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THE ANATOMY OF THE ROOT SYSTEM IN YAM BEAN, PACHYRHIZUS EROSUS (L) URBAN (FABACEAE)

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ABSTRACT

Investigations have revealed that the anatomy of the primary radicular root was typically dicotyledonous except that the metaxylem was not completely developed centripetally. Most of the roots had tetrarch xylem although a few pentarch conditions were observed. Tuberization was initiated by the formation of the vascular cambium which divided to form secondary tissues in a normal fashion. Later on, anomalous secondary and tertiary cambia developed around vessel elements and these produced mostly parenchyma storage cells. Activity of this anomalous secondary cambia thickening was chiefly responsible for the growth of the mature tuber.

RESUME

L'ANATOMIE DU SYSTEME RACINAIRE CHEZ LE DOLIQUE TUBEREUX, *PACHIRHIZUS EROSUS* (L) URBAN (*FABACEAE*)

Des études ont révélé que l'anatomie de la première racine radiculaire était du type dicotylédone excepté que le métaxylème n'était pas développé entièrement de façon centripète. La plupart des racines avaient un xylème tétrarche bien que quelques cas de pentarchie aient été observés. La tubérisation était initiée par la formation d'un cambium vasculaire qui se divise pour former des tissus secondaires normaux. Plus tard, des cambiums anormaux secondaires et tertiaires se développent autour des éléments des vaisseaux et produisent principalement des cellules de stockage du parenchyme. L'activité de cet épaississement des cambiums anormaux secondaires est responsable du grossissement du tubercule adulte.

INTRODUCTION

The recent increasing interest in the genus *Pachyrhizus* has resulted from its recognition of the various species (*P. erosus, P. tuberous, P. ahipa*) as potentially high-yielding tuber crops of high nutritional value with the possibility of large scale cultivation in third world countries (Kay, 1973 ; Anonymous, 1979). The plant known to have been cultivated by the Atzecs and Mayans in pre-Colombian times for its edible tubers (Lundell, 1984 ; Dibble and Anderson, 1963) presently enjoys a tropical and neo-tropical distribution and cultivation. It is mainly seed-propagated, but new plants may be regenerated from adventitious buds produced at the proximal end only of the tubers.

An extensive literature on the taxonomy (Clausen, 1945 ; Sorensen, 1988), morphology (Baker and Quimby, 1953), cytology (Roy, 1933) and chemistry (Norton, 1943, Norton and Hansberry, 1945, Hansberry et al, 1947 ; Krishnamurti and Seshadri, 1966, Duke, 1981) of *P. erosus* has been produced ; however, there exists an extreme paucity of information on its anatomy, especially of the root system. Carew and Quimby (1955) reported briefly on the anatomy of the "mature root" and lacked the information needed to provide an understanding of the processes and production of tissues leading to tuber formation.

Anatomical investigations of tuber development of a widely cultivated tropical root crop, sweet potato (Togari, 1950, Wilson an Lowe, 1973) have shown that fleshiness was primarily due to anomalous secondary thickening resulting from the activities of anomalous cambia.

The objective of this investigation was to describe the developmental anatomy of the root systems of *P. erosus* and to compare it with that reported for sweet potato.

MATERIALS AND METHODS

Seeds were sown in 400 ml capacity plastic pots containing a potting medium compound of three parts of garden top soil and one part of washed sand. Seedlings were harvested at different time intervals and portions of the root at different stages of development up to the mature tuber stage were excised and fixed in formaldehyde-acetic acid (1:3v/v) for light microscopy. Roots were cut into lengths of about 5 mm and dehydrated through an ethanol-tertiary butanol series prior to embedding in paraffin wax. Sections were cut about 12 µm on a AO Spencer 820 rotary microtome and stained with safranin and fast green (Johansen, D. A., 1940).

RESULTS AND OBSERVATIONS

Features of Root System

The primary root generally produced a turnip-shaped fleshy tuber approximately 30 cm in diameter and 25 cm long at the base of the stem. Occasionally a branch of the radicular root also formed a tuber which fused partially or wholly with the primary tuber to form a composite structure. At the distal end

of the tuber a portion of the elongated primary root remained non-tuberous and produced secondary roots. This extra-tuber region persisted to tuber maturation and attained a diameter of up to ten centimetres.

OBSERVATIONS

Primary Differentiation

The root of *P. erosus* were normally tetrach but occasionally a pentarch configuration was observed. In both cases there was incomplete centripetal development of the primary xylem resulting in the formation of a parenchymatous pith. The metaxylem elements in each arm, in close proximity to the pith parenchyma were comparatively large and relatively few (1-2 cells) while the protoxylem consisted of about 10-12 cells, the smaller outer ones abutting the pericycle. Groups of phloem cells alternated with the primary xylem arms being separated from them by fundamental parenchyma. The parenchymatous cortex was limited centripetally by a well defined endodermis and its outer surface was bounded by the epidermis. (Fig. I).

Secondary Thickening of the Root

Secondary growth generally occured in roots about one week after the emergence of the radicle.
Anatomical events at the onset of secondary thickening were similar to those in a typical root. At about the time that the primary xylem reached maturity, the vascular cambium was initiated. Procambial cells separating the primary xylem and phloem differentiated into cambial initials forming strips of cambial tissues which were eventually connected to form a continuous and irregular cylinder through the meristematic activity of the single layered pericycle.

Subsequent periclinal divisions of the initials of the vascular cambium led to

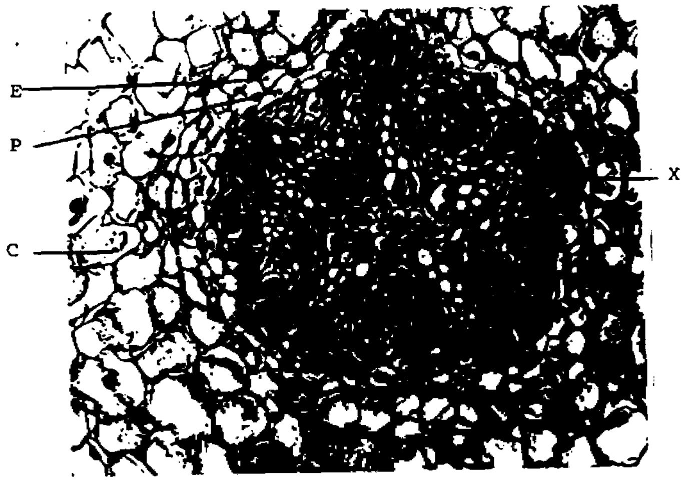

Fig. 1. T.S. of Young primary root showing the distribution of the primary tissues, the pentarch stele and the incomplete centripetal development of the xylem (pith).
C = cortex, E = Endodermis, P = Pericycle, X = Xylem

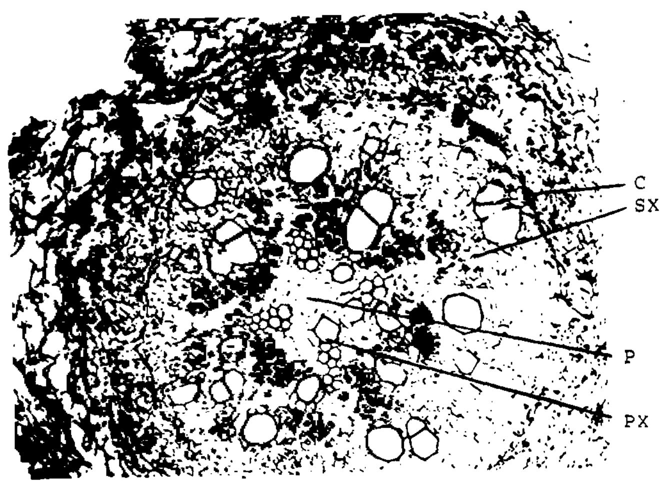

Fig. 2. T.S. of Primary Root, showing early stage of secondary thickening. Note the tetrarch stele. C = cambium, SX = secondary xylem P = pith, PX = primary xylem.

the production of secondary vascular tissues resulting in the formation of a symmetrical cylinder of cambium (Fig. 2).

The meristematic activity of the vascular cambium resulted in an enlargement of the axis and caused tangential stretching of the cells of the tissues outside the dividing pericycle layer, and to accommodate the increasing pressure exerted by the enlarging stele, the cells of the tissues especially the cortical cells divided anticlinally and expanded tangentially. Eventually, however, the cells of the extrapericylic tissues, ceased to divide and expand thus causing the cortex to be ruptured and cast off together with the epidermis and endodermis by the increasing pressure of the expanding (cortex). As this occurred, a phellogen formed in the outer layer of the pericycle and produced the periderm of the mature root. Normal secondary growth as described above, only occurred in secondary non-tuberous roots, i.e. branches of the primary roots.

In secondarily thickened non-tuberous roots the centrally located secondary xylem was heavily lignified and occupied the greater portion of the axis. The secondary phloem with its characteristic cell types occupied about a third of the volume of the secondary tissues and was interspersed with fan-shaped rays. A well defined periderm formed the outer protective tissue (Fig. 3).

The distal region of the tuberous root axis showed normal secondary growth but the formation of a small amount of anomalous cambial tissue on the periphery of some xylem elements was also observed (Fig. 4).

In primary tuberous roots certain anomalous developments in addition to the normal secondary growth occurred during formation of the tuber.

Growth of the tuber

The development and growth of the tuber occurred by continued activity of both the vascular cambium as well as anomalous secondary cambia which developed from parenchyma cells of the secondary xylem and frequently occurred as cylinders which surrounded groups of tracheary elements that were in various stages of maturation (Figs. 5, 6). Secondary cambia were also formed in the parenchyma of the secondary xylem not related spatially to any vascular elements (Fig. 7). As growth proceeded, anomalous "tertiary" cambia i.e. cambia developed in tissues derived from secondary cambia became evident throughout the central portion of the tuber (Fig. 8). It was occasionally observed that cells of the secondary xylem rays located at opposite sides of the primary xylem, and connected by pith parenchyma, became meristematic and formed broad bands of storage parenchyma (Fig. 9). While the development of these anomalous cambia was taking place, the

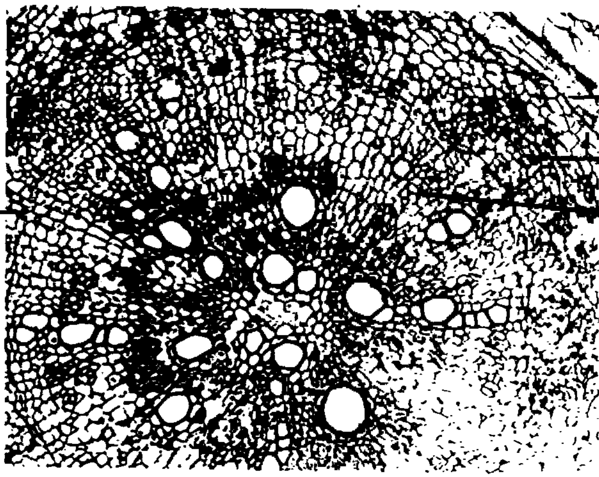

Fig. 3. T.S. of Tuberous root showing secondary thickening and intraxylary phloem
P = periderm, SP = secondary phloem VC = vascular cambiu
IP = Intraxylary Phloem

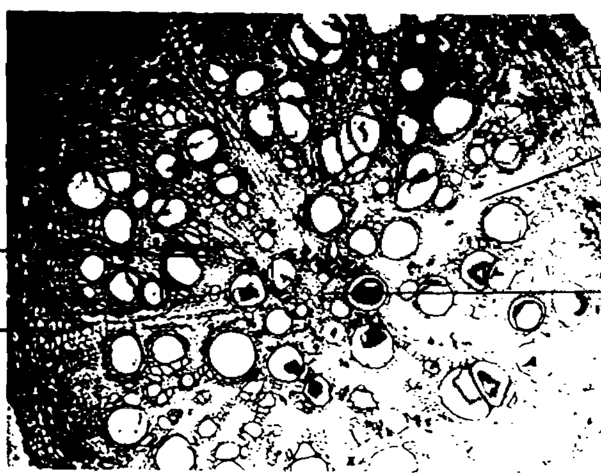

Fig. 4. T.S. of Distal region of primary root owing transitional features between a tuber and a non-tuberous secondarily thickened root. Note anomalous secondary cambia and heavy liqnification of tissues. ASC = Anomalous secondar cambium SP = Secondary phloem PX = Primary Xylem
P = periderm, SX = secondary xylem

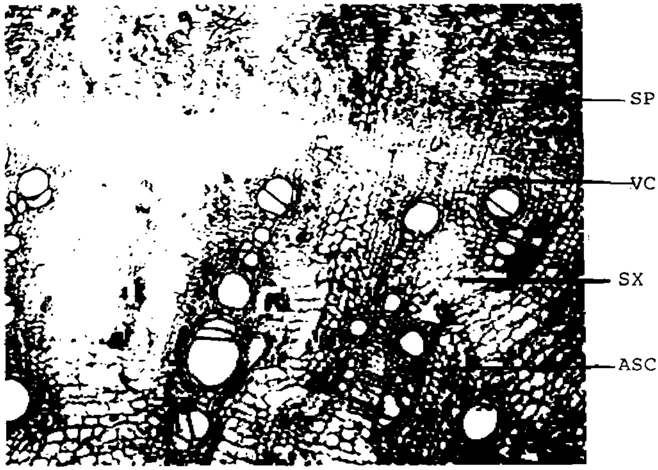

Fig. 5 T.S. of tuber showing activity of vascular cambium and secondary anomalous cambia associated with xylem elements VC = vascular cambum ASC = anomalous secondary cambium SP = secondary phloem SX = secondary xylem

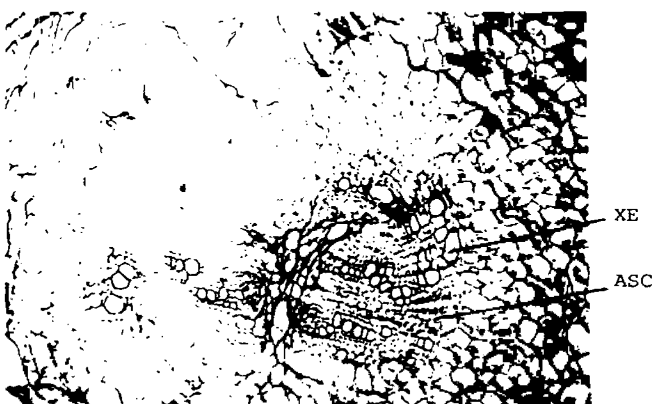

Fig. 6 T.S. of tuber showing anomalous secondary cambium associated with xylem elements ASC = Anomalous secondary cambia, XE = Xylem elements

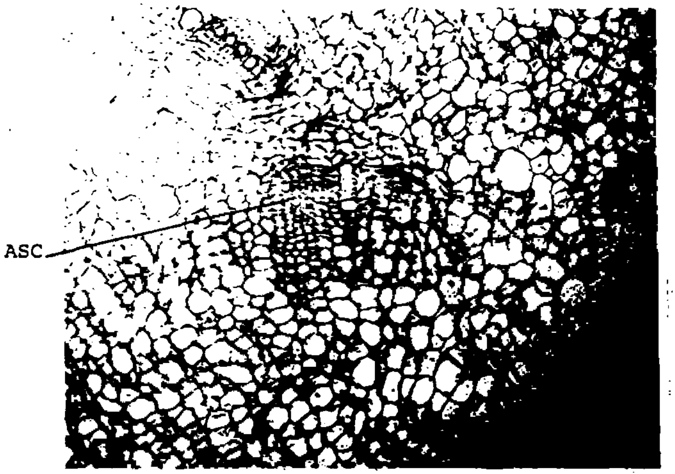

Fig. 7. T.S. of Tuber showing anomalous secondary cambium not spacially associated with xylem elements.

ASC = Anomalous secondary cambium

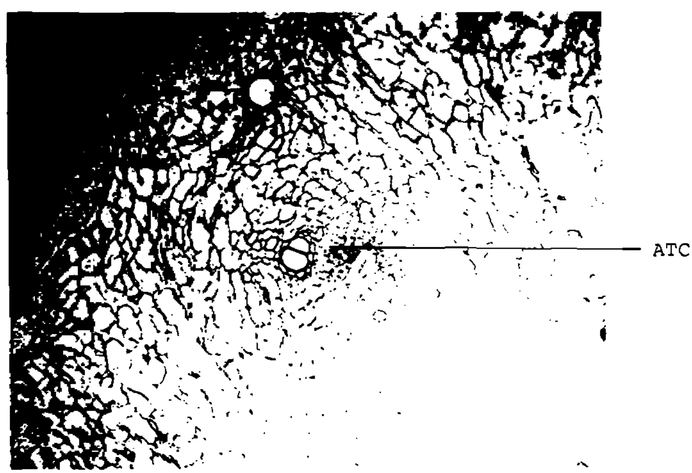

Fig. 8 T.S. of tuber showing anomalous tertiary cambium
ATC = Anomalous Tertiary Cambium

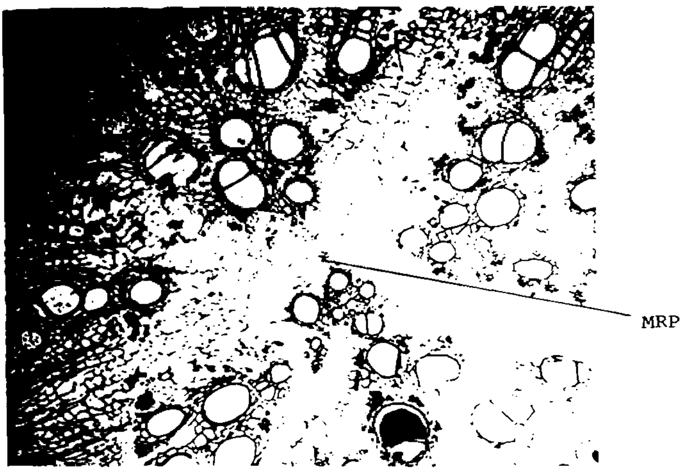

Fig 9. T.S. of tuberous root showing meristematic activity of secondary xylem rays to form bands of parenchymatous storage cells.

M R P = Meristematic Ray Parenchyma.

vascular cambium continued to function producing secondary xylem and phloem and large amounts of storage parenchyma. Activity of all cambia therefore resulted in the enlargement of the tuber.

The Mature Tuber

In the mature tuber, the epidermis, cortex and endodermis were no longer present and the protective tissue consisted of a pericyclic periderm produced and maintained by an active phellogen throughout tuberization. The periderm composed of an outer phellem, the phellogen and an inner phelloderm was about 10-12 layers of cells arranged in definite radial rows. The secondary phloem with normal cell types had flared rays with their wider parts abutting the phelloderm. The vascular cambium including its immediate derivatives situated between the secondary xylem and phloem was composed of about five layers of characteristic cells. The region within the vascular ambium formed the bulk of the tuber and was composed predominantly of storage parenchyma in which small groups of vascular tissues and anomalous cambia were interspersed. Some intraxylary phloem was observed in the secondary xylem.

DISCUSSION

Observations on the anatomy of primary *P. erosus* roots have revealed a great similarity to the basic dicotyledonous plan. There was however one significant deviation in that the generally tetrarch xylem had incomplete centripetal development. Anatomical events leading to the formation of the vascular cambium and the production of secondary xylem and phloem were similar to those in a typical root and to that of the fleshy roots of sweet potato.

The activities of both the vascular cambium and anomalous cambia led to localized thickening of the root which was indicative of early tuberization. This thickened zone did not extend over the entire region of the root, so that the tuber was delimited at the proximal end by the hypocotyl and at the distal end by the extra-tuber region which remained non-tuberous. A similar situation was described for sweet potato by Wilson and Lowe, 1973.

Tuberisation in *P. erosus* always occurred in the primary root regardless of whether the state was tetrarch or pentarch. In sweet-potato, only pentarch and hexarch roots with complete or incomplet centripetal development of the xylem tuberized. Tuberous roots with tetrarch steles were never observed (Wilson and Lowe, 1973). In *P. erosus* anomalous secondary and tertiary cambia were involved in tuber growth, but in sweet potato, additional anomalous primary cambia was formed around the central metaxylem vessel and protoxylem arms (Artschwager, 1924, Togari, 1950 ; Wilson and

Lowe, 1973). No such anomalous primary cambia was observed in *P. erosus*.

Generally only the primary root of *P. erosus* formed a tuber and all secondary branches underwent normal secondary thickening showing heavy lignification within the secondary tissues. The majority of these root did not persist to tuber maturation and thus only a few remained attached to the tuber. The presence of small amounts of cambial tissues within the secondary tissue of the distal region of the mature tuber suggested that this region was transitional between the tuber and the root and that early development in this region was similar to that in the tuber itself.

The primary roots of *P. erosus* are obviously specialized for tuber development resulting from the appearance of anomalous secondary and tertiary cambia and a vascular cambium capable of rapid cell proliferation to produce parenchymatous starch-storing cells.

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