

ENDODERMIS WITH MERISTEMATIC ACTIVITY IN ROOTS OF SPECIES OF *SCLERIA* BERG. (CYPERACEAE)

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Abstract. (Endodermis with meristematic activity in roots of species of *Scleria* Berg. (Cyperaceae)). The root system of *Scleria* is, as in the remaining Cyperaceae, a system of adventitious roots. In the study of root anatomy of seven species from Minas Gerais state, Brazil, one relevant aspect is the presence of a cortex, formed by radially placed cells, resulting from an endodermis with meristematic activity, formed by initial cells. More than half the thickness of the cortex is the result of this activity, constituting the Derivatives of the Meristematic Endodermis (DME). After endodermal initials divisions ceases, this tissue undergoes differentiation, first forming casparian strip, proceeding to, and at the farthest levels from the apex, secondary thickening of these cell walls. The internal cortex presents thickening of cell walls at the level whereat the endodermis denotes casparian strip.

Resumo. (Endodermis with meristematic activity in roots of species of *Scleria* Berg. (Cyperaceae)). O sistema radicular de *Scleria* é, como nas demais Cyperaceae, um sistema de raízes adventícias. No estudo anatômico da raiz de sete espécies procedentes do estado de Minas Gerais, Brasil, um aspecto relevante é a presença de um córtex formado por células radialmente dispostas, resultante de uma endoderme com atividade meristemática, formada por células iniciais. Mais da metade da espessura do córtex é resultante dessa atividade, constituindo as Derivadas da Endoderme Meristemática (DEM). Após cessarem as divisões das iniciais endodérmicas, esse tecido sofre diferenciação, primeiro formando estrias de Caspary, apresentando posteriormente, em níveis mais distantes do ápice, espessamentos secundários das paredes das células. O córtex interno exhibe espessamento das paredes das células no nível em que a endoderme já apresenta estrias de Caspary.

Key words: derivatives of the meristematic endodermis, monocotyledons, Cyperaceae.

Introduction

Since the 19th century, work has been done on roots, mainly dealing with morphology, and focalizing three basic aspects: apical meristems protected by root caps, the presence and physiology of absorbing hairs, and the development of lateral roots (Mangin 1882; Van Tieghem 1898). Later, there was wide preoccupation regarding to the organization of the vascular system, and its adequateness to stellar theory (Brebner 1902; Eames & McDaniels 1947; Esau 1965; Sporne 1974; Gifford & Foster 1989; Fahn 1990).

Besides Metcalfe (1971), who in a classical write on Cyperaceae anatomy dealt with the general aspects of various organs, root anatomy in species of this family is also described in the works of Kadej (1963), Kukkonen (1967), Davies *et al.* (1973), Estelita (1993), Rodrigues & Estelita (2004), Menezes *et al.* (2005), amongst others.

One of the important aspects in the study of root anatomy, is perceiving a cortex formed by radiately arranged

cells. Many authors (Guillaud 1878; Van Tieghem 1898; Sporne 1974; Esau 1977) amongst others, showed in their works, the radiate rows of radicular cortex cells, although not emphasizing this aspect in their considerations. Only Mangin (1882) reported to this organization, without presenting any idea as to its origin and formation.

Innumerous recent papers displayed the radiate arrangement of cells from the internal region of the root cortex in Cyperaceae: Govindarajalu (1966, 1974) in *Bulbostylis*, *Cyperus* and *Lipocarpha*; Kukkonen (1967) in *Uncinia*; Eiten (1969) in *Eleocharis*; Rodrigues & Estelita (2004) in *Cyperus esculentus*, *C. rotundus*, *C. odoratus*, *Fuirema umbellata* and *Hypolytrum schraderianum*. Menezes *et al.* (2005) attribute the origin of these radiate layers in the cortex of *Cyperus papyrus*, *Lagenocarpus* and *Cephalostemon riedelianus* (Rapateaceae), to endodermal initials, recognizing as Williams (1947), the meristematic activity of these cells. This author noted, when studying the roots of 76 botanical families (18

from monocotyledons), that cortex radiation in all the species studied originated from the endodermis and, according to him, the endodermis should function as a cambium, giving origin to all the cortex.

Hurst (1956 *apud* Van Fleet 1961) also confirmed the origin of the radiate layers, according to him, starting from a proendodermis, while Van Fleet (1961) called attention to the work of Williams (1947), by naming, as did Hurst (1956 *apud* Van Fleet 1961) as proendodermis, the layer that originates the radiate rows, in the same way as Popham (1955).

When working on *Richtera* (Asteraceae), Melo-de-Pinna & Menezes (2003) pointed out the occurrence of the endodermis with meristematic activity in adventitious roots, as being responsible for formation of the inner cortex. This was likewise detected by Alonso *et al.* (2004) in *Canna edulis* (Cannaceae).

The presence of the exoderm is also considered as an adaptative characteristic, seeing that this structure contributes to protecting the root against radial loss of oxygen (Koncalova 1990). Root survival in anaerobic soils requires escape mechanisms, for without these, the roots of most species would quickly die (Armstrong *et al.* 1991).

In the roots of Eriocaulaceae, Scatena & Menezes (1996) observed anatomic characteristics such as the presence of cavities in the cortex, these being interpreted by the authors as adaptations to periodically dry or flooded soils.

Those plants which occur in flooded soils, generally possess a highly conspicuous cortex, formed by aerenchyma, in other words, with a large amount of air spaces (Justin & Armstrong 1987; Armstrong *et al.* 1991). Roots that develop in these environments possess constitutive aerenchyma, or rather, genetically defined, whereas roots which develop in periodically flooded environments, are capable of responding by the formation of lysigenous or schizogenous aerenchyma (Peterson 1992).

According to Schreiber *et al.* (1999), due to the occurrence of suberin, lignin and proteins on the endodermis cell walls, these same cells could also present an important function as a barrier against the entrance of pathogens.

The aim of the present work is to analyse the anatomic structure of adventitious roots in species of *Scleria*, as well as to confirm the origin of the radiate cortex.

Materials and Methods

Seven species of *Scleria* Berg. were analysed, all coming from the Serra do Cipó, located in the state of Minas Gerais, southeastern Brazil. The species were identified by experts in the family Cyperaceae, Marccus Alves e Ana Paula Prata, and voucher specimens are deposited in the Herbarium of the Instituto de Botânica de São Paulo (SP). They are: *Scleria bracteata* Cav. (M. Alves *et al.* 2120), *S. distans* Poir. (M. Alves *et al.* 2174), *S.*

latifolia Sw. (M. Alves *et al.* 2123), *S. leptostachya* Kunth (M. Alves *et al.* 2163), *S. microcarpa* Nees (M. Alves *et al.* 2144), *S. scabra* Willd. (M. Alves *et al.* 2181) and *S. secans* (L.) Urb. (A. P. Prata *et al.* 1165).

Another part of the material was fixed in Allen-Bouin (Berlyn and Miksche 1976) and conserved in ethanol 70° G.L. (Jensen 1962), aiming at later morpho-anatomical and microchemical analysis.

Transverse sections were done near to the radicular apex, and also in the region corresponding to the branching zone. Afterwards, all the sections were submitted to coloring by a mixture of astrablue and safranin in ethanol 50% (Bukatsch 1972). A part of the sections were mounted in synthetic Canadian balsam and part in glicerine 50%.

For microchemical tests, the sections were submitted to Sudan IV (Jensen 1962), for observation of suberin and lipid substances, ferric chloride, ferrous sulphate and formaline (Johansen 1940) for characterisation of phenolic compounds; and iodated zinc chloride (Jensen 1962) for cellulosic and lignified walls, as well as starch grains.

The anatomic analyses were done with a photon microscope, and the photomicrographs obtained through an Olympus-Vanox microscope.

Results

Scleria roots are adventitious, appear in the knots of the rhizome, and when young, present a succulent appearance, whereas when mature they become fibrous and of a dark color. In all the species analysed, the root cap consisted of several layers of cells which covered all the apical region containing the initials and their derivatives.

In cross-section, the epidermis appears as uniseriate, with normal cells and hairs, and walls without thickening (Fig. 1). In the cortex, the exoderm is identified as being constituted of a layer of hexagonal shaped cells with secondary walls, impregnated with lignin (Figs. 1 and 5). Internal to the exoderm, the cortex is composed of several layers of parenchyma, with radiate disposed cells (Figs. 1 to 4). A difference is noted in the size of the radiate cells from inside out. In figure 2, arrows 1 and 2 indicate, respectively, an endodermal cell which has not divided and a cell presenting one more division. The arrows of figure 3 indicate two recently divided endodermal initials, side-by-side with initials which have not yet done so. Before, differentiating, endodermal initials undergo a series of periclinal divisions (Fig. 3), giving rise to those cells which will form the greater part of the cortex, composing the Derivates of Meristematic Endodermis (DME, Fig. 4). The inner cortex is formed of one or more layers of thickened cells (Figs. 4-6). In the cortex, in the region furthest from the apex, there appear spaces of lysigenous origin, which accumulate air.

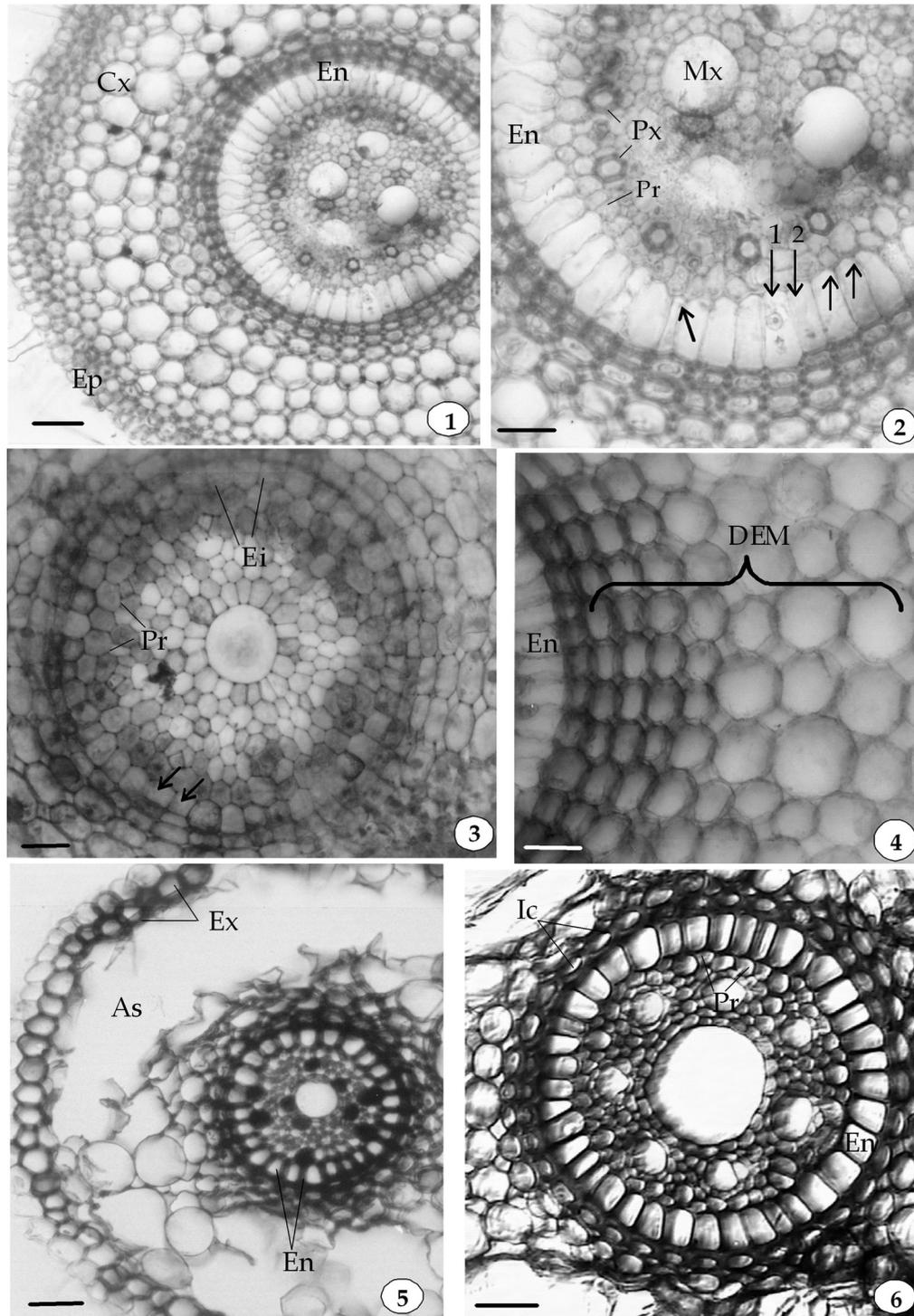


Fig. 1. Root cross section of *Scleria scabra* showing epidermis (Ep) with hairs and a cortex with cells disposed in a radiate fashion. **Fig. 2.** The same section as the previous, in which arrow 1 indicates a differentiated cell without showing the division that occurred in the cell showed by arrow 2. The minor arrows indicate Casparian strip. **Fig. 3.** Root apex cross section of *Scleria bracteata* with endodermal initials (Ei) at division phase; arrows indicate a pair of initials that have just divided. **Fig. 4.** Root cross section of *Scleria microcarpa*, showing meristematic endodermal derivatives (MED); inner cortex is composed of cells with thick walled cells. **Fig. 5.** Root cross section of *Scleria latifolia* showing a farly distinctive exodermis (Ex) among the parenchymatous cells of the cortex with aerial spaces (As). **Fig. 6.** Root cross section of *Scleria leptostachya* showing inner cortex (Ic) composed of cells with lignified secondary walls. En – Endodermis; Mx – Metaxylem; Pr – Pericycle; Px – Protoxylem. Scale bars of 50 μ m, 20 μ m, 20 μ m, 20 μ m, 50 μ m, and 20 μ m respectively.

The pericycle is uniseriate, with primary walls (Figs. 1-3 e 6) becoming thickened when the endodermis also thickens (Fig. 5).

The vascular tissues present poliarch organization, and, in the species *Scleria bracteata*, *S. latifolia*, *S. leptostachya* and *S. distans*, one only (Figs. 3, 5 and 6) or several (Figs. 1 e 2) elements of delayed metaxylem are formed in the region of the pith.

Several idioblasts with phenolic substances, can be detected in the vascular cylinder as well as in the pith (Fig. 5).

Discussion

The root system of the *Scleria*, as in the rest of the Cyperaceae, is a system of adventitious roots. Despite never having had cambium (Holtum 1955), the primary root of the monocotyledons do not thicken, thus being too thin for absorbing and translocating the necessary water. According to that author, this could be the reason for new roots, all adventitious, appearing on the stem nodes.

Porembski & Barthlott (1995) reported the existence of velamen in Cyperaceae roots, although this was not found in the species here in studied.

As has already been seen, one aspect which deserves the attention of authors in their observations on roots, is regarding the radiate arrangement of cortex cells of angiosperm roots. Already in 1882, Mangin stated that the cortex of monocotyledons roots is formed of two regions: the outer, with unorganized parenchymatic cells, and, more internally, with cells organized in radiate rows. Nevertheless, the author did not refer to the origin of this radiation. The person who first demonstrated that the endodermis displays meristematic activity similar to that of the cambium, and so could be responsible for the formation of radial rows of cells in the cortex was Williams (1947).

Menezes *et al.* (2005) opted for considering the proendoderm as being a layer of endodermal initials, through presenting a cambium type activity, exactly as proposed by Williams (1947). According to these authors the same initial cell is the one that always divides, giving origin to two cells, one of which will be derivated, whereas the other will remain as initial cell. Therefore it is one and the same cell which is always dividing, and when the divisions cease, it differentiates into endodermis.

Seago Jr *et al.* (1999) worked with the aquatic species *Hydrocharis morsus-ranae*, and in this work the authors reported to this layer of cells of a meristematic nature, as being a pro-endodermis which undergoes periclinal division giving origin to part of the cortex. This same layer was referred to as proendodermal by other authors (Pophan 1955; Mueller 1991). Nevertheless, none of these authors referred to Williams (1947), and neither

did they attribute to the endodermis (nor to the proendodermis), the origin of the radial layers of the cortex. Heimsch (1951), when studying *Hordeum sativum* L. (Poaceae), on page 529 established: - "In the meristematic region repeated periclinal divisions in the inner layer of cortical cells produce the radial rows of cells of the inner cortex". Even though this author refers to the work of Williams (1947), neither he attributes the origin of the radiate layers of the cortex to the endodermis nor, at least, to a pro-endodermis.

Only Melo-de-Pinna & Menezes (2003), Machado *et al.* (2004), Alonso *et al.* (2004) and Menezes *et al.* (2005), citing Williams (1947) described recently, the layers of radiate cortical cells as being the result of an endodermis with meristematic activity. In the present work, corroborating that established by Menezes *et al.* (2005), these same radiate rows of cells are denominated Derivatives of the Meristematic Endodermis (DME).

It is very easy to perceive that the endodermis is the layer which generates the radiate cortex. It is enough to check that these cells, thin at the beginning, become larger from the endodermis on towards the surface of the organ.

The pericycle is placed internal to the endodermis, constituting a single layer of cells.

In the studied species, it is observed that in differentiated roots, there is an aerenchyma in the cortical region. For some authors, the appearance of aeriferous cavities in roots is generally related to temperature (Sojka *et al.* 1972), to light intensity (Luxmoore *et al.* 1972), and the concentration of nutrients (Konings & Verschuren 1980). As regards the species of *Scleria*, the appearance of aerenchyma in the roots could be a result of the environment conditions observed in the Serra do Cipó, where plants grow under stress. Sajo & Menezes (1986) demonstrated, by differences in dry weight, that in *Vernonia* (Asteraceae), in dry periods spaces remain full of water, and during rain periods, full of air.

Aerenchyma could be the result of either the separation of cells (schisogenous aerenchyma) or of cell lysing (lysigen aerenchyma). Metcalfe (1971) states the formation of air cavities in Cyperaceae as being the origin of schizolysigenous, in the same way as Rodrigues & Estelita (2004). Govindarajalu (1974), in species of *Cyperus* and *Lipocarpha*, mentioned an empty external cortex with concentrically organized air-cavities, separated by radial rows of parenchyma, as observed in *Syngonanthus* by Scatena & Menezes (1996).

Mani (1962) describes the formation of lysigenous spaces as a common characteristic in the roots of various species of *Cyperus*. Also according to this author, the main factor involved in the formation of lysigen intercellular spaces could be the lack of oxygen which these cells undergo, caused by the high lignification of

some of the innermost cortical cells, as well as those of the exodermis. Such an idea may possibly explain the emptiness observed in the cortex of the roots of the species studied, since the endodermis and its resulting first layers proved to be intensely lignified.

Maybe the presence of an internal cortex with cells possessing lignified secondary walls, might be evidence of what was proposed by Schreiber *et al.* (1999), in that these thickened cells, would have an important function in preventing the entrance of pathogens into the vascular cylinder.

In this work, the meristematic activity of the endodermis in the root responsible for formation of part of the cortex, is confirmed, showing cells organized in radial rows, besides the presence of air spaces of lysigen origin, between the exoderm and the lignified internal cortex.

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