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THE ARRANGEMENT OF THE VASCULAR BUNDLES IN THE NODES OF THE DIOSCOREACEAE

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With plates I–II

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INTRODUCTION

In 1926 MASON (1) drew the attention to the fact that in the nodes of the stem of the *Dioscoreaceae* special xylem and phloem structures are found which join respectively the xylem and phloem elements of the vascular bundles running in the successive internodes. He called these structures wood plexus and phloem plexus. Especially the phloem plexus was further described by him.

MASON's results can be briefly summarized as follows. The sieve tubes of the successive internodes do not join up with each other directly, but via a glomerulus, a great number of oblong thin-walled parenchymatous cells running fairly parallel, with a distinct nucleus and densely plasmatic contents. These glomeruli are connected with the ends of outgoing and incoming sieve tubes by similar cells (bast tubuli) lying less compactly and being according to the distance to be bridged, of different lengths. On the ground of this anatomic structure, MASON concludes to a secretory function of the glomeruli, thinking it at the same time probable that these glomeruli form an obstacle for a rapid moving of carbohydrates along the phloem. Whereas, therefore, a mass transport in the internodes through the sieve tubes is conceivable, the substances transported through the phloem must pass the plasm at the nodes. An analogous case SCHUMACHER (2) sees in the anatomical relations, as they appear in the haustorial connections of the parasite *Cuscuta odorata* on *Pelargonium zonale*.

ROECKL, quoted by ESAU (3) also examined the structures in the *Dioscoreaceae* and her conclusion was that their anatomic structure did not differ sufficiently from the normal phloematic tissue, to justify MASON's speaking of non phloematic tissue in this case. HAPP, quoted by HUBER (4) speaks in this connection of sieve cells, verbatim: "reich getüpfelten, aber keine Siebplatten führenden Parenchymzellen (wohl richtiger Siebzellen)".

In connection with the theoretical importance of this matter, a description of the anatomical structures observed by me, may be useful.

The course of the vascular bundles in a number of *Dioscoreaceae* has been examined at the hand of free-hand and microtome sections. The free-hand sections made of the fresh material were stained in coralline soda, according to STRASZBURGER's (5) directions, whereas the microtome sections, in imitation of MASON were stained in haematoxyline. As evidence all particular structures described were fixed on photographs. The research was performed in the Botanical Laboratory of Groningen, Department Systematic Botany, director Prof. Dr R. v. d. WIJK.

ANATOMICAL INVESTIGATIONS

In the internodes in the outer layers of the central cylinder run a number of vascular bundles, arranged in a circle. We find always one opposite a rib and one or two between two ribs. The number depends on the species examined and in the species on the thickness of the stem. The vascular bundles opposite the ribs pass at the nodes into the petiole, that is three per leaf, the others continue uninterrupted. If more than one leaf is inserted at one node (binary, ternary and sometimes quaternary false whorls may occur side by side on the same stem) all vascular bundles opposite the ribs may leave the stem. The relation between phyllotaxis and course of the vascular bundles was extensively described by QUÉVA (6).

The leaf traces leave the stem at the nodes by curving outwards about rectangularly and disappearing into the petiole in that way. The wood parenchyma, which encloses the xylem vessels, and the sclerenchyma, which encloses the phloem vessels, is developed more strongly locally, so that a picture arises as has been given schematically in Fig. 1.

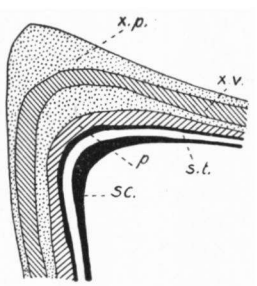


Fig. 1. Schematic drawing of the arrangement of a vascular bundle passing into the petiole.
x.p. xylem parenchyma s.t. sieve tubes x.v. xylem vessels p. parenchyma sc. sclerenchyma

At the nodes the number of vascular bundles vanishing into the petiole are supplemented by branching. Besides that supplement this branching also supplies the vascular bundles going into the axillary buds. Per leaf about one third of the total number of vascular bundles found in the stem, participate in the branching, so that of a ternary whorl all vascular bundles are involved in the branching. Now this branching has a special character in the *Dioscoreaceae*. In a longi-

tudinal section of the stem, made in such a way that the petiole is about cut in halves, there is in the stem just below the leaf insertion a suboval complex tissue, macroscopically visible. This complex consists of tracheids, running in all directions, among which especially at the base and at the top in open spaces, conglomerates of oblong parenchymatous cells are conspicuous. At the base the vascular bundles disappear into this complex, at the top they emerge from it, the vascular bundles to the axillary bud arising from it too. The complex itself is formed by repeated splitting up of xylem and phloem elements into elements getting narrower and narrower, next uniting again and so forming the vascular bundles of the next internode. In principle this branching runs parallel for xylem and phloem; this is clearly shown in the schematic figures 2 and 3.

On first considering the xylem (Fig. 2), we note that the course of things is as follows. The vessel running in an internode (v_1) splits up

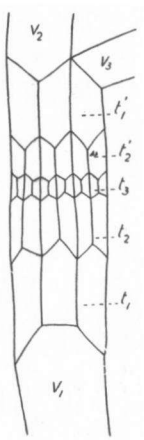


Fig. 2. Schematic drawing of the splitting up of a wood vessel via a complex of tracheids into two vessels, one of which remains in the stem (v_2) and the other going into the axillary bud (v_3). t_1 and t'_1 tracheids of the first order, t_2 and t'_2 tracheids of the second order, t_3 tracheids of the third order.

at the end in three (in reality in a varying number) tracheids of the first order (t_1). These tracheids of the first order pass in a corresponding way into tracheids of the second order (t_2), these again into tracheids of the third order (t_3). It is difficult to trace how often this splitting up is repeated, but finally it takes place in a reverse direction and we get through a confluence of a number of tracheids of a higher order, tracheids of a lower order, so $t_3 \rightarrow t'_2 \rightarrow t'_1$. These last pass into the vessels for the next internode (v_2) and for the axillary bud (v_3).

Of course things are greatly simplified in this scheme. In fact the splitting up at the end of v_1 does not only take place in the longitudinal axis but also laterally. Owing to this the branching of the xylem elements gets a very erratic character and looks like an intricate complex of tracheids, in which there also occur interconnections between tracheids originating from vessels of neighbouring vascular bundles. Where the tracheids are not adjoining, they are surrounded by wood parenchyma (living contents, starch grains).

At the hand of a number of photographs (Plate I–II) we can now imagine the exact arrangement. Photograph A shows a vessel of a vascular bundle of the stem splitting up just below the complex into two tracheids of the first order. These tracheids split up in the same way into tracheids of the second order, which is shown in photograph B. The partition walls between vessels and tracheids and between tracheids among themselves, have besides greatly thickened wall parts also non-thickened ones, which give us a very strong impression of their being perforations. In photograph C we see at the end of a vessel, the partition walls from a number of tracheids. This gives us a clear picture of the structure of the transverse walls. Photograph F (1) gives a survey of a part of a wood complex, from which the erratic arrangement of the tracheids clearly appears. The partition walls between wood parenchyma and tracheids bear bordered pits or have net-like thickenings (photo D).

Mutatis mutandis the branching of the phloem elements has taken place in the same way (Fig. 3). As a rule the splitting up takes place

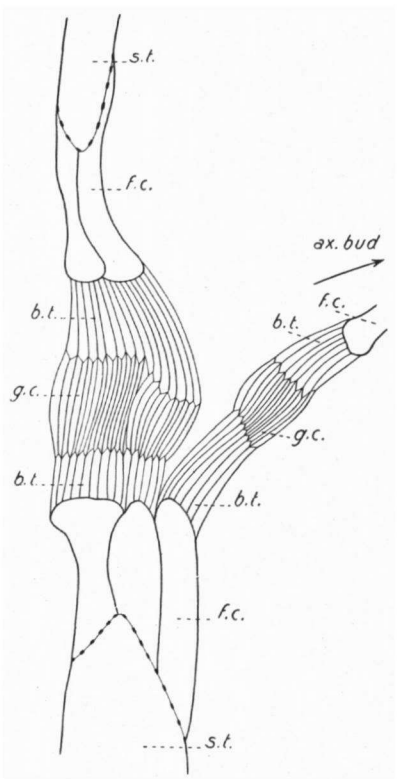


Fig. 3. Schematic drawing of the splitting up of a sieve tube via glomeruli into two sieve tubes, one of which remains in the stem and the other going into the axillary bud.
s.t. sieve tubes, b.t. bast tubulus cells, f.c. funiculus cells, g.c. glomerulus cells.

three times in this case. The elements formed by splitting up and confluencing are called in imitation of MASON: sieve tubes → funiculus cells → bast tubuli → glomerulus cells → bast tubuli → funiculus

cells → sieve tubes, respectively. As contrasted with the xylem the arrangement is much less erratic. The cells which arise from the end of a certain element, run close together all in the same direction. A sieve tube passes into 2 or 3 funiculus cells, whereas each of these latter pass into a great number of bast tubuli. The length of the bast tubuli varies much and is dependent on the distance to be bridged between two sieve tubes that are being connected with each other. Each bast tubulus is connected with one to three glomerulus cells. While on splitting up each of the successive elements grows narrower and narrower, the total sectional surface becomes much larger owing to the great number. In my estimation the average sectional surface of a glomerulus (i.e. the total of the glomerulus cells, inserted between two sieve tubes merging into each other) is five to ten times larger than that of the sieve tubes joined by this glomerulus.

This arrangement has also been fixed in a number of photographs. Photo E shows, how a number of sieve tubes, running between two xylem parts, pass into glomeruli. In photo F (2) we see, higher magnified, how a sieve tube splits up into three funiculus cells. In the partition wall the sieve plate with thicker and thinner parts is distinguishable. The thicker parts are the sieve fields, the thinner ones the wall parts between them. A view of such a sieve plate from above, as printed on photo G, clearly shows that a single sieve field is also porous; the lighter parts consist of callus (coloured with coralline soda), which has been formed round sieve pores visible among them as dark patches. The funiculus cells originated in this way from a sieve tube end at the other extremity in a club shaped part.

As regards contents, they are not to be distinguished from the sieve tubes. In the wall of the club shaped end more sieve fields occur. To this the bast tubuli are joined, one per sieve field, sometimes one per two sieve fields. Photograph H shows this, while photograph K, more magnified, shows the connection of a bast tubulus with a sieve field. Both the basttubuli and the glomerulus cells have thin walls, being densely filled with protoplasm and possessing a distinct big nucleus. Seeing the fact that the terminal walls are slightly slanting, we had better speak of prosenchyma than of parenchyma (7). The partition walls between bast tubuli and glomerulus cells show besides thin parts also thickened patches provided with callus. The older the

EXPLANATION OF PLATE I

A. Splitting up of a wood vessel into two tracheids of the first order.
B. Splitting up of a tracheid of the first order into three tracheids of the second order.
C. Three partition walls between tracheids seen from above.
D. Partition wall between tracheids among themselves and relief figures on the wall of the wood parenchyma.
E. Two sieve tubes passing into glomeruli.
F. 1. The wood plexus.
   2. A sieve tube passing into three funiculus cells.

PLATE I

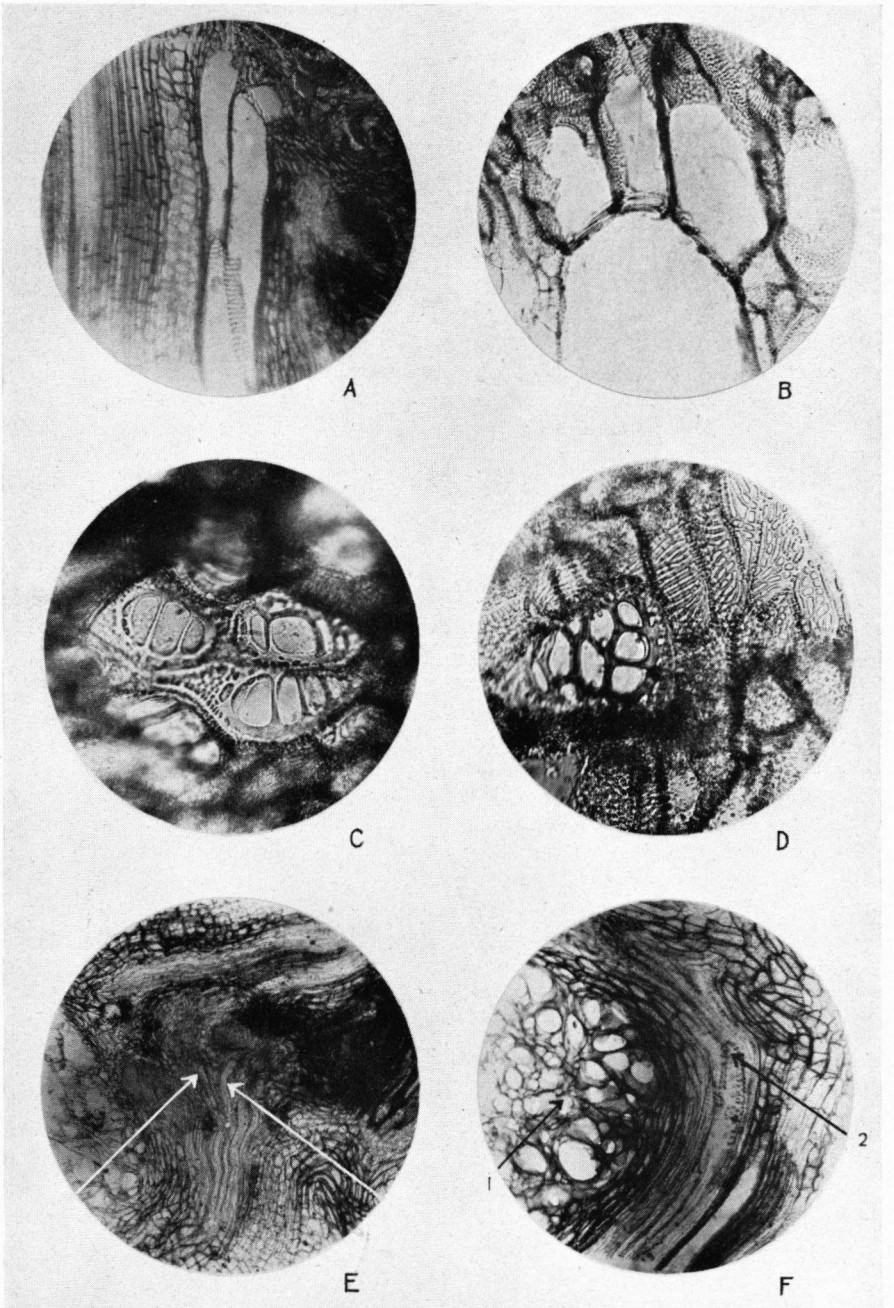
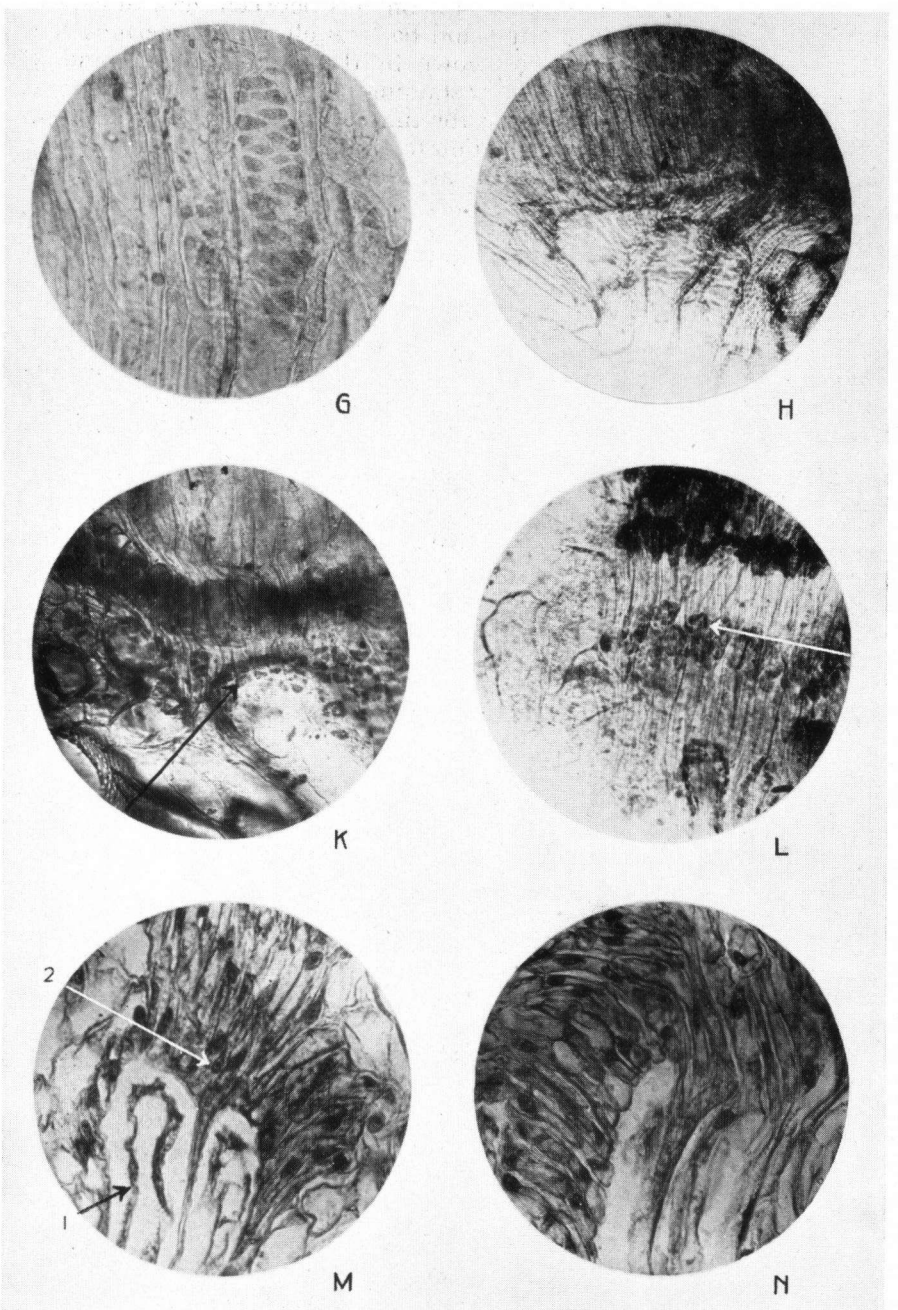


PLATE II



tissue, the stronger these thickenings come to the fore. This is shown by photograph L. The difference in contents between sieve tubes and funiculus cells on the one hand and bast tubuli and glomerulus cells on the other hand, is clearly shown by the photographs M and N, made of microtome sections after staining in haematoxyline. Whereas in sieve tubes and funiculus cells the thin layer of parietal protoplasm present has coagulated after fixation to an insignificant quantity (M_1), bast tubuli and glomerulus cells are densely filled with protoplasm (M_2). The sieve tubes and funiculus cells lack any trace of a nucleus, whereas in the bast tubuli and the glomerulus cells the nucleus is quite evident (photographs M and N).

Discussion

The above corroborates the facts described by Mason; besides a description of the xylem complex has been added and a further detailed description of the phloem complex. It appears that the occurrence of the complexes described is closely connected with the phyllotaxis.

A wood complex as described above, is not general in the plant kingdom. While in various plants tracheids occur in the xylem by the side of vessels, they usually behave independently of each other in branching. Yet this is not an isolated case. Rouschal (8) describes the same phenomenon for some grasses. There too vessels occur in the internodia, while on the nodes a complex of tracheids joins the vessels of two successive internodes. Meyer (9), who examined the vascular bundles of a great number of plants, states that in various species, the vessels running in an internode, just before or in the nodes pass into tracheids and here too, if not as such a complex tissue, the tracheids form the link between the corresponding vessels in the successive internodes. For the rest it appears from Meyer's publications that the difference between vessels and tracheids is not so great as is frequently assumed. As to the perforations of the walls and the size of the apertures in the transverse walls, every transition occurs between vessels and tracheids. The difference is, therefore, merely quantitative. Eames (10) mentions that sucking Indian ink through the tracheids clearly shows the quite open perforations in the partition walls.

EXPLANATION OF PLATE II

G. A sieve plate consisting of a great many sieve fields.
H. Transition of three funiculus cells into bast tubuli.
K. Connection of the bast tubuli with the sieve fields.
L. Thickened and thin parts in the partition walls between bast tubuli and glomerulus cells.
M. Transition of two funiculus cells into bast tubuli.
   1. Little protoplasm, no nucleus in the funiculus cells.
   2. Much protoplasm, distinct nucleus in the bast tubuli.
N. See M.

A, B, C, D, E, F, G, H, K and L have been made of free-hand sections stained with coralline soda.
M and N have been made of microtome sections stained in haematoxyline.

So it appears that a wood complex as occurs in the *Dioscoreaceae*, is also to be found in other plants and besides that the transition of vessels into tracheids (at the nodes) is no exception.

This does not hold for the phloem complex. As far as is known the occurrence of it is restricted to the *Dioscoreaceae*. It is essential whether there is a qualitative distinction between bast tubuli and glomerulus cells on the one side and sieve tubes and funiculus cells on the other side; a decision, therefore, in the controverse MASON–ROECKL. The grounds on which ROECKL and HAPP based their conclusion are unknown to me. MASON did not describe the thickenings in the wall, occurring on the partition walls between bast tubuli and glomerulus cells and consisting of callus (photo L); these indeed suggest phloem tissue. The only important difference between these elements and the sieve tubes which remains, is the contents of the cells. In order to give an opinion on the value to be attributed to this difference, it is necessary to examine the way of differentiation of the sieve tubes. Sieve tubes are differentiated from oblong parenchymatous cells. The initially very abundant plasma contents gradually disappear and a large vacuole is formed. Finally only a thin layer of parietal protoplasm is left and also the nucleus obliterates. Some investigators think that only after this maturing process is completely finished, the sieve tubes can perform their function, transport of assimilates, etc. This may be correct as long as mass streaming is assumed to be the only transport mechanism, but this is by no means probable. ARISZ (11) indicates that before this maturing is completed a specialized parenchyma transport should certainly be considered a possibility. Also the wall of the sieve tubes experiences considerable changes during the maturing process. The sieve plates develop, varying with the species, on the slantwise or oblique end walls and sometimes on the lateral walls of the sieve tubes. The plasm connections through these sieve fields are of the same nature as plasmodesms only much larger. On the thicker wall parts between the plasm connections callus is formed. In course of time this callus formation gets thicker and wider, so that consequently the plasm connection is finally being tied off. After complete closure the sieve tubes stop of course their functioning.

In the growing stem we find from top to base an increasing differentiation. In sections of the youngest nodes, the sieve tubes were already completely differentiated, i.e. the contents had been reduced to a thin layer of parietal protoplasm and the sieve plates were already clearly provided with callus. Of the appertaining bast tubuli and glomerulus cells the partition walls were slightly provided with callus (slightly stained in coralline soda), but marked differences between thickened and non-thickened wall parts were not there.

The contents were densely plasmatic and in each cell there was a clearly visible nucleus. In the older elements the callus deposit is more marked and also the perforation of the transverse walls is clearly visible. The contents, however, remain the same.

Seeing that the substances transported through the sieve tubes along the stem must pass the glomeruli in the nodes and consequently

have to pass through the plasm, a mass transport is surely impossible there. Whether this means a considerable inhibition of the rate of transport is not easily decided. In this connection we do well to consider that simultaneously with introducing "protoplasmic resistance" the track is considerably widened.

So the conclusion is that bast tubuli and glomerulus cells anatomically have a structure strongly departing from fully differentiated sieve tubes. For the transport through this system important consequences are connected with it.

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