The Root-Structure of *Dioscorea prehensilis*.

BY

T. G. HILL, A.R.C.S., F.L.S.,

Demonstrator in Biology at St. Mary's Hospital Medical School, London.

AND

MRS. W. G. FREEMAN, A.R.C.S.

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With Plate XIX, and a Figure in the Text.
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THE publication of a paper by Dr. D. H. Scott¹ placed botanists in possession of two new examples of spine-bearing roots. Of the plants considered one, *Dioscorea prehendens*, Benth., forms the subject of the present communication.

The plant described by Dr. D. H. Scott was grown at Kew, and the tuber was entirely a subterranean organ. It appears, however, that in the natural state the tuberous stem is almost entirely an aerial structure, a fact which is very clearly demonstrated by a photograph of the wild plant, taken by Mr. G. F. Scott-Elliot. The following interesting remarks are quoted from a letter from Mr. G. F. Scott-Elliot to Dr. Scott, which the writer has kindly allowed us to make use of. 'The plant was, I should say, 7 feet high and completely covered by the arched roots. . . . It was photographed and collected in a day's march, and there is not, I think, very much Natural History to be found from such hurried observations. I have an impression that this country has many wild boar who are possibly the enemy. It is not,

¹ Scott, D. H.: On two new instances of Spinous Roots, *Annals of Botany*, vol. xi, 1897.

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I think, a forest district, but it is in the "Acacia zone," i.e. scattered trees of Acacia at 20 to 30 feet apart and the colour of the soil showing through a scanty sedge and grass sward. Game is abundant in the neighbourhood, man is absent. The climate is very dry, but there is probably underground water within 20 feet of the surface. There may be no rain for nine months or so.'

In the material at our disposal the thick roots possessed spines which varied in their characters according to the state of their development. The youngest, although often fully grown, were quite soft and gradually tapered off into a fine termination bearing rootlets in the ordinary manner; others were quite hard and sharp. The question which here arises is whether the normal root-ending of some of the softer spines represents a normal condition or not. It will be borne in mind that the large spine-bearing roots are, in the natural state, aerial; and the possibility is not excluded, indeed it is very probable, that under these circumstances the spines when above ground do not terminate in a normal root; this condition only obtaining when the organs are buried.

It is not possible to clear up this point here, inasmuch as the necessary evidence is as yet wanting. However, dealing with the roots at our disposal, it is seen that the absorbing end of the spinous root sooner or later drops off, leaving behind a perfect sharply-pointed spine. This may be explained either on physical or physiological grounds. It was noticed that on dropping into clove oil a spine which had not yet lost its apical region, it immediately curled up at the tip, became brittle, and on being touched separation took place between the absorbent tip and the thick basal part. Something similar to this may occur naturally in the buried roots, although it is much more probable that the absorbent tip shrivels up hopelessly during the dry season. On the other hand the breaking may be due to the cutting off of food-supplies, for the cortex generally has a withered appearance before the actual severance takes place. And further, the sieve-plates in the basal parts of the spinous roots were

invariably blocked by callus, which fact probably points to the conclusion that the cause is physiological rather than mechanical.

The breaking is not effected at any one particular point; there is rather an ill-defined region where the transverse severance may occur.

Sections taken above and below the rupture, where the apical region was preserved, exhibited no anatomical characters such as are found in the separation-layer of a leaf.

The first sign of breaking in a young spine (Pl. XIX, Fig. 1 C) is a slight brown annular discoloration in the region indicated by the line *X-Y*, and sections show that here the softer tissues are withering. The portions of the root nearer the apex appear quite healthy, hence it is obvious that the rupturing is not caused by the mere dying of the tissues from the apex backwards.

In a more developed spine the discoloration-zone is seen to be still more marked and the separation is almost complete, connexion only being maintained by shreds of cortex (Fig. 1 D).

Besides these large spine-bearing roots the tuber also possesses much smaller roots, having numerous lateral root-lets which are clearly absorbent in function. These secondary roots, after dying off, also leave behind a small hard spine similar to those of the larger roots; a fact which has already been pointed out by Dr. Scott¹. Indeed, it may be stated at once that there is no essential difference either in the morphology or anatomy between the two varieties of roots, the dissimilarity being only in the size.

STRUCTURE.

Our knowledge of the anatomy of the roots of the Dioscoreaceae is based chiefly on the researches of Bucherer² who, in his work on the anatomy of this natural order, confines

¹ Loc. cit., p. 329.

² Emil Bucherer: Beiträge zur Morphologie und Anatomie der Dioscoreaceen, Bib. Bot., Heft 16, iii, 1889.

himself chiefly to the origin, &c., of the roots and the characters presented by their bundle-sheath in species of *Tamus* and *Dioscorea*. Further, he confirms Treub's¹ statements regarding the differentiation of the root-apex of *Tamus communis*, and disagrees with those of Janczewski.

Anatomy of the large spine-bearing roots.

These roots attain a diameter of .7 cm. and, as regards their structure, conform to the general monocotyledonous type. There are, however, certain interesting features exhibited which render a brief account of their structure not altogether out of place. The apex is somewhat blunt, and is made up of an enormous number of very small cells. Inasmuch as our material contained but one good and one indifferent apex, it was not possible unfortunately to investigate thoroughly the apical differentiation; however, it appears most probable that there is, in this plant, no definite calyptragen layer as has already been asserted by Treub¹, and confirmed by Bucherer², to be the case in the Dioscoreaceae among other Natural Orders.

From a series of transverse sections through the apex it may be seen that the central cylinder is of normal diameter, and before either the phloem or xylem is differentiated a number of canals or vessels are formed in the more central regions, roughly arranged in a circle within the zone which eventually will be occupied by the phloem and xylem. The development of these vessels is extremely remarkable and quite dissimilar to what obtains in other plants as far as is indicated by existing accounts. They are produced not merely by the obliteration of the end-walls of elements situated one above the other, but also by the breaking down of the lateral walls of contiguous cells in a transverse plane. It is not suggested, however, that these structures are formed wholly by such a lateral fusion of elements; for tracing them downwards from the apex it is found that they originate as

¹ Treub: Le méristème primitif de la racine dans les Monocotylédones. Leiden, 1876.

² Loc. cit.

a single row of elements somewhat larger than the surrounding cells. Only one case was seen in which the appearance of

FIG. 19.—1-6 illustrating the origin of one of the central vessels of the large spine-bearing roots. 7-12 showing the cell-walls within the lumen.

the first origin of a central vessel suggested an initial absorption of the lateral walls of contiguous cells (Text, Fig. 19, 1-6). Increase in size takes place, and sooner or later transverse walls, in varying stages of completeness, are seen stretching across the lumen. The majority of these

walls shows signs of disintegration, and their presence may be seen in several successive sections. Further, the nuclei of the cells originally bounded by these walls are very obvious (Pl. XIX, Fig. 2; and Text-Fig. 19, 7-12).

Further back the lumen is again quite clear and contains but few nuclei, but still nearer the base of the root a large number of nuclei, sometimes as many as twelve in a single transverse section, occur at various levels marking the regions where the fusion of a number of cells took place.

The only obvious explanation which will account for the foregoing facts is that these central vessels arise very generally as single rows of elements, but the initial cells of any one vessel may not always be situated immediately one above the other to form a continuous string as in many cases, but are separated by intervening cells the walls of which ultimately break down, and so there is produced a continuous vessel. It sometimes happens that these vessels may not reach a great length, for although many may be traced through, relatively speaking, long distances, some come to an end quite suddenly; this more especially was found to be the case when two had been formed quite close together and separated only by the common wall. Finally they become lignified in common with the other parts, with the exception of the phloem, of the vascular cylinder, and possess bordered pits. Whether or not this curious development is due to the fact that the roots examined were from an abnormally grown plant, cannot be decided at present. It is hoped that more material will be obtained and the matter investigated further.

The structures above described are not the only ones which are multinucleate, for certain of the *inner* vessels of the metaxylem, which are the *first* to originate, together with the larger sieve-tubes, frequently have as many as four or five nuclei at one level¹. It is doubtful whether these follow the

¹ Since this present paper was written, it has been found that Buscalioni in a recent preliminary communication ('Sull' anatomia del cilindro centrale nelle radici delle Monocotiledoni,' *Malpighia*, 15, 1902) has drawn attention to the fact that the mother-cells of the tracheae of the roots of the Dioscoreaceae and

course of development already described for the central vessels; in the case of the sieve-tubes there is absolutely no evidence to show that such is the case.

Before the differentiation of the xylem and phloem, adjacent cells fuse together at various parts of the cortex to form mucilage reservoirs. These are very numerous; in one transverse section as many as 130 were counted, and they develop rapidly. Eventually they become filled with bundles of raphides, and these may possibly subserve a protective function for the period during which the root remains soft. In longitudinal section these sacs are seen to be long, and they are situated one above the other forming long strings.

The central cylinder increases in diameter, and as it does so the vascular elements are differentiated. As in many roots of Monocotyledons the number of phloem- and xylem-groups is very large, thirty of each being not an uncommon number in the plant under discussion.

Sieve-areas occur on the lateral walls of the larger sieve-tubes, and a well-marked exodermis is present at the periphery of the cortex.

There is nothing further worthy of record until the general lignification of the vascular strand sets in. The first portions to thicken are the regions immediately external to the phloem-groups. This is illustrated in Figs. 3 and 4, from which it may be seen that a crescentic mass of fibres encase the external region of the phloem.

In order to ascertain whether or not this peculiarity obtained in other plants of the Dioscoreaceae, the roots of *Tamus communis* and an unnamed species of *Dioscorea* (labelled Pehio Yam) were examined. In both cases, although the lignification may become general, it was found that the regions external to the phloem-groups were not remarkable in being the first to be so markedly lignified.

Returning to the case of *Dioscorea prehensilis*, induration proceeds inwards towards the centre of the stele, and out-Asparagaceae are multinucleate; he also finds that the development of the xylem is centrifugal.

wards; the tissue external to and opposite the phloem-groups is, however, much thicker-walled.

Finally the cortex withers, and thus are formed roots of a high degree of hardness and bearing spines, the structure of which will be considered below.

For the sake of comparison the smaller and less modified roots, the essential function of which is absorption, were examined. These organs do not depart in any important feature from those of the larger roots as set forth above. Those differences that do obtain are to be solely attributed to the relatively large size of the latter as already described; thus instead of possessing thirty xylem-groups, the smaller roots never exhibited more than eight or ten. As regards histological features there are again no essential features of difference between the two forms, and in both the tissue directly bordering on the outer side of the phloem is the first to become lignified.

Figs. 5 and 6 illustrate the structure of these smaller roots.

Anatomy of the large spines.

These thorns originate as very thick lateral roots (Fig. 7), and it is only at the extreme apex that a normal root-structure can be discerned. The phloem and xylem of the spines are connected respectively to the similar tissues of the parent root by a large number of strands. In the case of the phloem these connecting strands are very numerous, being often related to as many as half the total number of phloem-groups present in the parent root (Fig. 7).

A transverse section near the base of a spine shows the phloem to be distributed around the periphery of the central cylinder in small groups isolated one from the other (Fig. 8), the xylem being restricted to two large lateral masses with smaller groups lying between them; these latter are the first to fuse with the xylem of the main root.

The examination of a series of sections from the base to the apex of a thorn shows that the phloem-strands travel in an irregular manner throughout the whole area of the stele.

Their course is sinuous, and as the apex is reached they anastomose with one another; hence just behind the extreme apex of a young spine it is found that there are but few phloem-groups, and these are arranged in quite a normal manner (Fig. 9, *a-e*).

This wide scattering of the phloem, coupled with the numerous connexions with the corresponding tissue of the main root, is probably to be correlated with the induration of the fully developed spine; for it is obvious that during the process of lignification much material, relatively speaking, must be required and must be well distributed for the purpose. The arrangement of the tissue in question is excellently adapted to facilitate such a process of lignification on a large scale.

Tracing the course of the xylem in a similar manner, it has already been stated that at the extreme base of the thorn the xylem is chiefly restricted to two large peripheral (just within the phloem-ring) masses, somewhat crescentic in shape, and that between these, smaller groups—which are the first to be connected with the xylem of the parent root—occur. The junction is effected chiefly by very short tracheides.

Sections cut nearer the main root exhibit longitudinal strands of xylem between the two crescentic masses; these represent the xylem rays of the parent root.

Passing towards the apex of the spine it is found that the xylem is more evenly distributed, and is generally restricted to the more central regions. As the apex is reached it diminishes in amount and gradually takes up a position towards the centre of the stele (Fig. 10). At the extreme apex it is generally aggregated into three or four groups alternating with the phloem in a normal root-like manner.

The abnormalities above described may at first sight appear remarkable, especially when a fully matured spine is examined; but it is to be borne in mind that no induration of the parenchymatous tissue sets in until the lateral root has attained its maximum size. The soft ground tissue of the basal region of the spine is the first to become lignified,

and the peripheral parts of the stele thicken up before the more central.

Fig. 11 illustrates the structure of a spine viewed in transverse section. A mature spine is seen to be made up chiefly of elements with very thick lignified walls, amongst which are scattered small isolated groups of phloem and conducting xylem-elements. The cortex of younger thorns possesses tannin-cells, and sometimes these elements may be found in the stele.

In longitudinal section it is seen that fibres predominate; the phloem pursues an irregular path, and cross-connexions occur between neighbouring groups. Sieve-plates may be observed at rare intervals, and the conducting xylem-elements are much longer in the central regions than those, already described, at the base.

SUMMARY.

1. In the natural state the tuberous stem is aërial.
2. The tuber possesses large spine-bearing roots, and smaller roots chiefly absorbent in function. The lateral rootlets of the latter, after dying off, leave behind a small hard spine similar to those of the larger roots.
3. The large spines of the material examined, when in the young state, tapered off into a normal root-ending. This absorbing end of the lateral spinous root eventually separates off, leaving behind a perfect spine.
4. Induration of the vascular cylinder of the thorn does not set in until the maximum size has been attained.
5. The apex of the large spine-bearing roots has no definite calyptrogen layer.
6. The central vessels of these organs are multinucleate and appear to be produced not merely by the obliteration of the end-walls of elements situated one above the other, but also partly by the breaking down of the lateral walls of contiguous cells in a transverse plane.
7. Certain of the inner vessels of the xylem-rays, the

development of which is centrifugal, are also multinucleate, as also are some of the larger sieve-tubes.

It is doubtful whether these structures follow the same course of development as the central vessels.

8. The vascular strands of the spine-bearing roots become very hard, the regions immediately external to the phloem-groups being the first to become lignified.

9. The large spines originate as thick lateral roots, and it is only at the extreme apex that a normal root-structure obtains.

10. At the base of these thorns the phloem-groups are arranged in a circle at the periphery of the central cylinder; as the apex is reached it is seen that the phloem-strands travel in an irregular manner throughout the whole area of the stele. Their course is sinuous, and they anastomose with one another; at the extreme apex the phloem consists of but few strands arranged normally.

This arrangement is probably to facilitate the extensive lignification of the spine.

11. At the base of the thorn the xylem is chiefly restricted to two large peripheral masses just within the phloem-ring. Towards the apex the xylem is more evenly distributed, and gradually takes up a position nearer the centre of the stele.

EXPLANATION OF FIGURES IN PLATE XIX.

Illustrating Mr. Hill's and Mrs. W. G. Freeman's paper on *Dioscorea prehensilis*.

Abbreviations: *end.*, endodermis; *p.c.*, passage cell; *ph.*, phloem; *ph.s.*, phloem-strand; *xy.*, xylem.

Fig. 1. Portion of a large spine-bearing root.

Fig. 2. Illustrating the development of the large vessels in the inner regions of the vascular cylinder of a large spine-bearing root.

Fig. 3. Part of a transverse section of a similar but older root, showing the highly lignified tissue external to a phloem-group.

Fig. 4. Similar section from an older root.

Fig. 5. Diagram of a transverse section of one of the smaller absorbent roots.

Fig. 6. Portion of Fig. 5 in detail.

Fig. 7. Diagram, showing origin of a large spine.

Fig. 8. Diagrammatic transverse section near the base of a spine, showing the disposition of the phloem and xylem.

Fig. 9. Diagrams of a series of transverse sections of a spine, illustrating the gradual fusion of the phloem, from the base (*a*) to the apex (*e*); stele only represented.

Fig. 10. Diagram of a transverse section of the vascular cylinder of an immature spine.

Fig. 11. Transverse section of part of the stele of an older spine, but still not fully developed.