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THE VASCULAR ANATOMY OF CALAMOVILFA LONGIFOLIA.*

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The present study of the anatomy of Calamovilfa was undertaken first because of the great difference observed between the mature vascular bundle of the rhizome and of the aerial stem. Both transverse and longitudinal sections were made of the rhizome and the writer was unable to find spiral tracheæ, although they occur in the aerial stem just as they occur in the other grasses. The investigation which followed then resolved itself into a study of the vascular strands: (1) the difference in the vascular structure of the aerial and subterranean stems, (2) the origin, development, and final organization of the vascular bundle of the stems, and (3) the development of the thickenings of the cell walls of the xylem vessels.

When one goes into the literature for a discussion of the above points there is an absence of definite data. Almost all the texts and reference books deal with the mature structures without taking up their origin and development. The figures that are used are mainly those of Zea, and only occasionally is some other grass figured. But though the vascular bundles of the aerial parts of grasses have many similarities, they are not all like corn and they are not all arranged in the stem, as they are in corn. It is possible because of these variations among the grass tribes to identify many genera and even species by their vascular anatomy. Schwendener, Duval-Jouve, Holm, Beal, Pammel, and others have studied the vegetative structures for the purpose of identification; and most of the anatomical studies have been of this type. For these studies in most

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instances the aerial parts were used. But in the grasses the stems vary in the composition of the mature vascular strand and in the arrangement of the vascular bundles, so that not only may the aerial stems of different species be dissimilar, but furthermore, (1) the underground stems of species are different and may form a basis for identification and (2) the aerial and underground stems of the same species are different from each other.

The writer has been unable to find papers which discuss the variation in the vascular anatomy between the rhizome and aerial stem of the same plant, or any discussing the origin and development of the vascular strands of the grasses.

THE RHIZOME.

The internode of the rhizome of Calamovilfa is very little elongated. There are few cells of the rhizome which are not lignified. All of the cells of the vascular bundle are thick walled and lignified, even those of the phloem (Fig. 1), although microchemical tests show that the cells of the phloem are not as highly lignified as those of the xylem and pericycle. The reduced leaves, merely scales, are also highly lignified and cutinized. The vascular bundle in the rhizome consists of the phloem with its sieve tubes and companion cells, protoxylem tracheids, and two to four large metaxylem tracheæ. It is without protoxylem annular or spiral tracheæ (Fig. 1), except in an occasional internode which has elongated or in a leaf trace. Instead, the protoxylem cells are thick walled, angular tracheids, and the pericycle is of thick walled, angular cells several layers wide. It forms a continuous band about the stele and the cortex on the inner side. The endodermis is not always well defined.

THE AERIAL STEM.

The aerial stem of Calamovilfa shows no differentation of cortex, for the vascular strands are scattered through the stem around a central pith. Each bundle is surrounded by a thick walled pericycle of several cell layers, and the phloem is made up of large, thin walled sieve tubes with companion cells usually irregularly placed, although they are sometimes quite regular. There are usually two large metaxylem pitted vessels, and from one to five annular and spiral vessels of the protoxylem surrounded by a few parenchyma cells, (Fig. 2).

The internode is said to develop basipetally. The writer has been unable to demonstrate any definite region of dividing cells at the base of the internode. The elongation in Calamovilfa occurs evidently from a diffuse region there which does not continue as cambium activity does, but is of limited development. Lignification begins at the top of the internode and progresses down the stem. The lignification of the base of the internode is the limit of the elongation phase of its development.

THE DEVELOPMENT OF THE INDIVIDUAL VASCULAR BUNDLE.

The desmogen strand is recognized first in the leaf primordium in both longitudinal and transverse sections. It begins with a single cell (Fig. 3), found and recognized with difficulty, that divides into two cells which are readily distinguished, (Fig. 4). Each of these cells divides longitudinally forming four cells (Fig. 5), and from here on the divisions are irregular. The cells of this strand press against the cells surrounding them and cause them to be elongated at right angles to the axis of growth (Fig. 6). This produces an appearance, which later disappears, of a sheath around the demogen strand.

When the strand reaches the condition shown in Figure 7, some of the cell walls both on the inner and outer edge of the strand may begin to thicken, but if elongation is rapid the thickening on the outer edge of the strand does not begin until after the metaxylem cells are differentiated. These outer cells, whose walls become thickened, are pericycle cells.

1. The Development of the Vascular Bundles of the Aerial System.

The cells which become thickened on the side of the strand toward the center of the stem are the annular and spiral tracheæ of the protoxylem. From one to five of these are differentiated. The mature condition is usually as follows: The first vessel is an annular one with the rings closer together than the first, or a spiral vessel very much stretched out. The succeeding ones formed centrifugally are spirals less and less elongated, and the youngest either has the tightest spiral or may be a reticulate vessel. Figures showing this are to be found in a number of text and reference works. Metaxylem vessels (pitted vessels when mature) appear after this; the phloem is differentiated about the same time. The metaxylem vessels are formed from the cells at the periphery of the strand (Fig. 8) in the inner half of the bundle, and the phloem begins to develop from the outer portion of the outer half of the bundle and develops centripetally.

At the outer edge of the strand the walls of the pericycle cells begin to thicken and lignification of the bundle begins. This continues until only the phloem cells and a few cells about the annular and spiral vessels remain as thin walled cells.

The protoxylem develops centrifugally, and the phloem develops centripetally for a time; then the cells of the phloem enlarge and in doing so press against the cells between them and the protoxylem so that these cells are flattened to appear as a cambium region. Chrysler has reported cambial activity in the grass bundle, but in Calamovilfa although the mature bundle of the aerial parts appears to have a cambium, it certainly does not, for the condition shown in Figure 9 is brought about in the manner described above. The divisions of the cells of the strand, before the xylem and phloem are differentiated, takes place throughout the whole strand as is shown by the accompanying figure (Fig. 10). Consequently the cells may continue to divide between the xylem and phloem in the region just above the nodes (Chrysler) which is the last to be completely lignified, and the pressure of the developing xylem and phloem causes the cells to take on the appearance of a cambium.

2. The Development of the Vascular Bundles Without Annular and Spiral Vessels.

The bundle (Fig. 1) found in the slow growing rhizome develops in a different manner. The desmogen strand develops just as in the bundle described above until the strand is made up of from twenty to fifty cells. Then there appear usually two (at times one to four) large cells which form the large pitted vessels of the bundle (Fig. 11). The cell walls of the pericycle at the outer edge of the bundle begin to thicken and the cells of the protoxylem become lignified, but no annular or spiral vessels are differentiated (except occasionally one and exceptionally two small ones) and all of the protoxylem cells are tracheids. The lignification, which started with the thickening of the cell walls of the pericycle and protoxylem, now continues until all of the cells of the bundle are thick walled and lignified (Fig. 1).

THE AMPHIVASAL BUNDLE.

The amphivasal bundle (Figs. 12 and 13) which one finds in the nodes and rhizome is brought about by the laying down of two vascular strands together which diverge and continue each as single strands. Sometimes the protoxylem vessels are not laid down, but usually in the aerial stem they are. Figure 12 shows the amphivasal bundle without annular or spiral vessels and Figure 13 shows an amphivasal bundle with a protoxylem spiral vessel. Chrysler has studied this condition in his paper on "The Nodes of Grasses" and states that the amphivasal bundle of the nodes is the fusion of two bundles and that in the basal portion of the plant this may continue through the internode. He also points out that the amphivasal bundle occurs more frequently in the rhizome and lower nodes of the plant than in the aerial nodes. This was found by the writer to be true in Calamovilfa. In Zizania, Chrysler finds that the amphivasal condition is most common where the nodes are crowded and that the same thing is true in the reproductive branch of corn, where the nodes are also crowded. Since the amphivasal bundle is so closely associated with the amount of elongation and the separation of the vascular strands, it is evident that here may be a means of studying the scattered vascular bundle that will lead to a better understanding of this condition in monocotyledons. That these structures will fit into the ordinary phylogenetic classification is not at all assured, although considered with other characters they may straighten up the relationships of the tribes and genera. Dr. Land, in his lectures, points out the great influence of the pericycle in the breaking up of the stele as the cambium activity becomes less pronounced. There is no doubt that a study of the pericycle and its development as well as a study of the endodermis will be of value for further investigations of the grasses and their inter-relationships.

THE MARKINGS OF THE XYLEM VESSELS.

According to Haberlandt there are five types of mature tracheæ in the xylem: annular, spiral, sclariform, reticulate, and pitted. All of these but the sclariform are found in Calamovilfa. As to the cause of the formation of these varying types, Haberlandt, Jeffrey, and others call attention to the fact that the annular and spiral vessels are related to the elongation of the stem or root, but they do not impress upon the reader the fact that annular and spiral thickenings are the direct result of elongation. Some writers even give the idea to their readers that they are annular and spiral to permit elongation rather than that they are the result of elongation.

In the rapidly growing aerial stem the first vessel to be laid down is usually observed to be either annular or spiral, succeeding vessels are closer spirals, and the last formed are reticulate or pitted. The writer finds that the type of vessels found in the mature condition varies with the amount of elongation, while the deposition of material forming the wall thickenings is going on. In very slow-growing stem tips no spirals are found, except occasionally a very tight one and occasionally an annular vessel. In elongating tips annular and spiral vessels of varying degrees are found in the protoxylem. The metaxylem tracheæ, laid down when elongation has practically ceased, are pitted vessels, or may be slightly reticulate.

In the rhizome with very short internodes the annular tracheæ are found occasionally, but few and scattered. These are the only protoxylem vessels found when any are found at all. In fast growing regions of the plant there are as many as five protoxylem annular and spiral vessels in the vascular bundles. In the internodes which are most elongated the elongation may be so great that the annular vessels are actually ruptured and even the surrounding parenchyma cells may be torn so that one finds the thickenings attached along the sides of a cavity. This is figured by Strasburger (page 122), and the cavity is readily demonstrated in corn and other grasses with a rapid development of aerial parts.

The above observation leads to a more careful study of the beginnings of these thickenings. Elongation occurs before these thickenings are lignified, and the thickened portion of the wall must be, therefore, in a more or less plastic state. A careful examination of the longitudinal sections of the desmogen strands showed that the first thickening is laid down in the pitted form, (Fig. 14). Still younger cells show a vacuolation of the cytoplasm, (Fig. 15), which causes it to line the wall in the same pattern as shown by the first wall thickenings. Apparently then, division and enlargement of the surrounding cells (Fig. 16) tears apart this wall thickening (Fig. 14) and the cell becomes annular, spiral or reticulate, depending upon the amount of stretching. If elongation has ceased, as it has when the thickenings of the metaxylem vessels occur, the wall remains in a pitted condition. In text figures one usually sees these vessels with the spirals and annular rings very regular. This is true to a remarkable degree; but there are many exceptions to this, for irregularity is common.

Thus it is shown that the types of tracheæ vary with the amount of elongation, maximum stretching causing the formation of the annular vessel, decreasing degrees of elongation causing spirals, reticulate, and finally pitted vessels, in the order named. This accounts for the fact that one does not find annular or spiral vessels in secondary wood, where sclariform, reticulate and pitted vessels occur.

It is common knowledge that plant structures vary when under different environmental conditions and it is evident from this study that the vascular structures are possibly not as static as they have been regarded, since the form of the protoxylem tracheæ, as well as the number of tracheæ, varies with the amount of elongation of the internode.

The physiology of the deposition of the thickenings of the xylem vessels is an open question. It may be that subsequent observations of anatomical variations of plants in extreme situations may throw some light upon the reasons for the thickening of the walls laid down in specific cells. It is known that less lignification occurs in hydrophytic than in xerophytic habitats, but this is a secondary thing, for, in Calamovilfa at least, lignification occurs after considerable thickening of the cell wall has taken place.

The failure of certain cells to divide in one plane and the ability to divide in another is the thing that leads to the development of the xylem vessels. The reason underlying the failure of the division at right angles to the main axis of the region of growth can at present be only a conjecture. (Dr. Land).

That the continued division and enlargement of the surrounding cells functions in the elongation of the protoxylem cells was called to our attention by Dr. Land from his work, as yet unpublished, on the origin of conductive strands. As soon as the division of the cells surrounding the xylem vessels ceases there are no more spiral vessels formed and all of the metaxylem vessels remain in the pitted condition.

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SUMMARY.

1. The first appearance of the vascular strands of Calamovilfa is the leaf primordia.

2. The vascular strand starts with a single cell.

3. In the elongating parts the order of development is as follows: Annular and spiral protoxylem elements, differentation of phloem and metaxylem at about the same time, and finally pericycle.

4. In the rhizome the vascular strand does not develop the annular and spiral protoxylem elements because of the failure of the elongation of the internode.

5. The amphivasal bundle of the nodes is brought about by the laying down of two bundles together which later diverge as simple strands.

6. There is no cambial activity in the vascular bundle of Calamovilfa.

7. A definite layer of dividing cells has not been found at the base of the internodes, but instead elongation occurs from a diffuse region of dividing cells.

8. The amount of elongation determines whether the tracheæ are annular, spiral, reticulate or pitted vessels.

9. The first thickening of all types of the tracheæ is pitted, and the walls are then stretched out by the division and enlargement of the surrounding cells so that they assume their mature form.

10. The original pitted thickening evidently arises by the vacuolation of the cytoplasm, this thickening being laid down by the thicker portions of the cytoplasm.

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EXPLANATION OF FIGURES.

Fig. 1. Vascular bundle of rhizome, no protoxylem vessels, phloem lignified.

Fig. 2. Vascular bundle of aerial stem, protoxylem vessels, (P).

Fis. 3, 4 and 5. Development of desmogen strand from single cell to four-celled stage.

Fig. 6. Desmogen strand showing appearance of sheath which disappears.

Fig. 7. Young vascular bundle showing beginning of lignification. The lower thickened cells are protoxylem vessels, the upper the first cells of the pericycle to be lignified.

Fig. 8. Young vascular bundle of aerial stem showing two protoxylem vessels and the beginning of the differentiation of metaxylem vessels and the phloem.

Fig. 9. Cross section of vascular bundle just above the node of aerial stem, showing four protoxylem vessels (one not showing thickening), and semblance of cambium.

Fig. 10. Desmogen strand showing the irregular division of cells throughout the strand.

Fig. 11. Young bundle of rhizome without protoxylem vessels, but showing the beginning of the differentiation of metaxylem vessels and phloem.

Fig. 12. Amphivasal bundle without protoxylem vessels.

Fig. 13. Amphivasal bundle showing a protoxylem spiral vessel, (X).

Fig. 14. A protoxylem cell showing the original pitted thickenings and spiral thickening in the same cell. The nucleus often remains after the cytoplasm disappears.

Fig. 15. Protoxylem cell showing characteristic vacuolation of the cytoplasm.

Fig. 16. Longitudinal section showing original cell of desmogen strand and divisions of surrounding cells which on enlargement stretch the cells in line with (X).

The Vascular Anatomy of Calamovilfa Longifolia,
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PLATE I.