

Root cortex: structural and functional variability and responses to environmental stress

Alexander Lux^{*})

Dept. of Plant Physiology, Faculty of Natural Sciences, Comenius University in Bratislava, Slovak Republic; Field Production Science Center, Graduate School of Agricultural and Life Sciences, The University of Tokyo, Japan

Miroslava Luxová

Institute of Botany, Slovak Academy of Sciences, Bratislava, Slovak Republic

Jun Abe

Dept. of Agricultural and Environmental Biology, Graduate School of Agricultural and Life Sciences, The University of Tokyo, Japan

Shigenori Morita

Field Production Science Center, Graduate School of Agricultural and Life Sciences, The University of Tokyo, Japan

Abstract: The cortex is the basic part of the primary root body and represents an important constituent of the root, both structurally and functionally. In monocotyledons, it might persist during the entire life of the root. In dicotyledons, with limited secondary thickening it might persist for a long time and be subject to dilatation growth. In intensively secondary-thickening roots, the cortex gradually deteriorates and is replaced by secondary tissues—the periderm. The functions of cortical tissues are diverse. The endodermis, and to some extent the exodermis, represent apoplastic barriers that control the uptake and radial transport of water and solutes by the root. However, these layers have several additional functions such as mechanically protecting the stele and protection against pathogens and parasites. Although the mid-cortex (or mesodermis) is primarily the site for reserve material deposition, it can also have several different functions that depend on the species and growth conditions. These include aeration in hypoxia (aerenchyma formation), and the location for symbiosis and even photosynthesis. The cortex varies widely amongst species and even in various root types of the same species. It might be designated as a root buffer zone, especially under stress conditions. Some aspects of the development, structure and function of cortical tissues are discussed in this report.

Keywords: cortex, endodermis, exodermis, hypodermis, mid-cortex

1. Introduction

Root cortical tissues have long attracted the attention of researchers because they are a complex of tissues at the site in which radial movement of water and solutes into the roots is regulated. Originally, it was mainly the endodermis that was considered the root apoplastic barrier—it controlled “free” water and ion movement through the apoplast and forced all transported solutes to pass through the plasma membrane and into the

symplast. The plasma membranes selective function regulated the passage of ions at this point of the transport pathway. In the early nineties, due to the introduction of new fluorescence staining techniques (Brundrett et al., 1988, 1991), a series of papers appeared that demonstrated the presence of a second apoplastic barrier in the majority of angiosperms—the exodermis (Perumalla et al., 1990; Peterson and Perumalla, 1990). However, this cortical layer is somehow ecologically

2004年8月31日受付

* 連絡先 Dept. of Plant Physiology, Faculty of Natural Sciences, Comenius University, Mlynská dolina B-2, SK-842 15, Bratislava, Slovak Republic
Fax: +421-2-65429064 E-mail: lux@fns.uniba.sk

dependent, and unlike the endodermis, does not usually represent a uniform sheath that covers the entire root (see Peterson, 1997). A partially neglected tissue is the mid-cortical layer, which is also called the mesodermis. It is often a multilayered tissue that plays an important role in the function of the root as a storage place for reserve materials, is metabolically active and produces various organic compounds, facilitates aeration of roots in anaerobic conditions and sometimes even provides assimilates and is a site for photosynthesis.

A structural and functional study of the root cortex currently provides some new information. In particular, the endo- and exodermis are the subjects of several recent reviews (Enstone et al., 2003; Ma and Peterson, 2003, and references therein). Thus, the main purpose of this review is to point out some of the less-discussed aspects of peripheral root tissues and to stimulate research in these areas. It is mainly aimed at (1) the structural (and, thus, also functional) variability of cortical tissues in various plant species, (2) differences between individual root types of the same plant, (3) the little studied processes occurring in the root cortex of plants with secondary thickened roots, (4) some aspects of various stress factors, and (5) inter- and intraspecific differences in the root cortex that are related to stress tolerance.

2. Concept of cortical layers

The root cortex is a well-defined part of the primary root body (Fig 1A). Its development is the result of periclinal, anticlinal and transversal cell divisions of the apical initials (see Morita, 2000; Barlow, 2002; Baum et al., 2002; Chapman et al., 2003; and references therein). Meristematic cells derived from initial cells divide: (1) transversally, which increases the number of cells in columns in a longitudinal direction, (2) periclinally, which increases the number of cell layers in a radial direction, and (3) anticlinally, which increases the number of cells in individual cell layers. Therefore, the root pattern, as can be observed in cross sections, is formed by periclinal and anticlinal divisions. In the majority of roots, the sequence of periclinal divisions is centripetal: the first cells that cease periclinal divisions are at the periphery of the root cortex, while the final periclinally dividing cells produce the innermost cortical cells, the cells of the endodermis (see Kawata and Lai, 1965).

However, exceptions to this rule exist, and the internal part of the cortex shows centripetal growth while the external part shows a division in a centrifugal direction in roots of some species. Despite this, the innermost cortical layer is the endodermis, and it is a mistake to describe the root structure as being composed of the cortex and endodermis, simply because the endodermis is part of the cortex. Unfortunately, this confusion is quite common in recent literature, mainly due to the incorrect interpretation of the *Arabidopsis* root structure. This excellent model plant has a beautifully simple and usually highly regular root structure. Its cortex often consists of only two cortical layers, the outer and inner, the innermost of which is the endodermis. It is quite common to describe this root structure as consisting of one layer of cortex and one layer of endodermis. However, this is not correct.

The external part of the root cortex can be of a very variable composition. In dicotyledonous plants, it is usually simple, while in monocotyledonous plants it is more complex. The most complicated structure of peripheral cortical tissues might be described as the complex hypodermis, which often consists of one or several (multiseriate) peripheral layers of exodermis situated below the epidermis and the centripetally developed internal sclerenchymatous layer(s) (Fig. 1B). This model is rather common in grasses (e.g., in rice, see Morita and Nemoto, 1995; Kondo et al., 2000). The term exodermis is reserved for the peripheral cortical layer(s) that develop Casparian bands and form the second (or first, if we start counting from the root surface) root apoplastic barrier (Peterson and Perumalla, 1990). However, this layer is somehow less constant, and unlike the endodermis does not usually form a compact and uninterrupted sheath covering the whole root body. It might develop in a patchy form, discontinuously, or even be absent in some roots of plants that possess the ability to form exodermis (see Zimmerman and Steudle, 1998). In species in which the exodermis is absent, the term hypodermis is used when the external (subepidermal) cell layer differs from the rest of the cortical tissues. This difference is sometimes only a result of the shape, but most frequently a result of the sclerenchymatous character of the hypodermal layer(s), which form a mechanical protection over the root surface.

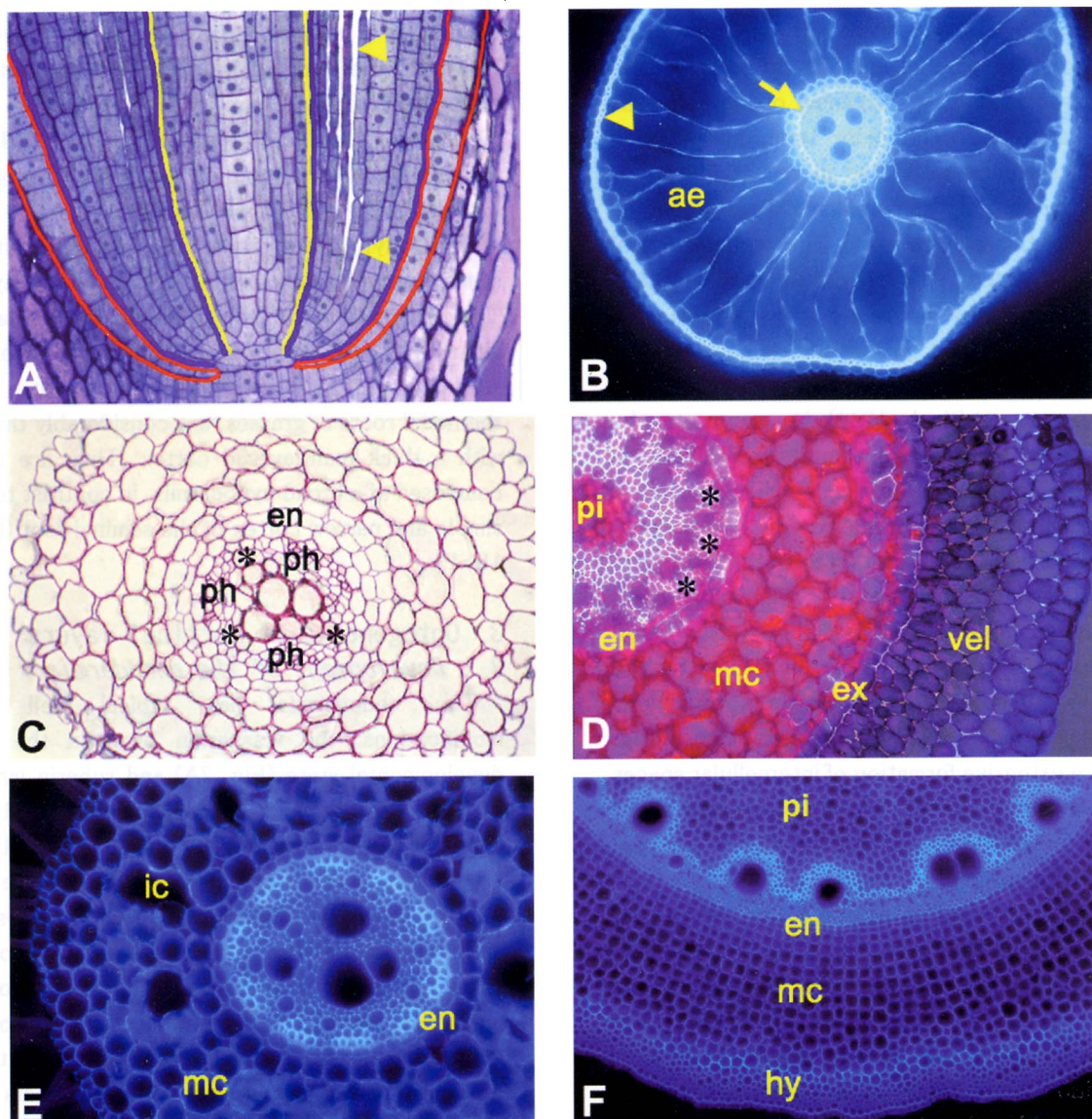


Fig. 1 White light and fluorescence microscopy of roots to show the development and variability of the root cortex in various species. (A) Median longitudinal section of the rice root apex. Formative divisions of three histogens: dermatogen, periblem and plerome, give rise to the epidermis (red), cortex (blue) and stele (yellow), respectively. Lower and lateral parts show the portion of root cap. Note the intercellular spaces close to the tip (arrows). Sample fixed in glutaraldehyde and osmium tetroxide and embedded in Spurr's resin. Semithin section, stained with toluidine blue and basic fuchsine, according to Lux (1981). (B) Cross section of mature nodal root of rice. Note the sclerenchyma layer in the outer cortex (arrowhead), thick-walled endodermis (arrow) and extensive intercellular spaces that form aerenchyma (ae). Freehand cross section, autofluorescence under UV light. (C) Cross section of the primary root of yarrow (*Achillea collina*). Example of simple primary structure of thin triarch root (*, xylem pole; ph, phloem pole) of a dicotyledonous plant. Preparation as in (1A). (D) Aerial root of the epiphytic orchid, *Oncidium sp.* Red color is the result of chlorophyll autofluorescence under UV light. Note the thick velamen (vel; multilayered epidermis), stele with numerous xylem and phloem poles (polyarch root), and the unequal development of endodermis due to the positional effect, with thick walls opposite the phloem poles (exhibiting light blue fluorescence) and thin walls opposite the xylem poles (*). Freehand cross section, autofluorescence under UV light. (E - F) *Sorghum (Sorghum bicolor)* roots. (E) Seminal root of the plant grown in hydroponics, note the lysigenous intercellular spaces (ic). (F) Thick nodal (adventitious) root. In contrast to the seminal root, nodal roots have multilayered sclerenchymatous hypodermis, more layers of radially arranged mid-cortical cells, higher number of xylem and phloem poles and broad pith (pi) in the center of the stele. The innermost cortical layer with small cells and thick inner tangential walls is the endodermis. Both (E, F) are freehand cross sections, autofluorescence under UV light. en, endodermis; ex, exodermis; hy, hypodermis; mc, mid-cortex; pi, pith.

The mid-cortical layers are sometimes called the mesodermis. Although this part of the cortex usually remains parenchymatous (Figs. 1C-E), in some cases secondary thickening of the cell walls might also occur. The older term, mesodermis, which is somehow neglected in recent literature, was rather useful, and referred to the middle position of this cortical part. The arrangement of mesodermal layers, as observed in cross sections, might be in orderly radial rows (radial cell arrangement, see Fig. 1F) or cells might alternate in successive concentric layers (alternate type, see Fig. 1D; Sinnot and Bloch, 1941). In some roots, the central radial arrangement changes to alternate in peripheral layers. The presence of schizogenous intercellular spaces is typical for the mesodermis, which usually starts to form close to the apex (Fig. 1A) and might become extensive in some roots. Lacunae are developed in this way. Large intercellular spaces might also be formed by the breakdown of cells through lysigeny; lysigenous intercellular spaces are formed in this manner (Fig. 1E). The extensive formation of intercellular spaces or lacunae is typical for aquatic plants and might also be induced by anaerobic conditions in some non-aquatic species.

Variability of root cortex composition in various species can be found in Guttenberg (1968) and more recently in the Root Atlas (Kutschera and Sobotik, 1992). In most cases, these two very extensive works depict the structure of seminal or adventitious roots. However, the variability of root structure within the given species is accomplished with lateral roots, which might be of two (or perhaps even more) types in some species (see Hochholdinger et al., 2004). Lateral roots represent the majority of the root systems external surface and are probably responsible for the bulk of nutrient absorption: at least in some species, as has recently become evident (Kirk, 2003). The structural study of these roots is still very limited, and a detailed comparison of various root types in a given species is rare. Kawata et al. (1977) found two anatomically distinct lateral root types in rice. Irrespective of the order of branching, the first type were thick lateral roots that had a similar structure to the nodal root (epidermis, exodermis, sclerenchyma, aerenchyma, endodermis and the stele, which included one late metaxylem, although the size of each tissue was smaller). The second

type, thin lateral roots, had the epidermis, exodermis, sclerenchyma and endodermis. However, the mid-cortical layer was absent (no aerenchyma existed) and the stele had no late metaxylem. Similarly, Yamauchi et al., (1996) classified the lateral roots of cereals into two types: L-type (large) and S-type (small).

Generally, lateral roots are thinner, with a smaller diameter and a lower number of cell layers. The cortical tissues might be reduced to two layers, even in species with a multilayered cortex in seminal roots. However, adventitious roots, e.g., the nodal roots of grasses, are considerably thicker, with a thick multilayered cortex. They are often composed of a broad hypodermis, in contrast to the simple and narrow cortex of the seminal root (Figs. 1E, F).

3. Ontogenesis of cortical layers

3.1 *Development of the endodermis*

The endodermis has typical cell wall modifications: the Casparian band in the first developmental state (Fig. 2A) and suberin lamella in the second (Fig. 2B) (Guttenberg, 1968; Clarkson and Sanderson, 1974; Sanderson, 1983; Barnabas and Peterson, 1992). Due to these cell wall modifications, the endodermis becomes an apoplastic barrier that regulates the radial flow of water and ions in younger root parts (Peterson et al., 1993; Steudle and Peterson, 1998; Morita, 2000). In the third state, development of thick secondary walls in the endodermis protects the vascular tissues in older root parts, and the function of the endodermis is already mostly mechanical (Fig. 2C). Secondary cell walls at this state are sometimes called tertiary walls because a secondary layer of suberin lamellae has been deposited on the primary cell wall.

Creation of Casparian bands might be the final stage in some dicotyledons and monocotyledons, e.g., in aquatic plants of the Nymphaeaceae (Seago, 2002). In other species, mostly dicotyledons, the development of the endodermis has finished by the second state. In some of these species, the difference between the second and third states might not be very clear (Esau, 1965).

Published results of developmental studies of individual ontogenetic states of the endodermis in various species and root types are still scarce. They indicate that the first state occurs as close as

0.1 mm from the root tip in *Libocedrus decurrens* (Wilcox, 1962), 2–3 mm from the root tip in rice (Kawata and Lai, 1967), and 10 mm in *Ranunculus acris* and *Zea mays* (Scott and Peterson, 1979; Perumalla and Peterson, 1986). There is usually a broad zone between the first-formed Casparian bands and the distance to all endodermal cells with the bands. Moreover, as growth of the various species studied was under specific conditions, it is difficult to compare the data. Generally, the faster a root grows, the longer the distance from the tip to where Casparian bands are formed (Enstone et al., 2003; Ma and Peterson, 2003). This also means that any stress that affects root growth will result in a reduced distance of Casparian band formation to the root tip (Reinhardt and Rost, 1995). In tea, the white adventitious roots of plants grown hydroponically developed Casparian bands at a distance of 4 mm from the tip, while in the soil this distance was shorter. In lateral roots of the same species, it was only 1 mm from the root tip (Tanimoto et al., 2004, and unpublished results). Variable distances of Casparian band formation were also found between clones of the same species (for *Salix*, see Lux et al., 2004b).

Precise data about the second and third states of endodermal development are even scarcer. The zone of gradual development of suberin lamellae along the root axis is usually very long. In hydroponically grown maize, the development of suberin lamellae occurred from 80 to 240 mm from the tip to where the first endodermal cells entered the second state and the distance to all endodermal cells with suberin lamellae (Zeier et al., 1999). In soil-grown gentian roots, these distances ranged 5–30 mm from the root tip (Šottniková and Lux, 2003). In hydroponically grown pea, the first endodermal cells of primary seminal roots were found in the second state at a distance of about 100 mm from the tip (Lux and Tanimoto, unpublished results). In adventitious roots of hydroponically grown tea this distance was 50 mm from the tip, while in lateral roots of the same species it was only 1.5 mm from the tip (Tanimoto et al., 2004; Lux and Homma, unpublished results). Considerable intraspecific differences in the second endodermal state were found in willow adventitious roots (Lux et al., 2004b). Equally, as was the case of the first state, distances to the second and third states were affected by the speed of root growth and, thus, also

by stress factors.

In the third state, a thick cellulose secondary wall (sometimes classified as the tertiary wall) was deposited over the suberin lamellae. This wall, together with the original primary wall, might become lignified. As an addition to organic substances, impregnation of walls with silicon might occur in some species (see section 4.1). In many species, this thickening is limited to radial and inner tangential walls, which results in a so-called U-shaped thickening (Fig. 1C). In other species, the thickening is uniform and O-shaped thickening occurs.

For additional details about endodermal development and chemistry, see recent reviews by Enstone et al. (2003) and Ma and Peterson (2003).

3.2 Development of the exodermis

The exodermis is defined as a special type of hypodermis that develops Casparian bands (Peterson and Perumala, 1990; Fig. 2D). This layer, similarly to the endodermis, can be developed in three states: (1) Casparian band formation, (2) suberin lamellae deposition, and (3) secondary wall formation (referred by some authors as tertiary walls). Since there is an excellent recent review of exodermal development by Ma and Peterson (2003), apart from a brief summary of this topic, only some additional notes will be mentioned here.

After considerable discussion about the existence of Casparian bands, and thus about the existence of additional apoplastic barriers in roots, it was finally shown by Peterson and co-workers that this layer existed in the roots of the majority of angiosperm species. However, some difficulties make this tissue less accessible to investigation than other cortical tissues. The second state of development, in which suberin lamellae are usually deposited immediately after Casparian band formation, often masks the Casparian bands. Progress in the study of exodermal development was mostly undertaken as a result of the berberine staining procedure introduced by Brundrett et al. (1988), which allowed the amorphous suberin of Casparian bands to be distinguished from the suberin of lamellae. This allowed to identify the exodermis also in species where it was previously unknown (e.g. in rice; Morita et al., 1996).

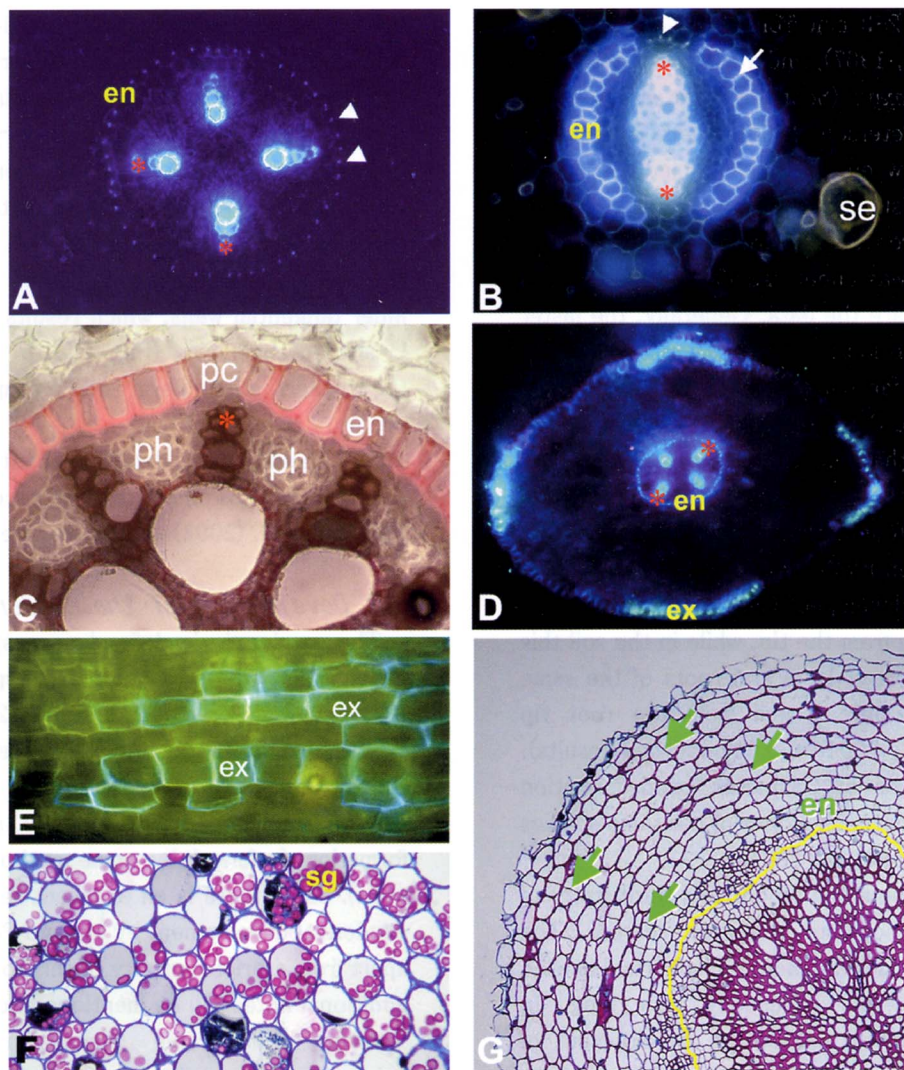


Fig. 2 Endodermis, exodermis and mid-cortical layers of various species observed in white light and fluorescence microscopy. (A) Endodermis in melon root with all cells possessing the Casparian bands (arrowheads). Cross section stained with berberine-toluidine blue, fluorescence under UV light. (B) Endodermis in *Karwinskia parvifolia* root. Positional effect, the endodermal cells opposite the two xylem poles (*) remain in state I, possessing the Casparian bands only (arrowhead), while cells opposite the broad phloem poles proceed to state II, suberin lamellae deposition (arrow). Note the bright yellow fluorescence of secretory structure in the mid-cortex. Autofluorescence under UV light. (C) Endodermis of *Iris germanica* adventitious root. All endodermal cells have developed thick U shaped lignified secondary walls (state III of endodermal development), except two passage cells opposite one of the xylem poles (*). Cross section, stained with phloroglucinol-HCl and observed under white light. (D) Endodermis and exodermis in the tetrarch adventitious root of *Salix*. Positional effect in the exodermis. Exodermal cells opposite the four phloem poles are ontogenetically advanced. Freehand cross section stained with berberine-toluidine blue and observed under UV light. (From Lux et al., 2004, reproduced with permission from *Physiol. Plant.*, Vol. 120, p. 541, © Physiologia Plantarum 2004). (E) Exodermis of the tea adventitious root in longitudinal view. Patchy development of the exodermal cells results in groups of cells with wall modifications (exhibiting light blue fluorescence) scattered between the cells without these modifications. Root segment cleared in lactic acid, stained with berberine and observed under UV light. (F) Mid-cortical cells in the adventitious root of *Primula acaulis* contain numerous starch grains. Preparation as in (1A). (G) Cross section of the secondary thickening root of yarrow (*Achillea collina*). Cambium (marked by yellow line) produces the secondary vascular tissues, resulting in increased diameter of inner tissues. Cortical layers react by dilatation growth. Cell extension and radial cell divisions (marked by yellow arrows) take place in all cortical layers in this species. Compare with the primary structure of the same root in Fig. (1C). Preparation as in (1A). *, xylem pole; en, endodermis; ex, exodermis; pc, passage cells; ph, phloem pole; se, secretory structure; sg, starch grains.

The exodermis might develop in a uniform fashion, composed of similarly sized and formed cells. This type has been most studied in maize. Another type of exodermis, which has mostly been studied in the onion, is dimorphic, with alternating long and short cells. Moreover, the exodermis can be uniseriate or multiseriate. The type, presence or absence of the exodermis appears to be a constant characteristic at the family level (Perumalla et al., 1990; Peterson and Perumalla, 1990).

Other difficulties in the study of the exodermis are the influence of external conditions on its development, and its absence under specific conditions (e.g., hydroponics), even in species where it is normally present. The exodermis usually forms at a greater distance from the root tip than the endodermis. In maize, cultivated in moist vermiculite, exodermal Casparian bands appear after four days of cultivation, when roots are 60 mm long (Enstone and Peterson, 1997). Similarly in onion, they appear after five days and about 50 mm from the tip. However, a reverse sequence of differentiation was found in some species, with the exodermis differentiating earlier (closer to the root tip) than the endodermis. This phenomenon was found in some wetland plants (Seago et al., 1999; Soukup et al., 2002) and in tea plants (Homma et al., 2000; Tanimoto et al., 2004).

Gradual and patchy development of exodermis along the root axis is another characteristic of this cortical layer. There is always a long root zone with non-mature exodermis, and what is most interesting is that development need not be continuous along the cell files. This results in the formation of "islands" or groups of cells with developed Casparian bands and suberin lamellae scattered between the cells without these wall modifications. This can best be seen in longitudinal views (Fig. 2E). Sometimes preferential development of exodermis against the phloem poles can be observed (see section 3.4)

3.3 Development of mid-cortex (mesodermis)

Mesodermal layers attract less attention than the endo- and hypodermis. Nevertheless, these cortical layers are important as storage places (mainly depositing starch). They are important metabolically, often depositing or synthesizing various secondary metabolites that are sometimes accumulated in specialized secretory structures

(see Lux et al., 2004a; Fig. 2B). They also represent a place for root symbiosis with fungi. Thickening of mesodermal cell walls, sometimes in a curious form of phi thickenings (resembling in cross sections the Greek letter Φ), is supposed to mostly serve for the mechanical strengthening of the cortex (Esau, 1965; Enstone et al., 2003). Aerial roots often contain chloroplasts in their mid-cortical layers, and also in the pith. This characteristic is typical and well known for aerial roots of epiphytes (Fig. 1D). However, parenchyma cells in grass nodal roots exposed to the light are also full of chloroplasts. This phenomenon requires a more detailed study.

The majority of recent structural work that deals with the mesodermis has focused on aerenchyma formation. Aerenchyma is defined as a tissue that contains enlarged gas spaces, which exceed the commonly present intercellular spaces. It can be formed constitutively or induced by abiotic stresses, usually by hypoxia that results from waterlogging. Sometimes it is induced by other stresses such as drought, high temperature or nutrient deficiency. The main reason for the interest in aerenchyma is its importance for crop survival under waterlogged conditions. Aerenchyma is also important, as it is a major pathway for the release of the global warming gas, methane, to the atmosphere in flooded soils. Therefore, an understanding of the regulation of its development is considered a research priority (Evans, 2003).

Aerenchyma formation has been intensively investigated in rice plants because of the vital importance of internal aeration to roots in paddy fields. It was found that the main roots (numerous nodal roots forming the skeleton of the root system) were aerenchymatous, with continuous gas channels from the root base to the tip. However, they were covered by gas-impermeable peripheral cortical layers (Morita and Nemoto, 1995; Colmer, 2003; Fig. 1B). This structural model conflicts with the need for efficient water and nutrient absorption, therefore the main water and solute uptake should be realized with short, fine lateral roots, which are considerably less aerenchymatous, and also with less-thickened peripheral cortical walls (Kawata et al., 1977; Matsuo and Hoshikawa, 1993). They account for the majority of the external surface of the rice root system and are supposed to be responsible for the bulk of water and nutrient

absorption by the root system (Kirk, 2003). Aerenchyma development has also been well studied in various wetland plants, with considerable differences in cortical layer composition noted (for details, see review by Seago, 2002). The entire topic of aerenchyma formation was recently published as the Tansley review (Evans, 2003).

3.4 *Effect of the radial organization of the stele, determined by xylem and phloem poles, on cortex development-positional effect*

Radial organization of the root vascular bundle with alternating xylem and phloem poles has a significant impact on the development of the cortex. This effect is clear and well known in the endodermis, starting from the proendodermal stage, and is particularly evident during the second state of development. The first state, Casparian band development, sometimes starts in all endodermal cells at the same distance from the root tip, or at least appears to. A more detailed study usually shows that, even at this state, the endodermal sectors opposite the phloem poles are "privileged" and form Casparian bands earlier than the endodermal cells opposite the xylem poles. The long distance along the root axis with gradually formed suberin lamellae (second state) is also subject to this positional effect. In some species (e.g., the lateral roots of the shrub, *Karwinskia* spp., family Rhamnaceae; Fig. 2B), endodermal cells opposite the xylem poles remain permanently in the first state, while cells opposite the phloem poles proceed to the second state. If delayed, development of certain cells continues to the stage in which the majority of endodermal cells pass to the third state. This results in the formation of so-called passage cells (Fig. 2C). However, in some species, passage cells might later complete their ontogenesis and proceed to the second or third state.

The positional effect was found not only in the endodermis, but also in mid-cortical layers during aerenchyma formation in maize and willow. Living cortical cells are located opposite the protoxylem, and air channels are formed opposite the phloem poles as a result of cell autolysis (Scott, 1928; Konings and Verschuren, 1980; Barlow, 2002). This indicates that the signals radiating from the phloem and/or xylem poles that regulate the events

of cell death and cell wall synthesis in cortical layers can extend across several cell layers. Recently, we found clear evidence of the positional effect in the exodermis of willow adventitious roots opposite the phloem poles with advanced development of this layer (Lux et al., 2004b). As these roots are usually tetrarch, four sectors of developed exodermis can be found at some distance from the root tip (Fig. 2D). Another evidence of signals radiating from the stele up to the exodermis is the formation of a "window" in the region of exodermis opposite the growing lateral root primordium. In this window, the exodermis lacks suberin and lignin (Soukup et al., 2002). New findings can be expected in connection with the positional effect phenomenon in cortical cells.

3.5 *Secondary dilatation growth of cortical tissues*

There is extensive literature that deals with early changes of root cortical layers, especially in regards to the endo- and exodermis. Much less studied are the older root parts. However, the cortex can persist, even in quite old secondarily thickening roots. In early stages of cambial activity, extension of peripheral layers that correspond to secondary thickening of vascular cylinders takes place in all roots. This enlargement of peripheral tissues is called dilatation growth. Thus, the secondary growth of roots comprises cambial growth (realized by vascular cambium and cork cambium activity) and dilatation growth (present in the primary cortex, rhizodermis, in axial phloem parenchyma and in the ray parenchyma of bark; Esau, 1965; Lev-Yadun and Aloni, 1992). Dilatation growth involves cell enlargement and/or cell renewed division.

Changes that occur in endodermal cells are probably the most interesting feature of dilatation growth. These cells develop specific wall modifications (see section 3.1) and represent highly specialized cells with extremely important functions for the regulation of radial transport in the roots. However, during dilatation growth, their cell walls must extend. Moreover, in some species these cells radially divide. The additional division of endodermal cells is a species-specific feature, and the number of cells along the circumference of the endodermal sheath increases as a result. The number of additional divisions of an individual

endodermal cell is also variable and species-specific, ranging from single division (e.g., in *Primula acaulis*; Lux and Luxová, 2003/4) up to 24 new radial walls being formed (*Gentiana asclepiadea*; Šottníková and Lux, 2003).

Previous reports by authors (e.g., Bond, 1930) indicate that the additional division of cells starts during endodermal developmental states I or III. After the division of endodermal cells during state I, the new radial walls gain a typical endodermal character and Casparian bands are deposited soon after the new wall forms. Thus, the endodermal apoplastic barrier is not interrupted by these new walls. If the additional division takes place in endodermal cells during state III, the new radial walls remain without Casparian bands in the majority of species. These new walls have the character of supporting prop walls, and protect strongly-expanded endodermal cells from collapse. An exception to this rule was found in *Primula*, with Casparian bands developing in new radial walls after the division of thick-walled endodermal cells (Lux and Luxová, 2001, 2003/4). The role of these Casparian bands remains obscure, as no apoplastic transport is expected across endodermal cell walls in state III.

Expansion of the cortex in secondary thickening roots also induces dilatation growth in mid-cortical and hypodermal layers. In some species, even these cells might additionally divide. Radial division in mid-cortical layers is relatively common (Fig. 2G),

while division of the hypodermis is rare. This was found in species of the genus *Gentiana* (Luhan, 1954; Šottníková and Lux, 2003)

The additional division of endodermal cells is a rather frequently occurring phenomenon in roots of dicotyledons (for a review, see Lux and Luxová, 2001). However, several cytological and functional aspects and consequences of this process remain to be elucidated.

4. Reaction of the cortex to stress

The reaction of the root and the specificity of its cortical tissues to stress factors is a very broad subject, and might be the topic of a separate review. Here, only some aspects of this subject will be discussed. Special attention would require the interaction of cortical cells with symbiotic and pathogenic organisms, which is outside the scope of this review. Despite this, some new data about this very interesting topic can be found in the review of arbuscular mycorrhiza (Strack et al., 2003) and in the review of root endo- and exodermal responses to the environment (Enstone et al., 2003). It is also interesting to note that a protective role of the exodermis against pathogenic fungi was recently proven in barley roots by Reissinger et al. (2003).

The entire cortex can be understood as a kind of root "buffer zone". Peripheral tissues, at least up to the endodermal layer, which includes the epidermis, hypodermis and mesodermis, might be damaged and even deteriorate in some root parts.

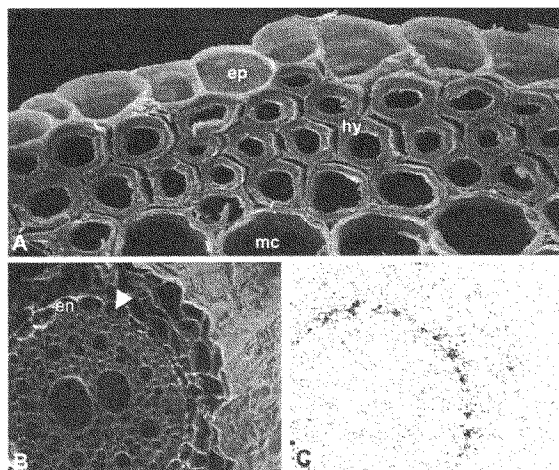


Fig. 3 Root cross sections observed in scanning electron microscope (SEM) and environmental scanning electron microscope (ESEM). (A) Thick-walled hypodermal layers in the old adventitious root of wheat (SEM). (B–C) Seminal root of Sudan grass (*Sorghum sudanense*). Endodermal cells are impregnated by silicon and specific silica aggregates are deposited on the inner tangential walls of the endodermal cells (arrowhead). (B) is an ESEM photo and (C) represents corresponding X-ray analysis using mapping mode to demonstrate the presence of silicon. en, endodermis; ep, epidermis; hy, hypodermis; mc, mid-cortex.

However, the root can still provide its most important function – to supply water and ions to the plant. The first cortical barrier, the hypodermis (or exodermis), is the first important part of this buffer zone. It usually reacts very sensitively to various stresses, as was demonstrated by the development of wall modifications characteristic to exodermal cells. For example, in maize, the exodermis is absent in hydroponically grown plants, but present in plants grown aeroponically and in the soil (Zimmermann and Steudle, 1998). Cell wall modifications and impregnation by suberin, lignin or some other unidentified substances were observed in hypodermal and deeper cortical layers as a reaction to mechanical injury. The exodermis develops up to the root apex in roots that are subject to stress and have stopped or substantially slowed their growth (Brundrett et al., 1990; Tanimoto and Lux, unpublished results from tea roots).

Specific adaptations of the roots of plants tolerant to various forms of stress factors require more attention. For example, in roots of drought-tolerant dicotyledonous succulents from the family Cactaceae, the hypodermal layer is composed of large cells thickened only in their outer tangential walls (Lux and Inanaga, 1997). These cells probably function mainly as water reservoirs. However, the hypodermal layers of grasses are frequently formed from small cells with thick walls (Fig. 3A), which is an important barrier that protects inner tissues. In sorghum, sclerification and wall thickness in a drought-tolerant cultivar was greater when compared with a drought-sensitive cultivar (Salih et al., 1999). Kondo et al. (2000) reported that some rice varieties (mostly upland varieties) formed two or three layers of sclerenchyma in the outer cortex, while most other rice varieties formed only one layer. Developmental plasticity of cortical layers in desert plants related to sources of water was shown by North and Nobel (1998, 2000).

Cell wall thickening of root cortical cells is associated with high salt and heavy metal stresses (Reinhardt and Rost, 1995). The endodermis was demonstrated to be an effective barrier to Na⁺ in the alkali grass, *Puccinellia tenuiflora* (Peng et al., 2004). The effects of salinity on the development of Casparian bands in the primary roots of maize were studied by Karahara et al. (2004). They found that

Casparian bands matured closer to the root tip in plants grown with an increased concentration of NaCl compared with the control. Moreover, the radial width of Casparian bands increased in the presence of salt. This suggests that the function of the bands is enhanced under salt stress.

Other types of stress can also induce changes in the cortical cell wall structure and composition. For example, a water deficit increased the lignification of the exodermis in tomato roots (Nakano et al., 2003). In maize roots, multiple environmental stresses (cultivation in municipal solid waste slag with high pH, high salt and heavy metal content) induced more intensive wall thickenings in the inner tangential walls of endodermal cells when compared with the roots of control plants. Slag-grown plants also had higher amounts of lignin in the endodermal and hypodermal layers when compared with control plants (Degenhardt and Gimmler, 2000). In wheat roots, hypoxia induced cell wall thickening. In this case, it accounted for an increase in cellulose, but not in lignin content (Albrecht and Muströph, 2003). However, cell wall thickening in the endodermis of rice only occurs in upland cultivars (Kawata and Lai, 1966). Some stresses result in specific root structural responses, e.g., aluminum induces radial cell expansion of cortical cells and callose formation in epidermal and outer cortical layers of cereals (Blancaflor et al., 1998; Budiková, 1999; Budiková and Mistrík, 1999; Čiamporová, 2002). However, species-specificity must be taken into account, even in this case, as it was shown that the absence of aluminum in the nutrient solution was a stress factor for hydroponically grown tea roots (Tanimoto, unpublished results).

4.1 *Silicon deposition in the endodermis and its relation to stresses*

In all these cases, the synthesis and deposition of organic substances represents a high cost to the plant, as these compounds cannot be reused in plant metabolism and represent a dead end for the metabolic pathways. In this manner, silicon deposition as an impregnating substance might be exceptionally advantageous. Silicon is metabolically “cheap” and is usually freely available to plants from the soil solution. Exceptions are some specific soils, and some intensively agriculturally used soils in which excessive extraction of silicon by plants

without its replacement could result in silicon deficiency symptoms (Ma and Takahashi, 2002). The mechanism of impregnation of cell walls by silicon has evolved in some plant species, and several so-called silicon accumulators deposit considerable quantities of this element in root endodermal cells (Sangster and Parry, 1976a, b; Lux et al., 1999, 2002, 2003a, b). In sorghum, and other species of the tribe Andropogoneae (family Poaceae), deposits of silicon form conspicuous silica aggregates on the inner tangential walls of the endodermis (Figs. 3B, C). We found that silicon accumulation in endodermal cell walls can even be higher than the silicification of leaves (Lux et al., 2003a). Silicon deposition was also found to be intraspecifically variable, and cultivars of both rice and sorghum with higher tolerance to drought have a higher silicification of endodermal cell walls than walls of drought-susceptible cultivars (Lux et al., 1999, 2002). Recently, it was found that sorghum supplied with silicon could extract a greater amount of water from the soil under drought conditions due to an acceleration of root growth and an enhancement of the water uptake ability (Hattori et al., in press). Root growth stimulation under dry conditions might be related to an increase of cell wall extensibility in an apical part of sorghum roots caused by silicon, as reported by Hattori et al. (2003). This high extensibility would allow the roots to elongate even when turgor pressure drops due to soil drying. Although silicon impregnation of endodermal walls acts as a protection against parasites (Bennett, 1982), this topic requires a more detailed study. Another beneficial effect of root silicification was to alleviate the effect on some toxic elements, mainly manganese, but also aluminum in some species (for a recent review of this subject, see Ma, 2004). Evidence appears to be accumulating about the unknown manner of silicon induced tolerance to several other toxic metals such as zinc (Neumann et al., 1997) and cadmium (Wang et al., 2000). This problem certainly requires more attention because of the importance of food contamination by toxic metals.

4.2 *Intraspecific differences of cortical tissues related with a reaction to toxic metals*

In our recent study, we analyzed the structural differences in roots of *Salix* clones that

substantially differed in the accumulation and translocation of cadmium and their sensitivity to this toxic metal (Lux et al., 2004b). An ontogenetic study of the endodermis indicated that the apoplastic movement of cadmium into the stele and the upward translocation might vary due to the development of this cortical layer. Development of Casparian bands in clones characterized with a high accumulation of cadmium started more distantly from the root tip than in clones with a low accumulation. Even more prominent were differences in the second state of endodermal development. The suberin lamellae were formed more distantly from the root tip in clones with a high translocation of cadmium (5–15 mm from the root tip) compared with those with a low translocation (2–5 mm from the tip). Furthermore, a quantitative comparison of area proportions of individual cortical layers showed a relationship with tolerance to cadmium. Clones with a high tolerance had a higher proportion of endo- and exodermis than sensitive clones. It is interesting to note that Rincon et al. (2003) found that the major genotypic differences in soybean root structure related with variations in resistance to water movement through the roots were in the surface area of the stele that approximates the dimension of the endodermal layer. Although there are several potential barriers to water conductance and ion uptake by the root system, the aforementioned results, together with the genotypic differences of cortical tissues related with the cadmium accumulation and sensitivity found in the willow, point to the importance of these tissues and the importance of research on this topic.

Acknowledgement

The work was partially supported by the Field Production Science Center, the University of Tokyo, grant 1/0100/03 from the Slovak Grant Agency VEGA and COST Action 859. We apologize to all colleagues whose works were not included due to the lack of space. The authors appreciate the generosity of the Keyence Company in allowing us to use their high sensitive CCD color camera to take some photos for this review.

References

Albrecht, G., Mustrup, A. 2003. Localization of sucrose synthase in wheat roots: Increased in situ activity of

- sucrose synthase correlates with cell wall thickening by cellulose deposition under hypoxia. *Planta* 217: 252-260.
- Barlow, P.W. 2002. Cellular patterning in root meristems: its origins and significance. In Waisel, Y., Eshel, A., Kafkafi, U. eds., *Plant Roots The Hidden Half*. 3rd Edition. pp49-82. (Marcel Dekker, Inc., New York, Basel)
- Baum, S.F., Dubrovsky J.G., Rost, T.L. 2002. Apical organization and maturation of the cortex and vascular cylinder in *Arabidopsis thaliana* (Brassicaceae) roots. *Am. J. Bot.* 89: 908-920.
- Barnabas, A.D.; Peterson, C.A. 1992. Development of Casparian bands and suberin lamellae in the endodermis of onion roots. *Can. J. Bot.* 70: 2233-2237.
- Bennett, D.M. 1982. Silicon deposition in the roots of *Hordeum sativum* Jess., *Avena sativa* L. and *Triticum aestivum* L. *Ann. Bot.* 50: 239-245.
- Blancaflor, E.B., Jones, D.L., Gilroy, S. 1998. Alterations in the cytoskeleton accompany aluminum-induced growth inhibition and morphological changes in primary roots of maize. *Plant Physiol.* 118: 159-172.
- Bond, G. 1930. The occurrence of cell division in the endodermis. *Proc. R. Soc. Edinb.* 50: 38-50.
- Brundrett, M.C., Enstone, D.E., Peterson, C.A. 1988. A berberine-aniline blue fluorescent staining procedure for suberin, lignin, and callose in plant tissue. *Protoplasma* 146: 133-142.
- Brundrett, M.C., Kendrick, B., Peterson, C.A. 1991. Efficient lipid staining in plant material with Sudan red 7B or Fluoral yellow 088 in polyethylene glycol-glycerol. *Biotech. Histochem.* 66: 111-116.
- Brundrett, M.C., Murase, G., Kendrick, B. 1990. Comparative anatomy of roots and mycorrhizae of common Ontario trees. *Can. J. Bot.* 68: 551-578.
- Budiková, S. 1999. Structural changes and aluminium distribution in maize root tissues. *Biol. Plant.* 42: 259-266.
- Budiková, S., Mistrik, I. 1999. Cultivar characterisation of aluminium tolerance of barley seedlings by root growth, aluminium and callose distribution. *Biologia* 54: 447-451.
- Chapman, K., Groot, E. P., Nichol, S. A., Rost, T. L. 2003. Primary root growth and the pattern of root apical meristem organization are coupled. *J. Plant Growth Regul.* 21: 287-295.
- Čiamporová, M. 2002. Morphological and structural responses of plant roots to aluminium at organ, tissue, and cellular levels. *Biol. Plant.* 45: 161-171.
- Clarkson, D.T., Sanderson, J. 1974. The endodermis and its development in barley roots as related to radial migration of ions and water. In: Kolek J. ed., *Structure and Function of Primary Root Tissue*. pp87-100. (Veda, Bratislava, Czechoslovakia)
- Colmer T.D. 2003. Long-distance transport of gases in plants: a perspective on internal aeration and radial oxygen loss from roots. *Plant Cell Environ.* 26: 17-36.
- Degenhardt, B., Gimmler, H. 2000. Cell wall adaptations to multiple environmental stresses in maize roots. *J. Exp. Bot.* 51: 595-603.
- Esau, K. 1965 *Plant Anatomy*. 2nd Edition. p767. (John Wiley & Sons, Inc., New York, London, Sydney)
- Evans, D.E. 2003. Aerenchyma formation. *New Phytol.* 161: 35-49.
- Enstone, D.E., Peterson, C.A. 1997. Suberin deposition and band plasmolysis in the corn (*Zea mays* L.) root exodermis. *Can. J. Bot.* 75: 1188-1199.
- Enstone, D.E., Peterson, C.A., Ma, F. 2003. Root endodermis and exodermis: structure, function, and responses to the environment. *J. Plant Growth Regul.* 21: 335-351.
- Guttenberg von, H. 1968. Der primäre Bau der Angiospermenwurzel VIII/5. In Linsbauer K. ed., *Handbuch der Pflanzenanatomie*. (Gebrüder Borntraeger Verlagsbuchhandlung, Berlin-Stuttgart, Germany)
- Hattori, T., Inanaga, S., Araki, H., An, P., Morita, S., Luxová, M., Lux, A. Application of silicon enhanced drought tolerance in *Sorghum bicolor* (L.) Moench. *Physiol. Plant.* - in press
- Hattori, T., Inanaga, S., Tanimoto, E., Lux, A., Luxová, M. 2003. Silicon-induced changes in viscoelastic properties of sorghum root cell walls. *Plant Cell Physiol.* 44: 743-749.
- Hochholdinger, F., Park, W.J., Sauer, M., Woll, K. 2004. From weeds to crops: genetic analysis of root development in cereals. *Trends Plant Sci.* 9: 42-48.
- Homma, T., Miyama, D., Lux, A., Tanimoto, E. 2000. Histological characteristics and acidic region observed in tea roots. *Bull. Tokai Branch Crop Sci. Soc. Jpn.* 129: 39-40. (in Japanese)
- Karahara I., Ikeda, A., Kondo, T., Uetake, Y. 2004. Development of the Casparian strip in primary roots of maize under salt stress. *Planta* 219: 41-47.
- Kawata, S., Lai, K-L. 1965. On the meristematic state of the endodermis in the crown roots of rice plants. *Proc. Crop Sci. Soc. Jpn.* 34: 210-216. (in Japanese with English summary)

- Kawata, S., Lai, K-L. 1966. On the cell wall thickening of the endodermis in the crown roots of rice plants. Proc. Crop Sci. Soc. Jpn. 34: 440-447. (in Japanese with English summary)
- Kawata, S., Lai, K-L. 1967. On the differentiation of Casparian dots of the endodermis in the crown roots of rice plants. Proc. Crop Sci. Soc. Jpn. 36: 75-84. (in Japanese with English summary)
- Kawata, S., Sasaki, O. and Yamazaki, K. 1977. On the structure of the crown root and the lateral root, and vessel connection between them, in rice plants. Jpn. J. Crop Sci. 46: 569-579. (in Japanese with English summary)
- Kirk, G.J.D. 2003. Rice root properties for internal aeration and efficient nutrient acquisition in submerged soil. New Phytol. 159: 185-194.
- Konings and Verschuren, 1980; Formation of aerenchyma in roots of *Zea mays* in aerated solutions, and its relation to nutrient supply. Physiol. Plant. 49: 265-270
- Kondo, M., Aguilar, A., Abe, J. and Morita, S. 2000. Anatomy of nodal roots in tropical upland and lowland rice varieties. Plant Prod. Sci. 3: 437-445.
- Kutschera, L., Sobotik, M. 1992. Wurzelatlas mitteleuropäischer Gründlandpflanzen. Band 2, Teil 2 Anatomy. (Gustav Fisher Verlag, Stuttgart, Germany)
- Lev-Yadun, S., Aloni, R. 1992. Experimental induction of dilatation meristem in *Melia azedarach* L. Ann. Bot. 70: 379-386.
- Luhan, M. 1954. Zur Wurzelanatomie unserer Alpenpflanzen: III. Gentianaceae. Sitzungsberichte der Akademie der Wissenschaften Wien, Mathematisch-Naturwissenschaftliche Klasse, Abteilung I. 163: 89-107.
- Lux, A. 1981. Rapid method for staining of semi-thin sections from plant material (in Slovak). Biológia 36: 753-757.
- Lux, A., Inanaga, S. 1997. Die atypische Struktur der jungen Wurzeln einer Wuestensukkulente *Echinocactus platyacanthus*. Stapfia 50: 289-293.
- Lux, A., Lišková, D., Masarovičová, E., Kákoniová, D., Hanáčková, Z., Argalášová-Šutovská, K., Kollárová, K., Henselová, M., Ordoñez, J. R. 2004a. Biology of *Karwinskia* spp., experimental cultivation and secondary metabolites production. In J.N. Govil, P.A. Kumar, V.K. Singh, eds., Recent Progress in Medicinal Plants - Vol. 4. Biotechnology and Genetic Engineering. pp175-200. (Studium Press LLC, U.S.A.)
- Lux, A., Luxová, M. 2001. Secondary dilatation growth in the root endodermis. In: Gašparíková, O., Čiamporová, M., Mistrík, I., Baluška, F., eds., Recent Advances of Plant Root Structure and Function. pp31-37. (Kluwer Academic Publishers, Dordrecht, The Netherlands)
- Lux, A., Luxová, M. 2003/4. Growth and differentiation of root endodermis in *Primula acaulis* Jacq. Biol. Plant. 47: 91-97.
- Lux, A., Luxová, M., Abe, J., Morita, S., Inanaga, S. 2003a. Silification of bamboo (*Phyllostachys heterocycla* Mitf.) root and leaf. Plant Soil 255: 85-91.
- Lux, A., Luxová, M., Abe, J., Tanimoto, E., Hattori, T., Inanaga, S. 2003b. The dynamics of silicon deposition in the sorghum root endodermis. New Phytol. 158: 437-441.
- Lux, A., Luxová, M., Inanaga, S., Sugimoto, Y. 2002. Silicification in sorghum (*Sorghum bicolor*) cultivars with different drought tolerance. Physiol. Plant. 115: 87-92.
- Lux, A., Luxová, M., Morita, S., Abe, J., Inanaga, S. 1999. Endodermal silicification in developing seminal roots of lowland and upland cultivars of rice (*Oryza sativa* L.). Can. J. Bot. 77: 955-960.
- Lux, A., Šottníková, A., Opatrná, J., Greger, M. 2004b. Differences in structure of adventitious roots in *Salix* clones with contrasting characteristics of cadmium accumulation and sensitivity Physiol. Plant. 120: 537-545.
- Ma, F., Peterson, C.A. 2003. Current insights into the development, structure, and chemistry of the endodermis and exodermis of roots. Can. J. Bot. 81: 405-421.
- Ma, J.F. 2004. Role of silicon in enhancing the resistance of plants to biotic and abiotic stresses. Soil Sci. Plant Nutr. 50: 11-18
- Ma, J.F., Takahashi, E. 2002. Soil, Fertilizer, and Plant Silicon Research in Japan. (Elsevier Science, Amsterdam)
- Mager, H. 1932. Beiträge zur Kenntnis der primären Wurzelrinde. Planta 16: 666-708.
- Matsuo, T., Hoshikawa, K. 1993. Science of the Rice Plant. I Morphology. (Food and Agriculture Policy Research Center, Tokyo)
- Morita, S. 2000. Root Growth and Root System Development. (University of Tokyo Press, Tokyo). (in Japanese)
- Morita, S., Lux, A., Enstone, D.E., Peterson, C.A., Abe, J. 1996. Reexamination of rice seminal root ontogeny using fluorescence microscopy. Jpn. J. Crop Sci. 65(Extra issue 2): 37-38.

- Morita, S., Nemoto, K. 1995. Morphology and anatomy of rice roots with special reference to coordination in organo- and histogenesis. In F. Baluska et al. eds., Structure and Function of Roots. pp.75-86. (Kluwer Academic Publ. Dordrecht, The Netherlands)
- Nakano, Y., Nakano, A., Watanabe, S., Okano, K., Tatsumi J. 2003. External and internal root structures of tomato plants grown hydroponically in a humid atmosphere or in a nutrient solution. J. Jpn. Soc. Hort. Sci. 72: 148-155.
- North, G.B., Nobel, P.S. 1998. Water uptake and structural plasticity along roots of a desert succulent during prolonged drought. Plant Cell Environ. 21: 705-713.
- North, G.B., Nobel, P.S. 2000. Heterogeneity in water availability alters cellular development and hydraulic conductivity along roots of a desert succulent. Ann. Bot. 85: 247-255.
- Neuman, D., Niedel, U.Z., Schwieger, W., Leopold, I., Lichtenberger, O. 1997. Heavy metal tolerance of *Minuartia verna*. J. Plant Physiol. 151: 101-108.
- Peng YH, Zhu, YF, Mao YQ, Wang SM, Su WA, Tang ZC 2004. Alkali grass resists salt stress through high [K⁺] and an endodermis barrier to Na⁺. J. Exp. Bot. 55: 939-949.
- Perumala, C.J., Peterson, C.A. 1986. Deposition of Casparian bands and suberin lamellae in the exodermis and endodermis of young corn and onion roots. Can. J. Bot. 64: 1873-1878.
- Perumala, C.J., Peterson, C.A., Enstone, D.E. 1990. A survey of angiosperm species to detect hypodermal Casparian bands. I. Roots with a uniseriate hypodermis and epidermis. Bot. J. Linnean Soc. 103: 93-112.
- Peterson, C.A. 1997. The exodermis and its interactions with the environment. In Flores, H.E., ed. Radical Biology: Advances and Perspectives on the Function of Plant Roots. pp131-138. (An American Society of Plant Physiologists Series 18)
- Peterson, C.A., Murrmann, M., Steudle, E. 1993. Location of major barriers to water and ion movement in young roots of *Zea mays* L. Planta 190: 127-136.
- Peterson, C.A., Perumalla, C.J. 1990. A survey of angiosperm species to detect hypodermal Casparian bands. II. Roots with a multiseriate hypodermis or epidermis. Bot. J. Linnean Soc. 103: 113-125.
- Reinhardt D.H., and Rost T.L. 1995. Salinity accelerates endodermal development and induces an exodermis in cotton seedling roots. Environ. Exp. Bot. 35: 563-574.
- Reissinger A., Winter, S., Steckelbroeck, S., Hartung, W., Sikora, R.A. 2003. Infection of barley roots by *Chaetomium globosum*: evidence for protective role of the exodermis. Mycol. Res. 107: 1094-1102.
- Rincon, C.A., Raper, C.D., Patterson, R.P. 2003. Genotypic differences in root anatomy affecting water movement through roots of soybean. Int. J. Plant Sci. 164: 543-551.
- Salih, A.A., Ali, I.A., Lux, A., Luxová, M., Cohen, Y., Sugimoto, Y., Inanaga, S. 1999. Rooting, water uptake, and xylem structure adaptation to drought of two sorghum cultivars. Crop Sci. 39: 168-173.
- Sanderson, J. 1983. Water uptake by different regions of the barley root. Pathways for radial flow in relation to development of the endodermis. J. Exp. Bot. 34: 240-253.
- Sangster A.G., Parry, D.W. 1976a. Endodermal silicon deposits and their linear distribution in developing roots of *Sorghum bicolor* (L.) Moench. Ann. Bot. 40: 361-371.
- Sangster A.G., Parry, D.W. 1976b. Endodermal silicification in mature, nodal roots of *Sorghum bicolor* (L.) Moench. Ann. Bot. 40: 373-379.
- Scott, L.I. 1928. The root as an absorbing organ. II. The delimitation of the absorbing zone. New Phytol. 27: 141-174.
- Scott, M.G., Peterson, R.L. 1979. The endodermis in *Ranunculus acris*. I. Structure and ontogeny. Can. J. Bot. 57: 1040-1062.
- Seago, J.L.Jr. 2002. The root cortex of the Nymphaeaceae, Cabombaceae and Nelumbonaceae. J. Torrey Bot. Soc. 129: 1-9.
- Seago, J.L.Jr., Peterson, C.A., Enstone, D.E., Scholey, Ch.A. 1999. Development of the endodermis and hypodermis of *Typha glauca* Godr. and *Typha angustifolia* L. roots. Can. J. Bot. 77: 122-134.
- Sinnott, E.W., Bloch, R. 1941. The relative position of cell walls in developing plant tissues. Am. J. Bot. 28: 607-617.
- Šottníková, A., Lux, A. 2003. Development, dilatation and subdivision of cortical layers of gentian (*Gentiana asclepiadea* L.) root. New Phytol. 160: 135-143.
- Soukup, A., Votrubová, O., Čížková, H., 2002. Development of anatomical structure of roots of *Phragmites australis*. New Phytol. 153: 277-287.
- Steudle, E., Peterson, C.A. 1998. How does water get through roots? J. Exp. Bot. 49: 775-788.
- Strack D., Fester, T., Hause, B., Schlieman, W., Walter M.H. 2003. Arbuscular mycorrhiza: Biological, chemical and molecular aspects. J. Chem. Ecol. 29:

1955-1979.

- Tanimoto E, Homma T, Matsuo K, Hoshino T, Lux A and Luxova M 2004. Root structure and cell-wall extensibility of adventitious roots of tea (*Camellia sinensis* L. cv. Yabukita). *Biologia* (in press)
- Wang L., Wang, Y., Chen, Q., Cao, W., Li, M., Zhang, F. 2000 Silicon induced cadmium tolerance of rice seedlings. *J. Plant Nutr.* 23: 1397-1406.
- Wilcox, H. 1962. Growth studies of the root of incense cedar, *Libocedrus decurrens*. I. The origin and development of primary tissues. *Am. J. Bot.* 49: 221-236.
- Yamauchi, A., Pardales Jr., J. R. and Kono, Y. 1996. Root system structure and its relation to stress tolerance. In Ito, O. et al. eds. *Dynamics of roots and nitrogen in cropping systems of semi-arid tropics*. pp. 211-233. (Japan International Research Center for Agricultural Sciences, Tsukuba)
- Zeier, J., Ruel, K., Ryser, U., Schreiber, L. 1999. Chemical analysis and immunolocalisation of lignin and suberin in endodermal and hypodermal/rhizodermal cell walls of developing maize (*Zea mays* L.) Primary roots. *Planta* 209:1-12.
- Zimmerman, H.M., Steudle, E. 1998. Apoplastic transport across young maize roots: effect of the exodermis. *Planta* 206: 7-19.