Vol.52, n. 6: pp. 1473-1483, November-December 2009
ISSN 1516-8913 Printed in Brazil

BRAZILIAN ARCHIVES OF
BIOLOGY AND TECHNOLOGY
A N I N T E R N A T I O N A L J O U R N A L

Morpho-Anatomical Analysis of the Rhizome in Species of *Scleria* Berg. (Cyperaceae) from Serra do Cipó (MG)

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ABSTRACT

Aspects related to the nature of stem thickening in monocotyledons have been the subject of many studies. Primary thickening has been attributed to the Primary Thickening Meristem (PTM). According to most authors, it gives rise, besides the adventitious roots, to the vascular tissues and part of the cortex. In other words, it has centripetal and centrifugal activity. For some authors, however, it gives rise only to the vascular system, and for others, only to part of the cortex. However, this work demonstrated that PTM corresponds to the pericycle in the meristematic phase or to the pericycle associated with the endodermis, also with meristematic activity. It was observed that the pericycle was responsible for the formation of the vascular system of the rhizome and of the adventitious roots; the endodermis gave rise to cell layers with radial disposition which comprised the inner portion of the stem cortex, and which corresponded to the region known as the derivatives of the meristematic endodermis (DME). A continuity was also demonstrated between the tissues of the stem and root in species of Scleria Berg. (Cyperaceae).

Key words: meristematic endodermis, rhizome, Cyperaceae

INTRODUCTION

The main type of underground stem found in Cyperaceae is the rhizome (Metcalfe, 1971), although in some species, such as *Cyperus rotundus* and *C. esculentus*, the stem system consists of branches which combine to form a true underground network (Wills and Briscoe, 1970; Gifford and Bayer, 1995). According to Holm (1929), due to the difficulty of applying a term which is appropriate for the various underground structures found in Cyperaceae, the term rhizome is used for nearly all the underground stems.

Anatomical aspects of the rhizome which are characteristic of some species of the Cyperaceae family have been summarized by Wills and Briscoe (1970), Metcalfe (1971), Bendixen (1973), Wills et al. (1980) and Gifford and Bayer (1995). Within the family, the rhizome presents morphological variations, and a thickened axis may occur with reduced internodes and sympodial growth.

Aspects related to the nature of stem thickening in monocotyledons have been the subject of many studies. Primary thickening has been attributed over the last fifty years (Rudall, 1991) to the Primary Thickening Meristem (PTM) and secondary thickening, to the Secondary Thickening Meristem (STM).

The function of promoting the formation of adventitious roots is also attributed to the PTM and STM (Cheadle, 1937; Krauss, 1948; Rudall,

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1991; Gifford and Bayer, 1995; Sajo and Rudall, 1999). Other authors working with Cyperaceae have demonstrated that the adventitious roots derives from the endodermis (Wills *et. al.*, 1980) or from the pericycle (Bendixen, 1973; Menezes et al., 2005).

In a recent work, Menezes et al. (2005) demonstrated that the meristem known as the PTM could either be the pericycle itself in the meristematic phase, or the pericycle in the meristematic phase associated with the endodermis, which also has meristematic activity. For these authors, the entire vascular system derives from the pericycle, as well as, naturally, from those elements formed by the procambium. On the other hand, although the entire cortex may be directly formed by the fundamental meristem it may also be formed partly from endodermal initials all which, in turn, derives from the fundamental meristem.

The aim of this work was to demonstrate that in *Scleria* species the rhizome was the stem which, in primary growth, presented an atactostelic structure, and also to verify and confirm the proposal which explained the primary growth in thickness in Cyperaceae, based on the meristematic activity of the pericycle or of the pericycle and the endodermis with meristematic activity.

MATERIALS AND METHODS

The seven species of *Scleria* Berg. analyzed in the present study were collected in the Serra do Cipó region, in the State of Minas Gerais. Part of the material was separated for herborization, according to the usual techniques for the preparation of exsicates, which have been deposited in the Herbarium of the University of São Paulo (SPF) and in the Instituto de Botânica de São Paulo (SP). Another part of the material was fixed in Allen-Bouin fixative (Berlyn and Miksche, 1976) and maintained in ethanol 70º G.L. (Jensen, 1962) prior to morpho-anatomical and microchemical analysis.

The species were identified by specialists in the family Cyperaceae, Marccus V. S. Alves and Ana Paula Prata. These are: *S. bracteata* Cav. (M. Alves et al. 2120), *S. distans* Poir (M. Alves et al. 2174), *S. latifolia* Swartz (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).

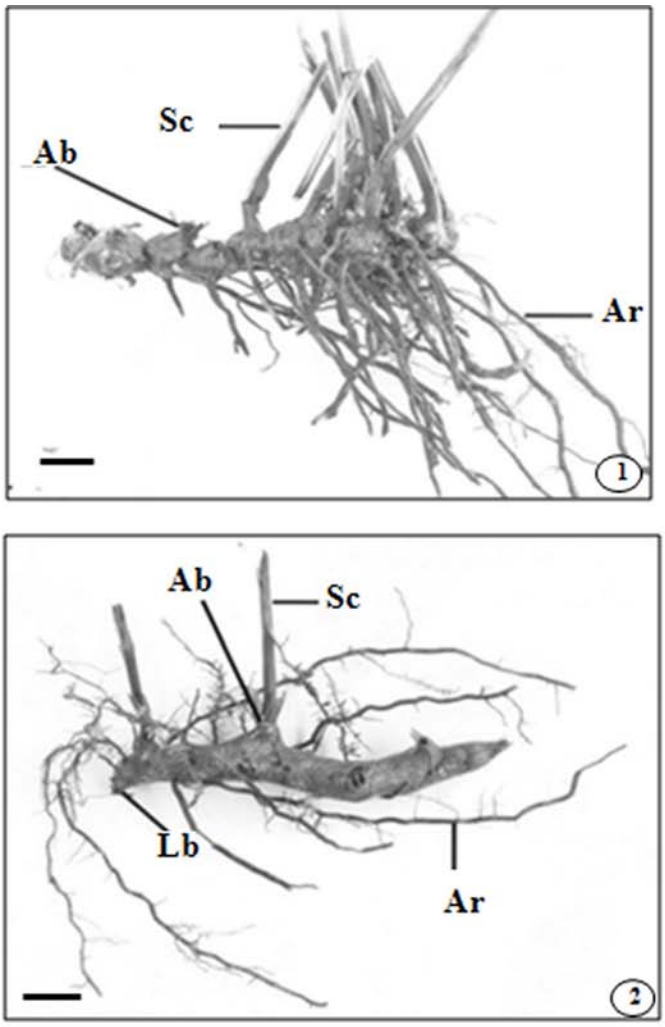
For morpho-anatomical analysis, fixed material was used to obtain cross-sections in a rotary microtome, by immersing the material in paraffin (Johansen, 1940) and polyethyleneglycol 1500 (Gerlach, 1984). Transversal and longitudinal sections were made on mature rhizomes, as well as stem apexes. Subsequently, the sections were stained in the following dyes: a mixture of Astra blue and Safranin in 50% ethanol (Bukatsch, 1972); crystal violet in 50% ethanol and orange G in clove oil (Purvis et al., 1964) and Safranin and fast green (Berlyn and Miksche, 1976). For permanent and semi-permanent mountings, synthetic Canada balsam and 50% glycerin were used, respectively.

For cytochemical tests, the sections were submitted to the reagents Sudan IV (Jensen, 1962) for observation of the cutin, suberin and lipid substances; lugol (Langeron, 1949) for identification of starch granules; iron chloride and iron sulphate and formalin (Johansen, 1940) for characterization of phenolic substances; and iodinated zinc chloride (Jensen, 1962) for cellulose and lignified walls and for starch grains.

Photomicrographs were obtained using an Olympus-Vanox microscope.

RESULTS

Morphologically, rhizome varied in the different species studied from horizontal and articulated forms (Fig. 1), as in *Scleria bracteata*, *S. secans*, *S. scabra* and *S. latifolia*, to horizontal, but elongated (Fig. 2), as in *S. microcarpa*, *S. leptostachya* and *S. distans*. In all species, the branching system of this origin was of the sympodial type. The rhizome internodes were short, varying in number, and cataphylls were found in the nodes protecting the apical (Figs. 3, 5 and 6) and lateral buds.

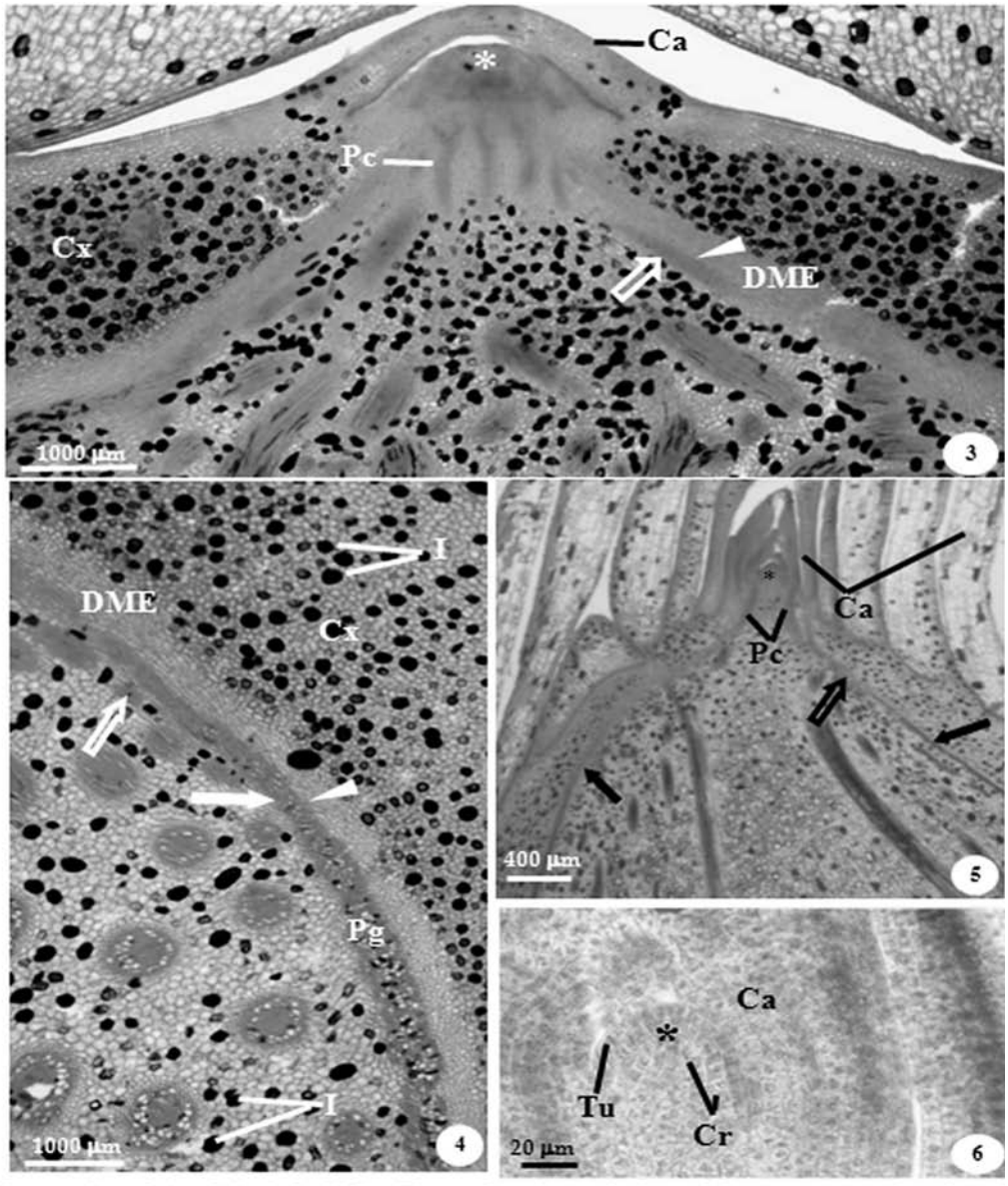


Figures 1 and 2 - Scleria bracteata and Scleria leptostachya**.** Fig. 1. General view of the articulated rhizome of *S. bracteata.* Fig. 2. General view of the elongated rhizome of *S. leptostachya.* Ab = apical bud; Sc = scape; Lb = lateral bud; Ar = adventitious root.

The promeristematic region - * (Figs. 3, 5 and 6) showed a tunica-corpus organization (fig. 6), with a layer of tunica and two or three layers of corpus.

In the apical meristems, procambium strands were observed in the inner region, and also surrounding the vascular cylinder (Figs. 3 and 5), adjacent to the endodermal inicial. The pericycle in the meristematic phase (Figs. 3-5 and 7) was arranged as a continuation of the procambium (Figs. 3, 4 and 5). The procambium gave rise to leaf traces and stem bundles (Figs. 8, 10-12), while the pericycle only gave rise to stem bundles (Figs. 7-9). Only the leaf traces, all of procambial origin, presented protoxylem and protophloem, as well as metaxylem and metaphloem (Fig. 11). The stem bundles, either of procambial or pericyclic origin, had only the metaxylem and metaphloem from the primary xylem (Fig. 12).

In a region of the rhizome furter away from the apex, the cross-section showed the epidermis (Fig. 14), the cortex (Figs. 8, 13 and 20) and the vascular bundles comprising an atactostele, distributed randomly in the fundamental tissue (Figs. 8 and 20). When present (Figs. 13, 14 and 20), the epidermis appeared to comprise a layer of cells, which could become detached in the most differentiated region of the rhizome remaining simply as subepidermic fibers, as shown in Figure 8.

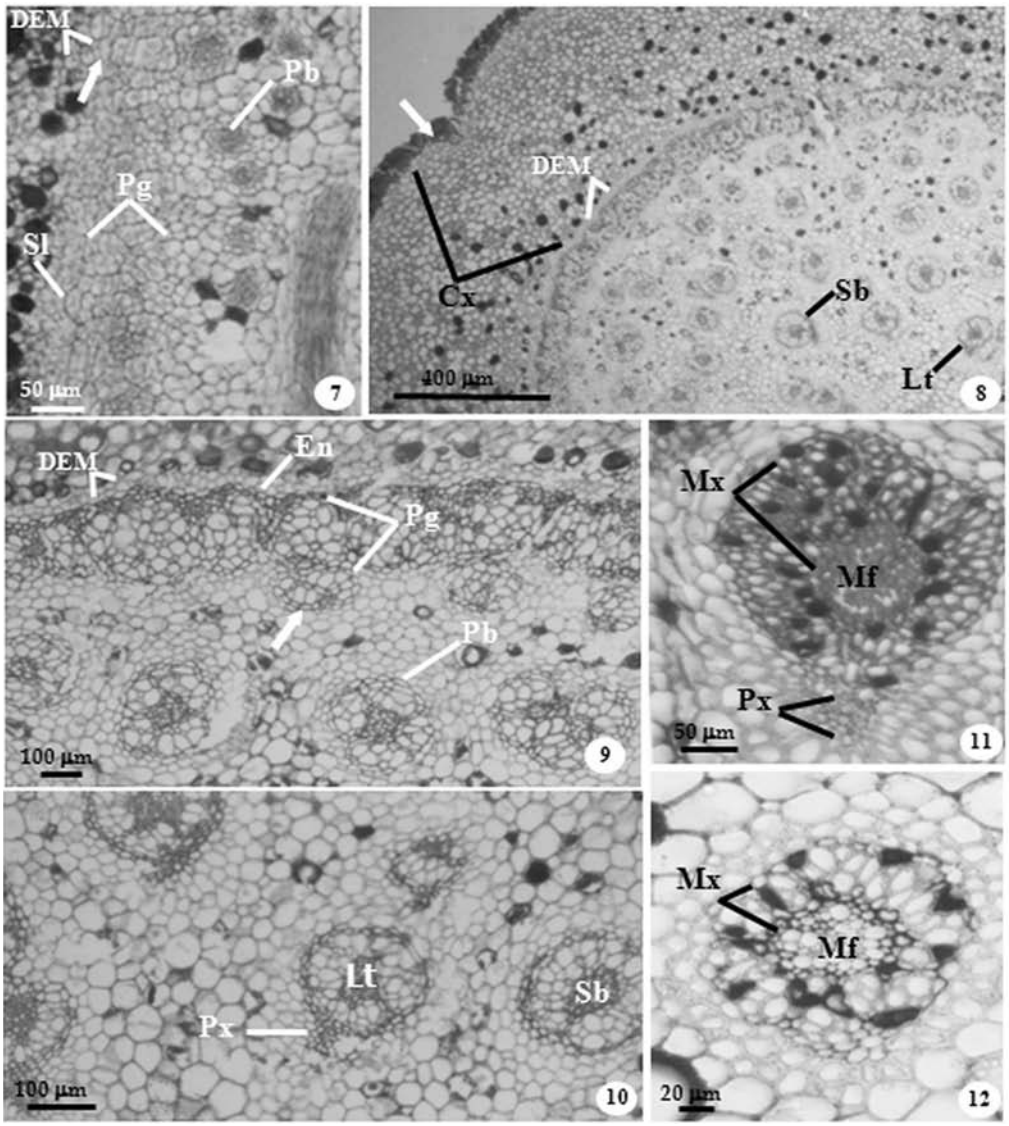


Figures 3 to 6 - *Scleria latifolia*. Fig. 3 - General view of the stem apex, showing the promeristematic region (*) protected by cataphylls (Ca), procambium strands (Pc), and also showing the derivatives of the meristematic endodermis (DME), and the procambium adjacent to the DME (hollow arrow); tip of the arrow indicates endodermal initials position. Fig. 4 – Detail of the pericycle in the meristematic phase (hollow arrow) and of the pericycle giving rise to the vascular system (filled arrow); tip of the arrow indicates endodermal initials position. Fig. 5 – *S. distans.* General view of the stem apex, showing the cataphylls, procambium strands, the meristematic region of the pericycle (hollow arrow) and the bundle-forming pericyclic region (filled arrow). Fig. 6 – *S. leptostachya*. Detail of the meristematic apex, showing the promeristematic region (*) and the cells which form the tunic (Tu) and the corpus (Cr). Cx = cortex; I= idioblasts with phenolic substances.

The cortex in the species *Scleria bracteata*, *S. latifolia*, *S. secans*, *S. microcarpa* and *S. scabra* appeared to be formed by three distinct regions: an internal region, which was more translucid, an intermediate region, with a high number of idioblasts containing phenolic substances, and an external region, with few of these idioblasts (Fig.8).

The inner cortex of these species was the result of the meristematic activity of the endodermis, comprising the region formed by the derivatives of the meristematic endodermis (DME) (Figs. 3, 4, 7-9, 15, 16, 20-22). In the parenchyma of the vascular cylinder, idioblasts were detected, containing phenolic substances (Fig. 4).

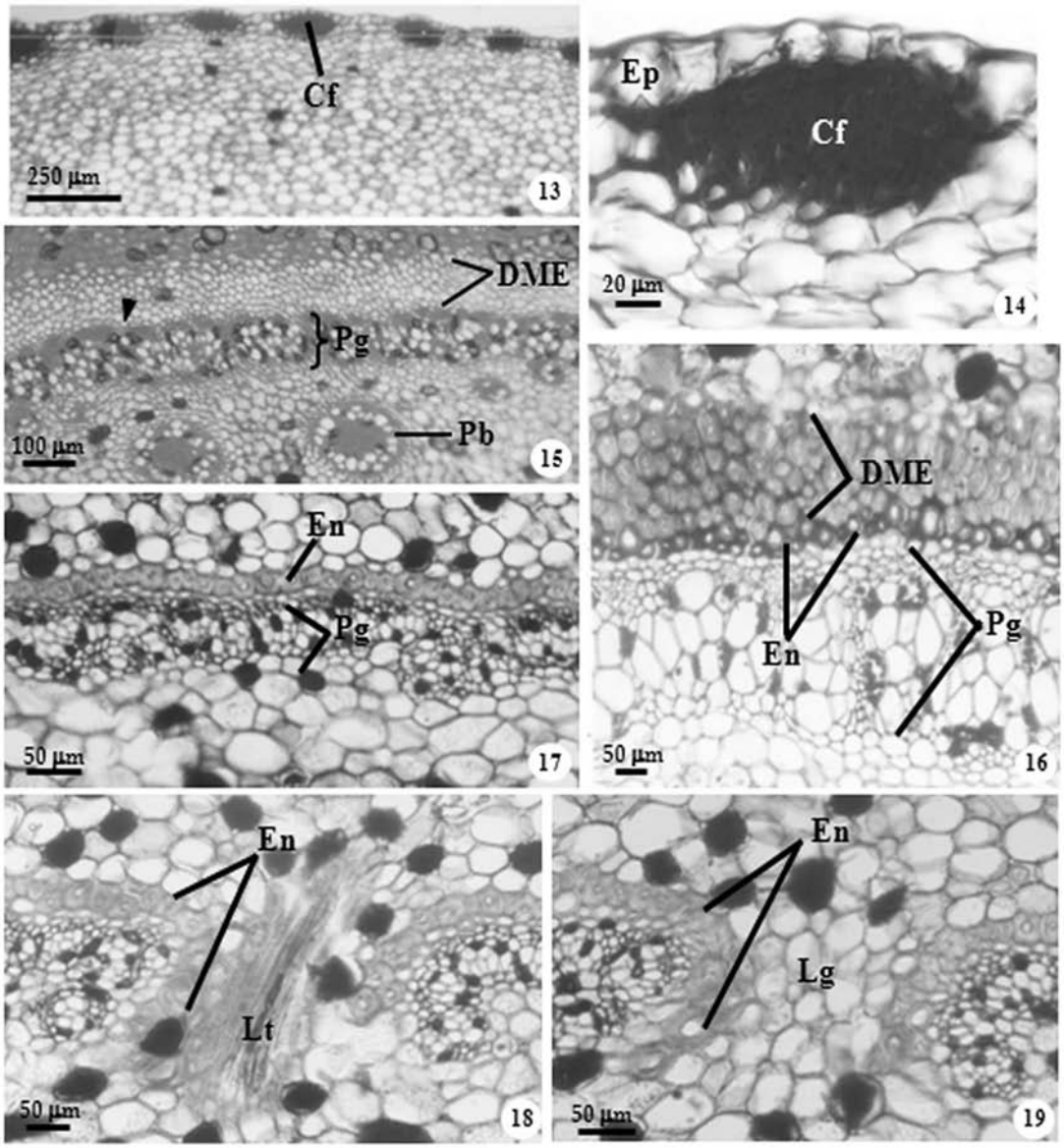
In the cross-section, it was observed that the cells that comprised the DME, next to the apex, were parenchymatous (Fig. 15), becoming thickened in the rhizome base, comprising a lignified inner cortex corresponded to the DME (Figs. 16, 20 and 21). In *S. distans* and *S. leptostachya*, the inner cortex was formed exclusively by the uniseriate endodermis (Figs. 17-19). In *S. bracteata* (Fig. 9), the endodermis gave rise to only two layers of cortex cells.



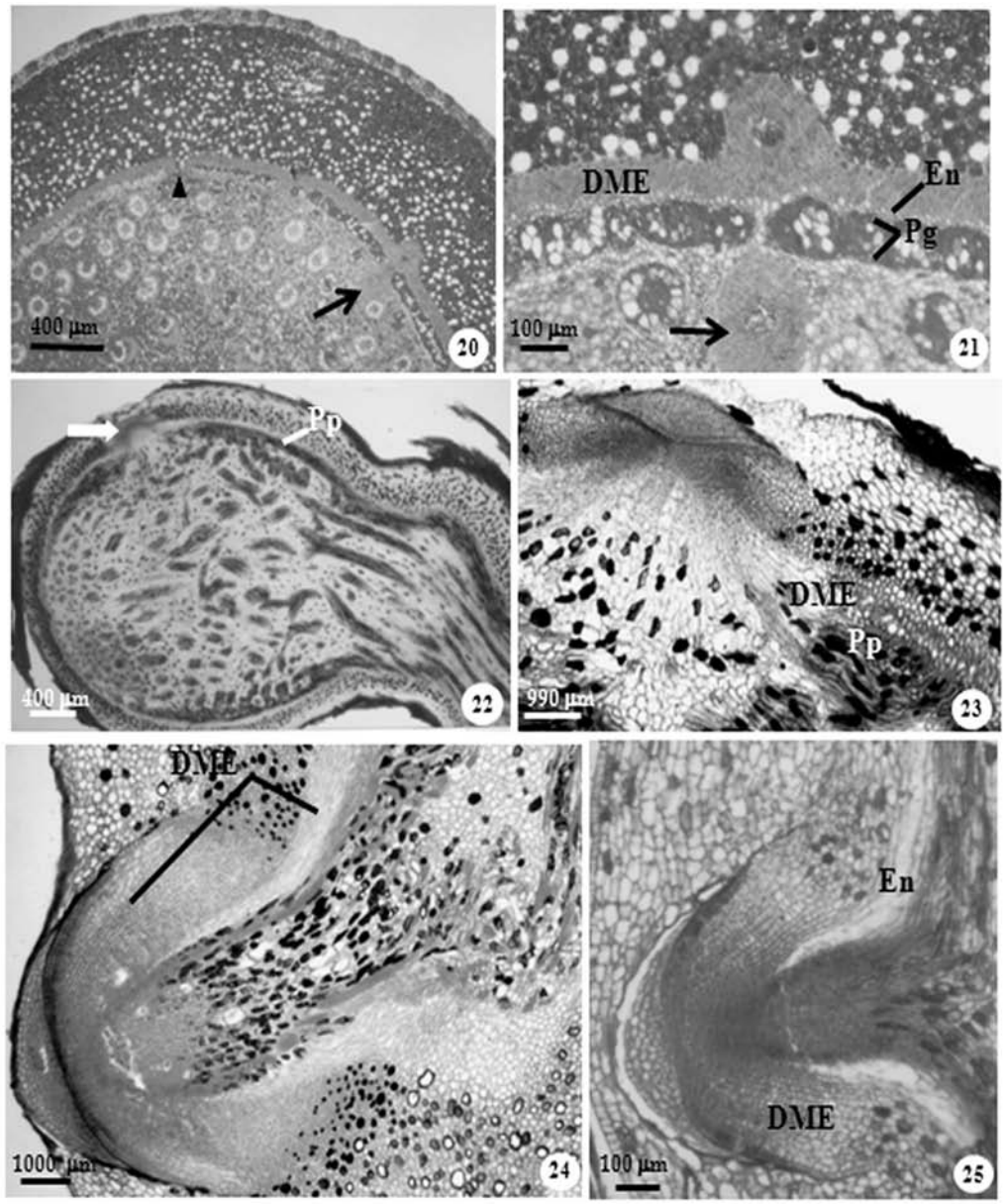
Figures 7 to 12 - *Scleria bracteata*. Fig. 7 – In the region next to the apex, detail showing the pericyclic region (Pg), the new pericyclic bundles (Pb) and the local of the suberin lamella (Sl), in the endodermic contact wall; endodermal initial (arrow). Fig. 8 – General view of the cross-section of the rhizome showing subepidermic fibers (arrow), the cortex (Cx) and, in the central cylinder, a stem bundle (Sb) and a leaf trace (Lt). Fig. 9 – Detail of the pericyclic bundle-forming region, a new bundle (arrow), and the pericyclic bundles. Fig. 10 – Detail of the central region of the vascular cylinder, containing a stem bundle and a leaf trace, both of procambial origin. Fig. 11 – *S. secans.* Detail of a leaf trace. Fig. 12 – *S. secans.* Detail of a stem bundle. En= endodermis; Mf = metaphloem; Mx = metaxylem; Px = protoxylem.

In longitudinal sections of rhizomes (Figs. 22-25), the formation of lateral roots was observed, and their respective peripheral plexus (Fig. 22). The emergence of a lateral root showed a perfect continuity between the corresponding tissues of the root DME and of the stem DME (Figs. 23 and 24) or between the endodermis of the root and of the stem (Fig. 25).

It was observed that the region where the leaf trace emerges was preceded by an invagination of the endodermis (Figs. 18 and 19) or of the endodermis and its derivatives (Figs. 20, 21, 22) to the interior of the vascular cylinder. In Figures 20 and 21, the leaf trace was still in the interior of the cylinder, already surrounded by the endodermis and its derivatives.



Figures 13 to 19 – *Scleria latifolia*. Fig. 13 – General view of the peripheral region, noting the cortical fibers (Cf). Fig. 14 – Detail of the epidermis (Ep) and cortical fibers (Cf). Fig. 15 – Detail of the derivatives of the meristematic endodermis (DME), the pericyclic region (Pg) and the pericyclic bundles (Pb); the tip of the arrow indicates the endodermis. Fig. 16 – *S. microcarpa*. Detail of the pericyclic region, endodermis (En) and DME completely lignifieds. Fig. 17 to 19 – *S. distans*. Fig. 17 **–** Detail of the uniseriated endodermis, without meristematic activity, and the pericyclic region. Fig. 18 – Exit of a leaf trace (Lt) and the invagination of the endodermis inside the vascular cylinder. Fig. 19 – Leaf gap (Lg) left by the exit of a trace and the endodermic boardering the gap.



Figures 20 and 21 – *Scleria microcarpa*. Fig. 20 – General view the rhizome, showing a leaf trace (arrow) surrounded by the DME (derivatives of the meristematic endodermis) in the interior of the vascular cylinder; the tip of the arrow shows the leaf gap and the invagination of DEM inside the vascular cylinder. Fig. 21 – Detail showing the DME completely lignified of the rhizome and, indicated by arrow, the leaf trace. Fig. 22 - General view of the rhizome of *S. secans* showing the organization of the peripheral plexus (Pp) towards the adventitious root (arrow). Fig. 23 – The same root indicated in Fig. 22. Fig. 24 – Exit of an adventitious root in the rhizome of *S. latifolia*, showing the continuity between the DME of the rhizome and the root. Fig. 25 – Detail of the exit of an adventitious root of *S. distans* showing the continuity between the uniseriated endodermis of the rhizome and the root. En = endodermis; Pg = pericyclic region.

DISCUSSION

The rhizome is an organ of resistance and storage of nutrients, in addition of being the principal means by which a single plant can cover wide areas and continue to spread itself indefinitely due to its continual growth (Holtum, 1955). Font Quer (1979) defines the rhizome as an underground stem with cataphylls that is capable of producing roots. Also according to this author, in temperate climates or regions with a marked dry season, the rhizome protects the plant from unfavorable environmental factors.

As seen above, in the species studied, the rhizome was horizontal and articulated in *Scleria bracteata*, *S. latifolia*, *S. secans* and *S. scabra* or horizontal and elongated in the other species. Both types of rhizome had sympodial growth, as described by Holtum (1955).

In relation to the shoot apex of the rhizome, according to Santos and Silva (1997), the monocotyledons often presented a one-layered tunica while the region of the corpus comprised various cellular strata, which exhibited divisions at all levels. In *Scleria*, a cellular layer consisting of the tunic and two or three cellular strata comprising the corpus were also observed in the promeristematic region.

The rhizome covering consisted of a uniseriated epidermis, the cells of which were eliminated in more advanced stages of development of this organ and replaced by the cells with thickened, lignified walls of the external cortex. The same could be observed in relation to the other Cyperaceae, such as *Cyperus giganteus* (Rodrigues and Estelita, 2002).

Besides the fibrous strands of the external cortex, the high number of cells with phenolic substances certainly represent protection against herbivores. These substances protect the organ against microorganisms and herbivores, such as tannins which reduce the digestibility of the vegetal tissues (Howe and Westley, 1988).

In *Scleria distans* and *S. leptostachya*, the internal cortex corresponded to the uniseriate endodermis, while in the other species, it corresponded to the endodermis and its derivatives. The occurrence of the endodermis in the rhizome of Cyperaceae has already been mentioned by various authors (Eiten, 1969; Wills and Briscoe, 1970; Bendixen, 1973; Govindarajalu, 1974; Wills et al., 1980; Gifford and Bayer, 1995; Rodrigues and Estelita, 2002; Menezes et al., 2005). However, the endodermis with meristematic activity, forming the inner cortex of the rhizome, was uniquely demonstrated by Menezes et al. (2005).

Many authors did not state categorically that the endodermis was the innermost layer of the cortex, preferring to call it the "endodermoid sheath" (Plowman, 1906), "the endodermoid layer" (Metcalfe, 1971; Kukkonen, 1967) or the "endodermal cells" (Govindarajalu, 1966; Gifford and Bayer, 1995). This fact, in general, occurs due to the absence of Casparian strips. However, Rodrigues and Estelita (2002) and Menezes et al. (2005) observed the presence of Casparian strips in the endodermis of stems belonging to different Cyperaceae.

Internally to the endodermis is the pericycle, which is the layer that generates the vascular tissues, as has been emphatically stated by Menezes et al. (2005). Next to the stem apex, a pericycle is distinguished from the endodermis, also in meristematic phase, by a discrete thickening of suberin on the the periclinal walls of the endodermal cells, as already demonstrated by Williams (1947) and detected by Melo-de-Pinna and Menezes (2003) in the roots of *Richterago*.

In all the longitudinal sections, the procambium arrangement adjacent to the endodermis was observed in the apex, making difficult to state whether the tissue was the procambium or already the pericycle in the meristematic phase. Only studies using molecular markers can determine the true nature of these cells. The same difficulty has been emphasized by Esau (1965), Fahn (1990) and other authors, who claimed that the tissue of the vascular bundle, between the primary xylem and phloem in dicotyledons, was no longer the procambium, but became the cambium. It is not known that exactly when one finishes and the other starts. In any case, it could be shown here that in species of *Scleria*, the origin of the pericycle was procambial.

In these plants, the vascular system was organized as an atactostele, as defined by Brebner (1902), and corroborated by Ogura (1972) and Gifford and Foster (1989). In the endodermis and surrounded by the pericycle, the vascular bundles are randomly arranged. In the region of the vascular cylinder, it is observed that the bundles are concentric, and that besides being of procambial origin, they are also of pericyclic origin. The bundles of procambial origin were of two types, as demonstrated by Menezes (1971) in Velloziaceae: bundles which presented protoxylem/protophloem

and metaxylem/metaphloem and bundles uniquely formed of metaxylem/metaphloem. The former consist of leaf traces, while the latter are stem bundles. Zimmermann and Tomlinson (1969) also highlighted in Arecaceae only leaf traces with protoxylem/protophloem. All bundles of pericyclic origin consisted solely of metaxylem/metaphloem, and all were, therefore, stem bundles, as shown by Menezes (1971).

Schach (1852 *apud* Mangin, 1882), stated that in all vascular plants dividing cells were found between the medulla and the cortex. He denominated these cells the "cambial circle" or "thickening ring". Also, according to this author, when this activity remained, as observed in the stem of *Pandanus* and *Dracaena*, it could acquire considerable thickening, with the formation of a lateral meristem (such as a cambium). Menezes et al. (2005) accepted that Schach's "cambial circle" was the pericycle associated with the endodermis with meristematic activity in the rhizome, and that the "thickening ring" corresponded to the thickened derivatives of the meristematic endodermis (DME). In *Cyperus papyrus*, *Cephalostemon riedelianus* and *Lagenocarpus rigidus,* these authors demonstrated that the layers of the DME became thickened, as there was no secondary growth in these plants, while Rodrigues and Estelita (2002), working with *Cyperus giganteus*, accepted secondary growth inside the lignified layer.

The primary thickening in monocotyledons was due to the presence of a primary thickening meristem (PTM), according to the terminology proposed by Ball (1941). This type of thickening, however, had already been mentioned by Petersen (1892 *apud* Ball, 1941) and Schoute (1903 *apud* Ball, 1941). Subsequently, various other authors, including DeMason (1979), Stevenson and Fisher (1980), DeMason (1983), Diggle and DeMason (1983), DeMason and Wilson (1985), Rudall (1991) and Gifford and Bayer (1995), have referred to PTM as a factor responsible for primary thickening in monocotyledons. These ideas were completely rebuffed by Menezes et al. (2005), who demonstrated that the thickening occurred through the activity of the pericycle or the pericycle and the endodermis.

On the other hand, Krauss (1948), Rudall (1991) and Sajo and Rudall (1999) accepted a translucid zone as being the PTM, and which, in older stems, became lignified. Fisher (1978) described this layer in *Musa* as consisting of vacuolated cells, with a translucid appearance, known as the "clear zone". Menezes et al. (2005) clearly demonstrated that this translucid zone corresponded to the derivatives of the endodermis with meristematic activity in the rhizome, and that it sclerified, subsequently, as seen in *Scleria*.

Rodrigues and Estelita (2002), corroborating the idea of the existence of the PTM, forwed that it emerged in later states of differentiation and consisted of layers of cells positioned laterally, close to the base of the leaf primordia, which divided periclinally. The authors observed that in *Cyperus giganteus* PTM was located externally to the procambium strands and its cells divided in both directions: the centrifugal activity gave rise to the radial branches of the parenchyma and the centripetal activity to the amphivasal vascular bundles. Menezes et al. (2005) contradicted this and mentioned that a single meristem could not form both the cortex and vascular cylinder. According to them, the endodermis and pericycle, both in meristematic phase, simulated single meristem, a fact that has misled many authors.

In *Scleria bracteata*, *S. latifolia*, *S. secans*, *S. microcarpa* and *S. Scabra*, the same region can be identified and differentiated into meristematic cells, which comprise the innermost region of the cortex. This zone derives from the endodermis which, just as observed by Menezes et al. (2005), undergoes various divisions before differentiating, giving rise to derivatives that will comprise the inner cortex of the rhizome.

It could be emphasized here that based on the observation of the longitudinal sections of the apex of the rhizome of the species of *Scleria*, the continuity of the endodermis and its derivatives in all vegetative organs has been clearly demonstrated, as claimed by Menezes et al. (2005). Also, according to these authors, the same type of division of the endodermic initial cells could also be observed in other monocotyledons, as demonstrated in the leaves of *Echinodorus paniculatus* (Menezes et al., 2005), where the cells resulting from the meristematic activity of the endodermis formed part of the mesophyll, as also seen in the leaf traces of *Cyperus papyrus*.

The invagination of the endodermis to the interior of the vascular cylinder, in the region where the leaf trace emerges from the vascular cylinder toward the cortex is an important aspect. This invagination enables the trace to emerge totally surrounded by the endodermis, as seen in *Scleria distans* and in the case of *S. microcarpa*. Besides

the endodermis, the lignified derivatives of the endodermis are also observed inside the vascular cylinder.

ACKNOWLEDGEMENTS

The authors thank to Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) for the financial support.

RESUMO

Aspectos relacionados à natureza do espessamento em caules de monocotiledôneas têm sido objeto de estudo de muitos pesquisadores. O espessamento primário vem sendo atribuído ao meristema de espessamento primário (MEP). Segundo a maioria dos autores origina, além das raízes adventícias, os tecidos vasculares e parte do córtex. Para alguns autores, no entanto, origina apenas o sistema vascular e para outros, apenas parte do córtex. Entretanto, demonstra-se neste trabalho, que o MEP corresponde ao periciclo em fase meristemática ou ao periciclo associado à endoderme, também com atividade meristemática. Verificou-se que o periciclo é responsável pela formação do sistema vascular do rizoma e pela formação das raízes adventícias; a endoderme origina fileiras radiais de células que constituem a porção interna do córtex caulinar e que correspondem à região denominada derivadas da endoderme meristemática (DEM). Demonstra-se também, a continuidade entre os tecidos do caule e da raiz nas espécies de *Scleria* Berg. (Cyperaceae).

REFERENCES

Ball, E. (1941), The development of the shoot apex and of the primary thickening meristem in *Phoenix canariensis* Chaub., with comparisons to *Washingtonia filifera* Wats. and *Trachycarpus excelsa* Wendl. *Am. J. Bot.*, **28**, 820-832.

Bendixen, L. E. (1973), Anatomy and sprouting of yellow nutsedge tubers. *Weed Sci.*, **21**, 501-503.

Berlyn, G. P. and Miksche, J.P. (1976), *Botanical microtechnique and cytochemistry.* The Iowa State University Press, Arnes. 326p. ill.

Brebner, G. (1902), On the anatomy of *Danaea* and other Marattiaceae. *Ibid*, **16**, 517- 552.

Bukatsch, F. (1972), Bemerkungen zur Doppelfärbung Astrablau-Safranin. *Mikrokosmos*, **61** (8), 255.

Cheadle, V. I. (1937), Secondary growth by means of thickening ring in certain monocotyledons. *Bot. Gaz.*, **98**, 535-555.

DeMason, D.A. (1979), Function and development of the primary thickening meristem in the monocotyledon, *Allium cepa* L. *Bot. Gaz.*, **140** (1), 51-66.

DeMason, D. A. (1983), The primary thickening meristem: definition and function in monocotyledons. *Am. J. Bot.*, **70** (6), 955-962.

DeMason, D.A. and Wilson, M.A. (1985), The continuity of primary and secondary growth in *Cordyline terminalis* (Agavaceae). *Can. J. Bot.*, **63**, 1907-1913.

Diggle, P. K. and DeMason, D.A. (1983), The relationship between the primary thickening meristem and secondary thickening meristem in *Yucca whipley* Torr. I. Histology of the mature vegetative stem. *Am. J. Bot.*, **70** (8), 1195-1204.

Eiten, L. T. (1969), The vegetative anatomy of *Eleocharis interstincta* (Vahl) Roem and Schult. *Arqs. Bot. Est. S. Paulo*, **4**, 187-228.

Esau, K. (1965), *Plant Anatomy.* 2nd ed. Wiley, New York. 767 p. ill.

Fahn, A. (1990), *Plant Anatomy.* 4th ed. Pergamon Press, Oxford.

Fisher, J. B. (1978), Leaf-opposed buds in *Musa*: their development and a comparison with allied monocotyledons. *Am. J. Bot.*, **65** (7), 784-791.

Font Quer, P. (1979), *Diccionario de Botánica.* Editorial Labor S. A. 1244 p.

Gerlach, D. (1984), *Botanische Mikrotechnik.* Georg Thieme, Stuttgart. 311p.

Gifford, E. M. and Foster, A. S. (1989), *Morphology and Evolution of Vascular Plants.* W. H. Freeman and Co, New York. 626 p. ill.

Gifford, E. M. and Bayer, D. E. (1995), Developmental anatomy of *Cyperus esculentus* (yellow nutsedge). *Int. J. Plant Sci.*, **156** (5), 622-629.

Govindarajalu, E. (1966), The systematic anatomy of South Indian Cyperaceae: *Bulbostylis* Kunth. *Bot. J. Linn. Soc.*, **59** (379), 289-304.

Govindarajalu, E. (1974), The systematic anatomy of south Indian Cyperaceae: *Cyperus* L. subgen. *Juncellus*, *Cyperus* subgen. *Mariscus* and *Lipocarpha* R. Br. *Bot. J. Linn. Soc.*, **68**, 235-266.

Holm, T. (1929), The application of the term "Rhizome". *Rhodora* , **31,** 5-23.

Holtum, R. E. (1955), Growth-habits of monocotyledons – variations on a theme. *Phytomorphology*, **5** (4), 399-413.

Howe, H. F. and Westley, L. C. (1988), *Ecological relationships of plants and animals*. Oxford University Press, New York. 273 p. ill.

Jensen, W. A. (1962), *Botanical Histochemistry, Principles and Practice.* W. H. Freeman, San Francisco. 408p. ill.

Johansen, D. A. (1940), *Plant microtechnique*. McGraw-Hill Book Co. Inc., New York. 523p. ill.

Krauss, B. H. (1948), Anatomy of the vegetative organs of the pineapple, A*nanas comosus* (L.) Merr. I. Introduction, organography, the stem and the lateral branch or axillary buds. *Bot. Gaz.*, **110** (2), 159-217.

Kukkonen, I. (1967), Vegetative Anatomy of *Uncinia* (Cyperaceae). *Ann. Bot.*, **31** (123), 523-544.

Langeron, M. (1949), *Précis de microscopie*. Paris, Masson. 1430p. ill.

Mangin, L. (1882), Origine et insertions des racine adventives et modifications correlatives de la tige chez les monocotyledons. *Anna. Sci. Nat. Bot*., **14**, 216-363.

Melo-de-Pinna, G. F. de A. and Menezes, N.L. (2003), Meristematic endodermis and secretory structures in adventitious roots of *Richterago* Kuntze (Mutisieae-Asteraceae). *Revista Brasil. Bot.*, **26** (1), 1-10.

Menezes, N. L. (1971), Traqueídes de transfusão no gênero *Vellozia* Vand. *Ci. and Cult.*, **23**, 389-409.

Menezes, N. L.; Silva, D. C.; Arruda, R. C. O.; Cardoso, V. A.; Melo-de-Pinna, G. F. A.; Castro, N.M.; Scatena, V. L. and Dias, E.S. (2005), Meristematic activity of the endodermis ericycle in the primary thickening in monocotyledons. Considerations on the "PTM". *An. Acad. Brasil. Ciên.*, **77** (2), 259-274.

Metcalfe, C. R. (1971), *Anatomy of the Monocotyledons, Cyperaceae*. Clarendon Press, Oxford, v. 5.

Ogura, Y. (1972), *Comparative anatomy of vegetative organs of the Pteridophytes*. Gebrüder Borntraeger, Berlin. 500p.

Plowman, A. B. (1906), The Comparative Anatomy and Phylogeny of the Cyperaceae. *Ann. Bot. (London)*, **20** (77), 1-33.

Purvis, M. J., Collier, D. C. and Walls, D. (1964), *Laboratory Techniques in Botany*. Butterworths, London. 371 p. ill.

Rodrigues, A. C. and Estelita, M. E. M. (2002), Primary and secondary development of *Cyperus giganteus* Vahl rhizoe (Cyperaceae). *Revista Brasil. Bot.*, **25**(3), 251-258.

Rudall, P. (1991), Lateral Meristems and Stem Thickening Growth in Monocotyledons. *Bot. Rev.*, **57**(2), 150-163.

Sajo, M. G. and Rudall, P. (1999), Systematic vegetative anatomy and ensiform leaf development in *Xyris* (Xyridaceae). *Bot. J. Linn. Soc.*, **130**, 171-182.

Santos, G. O. and Silva, E. A. M. (1997), Growth and development of rhizome of ginger (*Zingiber officinale* R.). *Arq. Biol. Tecnol.*, **40**(3), 651-656.

Stevenson, D.W. (1980), Radial growth in *Beaucarnea recurvata. Am. J. Bot.*, **67** (4), 476-489.

Stevenson, D. W. and Fisher, J. B. (1980), The developmental relationship between primary and secondary thickening growth in *Cordyline* (Agavaceae). *Bot. Gaz*, 141(3), 264-268.

Williams, B. C. (1947). The structure of the meristematic root tip and origin of the primary tissues in the roots of vascular plants. Am. J. Bot. 34: 455-462.

Wills, G. D. and Briscoe, G. A. (1970), Anatomy of purple nutsedge. *Weed Sci.*, **18** (5), 631-635.

Wills, G. D., Hoagland, R. E. and Paul, R. N. (1980), Anatomy of yellow nutsedge (*Cyperus esculentus*). *Weed Sci.*, **28** (4), 432-437.

Zimmermann, M. H. and Tomlinson, P. B. (1969), The vascular system in the axis of *Dracaena fragans* (Agavaceae), 1. Distribution and development of primary strands. *J. Arnold Arboretum*, **50** (3), 370-383.

Received: September 25, 2006;
Revised: August 28, 2007;
Accepted: November 19, 2008.