STRUCTURE, ARRANGEMENT AND COURSE OF VASCULAR BUNDLES IN THE STEM AND LEAVES OF HEPTAPLEURUM VENULOSUM SEEM

BY

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Introduction.

Heptapleurum Gaertn. is an Araliaceous genus. Its about 60 species are distributed all over the Old World tropics, but the only species occurring in northern India is *Heptapleurum venulosum* Seem. The writer's attention was first drawn to this plant from a casual study of the transverse section of the petiole which showed a peculiar arrangement of the primary vascular strands. These are arranged in two rings and the bundles of the inner ring show an inverse orientation to those of the outer ring. A similar transverse section of the stem revealed the presence of cortical bundles. As it was thought that a full knowledge of this peculiar arrangement of the bundles in the leaves and the stem, how it arises and its probable significance, would be of some interest, the present investigation was undertaken.

Previous Work.

Solereder (7) mentions a large number of workers who have investigated the central cylinder of the Araliaceæ. Among these are included Trécul, Sanio, Cedervall, Van Tieghem, Weiss, Gussow, Viguier and several others. All the earlier literature is cited by the last named author (8) and his researches along with those of Güssow (1) are the most comprehensive ones on the subject, though these were undertaken only from the systematic point of view and are accompanied by a large number of keys based on anatomical characters. Both of them used a very large number of plants in their investigations, Gussow about 43 genera and Viguier more than 60 genera. None of these authors, however, says anything about the structure of *Heptapleurum venulosum*. The only work in this direction has been done by Petit and Plitt (also quoted by Solereder) who have described the above mentioned peculiarity in the structure of the petiole. These investigators, however, restrict themselves to the structure of the petiole alone.

Habit and External Form.

According to Parker (6) *Heptapleurum venulosum* is met with in a wild state in the Sutlej and Ravi valleys but several cultivated plants are found in the various gardens of Lahore and the material from the latter has been used in the present investigation. The plants growing in Lahore usually assume the form of erect or suberect shrubs, with fairly large, alternate, stipulate and digitate compound leaves. The petiole is 6 to 9 inches long, dilated and clasping at the base. The stipules may be up to half an inch long and these are connate between the stem and the petiole. Leaflets are 3 to 7 in number, usually 5, 4 to 8 inches long and 2 to 4 inches broad. Their petiolules vary from half an inch to two inches in length. The middle leaflet is usually the largest. In their natural habitat, the plants flower in the months of January and February but in Lahore the flowering shoots make their first appearance in May and the flowers open in the month of June.

Structure of the Petiole.

The petiole is quite circular in cross section and as has already been told the vascular bundles here are arranged in two definite rings (fig. 1). Those of the outer ring are of two types. There are larger bundles mostly alternating regularly with smaller bundles. The structure of the two is, however, exactly similar. Each bundle consists of xylem and phloem. Xylem is internal and endarch and phloem external. To the outside of the phloem there is a cap of fibrous elements. These fibres are of the nature of substitute fibres. Their walls are greatly thickened and lignified but the protoplasmic contents are quite intact, as is characteristic of most herbaceous plants. The bundles of the inner ring are situated only opposite to the smaller bundles of the outer ring. Their number, consequently, is only one half of that of the bundles of the outer ring. Xylem and phloem of these internal bundles are arranged in a manner inverse to that of the bundles of the outer ring, the xylem here being external and phloem internal. Further these bundles lack the cap of fibres which is present to the outside of the phloem of the bundles of the outer ring. In one case only a deviation from the above arrangement was observed. Here a collateral vascular strand was found lying even inside the inner vascular ring without any definite position.

Resin canals which are characteristic of the family are situated in the petiole in a more or less definite manner. There are two rings of resin canals in the cortex, one near the periphery and close to the epidermis and the other close to the central cylinder. Further there is one resin canal to the inside of each of the larger vascular bundles of the outer ring.

A study of the cross-sections of the petioles of different ages shows that the larger bundles of the outer ring begin to develop earlier and then later on in between them are formed the smaller bundles. The bundles of the inner ring develop simultaneously with the latter. All these bundles, however, whether of the outer ring or of the inner ring, whether smaller or larger, develop from separate procambial strands and there development is quite normal, agreeing in every feature with that of the collateral bundles of an ordinary dicotyledon and such as is usually described in text-books. The xylem and the phloem begin to differentiate simultaneously at two opposite ends of the procambial strands, the middle portion of the procambium gives rise to the cambium and primary and secondary xylem are distinguishable. In the mature condition, however, although the smaller bundles of the outer ring and the bundles of the inner ring develop from quite separate procambial strands, the two become connected and appear to be situated within a more or less common sheath (fig. 10.) The walls of the cells intervening between the two bundles get thickened and lignified and these cells in a cross-section show the same structure as is shown by the cells of the fibrous caps of the bundles of the outer ring. Also the cells surrounding the inner bundles on the other sides get somewhat thickened and lignified. A sheath of lignified tissue surrounding the two bundles is thus differentiated and the whole thing assumes some resemblance with the internal bundles such as have been described in the stem of several perennial species of *Rumex* by Herail (2) and others. The resemblance is, however, only superficial, for as Maheshwari (5) has shown the internal bundles of *Rumex* develop from the same procambial strands from which the bundles of the outer normal ring are formed.

Course, Structure and Development of the Bundles in the Leaflets.

At the distal end of the petiole, the ring of vascular tissue, splits up into as many parts as the number of leaflets borne by it, so that a transverse section of the petiolule of a leaflet (fig. 2) shows an arc of bundles, several of which have internal bundles. In other words two arcs of bundles can be distinguished here also, as two rings in the main petiole, an outer and an inner one. The bundles of the outer arc are normally orientated and those of the inner one inversely orientated. In the outer arc larger and smaller bundles can be distinguished and most of the bundles of the inner arc are situated opposite to the smaller bundles of the outer arc, but the arrangement is not so definite as in the petiole This is caused by some of the internal bundles turning through an angle of 180 or less degrees and uniting with the bundles of the outer ring. Sometimes the arrangement of the bundles is such that in a transverse section there appears to be an outer bundle with an internal bundle and some bundles situated on the sides of the two (fig. 11).

Higher up where the petiolule begins to pass into the blade of the leaflet (fig. 3) the side bundles of the arc begin to pass outwards into the assimilatory region of the blade and only the central ones remain in the midrib. Further up, as one passes to the distal end of the leaflet, one finds the internal inversely orientated bundles all one by one turning through a smaller or bigger angle and fusing with the bundles opposite to them, so that all the bundles become normally orientated. The adjacent bundles begin to fuse with each other and the number of bundles decreases so that about the middle of the blade of the leaflet, in the region of the midrib, only a few large bundles are present and these are arranged in a deep arc the margins of which are turned inwards (fig. 4). Near the apex of the leaflet, all these bundles fuse and a single crescent-shaped vascular strand is formed. (fig. 5).

As regards the development, it may be mentioned that some of the bundles in the region of the petiolule show a different situation as compared with the normal development of collateral bundles, such as is found in the petiole and the stem of this plant also. The procambial strands here often only give rise to phloem. Then a cambium is differentiated on one side and all the xylem develops from this cambium, so that primary xylem is altogether eliminated. In such cases (fig. 11), a certain amount of resemblance is shown with the medullary phloem of certain families like Cucurbitaceae. Fig. 11 for example may be compared with text-fig. 4 of Holroyd (3). There is, however, a good deal of difference in the origin of the internal bundles in the two cases, for in the Cucurbitaceæ the inversely orientated internal and lateral bundles develop from the same procambial strands as the bundles of the outer ring.

The Course of the Bundles at the Base of the Petiole and in the Stem.

At the base of the petiole, the smaller bundles of the outer ring begin to pass inwards and the bundles of the inner ring either join the bundles of the outer ring opposite to which they are situated or simply turn through an angle of 180 degrees so that they lose their inverse orientation. In this way a transverse section of the base of the petiole (fig. 6) shows a large number of irregularly scattered bundles like those of a monocotyledonous stem, the majority of which are normally orientated and only a few here and there show inverse orientation.

Lower down the petiole joins the sheathing leaf base and the whole mass of bundles coming from the leaf begins to open out from the inner side (fig. 7) and gradually resolves itself simply into a ring of bundles surrounding the ring of primary vascular strands of the stem, when the leaf and the stem have fused (fig. 8). These foliar bundles do not join the bundles of the stem all at once. On the other hand they do so very gradually. No one leaf gap is formed but the bundles of the leaf trace pass into the central cylinder from all sides. The leaf trace consequently may be called multilacunar. This along with the sheathing leaf base are monocotyledonous characters. Further these leaf trace bundles do not pass into the central cylinder all at the same level. The foliar bundles on the side of the stem, away from the side on which the leaf is attached, pass first into the central cylinder (fig. 9) and then the other bundles slowly and slowly. It is only when the lower node has been reached that all the foliar bundles pass into the central cylinder. This explains the presence of cortical bundles in a cross-section of the stem.

The structure of the flowering peduncles is essentially similar to that of the vegetative stem and cortical bundles are present here also.

Discussion

The chief features in the anatomy of *Heptapleurum venulosum* are, firstly, the scattered disposition of the bundles at the base of the petiole, their arrangement in two rings through the greater length of the petiole and the inverse orientation of the bundles of the inner ring, and secondly, the occurrence of cortical bundles in the stem, due to a longitudinal course of the leaf trace bundles in that tissue. Similar abnormalities have also been described in other genera of the Araliaceae. Viguier (8) mentions about 30 genera which have got medullary bundles in the petiole. Gussow (1) mentions about 10 genera which have medullary bundles in the stem. Cortical bundles have been described in the stem of several genera like *Mydocarpus*, *Delarbrea*, *Heteropanax*, *Cussonia*, *Oreopanax*, *Pentapanax* and *Stilbocarpa*. Both medullary and cortical bundles are found in some cases. In no case, however, these bundles have been investigated in detail and their course described with the aid of modern technique. Nor any attempt has been made in this family to explain the significance of these structures which, although fairly common in some orders, are really deviations from the normal vascular cylinder of the dicotyledons.

A few years back Worsdell (9, 10) studied the anatomy of the Cucurbitaceæ and Compositæ, from which he arrived at some general conclusions applicable to the whole group of Angiosperms with the possible exception of the Amentiferæ. According to him the medullary bundles or a scattered disposition of the bundles, such as is found in monocotyledons, is an ancient character of the stem of flowering plants, which the monocotyledons have mostly retained and dicotyledons have mostly left behind. The medullary phloem found in the axis of some orders of dicotyledons is the last vestige of this ancestoral condition. Most of his evidence is drawn from a study of the petioles and the flowering peduncles which are regarded as conservative organs and are supposed to retain the ancestoral structure—medullary bundles or a scattered disposition of the bundles—more or less well preserved when it has become extinct or almost so in the stem.

Worsdell did not use the evidence from the anatomy of *Heptapleurum* or any other Araliaceæ in support of his conclusions, but he could have easily utilised it. In *Heptapleurum* medullary bundles are absent from the stem but these are found in a quite well developed condition in the petiole. Similar condition is also exhibited by several other genera of the Araliaceæ. *Aralia spinosa* possesses a ring of inversely orientated medullary bundles in the petiole, while these are absent from the stem, though found in the stem of several other species of *Aralia* and *Arthrophyllum*, according to Solereder (7). Similarly from the work of Viguier (8) and Gussow (1), one finds the absence of medullary bundles in the stem of *Schefflera* and *Didymopanax* and their presence in the petiole. There is, however, one feature which is not explainable on the basis of Worsdell's conclusions. His theory can explain the absence of medullary bundles in the stem and their presence in the petioles of several plants, but he has no consistent explanation to offer for such a condition as is found in *Heptapleurum venulosum*, where medullary bundles are found in the petiole and in their stead cortical bundles in the stem; and this little point can change our whole outlook on the question and make one seek some other explanation.

Opposed to Worsdell's theory, are the views of several other botanists who regard the medullary bundles in the stem of decotyledons as a new formation which originated as a response to certain physiological needs. Various causes have been mentioned and perhaps the evolution of medullary bundles in different groups is due to different causes. One of the most plausible causes has been mentioned by Jeffrey (4). He believes that there has been a gradual increase in the elaborative efficiency of the leaves from the earlier to the modern flowering plants and "this situation has brought about that many traces enter the stem at a node instead of three or at the most several traces which pass into the nodal region of the axis in the mass of dicotyledons. This multiplication of the conducting strands brings with it complications of arrangement in the stem for the number is too large to be accommodated on the periphery in a single ring as is the rule even among herbaceous dicotyledons. As a consequence of the necessities which have thus arisen the leaf traces are displaced from the margin of the central cylinder into the pith or medulla. Rarely the same object is effected by the running of the foliar traces for one or more internodes in the cortex."

After considering both these views about the nature of medullary bundles with special regard to the anatomy of *Heptapleurum venulosum*, I feel inclined towards the second one. The leaves of this plant are fairly large. I have not investigated their elaborative efficiency, so I cannot say anything on this point. The number of the leaf trace bundles, however, is very large and one actually sees while tracing the course of vascular bundles how congested these structures are both in the petiole of the compound leaves and in the stem, a fact also borne out by the very gradual passing of the leaf trace bundles into the central cylinder. This view further has the merit of explaining medullary bundles in the petiole and cortical bundles in the stem in accordance with one uniform principle.

As regards the inversely orientated bundles, Worsdell (9, 10) believes these to have been derived by reduction from amphivasal concentric type of bundles which he regards to be the most ancient form of vascular bundle in the Angiosperms. In *Heptapleurum*, however, one sees how easily while passing from the base of the petiole higher up, a normally orientated bundle becomes inversely orientated, simply by turning through an angle of 180 degrees. This suggests that in some plants at least inversely orientated bundles have not been derived from amphivasal bundles by reduction but by a simple rotation of the ordinary collateral bundles and these peculiar arrangements in most cases may be simply regarded as variations in design, all fulfilling the same need.

In the end it may be suggested that a comprehensive study of the course of the primary vascular strands in the leaves and the axis of the various genera of the Araliaceæ would be of great value in properly understanding the nature and origin of medullary bundles, not only in this but in other orders of dicotyledons as well.

Summary.

1. The vascular strands in the petiole of *Heptapleurum venulosum* are arranged in two rings. Those of the outer ring are alternately large and small. The bundles of inner ring are inversely orientated and situated opposite to the smaller bundles of the outer ring.

2. In the petiolule there is an arc of alternately large and small bundles, the latter mostly having inversely orientated bundles on their ventral side.

3. At the base of the petiole all the bundles are irregularly scattered.

4. A large number of leaf trace bundles enter the stem at every node from all sides. The leaf trace is multilacunar and the leaf trace bundles take an almost perpendicular course in the cortex for a longer or shorter distance and so give rise to cortical bundles in the stem.

5. It is suggested that these abnormalities, cortical bundles in the stem and medullary bundles in the petiole are recent formations which have originated in response to physiological needs.

I desire to express my thanks to Professor S. R. Kashyap for his several valuable suggestions and criticisms.

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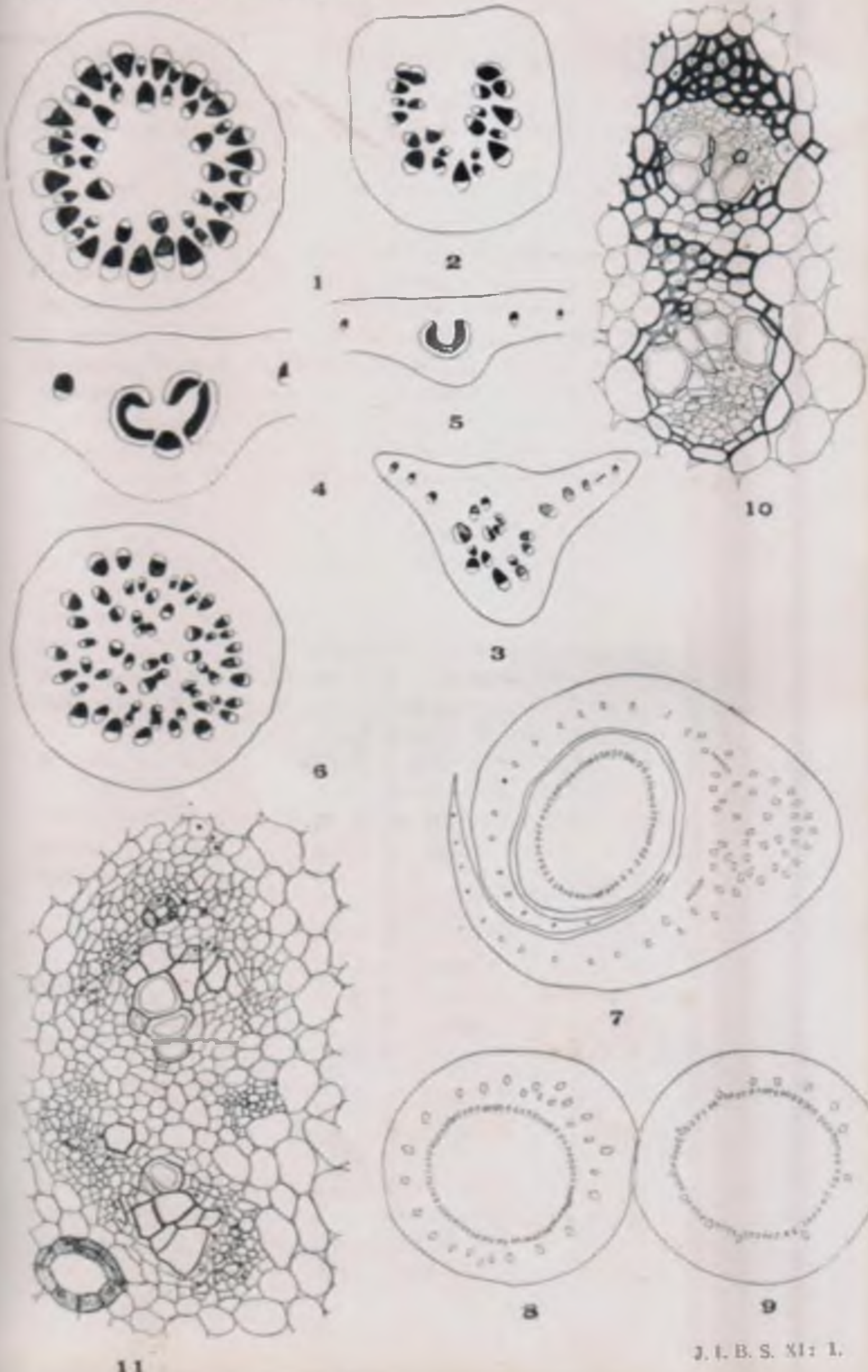
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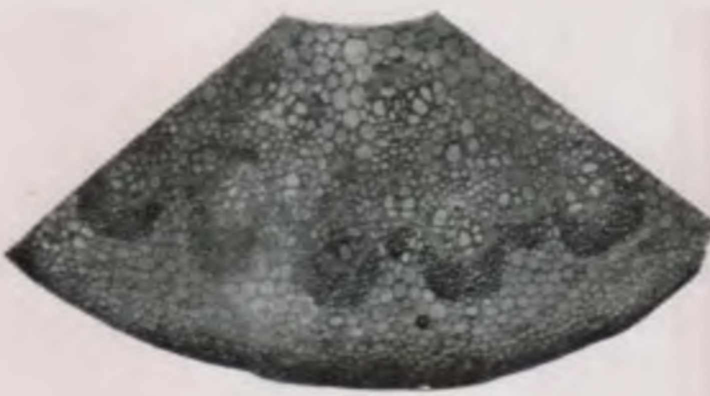

Explanation of Plates.

Fig. 1. Transverse section of the petiole, showing the arrangement of vascular bundles. Xylem in this and in figs. 2–6 is represented by black. × 20.

Figs. 2–5. Transverse sections of the leaflet at various places showing the arrangement of vascular bundles.

Fig. 2. Transverse section of the petiolule. × 25.

Fig. 3. Transverse section of the region where the petiolule just begins to pass into the blade of the leaflet. × 20.

Fig. 4. Transverse section of the mid-rib about the middle of the blade of the leaflet. × 25.

Fig. 5. Transverse section of the midrib near the apex of the leaflet. × 25.

Fig. 6. Transverse section of the base of the petiole showing the arrangement of the bundles. × 15.

Fig. 7. Transverse section of the stem and the sheathing leaf-base just above the node × 17.

Fig. 8. Transverse section of the stem just below the node. × 17.

Fig. 9. Transverse section of the stem lower down. × 17.

Fig. 10. One external and one internal bundle from fig. 1, showing the structure of the two × 200.

Fig. 11. A part of the transverse section of the petiolule, showing an outer bundle with its internal and lateral bundles. × 200.