J. Plant Production, Mansoura Univ., Vol. 6 (10):1679 -1691,2015

SECONDARY GROWTH PATTERN IN THE ROOTS OF TWO HERBACEOUS SPECIES BELONGING TO GENUS *Solanum*

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ABSTRACT

Two herbaceous species belonging to genus *Solanum* namely, *Solanum melongena* L. and *Solanum lycopersicum* L. were subjected to study the incidence of the secondary growth and consequently the formation of protective tissues in their roots. The main results were as follows :

1- At an early stage of growth, the xylem tissue at the base of the root accomplished a proportion of its final amount that was decidedly bigger than that needed for the shoot system already achieved by the plant.

2- In contrast to the eggplant, no development of any periderm-like structure at the periphery of the root of tomato was detected. In the successive ages, storage depletion of food stuff in root parenchyma of the eggplant was not found in the tomato root.

3- The whole vascular cylinder was dissected into differently sized sectors by rays of varied width ranging in cross section from 2 to 6 cells. This histological characteristic was not present in the root of eggplant.

4- The root xylem in the tomato root unlike that in the eggplant looked heterogeneously perforated.

INTRODUCTION

Detailed response of the primary tissue outside the xylem tissue to secondary growth, and sufficient information about the development of protective tissues in roots of the annual herbaceous dicotyledons is lacking in literature.

The development of protective tissues in roots was stated by Eames and Mc Daniels (1947) to be restricted to the perennial plants where a true periderm arises in the pericycle.

Luhan (1955) pointed out that a variety of protective tissues were observed in plants with a limited amount of secondary growth as do the herbaceous dicotyledons growing in the alpes : persisting thick-walled epidermis (*Ranunculus*); exodermis (*Primula*); exogenously originating periderm (*Artemesia*) and other *Asteraceae*; dead and collapsed but persisting cortex (*Polygonum*); subdivided and superized endodermis (*Gentiana*); polydermal (*Potentilla*); periderm of deep seated origin (*Saxifragaceae*).

Esau (1965) stated that the amount of secondary growth varies in roots of the different herbaceous plants as do the histology of the tissues and the distinction of periderm.

Owing to the recorded diversity in the way by which the herbaceous dicotyledons build up protective tissues during their secondary growth beside the scarce literature on this histological character, it was highly appreciated to carry out the present work.

Two herbaceous annual species of the *Solanaceae* belonging to the same genus were involved namely *Solanum melongena* L. and *Solanum lycopersicum* L., both of economic importance (Cronquist, 1981).

Metcalfe and Chalk (1979) generally recorded that in roots of the solanaceous plants, cork arises in the exodermis or may be deep-seated in origin.

The main aim of the present investigation was to study in some detail the response of the primary body and the histological tissue changes accompanying secondary growth of the roots of eggplant and tomato plant.

MATERIALS AND METHODS

The current work was carried out at the experimental station, Faculty of Agriculture, Cairo University, Egypt.

Seed lots of the two investigated solanaceous species listed before i.e. *Solanum melongena* L. (White Balady) and *Solanum lycopersicum* L. (Pearl Harbor) were secured from the Agricultural Society, A.R.E. Seeds were sown on April 18. Forty pots 40 cm diameter filled with Nile Clay were used, 20 for each species. When plants were 22 days old, they were thinned out to 5 plants for each pot.

All plants were fertilized with a combination of NPK as 3:2:1 at a rate of 10 g/plot. This amount was equally applied at the two ages 25 and 50 days after sowing.

For the histological study at every studied age, three samples from digging out plants of the tap-root at about 2 cm below the hypocotyl in the root axis were killed and fixed in F.A.A. solution.

The first root samples were taken after emergence of dicotyledons above soil (one week). Then daily samples were taken to detect the start of cambial activity.

From three weeks onwards, the root samples were secured every fortnight until the age of 9 weeks and after every three weeks until end of the vegetative growth.

Fixed materials were dehydrated by normal butyl alcohol method and embedded in paraffin wax of 56-58 ^{o}C. m.p Sections 15 µ thick were cut by a rotary microtome, stained with crystal violet/erythrosine before mounting in Canada balsam (Nassar and EL-Sahhar, 1998). The stained sections were examined by light microscopy and photographed.

RESULTS AND DISCUSSION

***Solanum melongena* L.**

Age of 3 weeks :

The general topography of the root (Fig. 1) revealed the following structure :

A nearly lost epidermis which was at occasional places represented by wall remnant or whole crushed cells. Fig. (2) which was taken one week earlier showed more clearly the remains of the epidermis. It also showed the primary diarch xylem and the early start of cambial activity. The sub-epidermis layer formed the exodermis. It is a distinguished layer compared with the underlying ones. The cells were nearly isodiametric; their outer walls were rather thick and in fresh material reacted positively with sudan III and phloroglucinol hydrochloric acid, proving therefore to have both suberized and lignified nature.

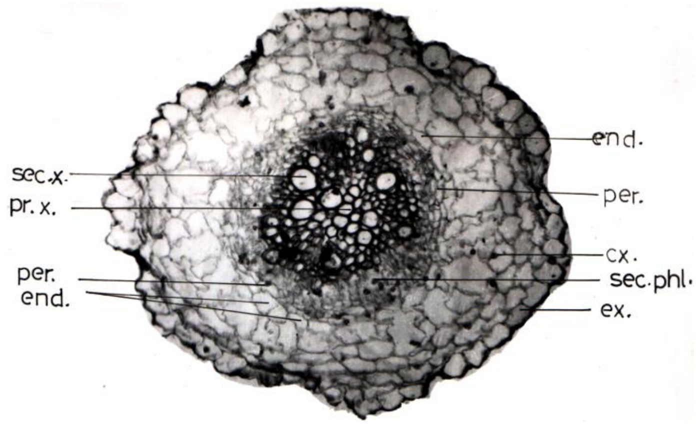

Fig. (1): Transection at the base of main root of eggplant, 3-weeks old plant (X170).
Sec.x: Secondary xylem, Pr.x: Primary xylem, Per.: Pericycle, end.: Endodermis, Cx.: cortex, ex.: exodermis.

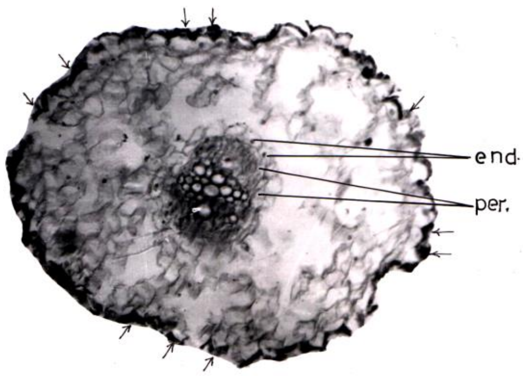

Fig. (2): Transection at the base of main root of eggplant, 2-weeks old plant; the arrows point to remains of the epidermis (X150).
Per.: Pericycle, end.: Endodermis.

At few places the cells were seen crushed, probably with the overlying epidermis to the extent that they lost completely their original outline.

The rest of the cortex excluding the endodermis had thin walled-parenchyma cells of different size and shape. The endodermis faced the outward pressure of increased size of the vascular cylinder by enlargement of its cells in one or more planes.

A one-layered pericycle generally of smaller sized cells than those of the endodermis. It enveloped the vascular cylinder whose xylem averaged 186.6 µ in diameter.

Age of 5 weeks :

During the following two weeks, secondary growth proceeded actively, thus bringing the diameter of the xylem to an average of 507.5 µ (Fig. 3). As a result, the following changes were observed by the end of this week.

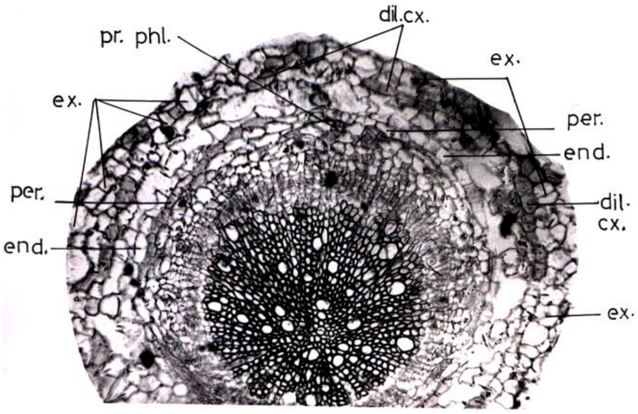

Fig. (3): Transection at the base of main root of eggplant, 5-weeks old plant (X150).

ex.: exodermis, Pr.phl.: Primary phloem, dil.cx.: Dilated cortex, Per.: Pericycle, end.: Endodermis.

The exodermal cells increased decidedly in size by enlarging in one or more plane. This was accompanied in many cells by their division either anticlinally or periclinally or both. This attempt of the exodermis to accommodate the increase in root diameter with such irregular behaviour of cell division made the outer periphery of the root of much uneven surface and the exodermis itself to be of a heterogeneous appearance compared with the preceding age. The epidermal remains were still visible. Dilatation of the cortical cells was demonstrated. Both endodermis and pericycle underwent dilatation growth, though it was difficult to demonstrate, this process due probably to its rapid incidence i.e. cell division followed rapidly cell elongation.

Age of 7 weeks :

It was clear that between 5 and 7 weeks after sowing, secondary growth slowed down than before (Fig. 4). The mean xylem diameter reached 656.7 µ while it was 507.5 µ in the preceding age.

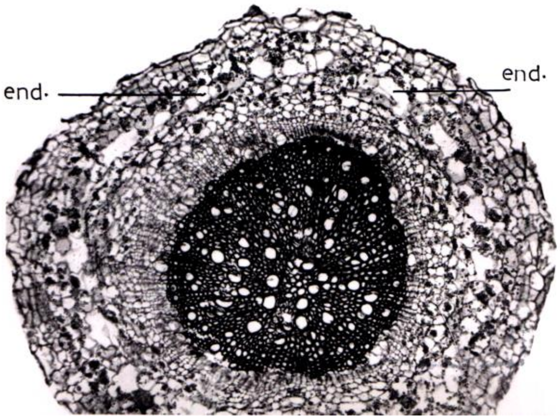

Fig. (4): Transection at the base of main root of eggplant, 7-weeks old plant (X150).
end.: Endodermis.

A conspicuous feature was that the endodermal cells were much enlarged in size, this made the stele easily distinguished from the outer tissues.

Another standing feature was that the root during these two weeks functioned as a store for food stuff. Starch grains were present in many cortical and phloem parenchyma filling them either partially or completely. The endodermal cells were the least filled with these grains.

Age of 9 weeks :

During the following two weeks there was a compensation of the preceding slowly down of secondary growth. The average diameter of the xylem reached 1220.9 µ (Fig. 5).

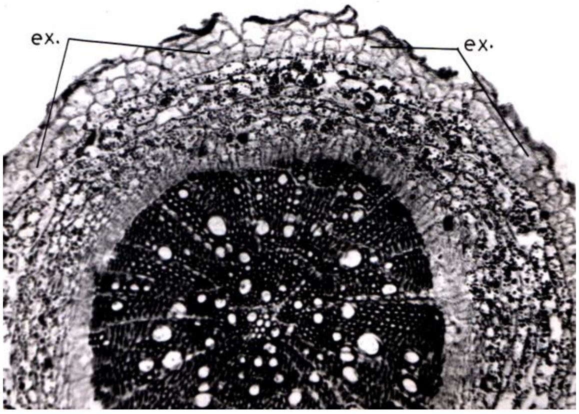

Fig. (5): Transection at the base of main root of eggplant, 9-weeks old plant. Notice the filling of all parenchyma cells outside the xylem with starch grains (X150).
ex.: exodermis.

The parenchyma cells of tissues outside the xylem especially those of the cortex and endodermis were actively dilated.

The former easy recognition of the endodermis by the bigger size of its cells was lost due partly to the abundant filling of all parenchyma cells outside the xylem with starch grains, and partly to the dilatation growth.

The protective exodermis showed increase of its component cells both in size and in number through further division but without having the appearance of a true periderm.

Age of 12 weeks :

When most of the vegetative growth was accomplished after about 3 months from sowing it was clear that additional secondary tissues were deposited, thus bringing the xylem core to a mean diameter of 1731.3 µ (Fig. 6). The cortical region became much narrowed due to the outward stelar pressure.

The stored starch grains were completely depleted. The exodermis at several places was ruptured or its outer cells were sloughed off. This was compensated by adding new cells especially by periclinal division. Division included also several cells underlying those of the original exodermis.

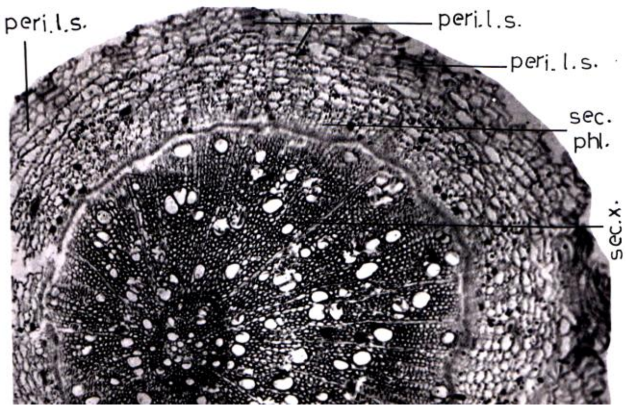

Fig. (6): Transection at the base of main root of eggplant, 12-weeks old plant (X125).

Peri. L.S.: Periderm-like structure, Sec. phl.: Secondary phloem, Sec. x.: secondary xylem.

Occasional short tiers of radially arranged cells were visible, and showing, therefore, patches of periderm – like appearance within the original exodermis.

Xylem characteristics :

The xylem is characterized by a ground tissue mainly of lignified parenchyma. Vessels round or oval, mostly solitary or present occasionally in clusters of 2 to 3 in tangential pattern. Development of the wider most vessels took place early since they are present close to the centre and they constitute a big portion of the whole xylem vessels, thus these tissues looked homogenously perforated. Rays are uniseriate in cross sections (Esau, 1965).

***Solanum lycopersicum* L.**

Age of 3 weeks :

The general structure of the root at the age of 3 weeks did not differ than in the eggplant. The average diameter of the xylem core was 260.2 µ.

Age of 5 weeks :

The diarch root showed a considerable amount of secondary growth, the average diameter of the xylem was 468.7 µ (Fig. 7).

The cortical region was seen crushed at several places. The outermost intact cells of the cortex formed the exodermis which until this age did not show any sign of cell division in contrast with *Solanum melongena* L. Its cells were conspicuously of irregular shape and size compared with the underlying dilated cortical ones.

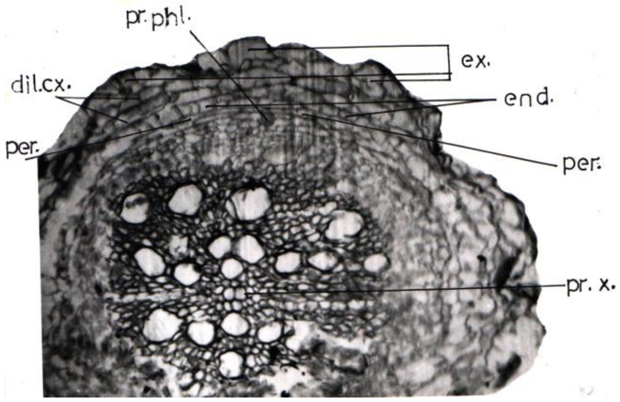

Fig. (7): Transection at the base of main root of tomato plant, 5-weeks old plant (X250).

Pr.phl.: Primary phloem, ex.: exodermis, Per.: Pericycle, Pr.x: Primary xylem, dil.cx.: Dilated cortex.

The endodermis kept pace with the enlarging vascular cylinder. It seemed that cell division during the dilatation growth was faster than in the overlying cortical cells, since the cells were still keeping their original size.

The pericyclic cells were tangentially elongated with or without cell division.

Age of 7 weeks :

Division of the exodermal cells in different planes in a manner similar to that described in *Solanum melongena* L. was obvious at this age where the xylem reached a mean diameter of 686.6 µ (Fig. 8).

Due to the dilatation growth, the underlying cortical cells varied much in size but on the whole they were bigger than the component cells of the exodermis. The layer which was still keeping its easy distinction was the endodermis; close examination revealed the presence still of casparian strips.

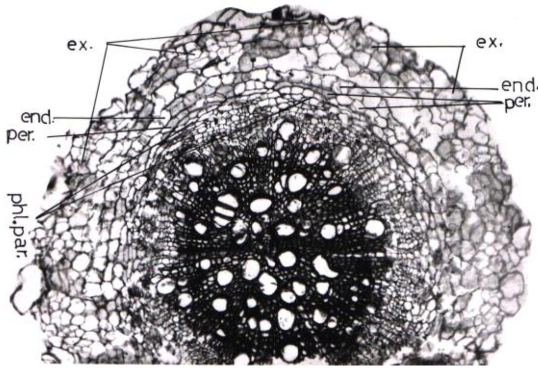

Fig. (8): Transection at the base of main root of tomato plant, 7-weeks old plant (X170).

ex.: exodermis, end.: Endodermis, Per.: Pericycle, Phl.par.: Phloem parenchyma.

The noticeable uniformity in size and shape of its cells might be attributed to a much regular rate of dilatation growth in this layer than in other cortical ones.

The pericycle which also underwent dilatation had cells with less uniform size and shape than those of the endodermis.

The parenchyma of primary phloem lying next to the pericycle was included in the dilatation process. Such phenomenon which was not noticed in root of the eggplant was probably due to the somewhat bigger amount of secondary growth with development of apparently wider vessels.

Age of 9 weeks :

During the following two weeks, the root as in the eggplant, showed higher rate of secondary growth resulted in the attaining of the xylem to an average diameter of 1014.9 µ (Fig. 9). The general effect on the tissues outside the xylem did not differ than in the preceding age.

The exodermis showed further division of its component cells at different planes, increasing particularly its circumference.

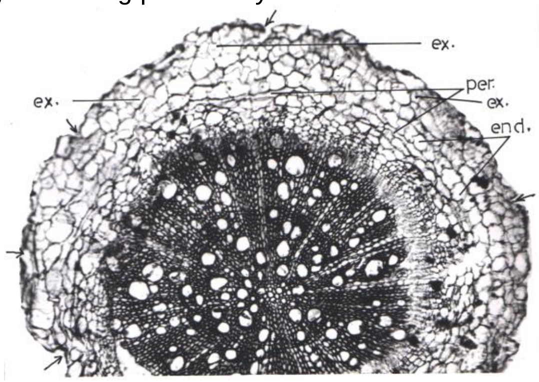

Fig. (9): Transection at the base of main root of tomato plant, 9-weeks old plant. At places pointed to by arrows the original exodermis was ruptured or crushed. The underlying cortical layer served for protection (X125).

ex.: Exodermis, Per.: Pericycle, end.: Endodermis.

The crushing or rupture of the original exodermis at occasional places was substituted by the underlying cortical layer whose outer walls became thickened and suberized. The other cortical cells and the endodermal ones continued dilatation. The endodermis was to a large extent able to keep its distinct appearance and uniformity in size and shape of its cells, in contrast with the cortex which some of its cells showed periclinal division.

Many pericyclic cells were radially flattened and their tangential walls at occasional places were seen very close to each other. It was difficult sometimes to define the outline of many of these cells.

The conducting elements of secondary phloem were present in distinct groups separated by somewhat dilated phloem parenchyma or ray cells, a structure which was not observed in the eggplant root, where the different phloem elements were intermingled.

Age of 12 weeks :

When the plant ceased its vegetative growth i.e. about 12 weeks after sowing, the vascular cylinder attained its final size and structure (Fig. 10). The xylem doubly increased in diameter being 1925.3 µ in the average. All the extra-stelar tissues from the outside exodermis to the inside endodermis were largely compressed. All cells had underwent very active dilatation growth. In contrast with the preceding ages it brought the cortical, endodermal and pericyclic cells to be nearly alike in size and shape since they all were radially narrowed and assumed more or less elliptical or spindle shape.

The big increase of xylem core was not only responsible for the ultimate histological state of the outer tissues just described but also active addition of secondary phloem was accomplished during the last 3 weeks of the vegetative growth. The phloem appeared in pyramidal-like structure consisting mostly of conducting elements separated by dilated parenchyma or ray cells.

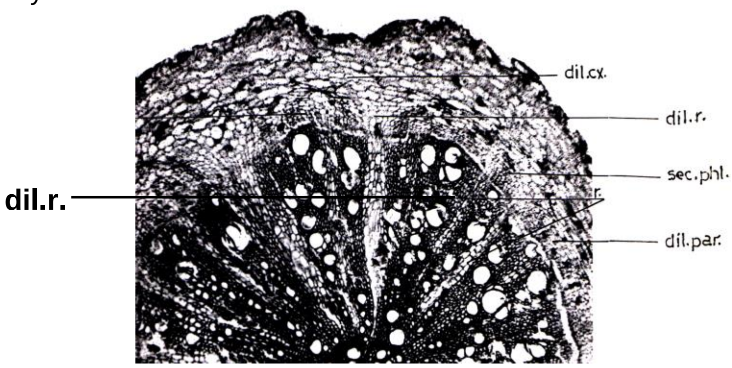

Fig. (10): Transection at the base of main root of tomato plant, 12-weeks old plant. Notice that the collapsed superficial cells and the still intact ones of the cortex all having suberized walls, from the protective tissue (X125).

dil.cx.: Dilated cortex, dil.r.: Dilated ray, sec.phl.: Secondary phloem, dil.par.: Dilated parenchyma.

In contrast to the eggplant, no development of any periderm-like structure at the periphery of the root was detected. It appeared that at this site the collapsed and the still intact cortical cells all having suberized walls serve for a protective tissue.

In the successive ages, storage depletion of food stuff in root parenchyma of the eggplant previously mentioned, was not found in the tomato plant.

Cambial activity in the root was much more pronounced during the last 3 weeks of the vegetative growth which lasted 12 weeks. About 50 % of the xylem tissue was developed during this period. This was in favour of supplying the growing shoot system with its requirements to build up about 60 % of its final growth of its shoot system as estimated by dry weight.

It was also noticed that cessation of cambial activity in the root which marked also the cessation of the vegetative growth preceded active start of blooming and fruiting of the plant. While the former was recognized 80 days after sowing, the first collection of marketable fruits took place after 99 fays from sowing.

The tomato plant did not differ in this respect than the eggplant (Rendle, 1967).

On the other hand, both the egg and tomato plants had relatively little vegetative growth and small amount of secondary growth; their roots showed an ill-defined periderm-like tissue or even its absolute absence (Pandey, 2003).

Xylem characteristics :

As seen in Fig. (11) the whole vascular cylinder was dissected into differently sized sectors by rays of varied width ranging in cross sections from 2 to 6 cells.

This histological characteristic was not present in the eggplant (Esau, 1977 and Fahn, 1977).

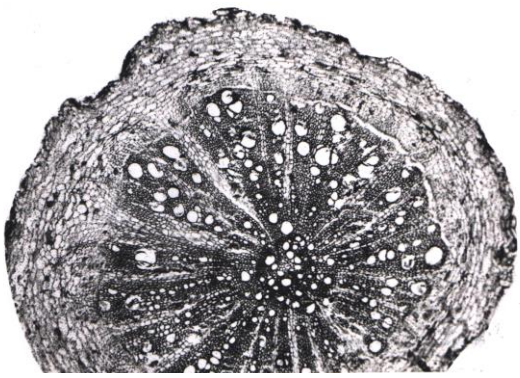

Fig. (11): Transection at the base of main root of tomato plant, 12-weeks old plant, notice the dissected vascular cylinder, and the absence of a true periderm or periderm-like structure (X100).

The ground tissue consists mainly of lignified parenchyma. The vessels are round and mostly solitary. Occasional clusters of 2 to 4 vessels in radial pattern are also present. While in the root of tomato plants wider most vessels were seen at the periphery of the xylem tissue which indicates their late development, they appeared earlier in the eggplant as described before. Thus, the root xylem in the tomato plant unlike that in the eggplant looked heterogeneously perforated (Hayward, 1938 and Hutchinson, 1973).

Comparing the xylem tissue at base of the root at end of vegetative growth, it was clear that the root possessed smaller number of vessels, but this was compensated by their bigger diameter, as tabulated below :

	Mean No. vessels	**Mean vessel diameter (µ)**
Solanum melongena	120	55.7
Solanum lycopersicum	185	57.6

It was interesting to notice that the increase in amount of vegetative growth as estimated by dry weight appeared to go parallel with the increase in vessel diameter and not in number of vessels in the roots.

The two investigated species could be arranged according to the amount of vegetative growth as follows :

Eggplant	Small amount	4.779 g/plant
Tomato plant	Small amount	4.124 g/plant

The same arrangement could also be made with respect to the vessel diameter tabulated before.

It seemed therefore, that more nutrition requirements of bigger vegetative growth needed the development of wider vessels rather than their bigger number.

The finding of different types of protective tissues in roots of the present investigated herbaceous species of the *Solanaceae* was also recorded by Luhan (1955) working on several herbaceous dicotylendons growing on the alpes.

The previous results on the amount of secondary growth and the accompanying histological changes in the primary body of roots of the two studied species showed that the annual herbaceous dicotyledonous plants behaved differently as to the distinction of periderm formation. The amount of secondary growth varied in the investigated plants and it was clear that the bigger the amount, the more readiness of the root to form a periderm-like structure until the true periderm was developed with the biggest amount as shown below :

	Mean xylem diameter	**Protective tissue**
Solanum melongena	1731.3	+
Solanum lycopersicum	1925.3	-

Where (+) indicates a weak development of a periderm-like structure while (-) is an indication for the absence of any periderm.

The periderm-like structure appeared in the exodermis or the underlying cortical layers according to the species. This structure is not histologically a true periderm for it lacks :

1- The continuity around the root circumference, 2- The presence of phellogen with its well-known structural characteristics in cross section i.e. rectangular, readily flattened cells and, 3- Suberization and may be also lignification of the outer cells of the radial files that comprise the phellem (Cork cells) in the true periderm.

In case of the untrue-periderm, the walls of the outermost cell of every radial tier serves as cork cell. The true periderm developed normally in the pericycle (Esan, 1977 and Fahn, 1977).

On the other side, eggplant had relatively little vegetative growth and small amount of secondary growth; the roots showed an ill-defined periderm like tissue or even its absolute absence.

Finally, the other obtained results or histological observations might be of physiological evolutional or taxonomic value.

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نظام النمو الثانوي في جذور نوعين من الأعشاب التابعة لجنس السولانم

عرفه أحمد عرفه
قسم النبات الزراعي - كلية الزراعة - جامعة المنصورة

نوعان من الأعشاب التابعة لجنس السولانم هما الباذنجان والطماطم كانا محل دراسة كيفية حدوث النمو الثانوي وما يتبعه من تكوين الأنسجة الواقية في جذورهما.

وكانت النتائج الرئيسية كما يلي :

١- لقد استكمل نسيج الخشب عند قاعدة الجذر نسبة من حجمه النهائي خلال مرحله مبكرة من النمو إذ كانت وبصورة واضحة أكبر مما يحتاجه المجموع الخضري عند هذه المرحلة .

٢- في المقابل لم يستدل على أي تطور لتركيب يشبه البريدرم في جذر نبات الطماطم. ظاهره نفاد الغذاء المخزن في بارنكيما جذور الباذنجان لم يستدل عليها في جذور نبات الطماطم خلال المراحل المتتالية من عمر النبات .

٣- لوحظ في جذور الطماطم أن الإسطوانة الوعائية كانت مجزئه إلى أجزاء متباينة الأحجام بواسطة أشعة متباينة الإتساع في القطاع العرضي حيث تراوح عرضها بين خليتين إلى ست خلايا. هذه الخاصية النسيجية لم تكن ظاهرة في جذور نبات الباذنجان.

٤- لقد ظهر واضحاً أن خشب جذور نبات الطماطم يبدو مثقباً بصورة غير متجانسة مقارنة بما هو عليه في جذور نبات الباذنجان.