5
Convolvulus sepium L.	184.0	150.4	11.3	19.4
Oenothera biennis L.	213.0	152.1	14.5	17.6
Solidago rigida L.	180.3	74.3	10.3	17.2
Plantago major L.	262.0	262.0	15.5	15.3
Arctium minus Bernh.	133.1	169.1	11.0	14.9
Viola cucullata Ait.	121.0	163.9	12.9	14.8
Impatiens biflora Walt.	109.7	183.6	18.1	13.0
Apocynum cannabinum L.	124.5	118.2	12.0	12.0
Ambrosia trifida L.	112.0	116.7	8.3	11.1
Taraxacum officinale Weber	118.3	116.3	9.2	11.1
Trifolium repens L.	100.4	121.3	12.0	10.7
Humulus Lupulus L.	138.3	139.3	9.6	10.5
Abutilon Theophrasti Medic.	165.8	96.5	15.0	10.3
Verbascum Thapsus L.	156.0	82.7	8.3	10.1
Average	181.1	137.1	13.2	15.7

TABLE III. CALIFORNIA WOODY PLANTS
(Data in microns)

	Total thickness	Vein interval	Vein diam.	Border parenchyma thickness
Raphiolepsis umbellata Mak.	578.4	260.8	34.1	28.8
Photinia arbutifolia Ait.	353.0	75.3	29.2	23.1
Coprosma Baueri Endl.	398.3	177.5	22.1	20.0
Eucalyptus globulus Labill.	249.0	187.9	28.0	19.9
Quercus agrifolia Nel.	211.5	152.2	16.3	17.4
Veronica salicifolia Forst.	396.4	202.0	34.4	16.9
Quercus douglasii Hand A.	259.6	187.3	30.6	15.8
Rhus integrifolia (Nutt) Benth. and Hook.	518.0	113.2	18.8	14.2
Ceratonia siliqua L.	376.6	187.2	28.1	14.1
Rhamnus californica Esch.	210.1	82.5	14.1	10.1
Average	355.0	162.5	25.5	18.0

TABLE IV. NEW ZEALAND WOODY PLANTS
(Data in microns)

	Total thickness	Vein interval	Vein diam.	Border parenchyma thickness
Coprosma robusta Raoul	461.3	256.8	32.2	25.2
Rubus australis Forst	281.7	203.3	27.7	23.3
Griselinia littoralis Raoul	628.1	205.3	31.8	22.7
Panax arboreum Forst	399.5	260.7	40.4	21.3
Pseudopanax crassifolium C. Koch	734.6	179.8	58.8	19.9
Meryta Sinclairii Seem	688.6	276.0	35.6	19.2
Vitex lucens T. Kirk	220.0	150.6	10.4	18.0
Metrosideros tomentosa A. Rich	353.0	171.7	24.5	16.7
Evonymus sp.	460.3	190.1	36.6	15.7
Elaeocarpus dentatus Vahl	305.8	176.4	20.5	13.0
Average	453.2	207.0	31.8	19.5

No close correlation was found between the border parenchyma thickness and any other measurement, or combination of measurements, for any group included in this survey. As noted earlier by Wylie (30), a feature of the border parenchyma is its relative constancy in thickness, though there may be considerable differences in other leaf tissues. While this uniformity is partly due to its being a single layer of cells, considerable greater range is found in epidermal thickness where also a single layer of cells is involved. It may be stated that the border parenchyma is the most nearly constant feature of leaves for all of the plant groups studied.

The relative volumes of the border parenchyma sheath and its enclosed vein were determined for each of the four plant groups surveyed. The volume of the sheath was always much greater than that of the invested vein. The average border-parenchyma/vein-volume ratio for Iowa herbaceous plants was 11.4:1; Iowa woody, 9:1; California and New Zealand broad-leaved evergreens, 5:1 and 4:1, respectively. In other words, the border parenchyma sheath had 1042 per cent greater volume than the invested minor vein in Iowa herbaceous plants and 800 per cent more in Iowa woody, while in the broad-leaved evergreens of California and New Zealand, this figure was 400 per cent and 300 per cent respectively.

The border parenchyma always has a much greater external surface than has its enclosed vein. The sheath/vein surface ratio averaged 3.1:1 for the Iowa herbaceous leaves: 3:1 in the Iowa woody; 2.3:1 in the California broad-leaved evergreens; and 2.2:1 in the New Zealand leaves. This means that the border parenchyma in these forms had from 122 per cent to 211 per cent greater area for mesophyll contacts than the enclosed vein would have exposed.

PENETRATION OF DYES

Some simple experiments were carried out to determine in a general way the conductive relations of veins, border parenchyma, and vein-ribs. A leaf was removed from the plant and its petiole was cut across under water. After a few minutes the cut end of the petiole with the blade attached was placed in a weak aqueous solution of Iodine green, Eosin, or Trypan red. The transpiration stream soon carried these dyes through the petiole into the tissues of the blade. Several other stains were tried including Aniline blue, Erythrosin bluish, Neutral violet, Methyl green, and Trypan blue, but were less satisfactory than the ones noted above.

The general progress of the absorbed dye could be readily followed. By using a hand lens or low powered objective, it was possible to identify by reflected light those portions of the blade where dye first reached the epidermis. With transmitted light the path of the stain could be traced through other leaf tissues. At frequent intervals after a leaf had been placed in dye, pieces were torn from the blade for study. Their ragged edges generally permittd a direct view into the various leaf tissues, revealing the extent of dye penetration. Free hand transverse sections, if quickly mounted dry, readily showed the dorsiventral course of the stain from the veins, through the vein-ribs, to the epidermis. Movement in a given vein was so rapid that it was impossible to follow the dye with a microscope as it moved lengthwise. However, dorsi-ventral and lateral conduction from the veins could be followed more successfully.

In all leaves used, penetration of dye from major veins into minor veins was very rapid. Immediately after dye was first observed in the major veins, it was also found in many minor veins, particularly those near the apex of the leaf. Paradermal and cross sections of all species confirmed the view that there was little lag in dye penetration from vein to border parenchyma, or between border parenchyma and vein-rib cells to the epidermis.

However, a definite lag was always noticed in the conduction from veins into the mesophyll. Often two or three hours passed between the time when the dye was first noticed in the minor veins, border parenchyma and vein ribs and its appearance in the sponge or palisade. When present the stain was never uniformly diffused, but tended to form clumps within certain cells. Even after an interval of three days there was little stain in the mesophyll of certain leaves, though they were still unwilted.

DISCUSSION

Since so much (approximately 99 per cent in the sample leaves measured) of the total vein length is completely invested by border parenchyma, and since experimentally this tissue has been shown to be conductive of injected dyes, we must assume that the intimate association of border parenchyma and enclosed vein involves also a close functional relationship.

All materials transported by the conductive system reach the leaf tissues through the border parenchyma. Similarly in translocation from the mesophyll, substances must pass through this sheath to enter the vein system. As extensions from the border parenchyma the vein-ribs provide dorsi-ventral conductive paths to or toward the epidermal layers. The fact that they show coloration by dye almost as promptly as the border parenchyma indicates a similarity in structure and function. Thus the border parenchyma and its vein-rib extensions are intermediaries between the conductive system and all other tissues of the blade.

Some longitudinal conduction also may occur through the sheath cells. While transfer through the border parenchyma is perhaps chiefly radial, there are possibilities for conduction along its length. The mere fact that border parenchyma cells, anatomically constructed as they are, are elongated parallel to veins, would insure, in some degree, a longitudinal movement of materials in these cells. The conductive importance of the border parenchyma and vein-ribs has not been appreciated.

The volume of the sheath is always much greater than that of the invested vein. For the groups of plants studied this difference ranged from 300 per cent to 1042 per cent. This volume provides, in some degree, for temporary storage of water and carbohydrates. It is known that photosynthesis may go on at so rapid a rate that translocation of photosynthate cannot keep pace. Under such conditions the border parenchyma might, with other living cells, provide some temporary storage for photosynthate.

On the other hand the border parenchyma in dicotyledons is seldom used for permanent storage of starch. Tests of leaves from fifteen species of Iowa plants including both herbaceous and woody forms, showed little starch in the border parenchyma at 7:00 P. M., following a sunlit day, except in the sheath of *Amaranthus retroflexus*. An appreciable amount in these leaves might be expected since this is one of the few species having many chloroplasts in the border parenchyma. The starch found in those cells may therefore have been derived from the photosynthetic activity of their chloroplasts.

The external area of the border parenchyma is also much greater than that of the enclosed vein. The ratio of border parenchyma/vein surface in the four groups of plants studied ranged from 2.2:1 in the New Zealand broad-leaved evergreens to 3.1:1 in the Iowa herbaceous leaves. Careful measurement of a mesophytic leaf of *Lepachys pinnata* showed that if the border parenchyma were lacking there would not be nearly enough vein surface to equal the total area of contacts between border parenchyma and mesophyll. In this leaf approximately 92.5 per cent of the sheath area was used in mesophyll contacts. Since the area of this sheath was 287 per cent greater than that of the enclosed vein, it is evident that if vein alone were present there would be space for only about 26 per cent of the actual mesophyll contacts with the border parenchyma.

Among the areas of mesophyll contacts there is always some border parenchyma surface exposed against intercellular space. In the in-

stance of *Lepachys pinnata* about 7.5 per cent of the sheath's surface bordered on mesophyll spaces. There could be evaporation from these areas into the intercellular space system. Any contribution to the humidity of these spaces would affect transpiration loss from the leaf. The border parenchyma may act, then, in some degree as a humidifier for the intercellular space system.

Cell turgor is an important factor in the support of foliage leaves. The border parenchyma as a continuous hollow cylinder of living cells is, when turgid, of some importance in a mechanical way. Dulgar (6) referred to this in her paper on the mechanical problems of foliage leaves but did not analyze its importance. As a hollow cylinder of living cells extending along much of the total vein length, the border parenchyma makes the best possible use of its tissue mass and supplements the support given to the blade by the enclosed vascular tissue. The vein-ribs, through their position as extensions toward the epidermal layers have also some mechanical value. When turgid they operate in some degree as vertical plate extensions from the veins at right angles to most stresses in the blade.

The border parenchyma is similar to the mesophyll in a general way and is usually included in that tissue, probably as a matter of convenience. However, critical analysis indicates that functionally it is more closely related to the veins. In contrast to the mesophyll, the border parenchyma usually has few chloroplasts, is always a single layer of cells in thickness, has no intercellular spaces, and is composed of cells which are elongated parallel to the vein. Experiments in this study have revealed that this sheath aids in the conductive responsibilities of the vein which it encloses and supports mechanically; it shares, then, rather more fully in the responsibilities of the vein than in the work of the mesophyll.

The border parenchyma cells, however, do not resemble those of the vein either in structure or arrangement. As living cells, they are not comparable with the lifeless tracheal elements, from which they differ also in form, wall thickness, and wall modifications. With their thin walls, living protoplasts, and included chloroplasts they retain their basic mesophyll organization. While the function of the border parenchyma and tracheal tissue might be considered similar in a general way, since both are conductive, the tracheids and vessels as dead cells obey the laws of hydraulics in their conduction, while the border parenchyma composed of living cells, translocates osmotically, with the main conduction at right angles to the vein length. The sheath cells are also different from the sieve tubes, since all border parenchyma cells have nuclei, never have sieve plates or large perforations in their walls, and always contain a few chloroplasts. They share with the phloem in translocation, but unlike the sieve tubes, all water must also pass through the border parenchyma to reach the blade tissues.

The border parenchyma, then, neither in structure nor in function is a part of the mesophyll which it contacts. It is also structurally wholly unlike the vein which it completely encloses, but *is more like* the conductive tissue in function. All of this stresses the intermediary

character of the border parenchyma and its individuality both in organization and function. Because of its presence about so great a percentage of vein length, and its relative constancy in a wide variety of leaves which differ greatly in size, thickness, and structure, and also because of its conductive and mechanical importance, the writer suggests that the border parenchyma should be considered as an organ of the foliage leaf. Its specializations are probably as distinctive as those of veins, epidermis, or mesophyll.

SUMMARY

1. The border parenchyma invested 99 per cent of the total vein length in the representative leaves that were measured. It forms an unbroken sheath and is primarily an intermediary between vein and mesophyll.
2. Dorsi-ventral extensions, named vein-ribs in this paper, usually extend from the border parenchyma to one or both epidermal layers, or may terminate in the mesophyll.
3. Experiments indicated that veins, border parenchyma, and vein-ribs cooperate in conduction.
4. The border parenchyma exposes from 111 per cent to 211 per cent more surface than that of the invested vein. It was found for a leaf of *Lepachys pinnata* that only 26 per cent of the actual mesophyll contacts could be provided by the vein surface, if the border parenchyma were not present.
5. The border parenchyma has a much greater volume than the invested vein. This increase ranged from 300 per cent to 1042 per cent and may aid to some degree in temporary storage.
6. Since the border parenchyma exposes considerable surface against intercellular spaces, the sheath may act as a humidifier for the space system and thus affect the transpiration loss from the leaf.
7. The border parenchyma is a continuous hollow cylinder of living cells which, if turgid, may be of some importance in a mechanical way in conjunction with the enclosed vein. The vein-ribs have some mechanical value, since, when turgid, they operate, in some degree, as vertical plate-extensions from the veins, at right angles to most stresses in the blade.
8. Since this sheath is uniformly present along the vein length, is relatively constant in a wide variety of leaves which differ in size, structure and longevity, and because of its conductive importance, the writer suggests that the border parenchyma should be considered an organ of the foliage leaf.

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BIBLIOGRAPHY

1. Avery, G. S. Jr. Structure and Development of the Tobacco Leaf. Amer. Jour. Bot. 20: 565-592. 1933.
2. Bary, A. de. *Comparative Anatomy of Phanerogame and Ferns.*

3. Cheesman, T. P. *Manual of the New Zealand Flora.* 1925.
4. Cockayne, L. Die Vegetation der Erde 14: *Vegetation of New Zealand.* 1921.
5. Crafts, A. S. A Technic for Demonstrating Plasmodesma. Stain Tech. 8 (4): 127-129. 1931.
6. Dulgar, D. G. The Mechanical Tissues of Foliage Leaves. The State University of Iowa, Thesis. 1931.
7. Foster, A. S. Investigations on the Morphology and Comparative History of Development of Foliar Organs. I. The Foliar Leaves and Cataphyllary Structures in the Horsechestnut. (*Aesculus Hippocastanum)*, first part. Amer. Jour. Bot. 16: 441-501. 1929.
8. ———— Investigations on the Morphology and Comparative History of Development of Foliar Organs. II. Cataphyll and Foliage Leaf Form and Organization in the Black Hickory, (*Carya Buckleyi var. arkansana*). Amer. Jour. Bot. 22: 88-149. 1935.
9. ———— A Histogenetic Study of Foliar Determination in *Carya Buckleyi var. arkansana.* Amer. Jour. Bot. 22: 88-147. 1935.
10. ———— *Practical Plant Anatomy.* 1935.
11. ———— Leaf Differentiation in Angiosperms. Bot. Rev. 2: 349-372. 1936.
12. Freundlich, M. F. Entwickling und Regeneration von Gefassbundeln in Blattgebilden. Jahrb. Wiss. Bot. 46: 136-206. 1908.
13. Haberlandt, G. Vergleichende Anatomie des assimilatorischen Gewebesystems der Pflanzen. Jahrb. Wiss. Bot. 13: 74-188. 1882.
14. ———— *Physiological Plant Anatomy.* Translation. 282-283, 328-329, 347-348. 1884.
15. ———— Ueber das Assimilations system. Ber. Deut. Bot. Ges. 4: 206-236. 1886.
16. Hanson, H. C. Leaf Structures as Related to Environment. Amer. Jour. Bot. 4: 553-560. 1917.
17. Lenz, C. P. The Intervascular Interval and the Islet Area of Some Monocotyledonous Leaves. The State University of Iowa, Thesis. 1932.
18. McMinn, H., and Maine, E. *Pacific Coast Trees.* 1935.
19. Maximov, N. A. *Textbook of Plant Physiology.* 181-184. 1930.
20. Mer, C. L. The Factors Determining the Resistance to the Movement of Water in the Leaf. Ann. Bot. N. S. 4 (14): 397-401. 1940.
21. Mounts, B. T. The Development of Foliage Leaves. University of Iowa Studies 14 (5). 1932.
22. Sachs, J. von. *Textbook of Botany.* Translation. 563-564. 1875.
23. Schimper, A. F. W. Uebber Bildung and Wanderung der Kohlehyrate in den Laubblattern. Bot. Zeit. 43 (47): 737-752, 43 (48): 753-768, 43 (49): 769-791. 1885.
24. Schubert, B. Ueber die Parenchymscheiden in den Blattern der Dicotylen. Bot. Centralb. 71 (37): 385-395, 72 (40): 13-21, 72 (41): 61-69. 1897.
25. Stevens, W. C. *Plant Anatomy.* 149-154. 1916.
26. Strasburger, E. *Das Botanische Practicum.* 227-231. 1884.

27. Tetley, U. The Development and Cytology of the Leaves of Healthy and "Silvered" Victoria Plum Trees. Ann. Bot. 46: 633-652. 1932.
28. Vries, H. de. Beitrage zur speciellen Physiologie Landwirtschaftlicher Culturpflanzen. Wachstumsgeschichte der Zuckerrube. Landw. Jahrb. 8: 417-499. 1879.
29. Wylie, R. B. Concerning the Conductive Capacity of the Minor Veins of Foliage Leaves. Amer. Jour. Bot. 25: 567-572. 1938.
30. ———— Relations Between Tissue Organization and Vein Distribution in Dicotyledon Leaves. Amer. Jour. Bot. 26: 219-225. 1939.
31. ———— The Role of the Epidermis in Foliar Organization and its Relations to the Minor Venation. Amer. Jour. Bot. 30: 273-280. 1943.