RESEARCH PAPERS

STRUCTURE OF THE ROOTS OF *DATURA STRAMONIUM* L. AND *DATURA TATULA* L.*

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Received February 3, 1955

INTRODUCTION

RECENT work on the locus of synthesis of alkaloids in plants belonging to the family Solanaceæ has directed attention especially towards the roots of these plants. Descriptions of the structural characters of belladonna root are included in some of the standard books of reference[1,2], and a detailed, fully illustrated account of this root and that of *Atropa acuminata* has been published by Melville[3]. The roots of species of datura, however, have not been so thoroughly investigated. The root of *Datura stramonium* was included in the United States Pharmacopœia from 1842 to 1863, but no description was given of the morphological or structural characters of the drug. A brief, unillustrated account of the structure of the root of this species was included in a description of the anatomy of the roots of several solanaceous plants published by Lewinsky[4] in 1924. The most complete account is that included in a thesis by Fischer[5] embodying the results of a study of the morphology of the entire plant of *Datura stramonium*. This description, however, is illustrated mainly by some photomicrographs from which it is difficult to interpret the details of the individual cells; also, very few records of measurements are given.

It seemed desirable, therefore, to make a more detailed, illustrated account of the macroscopical and microscopical characters of the root of *Datura stramonium* and its allied species *Datura tatula*.

MATERIAL

The mature plants used in this investigation of the anatomical structure of the roots of *Datura stramonium* and *Datura tatula* were obtained from several different sources. These are set out in the table on the opposite page.

No differences either in gross morphology or in structure were found between the roots of *Datura stramonium* and *Datura tatula*. Similarly, no differences were found in the root of the *inermis* variety of *Datura stramonium*. The description of the structure of the root of *Datura stramonium* which follows, therefore, would serve equally to describe the roots of *Datura tatula* and of *Datura stramonium* var. *inermis*.

MACROSCOPICAL CHARACTERS

The tap root (Fig. 1, A) grows to a length of from 12 to 30 cm., and has a diameter at the crown of 0·5 to 2 cm.; it is pale buff coloured

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* The subject-matter of this communication forms part of a thesis by one of us (B.P.J.) accepted by the University of London for the degree of Doctor of Philosophy.

externally and bears numerous slender side roots for a length of about 2 to 4 cm. from the crown, the lateral rootlets then diminish in number. These rootlets are attached to the tap root at positions scattered irregularly over the surface and no clear relationship can be traced between the arrangement of the laterals and the diarch structure of the primary xylem. Frequently a nearly full-grown tap root diminishes in vigour of growth towards the apex, and one or two lateral roots arising 4 to 6 cm. above the growing point develop more strongly and become larger than the tap root itself.

Sample number	Habitat	Date of collection
Datura stramonium		
1	Chelsea Physic Garden	August, 1949
2	Chelsea Physic Garden	October, 1950
3	Chelsea Physic Garden	September, 1952
4	Oxford Botanic Garden	October, 1949
5	Edinburgh Botanic Garden	October, 1949
Datura stramonium var. *inermis*		
6	Chelsea Physic Garden	October, 1949
7	Edinburgh Botanic Garden	October, 1949
8	Oxford Botanic Garden	October, 1949
Datura tatula		
9	Chelsea Physic Garden	October, 1949
10	Chelsea Physic Garden	September, 1952
11	Oxford Botanic Garden	October, 1949
12	Royal Botanic Gardens, Kew	October, 1949

The transversely cut surface (Fig. 1, C) exhibits an outer cortex about 0·25 mm. wide, a phloem region about 0·25 mm. wide; the xylem occupies the remainder of the diameter. The xylem is traversed by two primary and fairly numerous secondary medullary rays; the xylem proper is composed of lignified vessels embedded in a ground tissue which is composed of parenchyma with a few fibres, or mainly fibres with a little parenchyma, the whole being more or less lignified according to the age of the portion of the root examined. Nearer the crown of full-grown roots the secondary xylem cylinder becomes more parenchymatous in the central region owing to the presence of islands of unlignified parenchyma with interxylary phloem.

The lateral roots mostly attain a length of about 12 to 14 cm. but they remain quite slender, having a diameter rarely exceeding 3 mm.; they bear numerous tertiary rootlets about 0·5 mm. in diameter and 1 to 3 cm. in length.

Immediately above the crown of the root there is a region extending for about 0·75 to 1 cm. in which the gradual change from root to stem structure takes place (*d* to *e*, Fig. 1, A); above this the remainder of the underground part of the plant (about 0·5 to 1·5 cm. in length) is hypocotylary in origin and shows typical stem structure. This region continues to bear numerous scattered lateral rootlets and externally it is indistinguishable from the tap root below it. The scars of the cotyledons are seen about 2 to 4 cm. above the level at which the first rootlets are produced, so that the whole of the hypocotylary region extends for about 3 to 6 cm. (*d* to *f*, Fig. 1, A).

Although the root of *Datura stramonium* is normally a tap root, frequently, as a result of transplanting, the growth of the main root is arrested at an early stage and a fibrous root system is developed (Fig. 1, B).

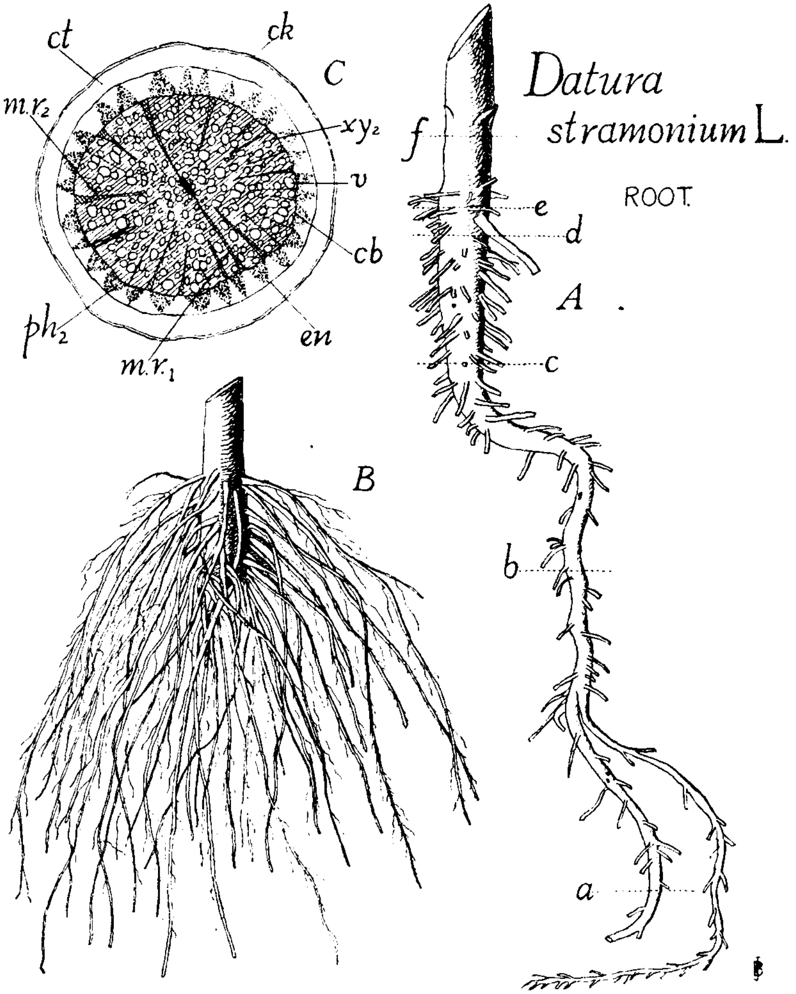


Fig. 1. Root of *Datura stramonium* L. *A*, mature tap root $\times \frac{1}{2}$. *B*, mature root of a plant from a transplanted seedling showing the resulting fibrous root system $\times \frac{1}{4}$. *C*, diagram of a transverse section cut near the apex of a mature tap root $\times$ 12. The broken horizontal lines marked *a* to *f* on the root *A* indicate the positions at which transverse sections have been made to illustrate the structure at these levels, see Figs. 2 and 8. *cb* = cambium; *ck* = cork; *ct* = cortex; *en* = endodermis; $m.r._1$ = primary medullary ray; $m.r._2$ = secondary medullary ray; ph_2 = secondary phloem; v = vessel; xy_2 = secondary xylem.

In such specimens the main root attains a diameter at the crown of up to 4·5 cm., but it is only about 6 to 7 cm. long. It bears along its length very numerous scattered lateral roots, most of which are about 15 to 20 cm. in length and up to about 5 mm. in diameter.

The structure of several of these transplanted roots was examined. It was found that the thickened crown of the roots is more strongly lignified than the corresponding position in a tap root; also the structure is complicated by the very extensive development of lateral roots. In general, however, there is no significant difference between the structure of such roots and that of the normal tap roots described in the following pages.

HISTOLOGICAL CHARACTERS

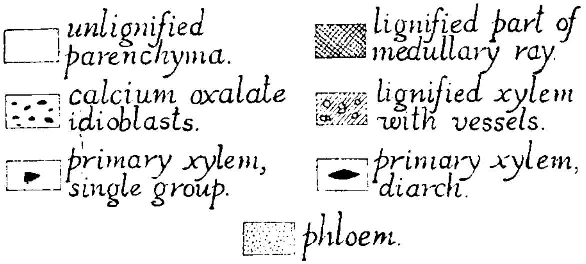
In general, the roots of the numerous plants examined showed similarity of structure, and the differences which were observed are probably attributable to variations in habitat, method of cultivation and time of collection. These differences consist of variations in the amount and distribution of the parenchyma and in the degree of lignification of the elements of the secondary xylem, and they are included in the account of the secondary structure which follows.

Sections cut at different positions along the length of the root demonstrate the increase of parenchyma as the root ages and the development of the groups of sieve tissue in the secondary xylem; for this reason the structure is described separately at the different levels *a*, *b*, *c* and *d* as indicated on root A, Figure 1, the position *d* corresponding to the crown of the root. The structure of the hypocotyl, including the changes which occur in the transition from root to stem, is described after considering the structure of the root proper.

A. STRUCTURE OF THE ROOT

Structure at a (see Fig. 1, A; Fig. 2, A).

PERIDERM. Externally there are 1 to 3 layers of rectangular cork cells measuring about R 18 to **30** to 52 μ, T 18 to **35** to 75 μ and L 60 to **85** to 120 μ, with suberised and sometimes slightly lignified walls (Fig. 3, B). Outside the cork the exodermis is occasionally found, the walls of which have become suberised; the piliferous layer is missing, or may be represented by fragments of the walls as shown in Figure 3, A. Frequently, probably as a result of damage, no periderm is found and the cell walls of the outer layers of the cortex have become suberised. Within the cork is a layer of *phellogen*, which arises in the layer of cortex immediately inside the exodermis (see Fig. 3, A). Phelloderm is not developed.



Key to Figures 2, 5, 6, 7 and 8.

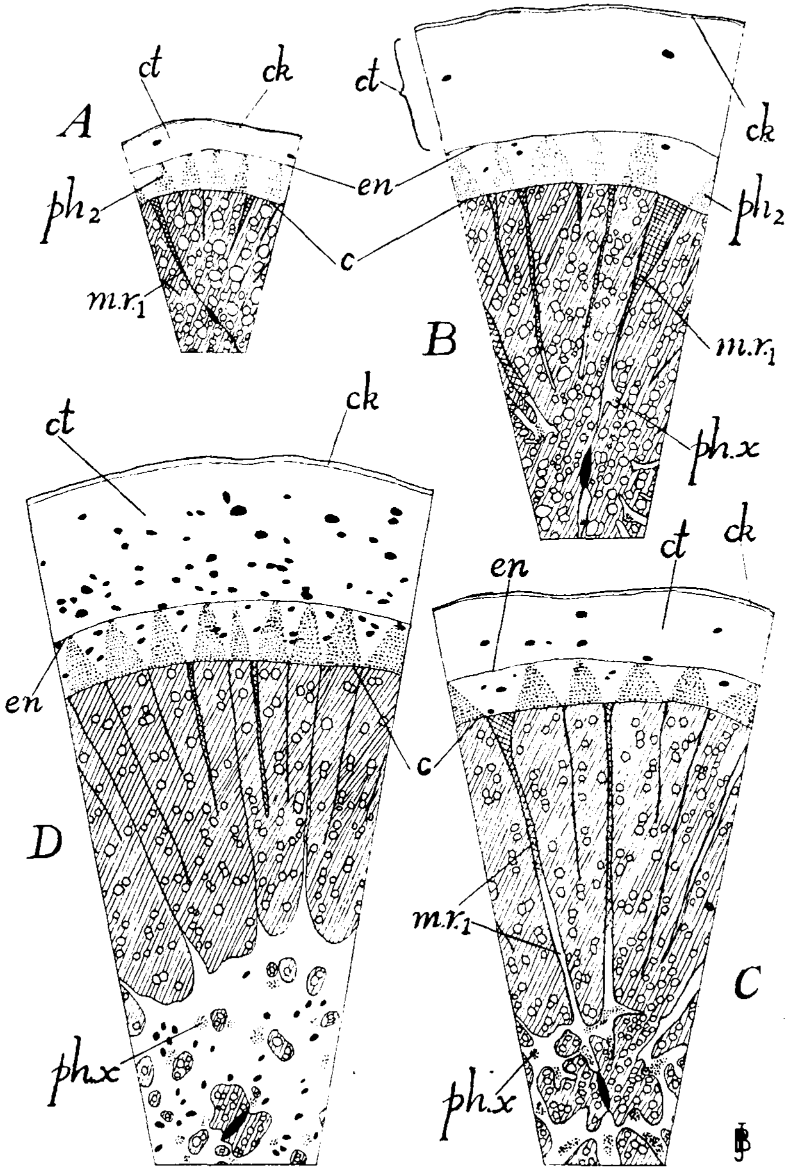


Fig. 2. Root of *Datura stramonium* L. *A*, *B*, *C* and *D*, diagrams of transverse sections of a tap root cut at four different levels marked *a*, *b*, *c* and *d* respectively on *A*, Fig. 1. *A*, from near the apex, shows a mass of secondary xylem in which unlignified parenchyma has not yet formed. *B*, which is 9 cm. above *A*, shows small areas of unlignified parenchyma in the secondary xylem; in several of these areas small phloem groups are present. *C* is a section taken 7 cm. above *B*, and shows the gradual increase in the unlignified parenchyma and in the development of the groups of phloem. In *D*, which represents the crown of the root, the rapid development of unlignified parenchyma in the central region has resulted in the splitting of the lignified elements into isolated groups and the formation of several interxylary groups of phloem; calcium oxalate is abundant in all the parenchymatous tissues. All × 15. *c* = cambium; *ck* = cork; *ct* = cortex; *en* = endodermis; *m.r.*$_1$ = primary medullary ray; *ph*$_2$ = secondary phloem; *ph.x* = interxylary phloem. For further details see Key on page 387.

The CORTEX consists of from 4 to 6 layers of thin-walled, somewhat tangentially-elongated cells about R 15 to **50** to 75 μ and T 60 to **90** to 120 μ, with small intercellular spaces; several of these cells contain microsphenoidal crystals of *calcium oxalate*; the size of the crystals varies considerably, the larger ones measuring up to 18 μ in greatest length. The *endodermis* is clearly distinguished; it is composed of a layer of

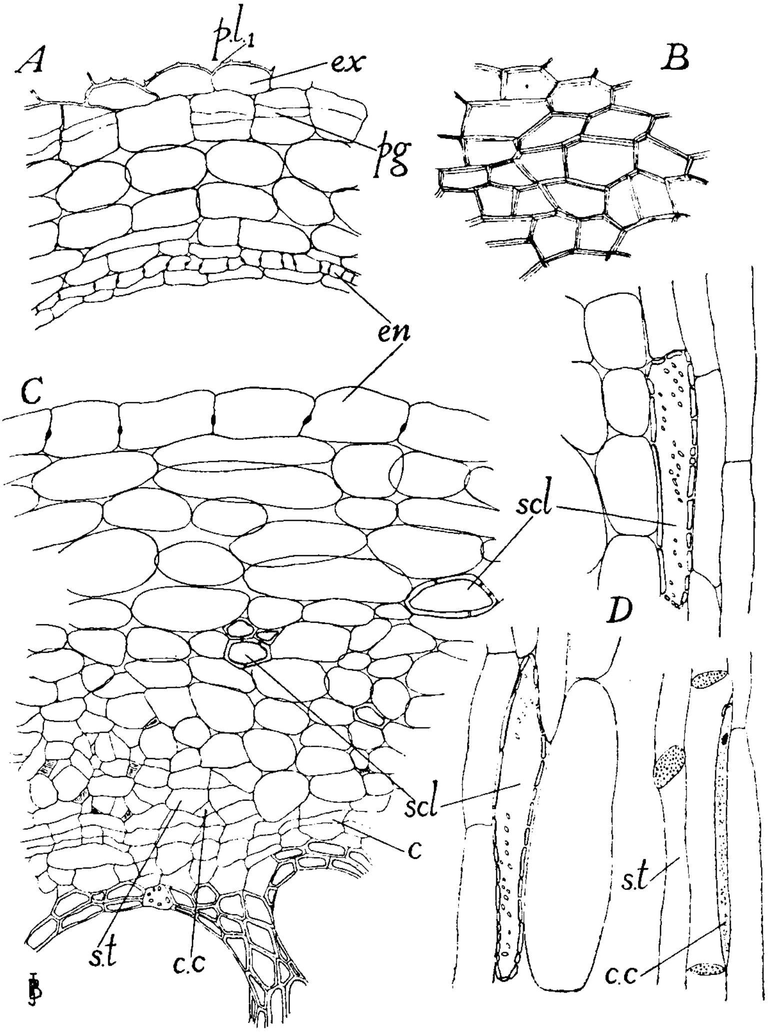


Fig. 3. Root of *Datura stramonium* L. Details of tissues external to the cambium. *A*, transverse section of the outer tissues of a young root showing the origin of the phellogen in the layer of cortex cells immediately inside the exodermis. *B*, cork in surface view. *C*, endodermis and phloem from a mature root as seen in transverse section. *D*, details of the phloem as seen in longitudinal sections. *A* and *B* × 115, *C* and *D* × 200. *c* = cambium; *c.c.* = companion cell; *en* = endodermis; *ex* = exodermis; *pg* = phellogen; *p.l.*$_1$ = remains of piliferous layer; *scl* = sclereid; *s.t* = sieve tube.

longitudinally-elongated, more or less regular cells, rectangular in transverse section, R 15 to 18 μ, and T 18 to 45 μ, with straight radial walls and no intercellular spaces. The casparian strip is narrow, being about one-quarter of the width of the radial wall; it varies somewhat in position and is most frequently found nearer the inner tangential walls of the cells. Starch is almost absent from these tissues; a very few small rounded granules occur measuring 3 to **4·5** to 6 μ in diameter.

The PERICYCLE, which is composed of a single layer of cells in the seedling, has become a band of 3 or 4 layers of large, thin-walled, somewhat tangentially-elongated parenchymatous cells.

The PHLOEM, which consists of sieve tubes and companion cells, with thin-walled parenchyma, forms a layer from 4 to 6—occasionally up to 12—rows in depth. The diameter of the sieve tubes is from 9 to **12** to 15 μ, and the length of the component elements varies from 180 to 220 μ (Fig. 3, C and D). The primary phloem is not clearly distinguishable. The *medullary rays* are numerous and from 1 to 4 cells wide; they are composed of large thin-walled parenchymatous cells which become elongated tangentially in the outer part of the phloem. Scattered in both the pericycle and the phloem, singly or in groups of 2 or 3, there occur occasional thick-walled sclereids measuring 21 to 40 μ in diameter, and 90 to 270 μ in length. The walls of these cells are slightly lignified, and have numerous simple pits in oblique rows (see Fig. 3, C and D). Microsphenoidal crystals of calcium oxalate are found in some of the cells of the pericycle and of the medullary rays of the phloem.

The CAMBIFORM TISSUE consists of 3 to 6 layers of rectangular cells R 6 to 12 μ, T 9 to 21 μ and L 65 to 90 μ, and forms a complete ring.

The PRIMARY XYLEM is diarch, and the 2 groups of primary xylem, each consisting of 4 to 6 protoxylem elements together with several larger metaxylem elements, are joined to form a double wedge-shaped strand appearing in transverse section as a narrow rhomboidal area at the centre of the root. The two *primary medullary rays* are clearly defined and usually can be traced through the diameter of the secondary xylem; they are from 2 to 4 cells broad in transverse section and are composed of lignified parenchyma, each having a small area of 1 to 6 smaller, thin-walled, unlignified cells abutting upon the protoxylem.

SECONDARY XYLEM. The structure of the secondary xylem varies in the specimens examined. In the majority of the roots the vessels occur singly or in groups of 2 or 3, and are scattered uniformly throughout the xylem; a few tracheids and a small amount of xylem parenchyma are associated with the vessels, and the remainder of the xylem, apart from the numerous secondary medullary rays, is composed of fibres, the whole being more or less lignified. In one specimen from the Oxford collection (sample 4), however, the transverse section at the position *a* shows a smaller number of vessels, which are arranged approximately in concentric rings, and the spaces between the vessels are filled almost entirely with unlignified parenchyma, the fibres occurring only in small groups near the vessels (see Fig. 5, A). In these roots the vessels and the fibres are the only lignified elements. A similar structure is shown by specimens from one of the Chelsea collections (sample 1).

The roots of the Edinburgh collection (sample 5) also show a different structure in the secondary xylem in this position. In these the xylem is more densely constructed, being composed mainly of thick-walled, strongly lignified fibres; the vessels are scattered and not very numerous, and the tracheids and xylem parenchyma associated with the vessels are strongly lignified, as also is the parenchyma of the medullary rays (see Fig. 6, A).

The *vessel elements* (Fig. 4, B2) measure from 72 to **115** to 135 μ in diameter, and are about 120 to 400 μ in length; usually the walls bear numerous spirally arranged bordered pits, but occasionally a reticulate type of thickening is developed. The end walls are frequently oblique; the perforations then appear as oval or rounded openings on the oblique walls, and the tips of the vessel segments are often elongated into narrow points. Many of the vessels, particularly those in the older, first-formed part of the secondary xylem, have thin-walled rounded thyloses, which are lignified and have a diameter of about 25 to 30 μ (Fig. 4, A). The *tracheids* (Fig. 4, B1) are associated with the vessels; they have a maximum diameter of 18 to 27 μ and measure 210 to 320 μ in length; their walls are lignified and fairly thick and bear numerous elliptical bordered pits which are spirally arranged. The ends are rounded or oblique and slightly tapering.

The *fibres* (Fig. 4, B1), which usually form the ground tissue of the xylem, measure 480 to 750 μ in length and 12 to 24 μ in diameter. The ends are frequently much elongated and often forked and notched to fit into adjacent elements. The walls are fairly thick, usually only slightly lignified, and have slit-shaped simple pits. Many intermediate forms between fibres and tracheids occur; they have elongated ends and elliptical bordered pits.

The *xylem parenchyma* (Fig. 4, B1) accompanies the vessels and consists of vertical rows of 2 to 4 cells with the end cell of each row tapering at one end. The walls are only slightly thickened, are usually lignified and bear numerous simple or bordered pits. They measure R and T 15 to 27 μ, and L 63 to 135 μ.

The *secondary medullary rays* (Fig. 4, C) are parenchymatous and are 1 to 3 cells broad in transverse section. The individual cells (Fig. 4, B2) are rectangular and measure R 21 to **30** to 66 μ, T 12 to **20** to 30 μ and L 30 to **42** to 65 μ; they have numerous simple or bordered pits and most of them are lignified to some extent.

Calcium oxalate and starch are absent from all the tissues within the cambium.

Structure from a *to* d (see Fig. 2, B and C).

In all the roots examined having the structure at *a* described above, the secondary xylem from *a* upwards towards the crown of the root becomes gradually more densely constructed in the outer region nearer the cambium and more parenchymatous in the central region, where also the interxylary phloem is developed. A transverse section cut in the region of *b* (Fig. 2, B) shows an increase in the size of the areas of unlignified parenchyma in the innermost part of the primary medullary rays, and

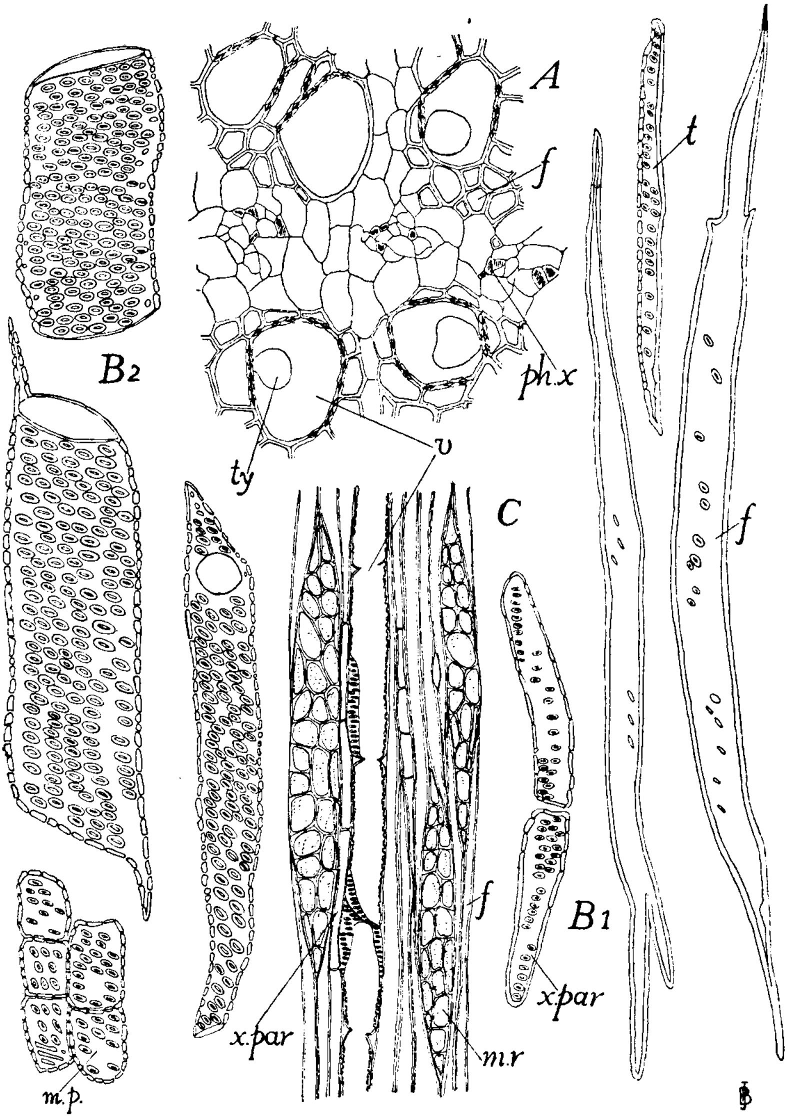


Fig. 4. Root of *Datura stramonium* L. Details of the structure of the secondary xylem. *A*, details of part of the section shown in *D*, Fig. 2, showing three groups of interxylary phloem and thyloses in the vessels. B_1, tracheid, fibres and cells of the xylem parenchyma. B_2, three vessel segments and a group of medullary ray parenchyma. *C*, part of a tangential longitudinal section from the lower part of a mature root. *A*, B_1 and B_2 × 200. *C* × 115. *f* = fibre; *m.p.* = medullary ray parenchyma; *m.r.* = medullary ray; *ph.x.* = interxylary phloem; *t* = tracheid; *ty* = thylose; *v* = vessel; *x.par* = xylem parenchyma.

other similar small areas of 2 to 3 cells have appeared in the central region adjacent to the broader secondary medullary rays. At the position corresponding approximately to *c* (Fig. 2, C), the number and size of

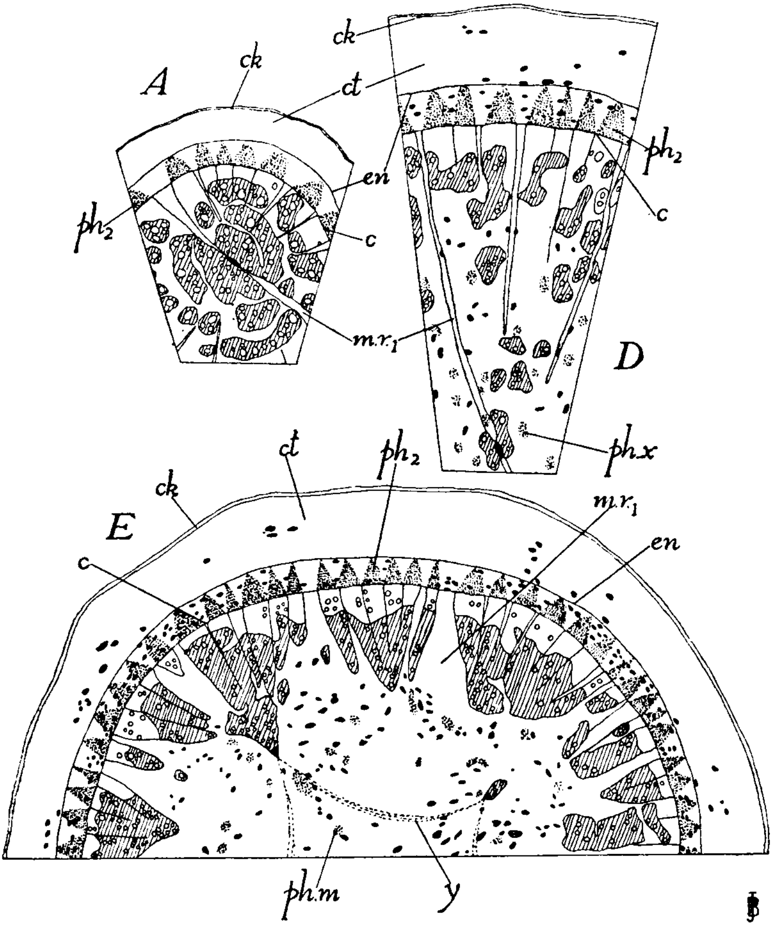


Fig. 5. Root of *Datura stramonium* L. Diagrams of transverse sections of the root of a plant grown at Oxford showing a type of root in which parenchyma has been abundantly developed amongst the elements of the secondary xylem. Diagrams *A*, *D* and *E* represent the structure at different positions on this root which correspond approximately to the levels marked *a*, *d* and *e* respectively on the more usual type of root shown in Fig. 1A (cf. Fig. 2, *A* and *D*). *c* = cambium; *ck* = cork; *ct* = cortex; *en* = endodermis; $m.r._1$ = primary medullary ray; ph_2 = secondary phloem; *ph.m.* = perimedullary phloem; *phx* = interxylary phloem; *y* = arcuate strand of parenchyma in the pith. *A* and *D* × 12, *E* × 10. For further details see Key on page 387.

the unlignified parenchymatous areas has increased and most of the medullary rays are unlignified for one-third to one-half of their length from the centre of the root. The more dense, lignified, outer part of the xylem, together with the lignified parts of the medullary rays, form a wide cylinder surrounding the largely unlignified central core. It is in these unlignified parenchymatous areas that the *interxylary phloem* first appears; it is differentiated as small groups of thin-walled sieve tissue embedded in the parenchyma.

As noted above, the roots of the Chelsea collection (sample 1) and the aberrant Oxford specimen show, at the position *a*, a structure in which the secondary xylem consists largely of unlignified parenchyma. Transverse sections cut at positions nearer the crown show the development of interxylary phloem in the parenchyma from the region of *b* upwards. The arrangement of the vessels and associated lignified elements in concentric rings gradually becomes replaced by a more scattered arrangement towards the central region, but a complete cylinder is maintained in the part nearer the cambium, although this remains largely parenchymatous and is not completely lignified as it is in the roots described above (Fig. 2, D; Fig. 5, D).

In the Edinburgh specimens which, owing to the presence of abundant tracheids and fibres, have a densely constructed xylem at the position *a*, development of islands of parenchyma with interxylary phloem occurs as in other roots. This results in producing in the upper part of these roots a distribution of tissues which closely resembles the condition found in the corresponding position on the roots already described (see Fig. 2, D), except that the wide outermost region of the secondary xylem is more densely constructed and more strongly lignified (Fig. 6, D).

Structure at d (*the crown of the root*) (see Fig. 2, D).

The *cork* has increased in amount and forms in this position a layer 6 or 7 rows in width; as at *a* phelloderm is not developed. The *cortex* also has increased in size and consists of up to 14 rows of thin-walled parenchymatous cells; the cells of the outermost layers are rectangular and enlarged, measuring about R 105 to 135 μ and T 120 to 225 μ; those towards the inside are smaller, measuring R 40 to 64 μ and T 60 to 90 μ, and they are more rounded as seen in transverse section. Many of the cortical cells contain microsphenoidal crystals of calcium oxalate. As previously noted in the more apical part of the root, starch is rare.

The *phloem* forms a layer up to 14 rows in width; the structure is similar to that described for the position *a*. There is an increase in the occurrence of calcium oxalate in the cells of the medullary rays; starch is also more frequent, but is not abundant.

The *primary xylem* strand is surrounded by a small irregularly-shaped area of secondary xylem consisting of a few vessels embedded in fibres and lignified parenchyma; these together form a lignified core in the centre of the root. Outside this, and continuing for about one-third to one-half of the radius of the secondary xylem, there is an area which consists of thin-walled unlignified parenchyma, in which are embedded small lignified groups composed of vessels and fibres with some xylem parenchyma, and numerous groups of interxylary phloem; microsphenoidal sandy calcium oxalate is abundant in this region. In the parenchymatous Chelsea and Oxford specimens described above, this arrangement continues as far as the cambium, except that there is no interxylary phloem or calcium oxalate in the outer part of the secondary xylem (Fig. 5, D). In all the other roots, including those from the Edinburgh collection, the outer part of the secondary xylem forms a hollow, completely lignified

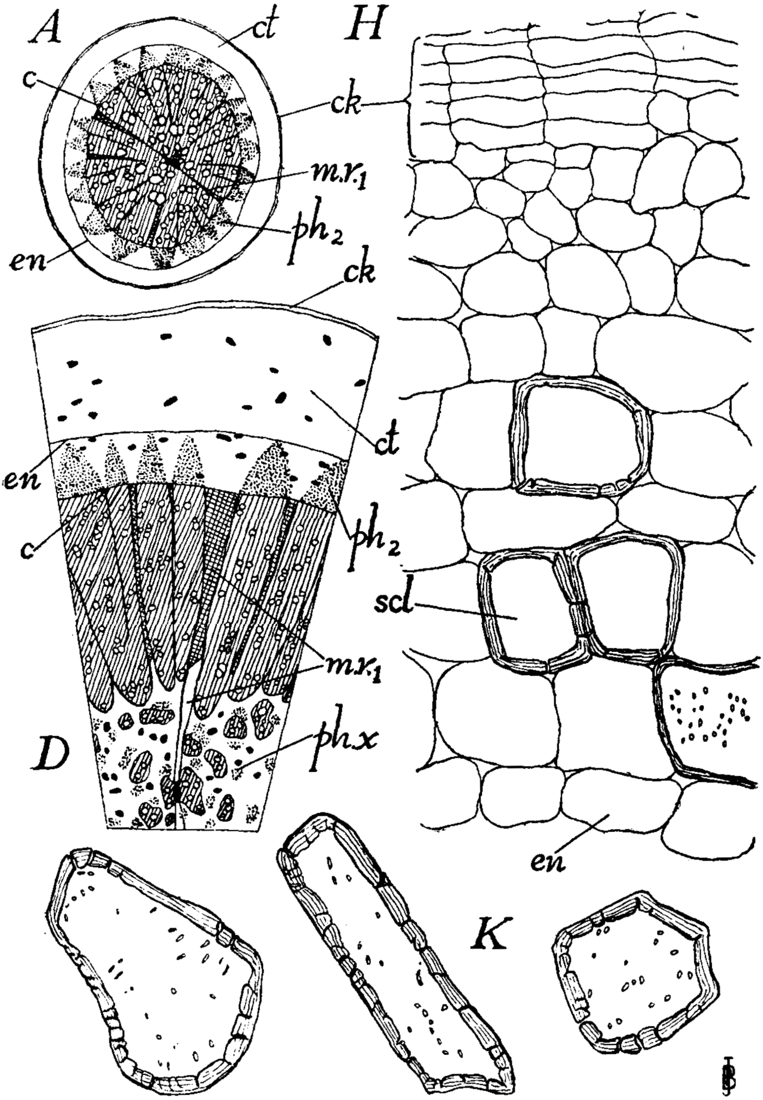


Fig. 6. Root of *Datura stramonium* L. *A* and *D*, diagrams of transverse sections of the root of a plant grown at Edinburgh showing a type of root in which the secondary xylem is more densely constructed, and unlignified parenchyma has not been so abundantly developed. The positions at which these sections have been cut corresponds to the levels *a* and *d* as marked on the root *A*, Fig. 1 (cf. Figs. 2 and 5). Both × 16. *H*, details of the outer tissues as seen at the crown of the same root, showing the sclereids in the cortex, × 130. *K*, isolated sclereids, × 130. *c* = cambium; *ck* = cork; *ct* = cortex; *en* = endodermis; $m.r._1$ = primary medullary ray; ph_2 = secondary phloem; *ph.x* = interxylary phloem; *scl* = sclereid. For further details see Key on page 387.

cylinder consisting of vessels and tracheids embedded in fibres and parenchyma with numerous narrow lignified medullary rays (Fig. 2, D; Fig. 6, D). The secondary xylem in this outer cylinder is more densely

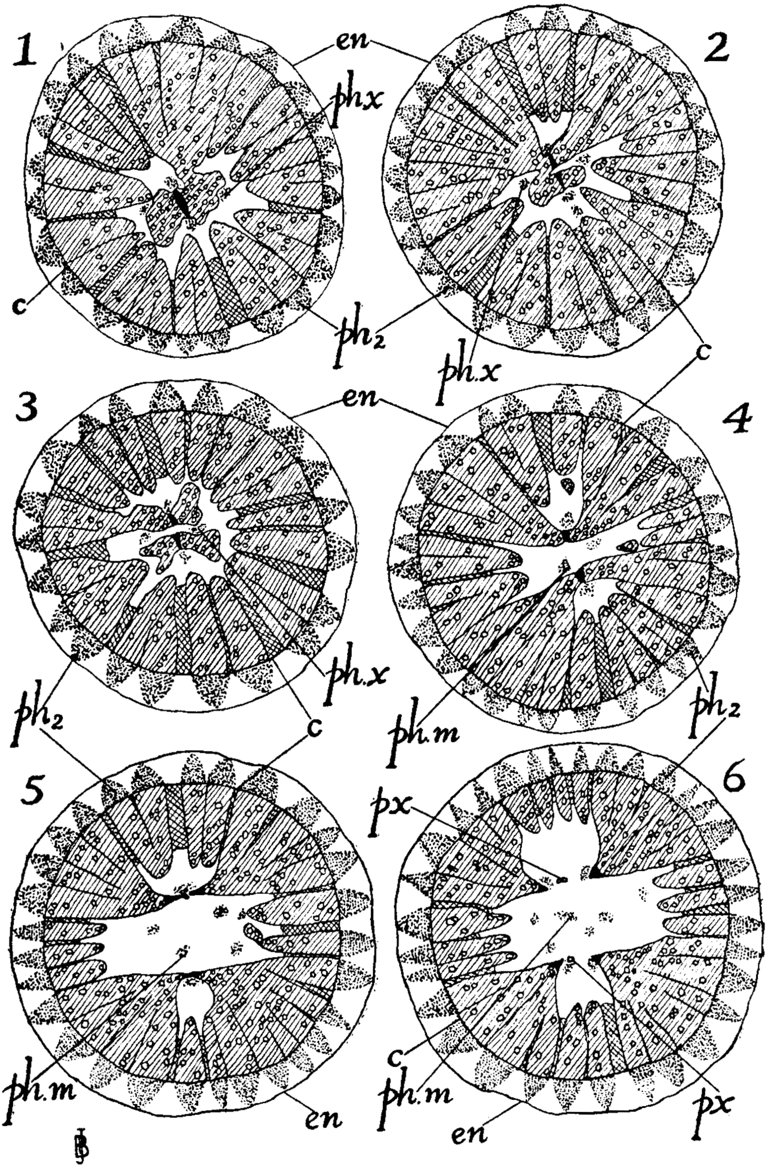


Fig. 7. Root of *Datura stramonium* L. Diagrams of six transverse sections cut successively in the region from *d* to *e* marked on the root *A*, Fig. 1, showing the transition from root to stem structure as seen in the stele of a mature root. All × 15. *c* = cambium; *en* = endodermis; ph_2 = secondary phloem; *ph.m.* = perimedullary phloem; *ph.x* = interxylary phloem; *px* = protoxylem. For further details see Key on page 387.

constructed than that seen in the position *a*; the vessels are somewhat smaller in diameter, measuring from 57 to **80** to 120 μ; the fibres have thicker walls and are more strongly lignified.

B. STRUCTURE OF THE HYPOCOTYL

Transition region (see Fig. 7, *1* to *6*).

The changes which occur in the stelar structure in the transition from the root to the upper end of the hypocotyl have been described in the seedling condition for species of datura by Gérard[6] and others[7,8]. These changes are seen in a modified form in the fully-grown root between the positions *d* and *e*, Figure 1, A, and the structure of the stele at 6 successive positions between *d* and *e* is represented in Figure 7. *1* shows the structure at the crown of the root, with the central core consisting of primary xylem together with lignified secondary xylem elements. In *2*, parenchyma is beginning to split this central region into two halves; the division is complete in *3*. The movement apart of the two halves and the development of small groups of phloem in the thin-walled parenchyma between them is shown in *4*. *5* shows the radial division of each primary xylem group into two; the division is complete on one side and beginning on the other. The final arrangement is shown in *6*; the 4 metaxylem groups are arranged on 4 inward-projecting points of the secondary xylem cylinder and there are numerous groups of perimedullary phloem in the central pith. In some of the roots examined the protoxylem has become separated from the metaxylem and lies between the 2 metaxylem groups; this arrangement is shown in *6*. Alternatively, the protoxylem remains attached to one of the metaxylem groups and is found with it on one of the points of the secondary xylem cylinder (Fig. 9, C), while the remaining metaxylem group is attached to the adjacent point (Fig. 9, D).

Structure at e (see Fig. 8, E; Fig. 5, E).

The outer layers of the *cork and cortex* are generally similar to those described at *d*; the endodermis contains a few starch granules, but a casparian strip is not distinguishable. In two specimens of the Edinburgh collection *stone cells* are present in the cortex in this position; they occur singly or in groups of 2, and are approximately similar in size to the surrounding parenchymatous cells, measuring R 60 to 180 μ, T 75 to 290 μ and L 105 to 330 μ. The walls are stratified, about 10 to 15 μ thick, and lignified, with numerous spirally arranged simple slit-shaped pits (Fig. 6, H and K). The presence of such cells in the cortex of the upper part of the root of *Datura stramonium* is mentioned by Fischer[5], but they are not an invariable feature of the root and were not present in any of the other specimens examined.

The *phloem* is about 20 rows in width; there is an increase in the amount of phloem parenchyma, otherwise the structure is very similar to that described for the position *a*. As at the position *d*, calcium oxalate is abundant, particularly in the parenchymatous cells of the medullary rays, where also a few starch granules are found. In the Edinburgh specimens described above, in which stone cells are developed in the cortex, there is a considerable increase in the number of sclereids (see Fig. 3, C and D) in the phloem and pericycle of this region; these are

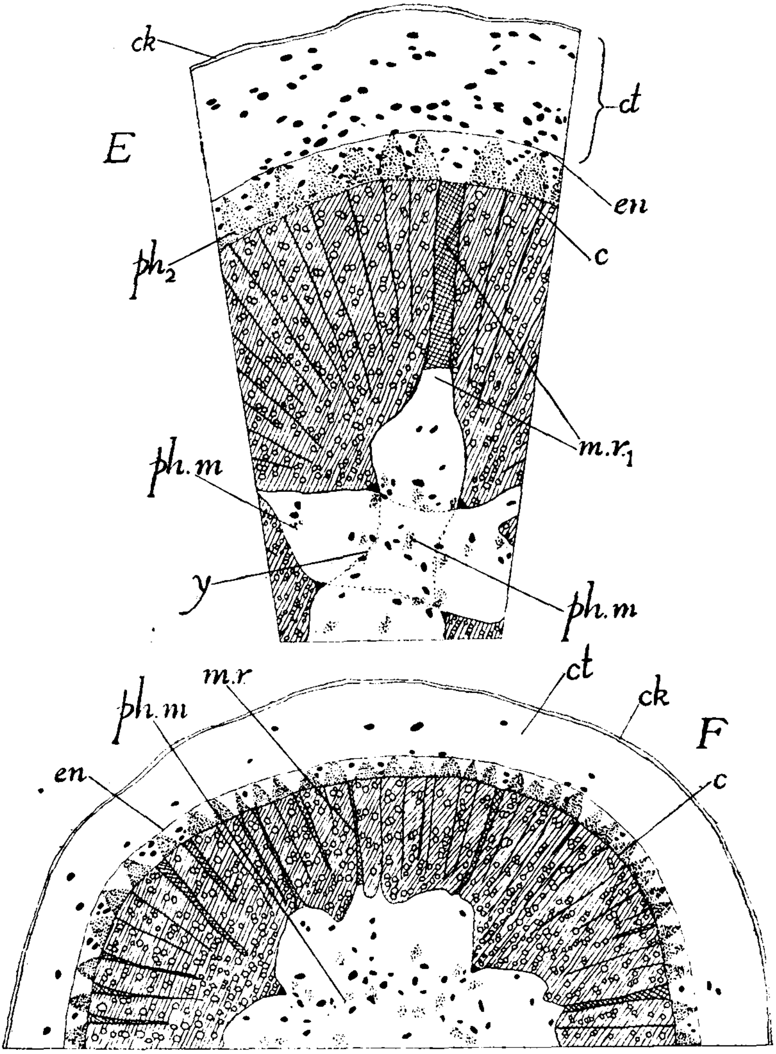


Fig. 8. *Datura stramonium* L. Structure of the hypocotyl. *E* and *F*, diagrams of transverse sections of the hypocotyl of a mature plant cut at the levels marked *e* and *f* respectively on *A*, Fig. 1. *E* shows the structure at the base of the hypocotyl, with four groups of primary xylem and numerous areas of perimedullary phloem; the secondary xylem forms a continuous cylinder of lignified tissue (cf. Fig. 5, *E*). *F* represents the structure at the top of the hypocotyl, just below the scars of the cotyledons. Both × 14. *c* = cambium; *ck* = cork; *ct* = cortex; *en* = endodermis; *m.r.* = medullary ray; *m.r.*$_1$ = primary medullary ray; ph_2 = secondary phloem; *ph.m* = perimedullary phloem; *y* = arcuate strand of parenchyma in the pith. For further details see Key on page 387.

similar to those already described at the position *a*, but the walls are somewhat thicker and are strongly lignified.

The *secondary xylem* forms a hollow cylinder surrounding the central pith; it is completely lignified except in the parenchymatous specimens from the Oxford and Chelsea collections, where it is broken up into lignified xylem groups separated by unlignified parenchyma and unlignified medullary rays (Fig. 5, E). The structure is similar to that described at the position *d*. On the inside the xylem cylinder is extended

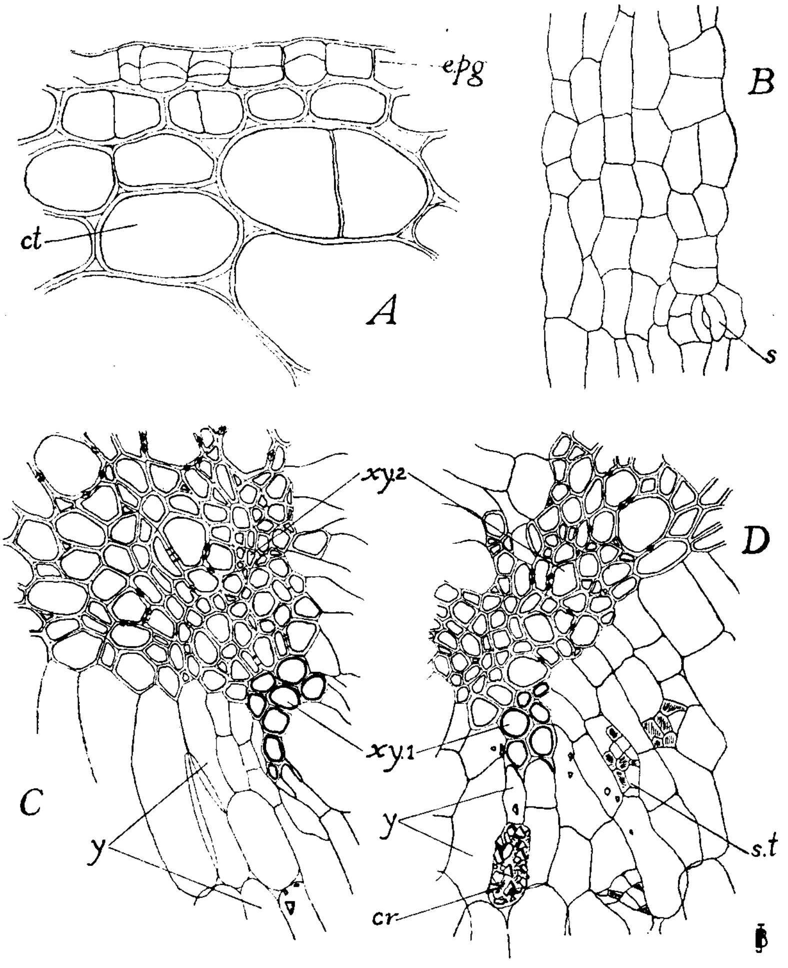


Fig. 9. *Datura stramonium* L. Structure of the hypocotyl. *A*, details of a transverse section of the peripheral tissues showing the origin of a phellogen in the epidermis. *B*, epidermis in surface view. *C* and *D*, details of the transverse section in Fig. 8, *E*, showing two points of primary xylem together with small portions of the adjacent secondary xylem and pith; see Fig. 8, *E*, for the relative positions of these groups in the section. *A* and *B* × 115; *C* and *D* × 200. *cr* = microsphenoidal crystals of calcium oxalate; *ct* = cortex; *e.pg* = epidermis showing origin of a phellogen; *s* = stoma; *s.t* = sieve tissue (perimedullary phloem); xy_1 = primary xylem; xy_2 = secondary xylem; *y* = arcuate strand of parenchyma in the pith.

to form 4 wedge-shaped projections into the pith, and on the point of each of these projections there is a small group of primary xylem elements (Fig. 8, E; Fig. 9, C and D); these groups, as explained above, arise by the division of the primary xylem into four during the transition from root to stem structure. The 2 wide primary medullary rays are still distinguishable.

The *pith* is composed of large irregularly-shaped parenchymatous cells measuring about R 60 to 150 μ and T 105 to 190 μ, with small intercellular spaces. The walls are sometimes slightly lignified and where the cells are in contact the walls bear simple slit-shaped pits. 2 or 3 rows of cells between the projecting points of the xylem are tangentially elongated to form arcuate strands (*y* in Fig. 8, E; Fig. 5, E; and Fig. 9, C and D). Scattered in the pith there are numerous groups of sieve tissue forming the *perimedullary* (*intraxylary*) *phloem*; these are of varying size, the smallest being composed of only 2 or 3 cells. Calcium oxalate microsphenoidal crystals measuring up to 24 μ in greatest length are found in many of the cells of the pith; very occasionally prisms or small cluster crystals also are present in this region. Starch is very rare.

Structure of the hypocotyl from e *to* f (see Fig. 8, F).

Above the position *e* the hypocotyl becomes stem-like in external appearance and further changes in the structural characters take place. A phellogen arises in the epidermis (Fig. 9, A) and a transverse section cut just below the cotyledonary scars (Fig. 8, F) shows to the outside several layers of cork together with the remains of the epidermis; as in the root, no phelloderm is developed. Immediately within the phellogen the first 1 or 2 layers of parenchyma have somewhat irregularly thickened walls (Fig. 9, A); there is no differentiated endodermis. Within the stele the structure remains very similar to that described at *e*; the 4 inwardly-projecting points from the secondary xylem cylinder are more evenly spaced round the central pith and other smaller points have developed between them. The arcuate strands of parenchyma (*y*) seen in the pith at *e* between the primary xylem points are no longer evident. Idioblasts containing microsphenoidal crystals of calcium oxalate are numerous in all the unlignified tissues.

C. LATERAL ROOTS

Origin of the lateral roots (see Fig. 10).

In the seedling the lateral roots arise in the pericycle just to one side of the protoxylem, and the xylem of the young lateral becomes attached to the side of the primary xylem of the tap root. The developing lateral may then continue along the course of the primary medullary ray, or it may gradually curve to one side, causing a displacement of the point of emergence to the right or left of a line directly opposite to the protoxylem. These conditions are illustrated in Figure 10, A and B; C and D show similar conditions as seen in a mature root.

In addition, a large number of the laterals are not initiated in the roots in the primary condition, but arise later after a considerable amount of

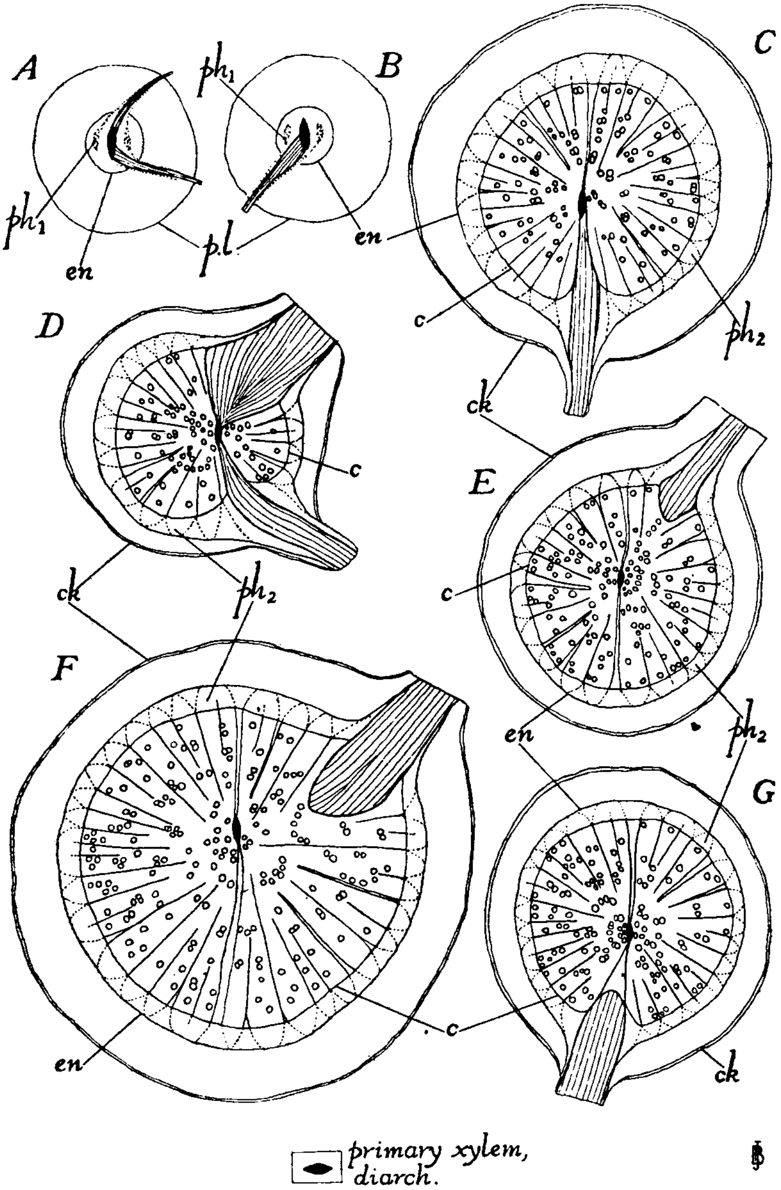


Fig. 10. Root of *Datura stramonium* L. Diagrams of transverse sections of tap roots showing the origin of the laterals and their course through the outer tissues resulting in the irregular arrangement of the laterals as seen on the outer surface of the tap root (see Fig. 1, *A*). *A, B, C* and *D* show laterals arising normally from the primary medullary rays; in *C* the course is straight whereas in *A, B* and *D* it is curved or slanting. *E, F* and *G* show laterals arising at various points after an appreciable development of secondary tissues has occurred. *A* and *B* × 25; *C* to *G* × 12. *c* = cambium; *ck* = cork; *en* = endodermis; ph_1 = primary phloem; ph_2 = secondary phloem; *p.l* = piliferous layer.

secondary growth has taken place. The vascular strands of these secondary roots are connected with the secondary xylem and phloem and not directly with the primary strand of the main root. They originate in the pericycle at various points which may be nearly in the line of the primary medullary rays (Fig. 10, G) or at divergences up to about 90° from them (Fig. 10, E and F); they also may make an appreciable lateral bend in the horizontal plane before emerging at the surface of the root.

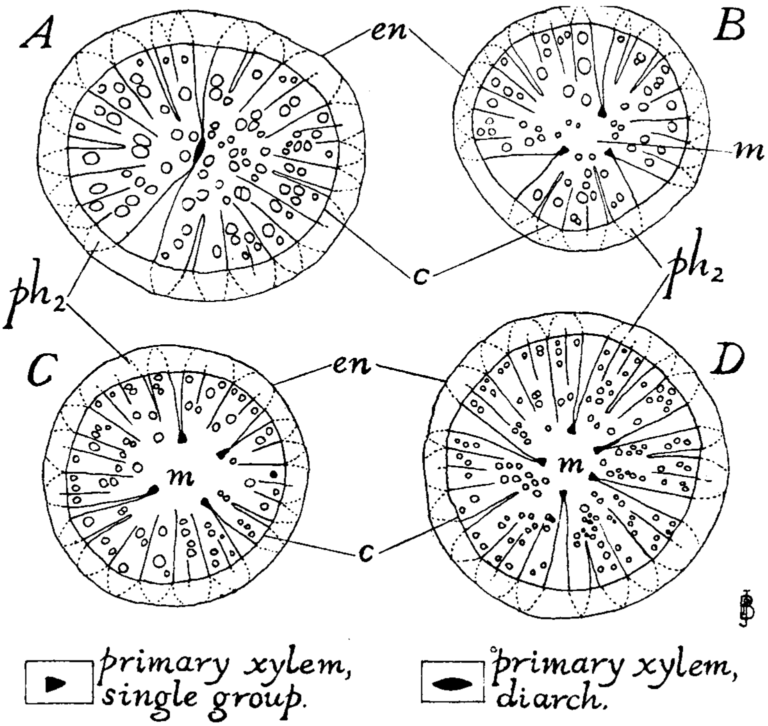


Fig. 11. *Datura stramonium* L. Structure of the lateral roots. Diagrams of transverse sections of the steles of lateral roots to show the variation in the number of primary xylem groups. *A* shows the diarch condition in one of the rootlets. *B*, *C* and *D* show the triarch, tetrarch and pentarch conditions respectively as seen in a single lateral root; *B* is cut near the apex, *C* about 2 cm. from the parent root and *D* close to the parent root. All × 30. *c* = cambium; *en* = endodermis; *m* = pith; ph_2 = secondary phloem.

As a result of this somewhat irregular behaviour the lateral roots are seen scattered indiscriminately over the outer surface of the tap root (Fig. 1, A), and they do not form two longitudinal lines as one might expect in a diarch root.

Structure of the lateral roots (see Fig. 11).

The outer layers, consisting of periderm, phellogen and cortex, are similar in structure to those found in the younger part of the main tap root and described for the position *a*; in some of the larger rootlets the cortex consists of up to 12 rows of cells. The endodermis is clearly distinguishable with a narrow casparian strip which varies in position as described for the main root.

The phloem forms a layer about 4 to 12 rows in width; generally there is an increase in the amount of phloem parenchyma and a reduction in the proportion of sieve tissue compared with that in the main root. Lignified sclereids are not present.

The number of groups of protoxylem varies; some of the lateral roots are diarch for the whole of their length and are thus similar to the main tap root. Others, including all those growing from the region above the crown, are triarch throughout the greater part of their length, the number of protoxylem groups increasing in the 2 or 3 cm. nearest to the main root to give a tetrarch or pentarch condition. Diagrams to show this range in a single lateral root are represented in Figure 11, B, C and D; Figure 11, A, shows the diarch condition in another of the rootlets.

In all the lateral roots the primary and secondary xylem, together with the numerous medullary rays and the small pith, when it is present, form a more or less completely lignified central core and the structure and arrangement of the elements of the secondary xylem are similar to those already seen and described in the main root at the position *a*. Microsphenoidal crystals of calcium oxalate are present in a few cells scattered throughout the cortex.

DISCUSSION AND SUMMARY

In the foregoing account the macroscopical and microscopical characters of mature roots of *Datura stramonium* and *Datura tatula* have been fully described and illustrated. Specimens obtained from 4 different habitats were examined, and no differences either in gross morphology or in structure were found between the roots of *Datura stramonium* and *Datura tatula*, so that the one description includes both species. In addition to the normal tap roots, the specimens included several roots from transplanted seedlings in which the main growth had been arrested and an extensive fibrous root system had developed; no essential differences in the internal structure were found between these 2 types.

In all the specimens examined the transition from root to stem structure was found to take place in a region from 2 to 3 cm. below the ground level; hence the upper part of the underground portion of the plant is hypocotylary in origin and shows stem structure.

The internal structure of the roots was found to be typical of members of the family Solanaceæ in that unlignified parenchyma is developed in the secondary xylem, and interxylary phloem is present. The detailed investigation has, however, revealed several characters which can be used as a means of identifying these roots, and the following brief summary of the secondary structure of the root of *Datura stramonium* includes the more important characters observed.

1. As illustrated in Figure 3, A, cork is formed by a phellogen which arises in the layer of cortex next on the inside of the exodermis. Owing to this rather unusual position of origin of the cork cambium the endodermis and inner layers of the cortex are still present in the mature root

and, as the endodermis is clearly defined, these are readily seen in transverse sections. No phelioderm is developed.

2. The secondary phloem is mainly parenchymatous with groups of sieve tissue and occasional stone cells. These stone cells are more numerous in the upper (older) parts of the root and in the hypocotyl; in roots from 1 sample (see Fig. 6) similar but more strongly thickened cells were also found in the cortex of the hypocotyl, but these were not present in the majority of the roots examined.

3. The secondary xylem shows some diversity in lignification owing to the presence of differing amounts of unlignified parenchyma in samples from different habitats. Interxylary phloem is present in all the roots as small groups of sieve tissue embedded in the parenchyma, and similar groups of sieve tissue form perimedullary phloem in the hypocotyl. The lignified elements of the secondary xylem consist of vessels, tracheids, fibres and xylem parenchyma. The vessels average about 115 μ in diameter and the walls bear numerous bordered pits; occasionally thyloses are found in the vessels from the older parts of the xylem. The tracheids are typical, and have elliptical bordered pits; many intermediate forms between tracheids and fibres occur. The fibres are moderately thin-walled, and the ends are frequently notched and branched to fit into adjacent elements.

4. The cell inclusions are some of the most interesting features of the root of *Datura stramonium.* Starch is almost completely absent from all the tissues; a few rounded granules occur in some of the parenchymatous cells of the cortex and secondary phloem, particularly in the upper part of the root and in the hypocotyl, but the great majority of the cells do not contain starch. On the other hand, calcium oxalate idioblasts are freely scattered throughout the parenchymatous tissues of both root and hypocotyl. Whereas, however, in the aërial parts of the plant (that is, the stem, leaves and flowers) calcium oxalate occurs chiefly in the form of cluster and prism crystals, in the root it is present entirely in the form of *microsphenoidal* crystals. These crystals show considerable variation in size, reaching a maximum of 24 μ in greatest length.

5. The tap roots are typically diarch, but examination of the external surface shows that the lateral roots do not form 2 vertical rows as one might expect, but are scattered indiscriminately. This is explained by the investigation of the origin of the lateral roots. It has been shown that they do not all arise opposite the primary xylem groups, but some originate at indeterminate points in the pericycle after some secondary xylem has formed; also, they bend considerably during their course through the tissues to the outer surface of the root (see Fig. 10). The lateral roots are mainly diarch in structure, but some show an increase in the number of primary xylem groups at positions close to the parent root; otherwise the internal structure of these roots is similar to that of the lower part of the main tap root.

As noted in the introduction, among the plants belonging to the family Solanaceæ which are used in medicine, *Atropa belladonna* and its allied species *Atropa acuminata* are the only ones for which the detailed structure of the roots has previously been described. It is of interest, therefore, to compare the structure of the root of *Datura stramonium* with that of *Atropa belladonna* and to determine the characters by which these roots can be distinguished from one another.

The 2 roots are similar in that the primary xylem strands are diarch, and that unlignified parenchyma is developed in the secondary xylem. Also, interxylary phloem is present in the roots, and perimedullary phloem occurs in the rootstock of belladonna and in the hypocotyl of stramonium. The elements which make up the lignified parts of the secondary xylem are also somewhat similar, consisting of vessels with bordered pits, tracheids and fibres. In both belladonna and stramonium roots stone cells occur in the secondary phloem; Melville[3] reports that they also occur in the cortex of the rootstock of belladonna, but they are more elongated and thinner walled than those found in the cortex of some of the samples of *Datura stramonium.* The form and occurrence of the calcium oxalate is also similar in both roots.

The main difference between the root of *Atropa belladonna* and that of *Datura stramonium* is the abundance of starch in belladonna and the almost complete absence of starch from stramonium. Another difference is seen in the position of origin of the phellogen, which results in differences in the arrangement of the tissues in the mature root. In belladonna root the cork cambium arises normally in the pericycle, and forms cork on the outside and several layers of phelloderm on the inner side; no cortex is present, therefore, in the mature root. In stramonium, on the other hand, the cork cambium arises in the outer part of the cortex, and no phelloderm is developed. In the mature root, therefore, both cortex and endodermis are present.

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