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STUDIES ON THE PHLOEM OF THE DICOTYLEDONS

II. THE EVOLUTION OF THE SIEVE-TUBE

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 169

ANSEL F. HEMENWAY

(WITH PLATE XI AND THREE FIGURES)

In 1909-10 the writer studied the phloem of some 30 species of lower dicotyledonous trees and found that the sieve-tubes in these species had the same general structure as those of the gymnosperms or vascular cryptogams.¹ Some 60 species of higher woody dicotyledons were investigated the next year, and this last year about 90 species of herbaceous dicotyledons and 12 monocotyledons have been studied.

As the literature on the subject of phloem has been rather well reviewed and catalogued recently, an exhaustive review of it will not be given here. In 1908 HILL² gave a good review of the literature from the histological standpoint. MANHAM³ similarly discusses the literature from the physiological side. CHAUVEAUD⁴ in an extensive paper gives a brief review of the literature of phloem.

The material for this investigation was collected in late summer or early fall, the object being to get the sieve-tubes in mature condition, so that they would best show callus formation. For the sake of comparison, several species were studied in seedling condition and in the adult growing condition.

Before proceeding to the discussion of the evolution of the sieve-tube, a few general observations on phloem anatomy may well be mentioned. The distribution of the hard bast in the woody

¹ HEMENWAY, ANSEL F., Studies on the phloem of the dicotyledons. I. Phloem of the Juglandaceae. *BOT. GAZ.* 51:131-135. *pl.* 13. 1911.

² HILL, A. W., The histology of the sieve-tube of angiosperms. *Ann. Botany* 22:245-290. *pls.* 17, 18. *figs.* 13. 1908.

³ MANHAM, S., The conduction of carbohydrates. *Science Prog.* Oct. 1910 and Jan. 1911.

⁴ CHAUVEAUD, G. L., L'appareil conducteur des plantes vasculaires et les phases principales de son évolution. *Ann. Sci. Nat. Bot.* IX. 13:113-438. *figs.* 218. 1911.

dicotyledons is very characteristic for each species and usually for each genus. In many cases it is arranged in bands concentric with the cambium, as in *Acer*, *Populus*, and *Crataegus*; in some cases in groups opposite the large or aggregate rays, as in *Alnus*, *Carpinus*, and *Drimys*; in other cases in irregular patches, as in *Ostrya* and *Celtis*; and finally, in various combinations of these arrangements, as in *Quercus*.

Plate figs. 1-3 show some of these peculiarities of phloem structure. Fig. 1 is a transverse section of *Acer macrophyllum*; the lighter horizontal bands are the hard bast cells; between these are the sieve-tubes and parenchyma cells; while the dark vertical lines are the phloem rays; in the lower portion of the figure the cambium and some xylem are seen. Fig. 2 is a similar view of *Alnus incana*; here we note that the hard bast occurs chiefly opposite the aggregate ray. Fig. 3 is a similar view of *Quercus Garryana*; a large group of hard bast is seen above the large ray in the lower left portion of the figure, while several smaller groups appear here and there in other parts of the phloem.

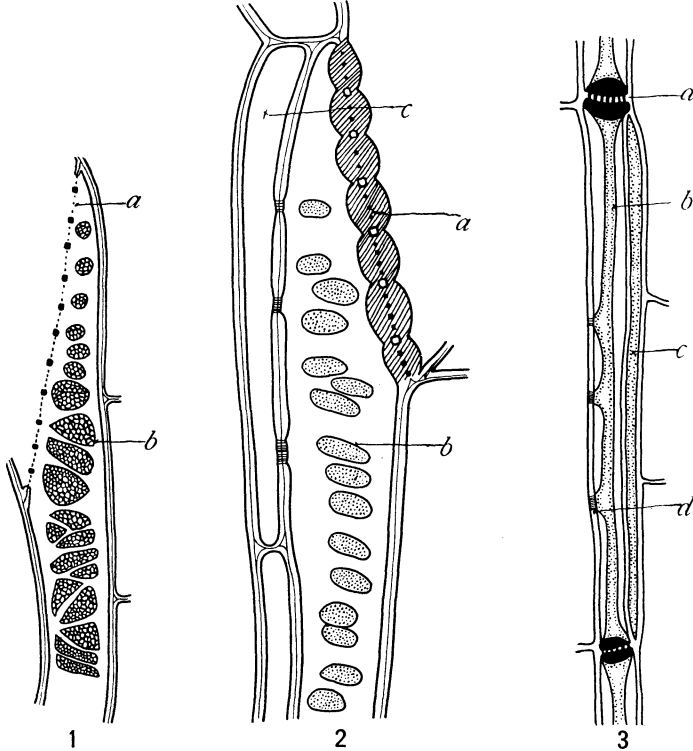
Fig. 4 is a transverse section of the stem of *Ranunculus fascicularis*; the central, lighter portion of the three bundles shown here is phloem. Fig. 5 is a similar view of *Chenopodium album*, and fig. 6, of *Amaranthus paniculatus*. The darker areas just above the groups of large vessels are phloem. This peculiar, scattered arrangement of bundles in a woody cylinder would suggest a possible point of origin for the monocotyledons.

Companion cells are rare if not wanting in many of the lower dicotyledons. It is probable that parenchyma cells play the part of companion cells here.

The end walls of the ray cells in the phloem of some woody dicotyledons show sieve-platelike pitting, but they did not show any callus formation. This formation is easily observed in tangential sections of *Phellodendron*, *Rhus*, *Ilex*, *Acer*, *Gymnocladus*, *Acanthopanax*, and many other species. There are often thick-walled, unlignified, phloem-parenchyma cells in both woody and herbaceous dicotyledons that show lateral sieve-platelike pittings, but no terminal sieve-plates or callus were seen.

In the herbaceous dicotyledons studied, often the most striking

feature was the relatively small amount of phloem present. In *Paeonia* and *Thalictrum*, for example, there may be only 6–12 sieve-tubes in a bundle having perhaps 30–50 times that number of xylem elements; but often in woody plants only a few rows of sieve-tubes, as seen in radial section, are really functional.



FIGS. 1-3.—Fig. 1, one-third of a sieve-tube of *Juglans nigra*: *a*, end sieve-plate in cross-section; *b*, lateral sieve-plate in face view; fig. 2, one-half of a sieve-tube of *Vitis labrusca*: *a*, end sieve-plate in cross-section; *b*, lateral sieve-plate in face view; *c*, companion cell; fig. 3, full length view of a sieve-tube of *Lactuca scariola*: *a*, end sieve-plate in cross-section, with callus; *b*, slime contents; *c*, companion cell; *d*, lattice or “sieve-field.”

No lignification of the phloem was observed in *Helianthus*. Perhaps the material used was collected too early or grew under different conditions from that described by BOODLE.⁵

⁵ BOODLE, L. A., Lignification of phloem. *Ann. Botany* 16:180. 1906; also *ibid.* 20: 319–321. 1910.

Species of over 140 genera, belonging to more than 60 families, have been studied. The sieve-tubes found in these different species, for the sake of convenience, may be grouped under three types, though perhaps most of them will come naturally between the first and second or second and third types.

The first type is like that found in *Pinus*. Here the lateral sieve-plates are the same as the terminal ones, and the end walls are very oblique, extending from one-fourth to one-half the length of the sieve-tube. Text fig. 1 shows one-third of a sieve-tube of *Juglans nigra* as seen in tangential view. The lateral sieve-plates are seen in face view on the tangential wall, while the terminal sieve-plates are seen in transverse section. The lateral sieve-plates on the tangential walls of the sieve-tubes in *Juglans* are usually more irregular and thinner than those on the terminal or radial walls.

The second type is like the first except that the lateral sieve-plates are less well developed, and the end walls are less oblique, and have 2-10 sieve-plates each. This type may be illustrated by *Vitis* (text fig. 2). The figure shows one-half of a sieve-tube in tangential section. The end wall here has 7 sieve-plates covered with callus. Poorly developed sieve-plates are shown in face view on the tangential wall. On the left is a companion cell related to the sieve-tube by fine pits.

The third type has end walls that are nearly at right angles to the side walls, and has only one sieve-plate to each end wall. The sieve-tubes of *Lactuca scariola* illustrate this type (text fig. 3). This sieve-tube, though shown in full length view, was drawn to the same scale as the other text figures. The three lattices on the left relate it to another sieve-tube.

The species studied may be grouped under these types as follows:

FIRST TYPE⁶

Alnus incana, *A. rugosa*, *A. oregana*, *Betula alba*, *B. lenta*, *B. lutea*, *Banksia Menziesii*, *Carya alba*, *C. ovata*, *Castanea dentata*, *Castanopsis chrysophylla*, *Casuarina Fraseriana*, *C. equisetifolia*, *Corylus americana*,

⁶ The nomenclature of GRAY'S *Manual* (Ed. 7) is followed as far as applicable; the names of plants indigenous to Oregon are those used in HOWELL'S *Flora of Northwest America*.

C. rostrata, *Carpinus caroliniana*, *Drimys colorata*, *Fagus grandifolia*, *Juglans cinerea*, *J. nigra*, *Myrica asplenifolia*, *M. cerifera*, *Nothofagus Menziesii*, *Ostrya virginiana*, *Populus balsamifera*, *P. grandidentata*, *P. tremuloides*, *P. trichocarpa*, *Quercus alba*, *Q. Garryana*, *Q. Kelloggii*, *Q. nigra*, *Salix fragilis*, *S. nigra*.

BETWEEN FIRST AND SECOND TYPES

Berberis aquifolium, *Celtis occidentalis*, *Aesculus glabra*, *A. Hippocastanum*, *Acer Negundo*, *A. macrophyllum*, *A. rubrum*, *A. saccharum*, *Crataegus coccinea*, *C. Douglasii*, *Calycanthus floridus*, *Fraxinus americana*, *F. oregana*, *Hamamelis virginiana*, *Holodiscus ariaefolia*, *Hydrangea vestita*, *Liriiodendron Tulipifera*, *Magnolia acuminata*, *M. Fraseri*, *Maclura pomifera*, *Morus rubra*, *Philadelphus Lewisii*, *P. grandiflora*, *Platanus occidentalis*, *Prunus serotina*, *Pyrus baccata*, *P. coronaria*, *Rosa gallica*, *Ribes sanguineum*, *Sassafras variifolium*, *Ulmus campestris*, *U. americana*.

SECOND TYPE

Ailanthus glandulosa, *Arbutus Menziesii*, *Catalpa bignonioides*, *Ceanothus sanguineus*, *Cephalanthus occidentalis*, *Cercis canadensis*, *Cladrastis lutea*, *Cornus Nuttallii*, *C. pubescens*, *Clethra alnifolia*, *Diospyros virginiana*, *Euonymus atropurpureus*, *Gymnocladus dioica*, *Gleditsia tricanthos*, *Ilex opaca*, *Kalmia latifolia*, *Lyonia ligustrina*, *Phellodendron amurense*, *P. japonicum*, *Robinia Pseudo-Acacia*, *Rhus glabra*, *R. Toxicodendron*, *Ricinus communis*, *Rhamnus cathartica*, *R. Purshiana*, *Sambucus glauca*, *Syringa vulgaris*, *Tilia americana*, *T. europaea*, *Vaccinium corymbosum*, *Vitis labrusca*.

BETWEEN SECOND AND THIRD TYPES

Abutilon Theophrasti, *Acanthopanax sessiliflorum*, *Actaea alba*, *Agri-
monia gryposepala*, *Amaranthus paniculatus*, *Aquilegia formosa*, *A. vulgaris*, *Aralia spinosa*, *Asarum canadense*, *Asclepias syriaca*, *Chenopodium album*, *Clematis ligusticifolia*, *Brassica alba*, *Datura stramonium*, *Daucus Carota*, *Dipsacus sylvestris*, *Euphorbia Preslii*, *E. corollata*, *Filipendula rubra*, *Geranium sanguineum*, *Geum triflorum*, *Hibiscus Moscheutos*, *Hypericum perforatum*, *Humulus Lupulus*, *Impatiens noli-tangere*, *I. pallida*, *Knautia arvensis*, *Paeonia montana*, *Potentilla rivalis*, *Polanisia graveolens*, *Polygonum Douglasii*, *Raphanus sativus*, *Rumex occidentalis*, *Saponaria officinalis*, *Solanum nigrum*, *Thalictrum dasycarpum*, *Tropaeolum majus*, *Urtica gracilis*, *Verbena officinalis*.

THIRD TYPE

Ambrosia artemisiifolia, *Arctium minus*, *Aster novae-angliae*, *Bryophyllum calycinum*, *Cichorium Intybus*, *Cicuta maculata*, *Cucurbita maxima*, *Cyclamen latifolium*, *Eupatorium purpureum*, *Echinocystis lobata*, *Eryngium yuccifolium*, *Helianthus annuus*, *Heracleum lanatum*, *Hieracium venosum*, *Lactuca scariola*, *Liatris squarrosa*, *Linaria vulgaris*, *Lobelia cardinalis*,

Lupinus polyphyllus, *Melilotus alba*, *Monarda punctata*, *Oenothera biennis*, *Opuntia Rafinesquii*, *Phaseolus vulgaris*, *Phytolacca decandra*, *Physalis heterophylla*, *Primula sinensis*, *Sium cicutaefolium*, *Scrophularia marilandica*, *Silphium laciniatum*, *Sonchus oleraceus*, *S. arvensis*, *Stachys palustris*, *Tephrosia virginiana*, *Trifolium pratense*, *Verbascum Thapsus*, *Veronica scutellata*, *Xanthium spinosum*.

The following monocotyledons were similarly studied, and all were found to have sieve-tubes of the third type.

Alisma *Plantago*, *Arisaema triphyllum*, *Dracaena scandia*, *Iris versicolor*, *Monstera deliciosa*, *Polygonatum commutatum*, *Potamogeton heterophyllus*, *Sagittaria latifolia*, *Scirpus validus*, *Smilax rotundifolia*, *Typha latifolia*, *Zea Mays*.

There are of course no sharp lines of division in grouping these species according to type; even in the same section there may be some variation. But in general there is no wide variation even with different genera of the same family, except where there are both woody and herbaceous genera; then the herbaceous ones showed the higher type, as for example in Rosaceae and Leguminosae. The sieve-tubes of the Leguminosae on the whole are of a higher type than those of the Rosaceae. The woody Rosaceae often have sieve-tubes about like the first type, with regular large lateral sieve-plates. While the woody Leguminosae may have occasionally well developed lateral sieve-plates, they are usually as small as in *Sambucus* or *Tilia*. The xylem of the Leguminosae has been likewise found to be a higher type, so perhaps these families do not belong so near each other as they are usually placed.

It will be noted that the woody dicotyledons studied are placed in the first and second types, while the herbaceous ones are in the intermediate type between the second and third, or in the third type. Three or four sieve-plates were the most seen on the end wall of any strictly herbaceous plant, as for example *Euphorbia* and *Thalictrum*. Even in these genera end walls with only one sieve-plate were often observed. In the Compositae studied, only one sieve-plate to each end wall of the sieve-tube could be found. When stained with Russow's callus reagent, the pores of the "sieve-fields" or lattices showed up as orange dots, but they never were large nor fused into callus pads.

Occasional lateral callus pads were observed in most of the

other herbaceous plants studied. In *Cucurbita maxima*, for example, as many as 9 lateral callus pads have been seen in a continuous row in a single sieve-tube.

The evolution of the sieve-tube parallels that of the tracheid or vessel. For example, in *Ephedra* the vessels have oblique end walls with several round or oval pits. This is supposed to be the primitive type of vessel. In *Liriodendron* the end wall of the vessel is still rather oblique, but the pits are of the scalariform type and close together. In the highest type, the pitted vessel, the little margin that is left of the end wall is usually at right angles to the side walls, as in *Fraxinus*.

Conclusion

In studying the phloem of the dicotyledons, it has been found that there is a gradual transition from the gymnospermous type of sieve-tube to the so-called dicotyledonous type as seen in the Compositae. At the first stage in advance the lateral plates are smaller and have smaller meshes than the terminal plates; then as the terminal wall becomes more and more at right angles to the lateral walls, the number of terminal plates decreases until there is only one terminal plate with relatively large meshes, and the lateral plates become "sieve-fields" or lattices.

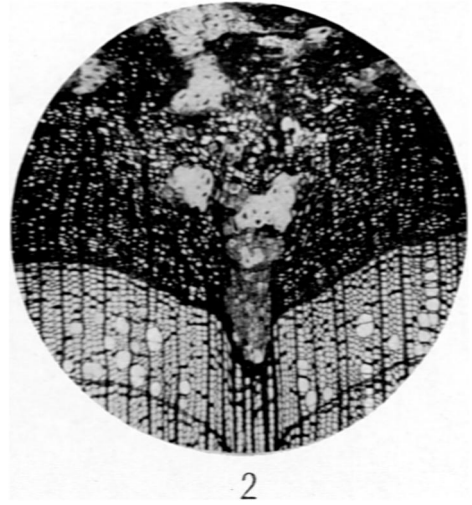
Paleobotany, ontogeny, and studies of xylem have induced many botanists to believe that herbaceous plants are more advanced in their evolutionary development than woody plants. This study of the sieve-tube adds another argument in favor of this view.

The first two years of this work were done in the Phanerogamic Laboratory of Harvard University under the direction of Professor E. C. JEFFREY, and the last year of work has been under the direction of Professors J. M. COULTER and W. J. G. LAND at the University of Chicago. The writer wishes to express his thanks to these instructors for their helpful advice.

TRANSYLVANIA UNIVERSITY
LEXINGTON, KY.



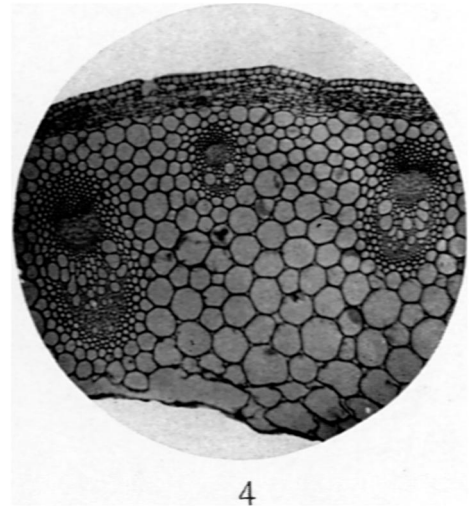
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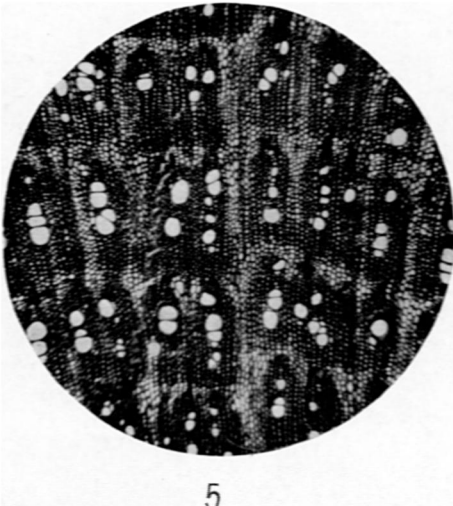
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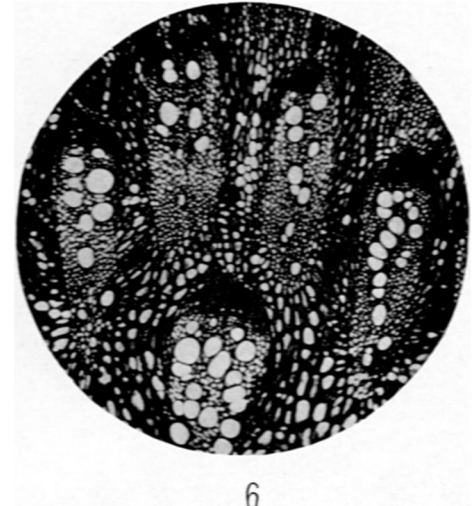
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EXPLANATION OF PLATE XI

FIG. 1.—Transverse section of phloem of *Acer macrophyllum*, showing horizontal bands of hard bast and general view of sieve-tubes and parenchyma cells.

FIG. 2.—A similar view of *Alnus incana*, showing that the hard bast occurs chiefly opposite the aggregate rays.

FIG. 3.—A similar view of *Quercus Garryana*, showing distribution of hard and soft bast.

FIG. 4.—Transverse section of stem of *Ranunculus fascicularis*, showing scattered bundles and relatively small amount of phloem.

FIGS. 5 and 6.—*Chenopodium album* (fig. 5) and *Amaranthus paniculatus* (fig. 6), showing peculiar scattered bundles that might suggest relationship to the monocotyledons.