Actin-Based Domains of the "Cell Periphery Complex" and their Associations with Polarized "Cell Bodies" in Higher Plants

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Abstract: Nascent cellulosic cell wall microfibrils and transverse (with respect of cell growth axis) arrays of cortical microtubules (MTs) beneath the plasma membrane (PM) are two well established features of the periphery of higher plant cells. Together with transmembrane synthase complexes, they represent the most characteristic form of a "cell periphery complex" of higher plant cells which determines the orientation of the diffuse (intercalary) type of their cell growth. However, there are some plant cell types having distinct cell cortex domains which are depleted of cortical MTs. These particular cell cortex domains are, instead, typically enriched with components of the actin-based cytoskeleton. In higher plants, this feature is prominent at extending apices of two cell types displaying tip growth – pollen tubes and root hairs. In the latter cell type, highly dynamic F-actin meshworks accumulate at extending tips, and they appear to be critical for the apparently motile character of these subcellular domains. Importantly, tip growth of both root hairs and pollen tubes is immediately stopped when the most dynamic F-actin population is depolymerized with low levels of anti-F-actin drugs. Intriguingly, MTs of tip-growing plant cells are organized in the form of longitudinal arrays, throughout the cytoplasm, which interconnect the extending tips with the subapical nuclei. This suggests that actin-rich cell cortex domains polarize plant "cell bodies" represented by nucleus–MTs complexes. A similar polarization of "cell bodies" is typical of mitotic and cytokinetic plant cells. A further type of MT-depleted and actomyosin-enriched plant cell cortex domain comprises the plasmodesmata. Primary plasmodesmata are formed during cytokinesis as part of the myosin VIII-enriched callosic cell plates, representing "juvenile" forms of the plant "cell periphery complex". In phylogenetic terms the association between F-actin and the PM may be considered for a more "primitive" form of cellular organization than does the association of cortical MTs with the PM. We hypothesize that the actin cytoskeleton is a natural partner of the PM in all eukaryotic cells. In most plant cells, however, it was replaced by a tubulin-based "cell periphery apparatus" which regulates, *via* still unknown mechanisms, the spatial deposition of nascent cellulosic microfibrils synthesized by PM-associated synthase complexes.

Introduction

The contemporary view of the eukaryotic cell is that it is a complex, composite system of endosymbiotic origin (Margulis, 1981[132]; 1996[133]; Sitte, 1993[195]; Gupta and Golding, 1996[80]; Gupta et al., 1994[81]). In addition to the more intuitively obvious endosymbionts of mitochondria and plastids, nuclei with their associated centrosome and microtubules (MTs) have also been considered as markers of ancient endosymbiotic events (Gupta et al., 1994[81]; Erickson, 1995[61]; Margulis, 1996[133]). In such composite systems there have been numerous opportunities for the relocation of genes from the endosymbiotic organelles to the host cell nucleus (Martin and Herrmann, 1998[134]). The external remains of the putative hosts to these endosymbionts may be traced to a plasma membrane (PM) which is primarily associated with an actin-based cytoskeleton. This type of cellular exterior is thought to be the result of an evolutionary step which contributed to the efficient phagocytotic feeding of the primitive cell as well as to its mobility. It was also an innovation which predisposed the emerging eukaryotic cell to the phagocytic acquisition of further endosymbionts (Mitchison, 1995[144]).

While the actin cytoskeleton has phylogenetically evolved in close association with the PM (see Fig. 5 in Mitchison 1995[144] for an evolutionary model; for more recent data see Zigmond, 1996[236]; Schmidt and Hall, 1998[190]; Machesky and Insall, 1999[131]), the MT cytoskeleton, by contrast, remains closely associated with the eukaryotic nucleus (for review see Baluška et al., 1997 b[11]; for more recent experimental data see Carazo-Salas et al., 1999[33]; Gindullis and Meier, 1999[71]). However, coincident with and perhaps dependent upon the evolution of a cellulose-rich cellular exterior of plant cells, MTs have secondarily populated the cell cortex where they have taken con-

trol over spatial aspects of the cellulose synthesis taking place at the external side of the PM (Giddings and Staehelin, 1991[70]). The structural/functional continuum of cortical MTs – cellulose synthase complexes – nascent cellulosic microfibrils (Hasezawa and Nozaki, 1999[86]) represents a highly specialized tubulin-based "cell periphery apparatus" of higher plant cells. Although cellulose synthesis also occurs in a few animal cells (e.g., Kimura and Itoh, 1996[110]), the involvement of MTs in this process is a major feature of plant cells (e.g., Cyr, 1994[44]; Barlow and Baluška, 2000[19]). Cortical MTs of plant cells align in parallel, transverse (with respect of growth axis) arrays under the extending PM. Putative links of cortical MTs with PM-associated cellulose synthase complexes (Hasezawa and Nozaki, 1999[86]; Kimura et al., 1999[111]) are considered to be responsible for the MT-dependent polarity of diffuse cell growth (Green, 1984[72]; Williamson, 1991[233]). The biophysical constraints of the system determine that the orientation of the MT/cellulose polymers and that of plant cell growth are at right angles to each other (e.g., Green, 1986[73]). Then, within the multicellular context of a growing apex, another outcome of these constraints is a regular pattern of plant organogenesis (Hardham et al., 1980[82]; Green, 1986[73]; Barlow, 1994[18]; Barlow and Baluška, 2000[19]). The highly organized cellulose wall covers the bounding PM of plant cells and renders them immobile, except in special cases where the stiff cellulosic cell wall is weakened (during root hair outgrowth) or is naturally absent (pollen tubes). In these cases the inherent motility of the plant cell periphery is expressed, allowing cellulose-depleted and actin-enriched subcellular domains to protrude and extend in an F-actin-dependent fashion called tip growth (e.g., Pierson and Cresti, 1992[173]; Volkmann and Baluška, 1999[222]; Baluška, 1999[16]; Miller et al., 1999[140]; Gibbon et al., 1999[69]). Many aspects of this unique mode of plant cell growth are reminiscent of events occurring at leading edges of migrating animal cells (for oomycetes see Gupta and Heath, 1997[79]; for pollen tubes see Lord and Sanders, 1992[128]; Sanders and Lord, 1992[187]; Lord et al., 1996[129]; Jauh et al., 1997[100]; Wilhelmi and Preuss, 1997[232]; for animal cells see Vasiliev, 1987[217]; Mitchison and Cramer, 1996[145]; Welch et al., 1997[227]). Recently, Bajer and Smirnova (1999[6]) provided convincing proof for the inherent motility of plant cells by plating endosperm cells of *Haemanthus,* lacking any cellulosic cell walls and cortical MTs, on agar-coated cover slips. *In vivo* observations revealed that post-telophase endosperm cells undergo pronounced cell shape changes forming lamellipodia-like lobes and filopodia-like processes. These cellular protrusions closely resemble those of diverse motile animal cells (e.g., Vega and Solomon, 1997[219]; Wessels et al., 1998[228]).

Without going over the arguments of an organismal *versus* a cellular conception of morphogenesis, it is fairly obvious that only animal cells are truly multicellular whereas higher plants are coenocyte-like organisms because their cellulosic walls (extracellular matrices) only partly enclose the cytoplasm of individual cells (Lucas et al., 1993[130]; Ding and Lucas, 1996[52]). In plants, the cellulosic cell walls serve as structural (supporting) rather than as isolating components of morphogenesis (Barlow, 1994[18]; Fowler and Quatrano, 1997[64]). It seems that the evolutionary pathway of plant cells towards multicellularity has been based on plant-specific plasma-membrane – extracellular matrix linker molecules, among which cellulose and callose synthase complexes are the prime candidates. Thus, identification of cytoskeletal partners of

these transmembrane complexes is one of the most urgent tasks of current plant cell biology (Fowler and Quatrano, 1997[64]). The embellishment of the plant cell protoplast with specific carbohydrate polymers and proteoglycans (Knox, 1992[113]; Showalter, 1993[193]; Du et al., 1996[57]; Nothnagel, 1997[157]) provides a matrix which is strong enough to mechanically support sessile plants. Plant specific extracellular matrices can, in addition, impart information for successful cellular and, hence, morphogenetic development (e.g., Pennell et al., 1992[166]; Langan and Nothnagel, 1997[121]). This is similar to the situation in animal cell systems (e.g., Ettinger and Doljanski, 1992[63]).

The microtubular cytoskeleton is inherently associated with the nucleus and together they comprise the "cell body" (Baluška et al., 1997b[11]; 1998a[13]) or "cytoplast" (Pickett-Heaps et al., 1999[172]). Complementary to the nucleus-based "cell bodies" are sites, or domains, at the cell cortex which organize the "cell periphery complex" – a term loosely used to comprise interactions among components of the cortical cytoskeleton, PM, and the extracellular matrix. In earlier articles (Baluška et al., 1997b[11]; 1998a[13]; 1998b[14]), we tried to amass evidence in support of the plant "cell body" concept and to show how it illuminates many aspects of plant cellular behaviour and development. In the present article, we wish to concentrate on associations of plant "cell bodies" with specialized actin-enriched domains of the plant "cell periphery complex" in the context of the plant-specific features of cell architecture, growth, and development. We hypothesize that actin-based cell cortex domains of higher plants polarize the "cell bodies" during mitosis, cytokinesis, and tip growth, and thus provide a polarity for morphogenetic processes.

Cortical MTs of Higher Plant Cells Represent the Most Abundant Cytoskeletal Component of their "Cell Periphery Complex"

A unique feature of cell walls in growing higher plants is that the spatial ordering of their nascent cellulose microfibrils, synthesized *via* poorly characterized and PM-associated synthase complexes (Kimura et al., 1999[111]), is controlled by dense arrays of cortical MTs located beneath the PM (Giddings and Staehelin, 1991[70]; Cyr, 1994[44]). This latter association, which forms some kind of "cell periphery apparatus" that is characteristic of most higher plant cells, seems to be organized *via* proteinaceous linker molecules (Hasezawa and Nozaki, 1999[86]; Akashi and Shibaoka, 1991[2]). It is this interdependence between cellulosic microfibrils and cortical MTs that determines the orientation of plant cell expansion. Typically, most plant cells elongate *via* bidirectional cell expansion which allows rapid extension of major plant organs, such as shoots and roots, a consequence of which is the effective exploitation of both the above- and below-ground environments. Bidirectional cell extension means that the longitudinal side walls grow in a more or less continuous fashion (diffuse plant cell growth) and, at the same time, incorporate new microfibrils by an appositional process mediated by numerous parallel arrays of cortical MTs. The transverse end walls, by contrast, expand little in width but increase in thickness. They are associated with fewer and less well organized cortical MTs but they are equipped with numerous primary plasmodesmata, attract abundant actin filaments (AFs), and are enriched with unconventional plant myosin VIII (for root apices

see Baluška et al., 1997 a[10]; Reichelt et al., 1999[180]; Baluška et al., 2000[17]).

Higher plant cells, like animal cells, display two basic PM-associated cytoskeletal systems which support two alternative modes of growth – tip growth and diffuse growth. For the F-actin-supported peripheral cytoskeleton of animal cells Vasiliev (1987[217]) coined the term "actinoplasm" whereas that part of the cytoskeleton supported by MTs was termed "tubuloplasm". The same terms could, perhaps, be applied to different cell cortex-associated domains of plant cells. In an evolutionary context, the secretion of a cellulosic extracellular matrix may have preceded, and then gone hand-in-hand with the development of cortical "tubuloplasm" and the plant type of multicellularity. This in turn forced the recession of the "actinoplasm", and the cells became immobile, requiring MTs to control the polarity of their extension by means of MT-directed diffuse growth. There are, however, two situations during plant cell development when plant cells escape their "coenocyte-like" and cellulose-supported multicellularity. In these cases the tubulin-based growth polarity recedes, and the actin-based growth polarity comes to the fore in the form of the tip growth of root hairs and pollen tubes. Such a resurrection of a phylogenetically "primitive" mode of plant cell growth is critical for the accomplishments of effective translocation of haploid plant "cell bodies" *via* rapidly growing pollen tubes and for the effective exploitation of nutrient-rich soil regions distant from the root surface by the rapidly growing root hairs.

Although the peripheries of growing plant cells are typically comprised of both cortical MTs and nascent cellulose (β, 1 → 4 glucan) microfibrils, forming some sort of plant "cell periphery apparatus", it is equally significant that sites sometimes arise on the cell periphery which are depleted of these two items. At apices of tip growing cells, like root hairs (e.g., Kumarasinghe and Nutman, 1977[118]) or pollen tubes (e.g., Hasegawa et al., 1996[85]; Derksen et al., 1999[48]), as well as at plasmodesmata or pit-fields (e.g., Radford et al., 1998[175]), the PM preferentially accomplishes the synthesis of callose (β, 1→3 glucan). This polymer is less structured and spatially organized (Delmer and Stone, 1988[45]) and, significantly, the sites of its synthesis are often enriched with components of the actin-based cytoskeleton (Reichelt et al., 1999[180]; Chaffey and Barlow, 2000[37]; Baluška et al., 2000[17]). We suggest that such actin-based and callose-rich cell periphery domains are a reminder (and a remainder) of the ancient mobile property of the plant cell predecessor.

Disassambly of Cortical MTs and Assembly of Cell Cortex-Associated AFs During Mitosis: Polarization of Mitotic Plant "Cell Bodies" *via* Selective Stabilization of Astral MTs?

Mitosis is one of the most conservative processes in eukaryotic cells. For the plant PM this represents the only situation when it becomes naturally free of underlying cortical MTs. Interestingly, mitosis is also accompanied by enrichment of the PM with F-actin and myosin VIII, especially at those sites which face the poles of the assembling spindle (Reichelt et al., 1999[180]; Chaffey and Barlow, 2000[37]; Volkmann and Baluška, 1999[222]; Baluška et al., 2000[17]). This feature occurs during the symmetric cell divisions in maize root apices (Baluška et al., 1997 a[10]). A similar situation, at least with respect to actin,

has also been reported for the asymmetric cell divisions from which arise the stomatal complexes in leaf epidermis (Cho and Wick, 1990[39]; 1991[40]; Cleary, 1995[42]; Cleary and Mathesius, 1996[43]; Kennard and Cleary, 1997[109]; for a review see in Wick, 1991[231]) where the pre-mitotic nuclei of subsidiary mother cells move towards localized actin-rich PM domains of the central guard mother cells (Kennard and Cleary, 1997[109]). The ensuing nuclear division and cytokinesis create the small, subsidiary cells on either side of the guard cells. Similarly, protonemata of the green alga *Chara* have actin-enriched growing tips which attract mitotic spindle poles when blue light induces mitosis in these cells (Braun and Wasteneys, 1998[28]). A similar feature was described in *Fucus* zygotes where an actin-enriched cell cortex domain selectively stabilizes one of its spindle poles, causing rotation of the whole spindle body in preparation for the first mitosis (Kropf et al., 1989[117]). Moreover, it also polarizes the exocytotic machinery which leads to the adhesion of the rhizoid pole of the zygote with the substrate (see Fig. 2 in Fowler and Quatrano, 1997[64]). Rotation of animal "cell bodies", *via* selective attraction of MTs at cell periphery domains, is critical for positioning of cleavage planes during embryogenesis (e.g., Nishikata et al., 1999[154]).

That these associations between polarized cell division, targeted exocytosis, and the actin-enriched PM domains are rather general phenomena for the eukaryotic organism is clear from other, phylogenetically distant, organisms. For example, local accumulation of mobile actin patches associated with the PM of budding yeast cells both imposes polarity on mitotic division and facilitates local exocytosis (Li et al., 1995[122]; Ayscough et al., 1997[3]; Welch et al., 1997[227]). This culminates in polarized outgrowth (budding) of post-mitotic cells (Drubin, 1991[55]; Chant, 1994[38]; Waddle et al., 1996[223]).

MT-Dependent Cytokinesis of Walled Plant Cells is an Actomyosin-Supported Process

Cytokinetic plant cells perform a unique form of exocytosis whereby numerous vesicles accumulate and fuse within tubulin-based but actin-enriched phragmoplasts. This transient structure is assembled at telophase by a highly polarized plant "cell body" (Baluška et al., 1998 a[13]), also known as a phragmoplast–nuclear complex (Kakimoto and Shibaoka, 1998[105]). It is responsible for partitioning the cytoplasm, or "cytoplast" (Pickett-Heaps et al., 1999[172]), with their newly divided "cell bodies" by means of a callosic cell plate. The phragmoplast body consists mainly of endoplasmic MTs radiating from post-mitotic nuclear surfaces (Nagata et al., 1994[151]; Baluška et al., 1996[9]; Baluška et al., 1997 a[10],c[12]; Hasezawa et al., 1997[87]) and these associate with MT-based motors carrying their vesicular cargoes (e.g., Asada et al., 1997[5]; Asada and Collings, 1996[4]). But phragmoplasts also contain abundant actin (Clayton and Lloyd, 1985[41]; Kakimoto and Shibaoka, 1987[104]; Palevitz, 1987[162]; Mineyuki and Palevitz, 1990[142]; Liu and Palevitz, 1992[125]; Baluška et al., 1997 a[10]; Endlé et al. 1998[59]), and the barbed ends of the AFs are oriented towards the phragmoplast interior (Kakimoto and Shibaoka, 1988[105]). A consequence of this is the polarization of the "cell body". Moreover, in concert with myosin motors AFs may also contribute to the active capture and accumulation of membranous material, dictyosome vesicles in particular, within the assembling cell plate. Notable is the association of plant myosin VIII

with assembling and maturing cell plates (Reichelt et al., 1999[180]; Baluška et al., 2000[17]).

The disintegration of AFs by means of the G-actin sequestering agent, latrunculin B (e.g., Gibbon et al., 1999[69]), fails to prevent cytokinesis but results in the aberrant positioning of newly-formed division walls (Baluška, unpublished). This confirms earlier observations of the resistance of phragmoplasts and cell plates to cytochalasins B and D (Palevitz and Hepler, 1974[164]; Palevitz, 1980[161]; 1988[163]; Gunning and Wick, 1985[78]; Lloyd and Traas, 1988[126]; Cho and Wick, 1990[39]). These observations point to the conclusion that F-actin does not play a vital role in the process of cytokinesis. What then is the role of F-actin in dividing cells? One possibility is that F-actin, because of its association with the preprophase band of MTs, may be responsible for where the cell plate docks with the side walls of the parental cell.

Callosic Cell Plate Precedes *De Novo* Formation of Cellulosic Cell Wall During Cytokinesis

Early cytological studies using the fluorochrome aniline blue revealed large amounts of callose in cytokinetic cell plates (Waterkeyn, 1961[225], 1967[226]; Fulcher et al., 1976[66]; Guens-Longly and Waterkeyn, 1976[75]). In fact, all cell walls of higher plants, irrespective of whether they are within the gametophyte or sporophyte generations, or within the primary or secondary tissues of the latter, are initiated as callosic cell plates during cytokinesis. Moreover, the recent use of monoclonal antibodies against callose has validated the "callose stage" for the cell plate in primary (Northcote et al., 1989[156]; Samuels et al., 1995[186]; Vaughn et al., 1996[218]) and secondary meristems (Chaffey and Barlow, unpublished observations). The generalization that every plant cell wall passes through an "embryonic" callose stage may also hold true for some lower plants (Schnepf and Sawidis, 1991[191]).

Following the fusion of dictyosome vesicles and the concomitant construction of a labile, membrane-enclosed callosic cell plate (Samuels et al., 1995[186]; Verma and Gu, 1996[221]; reviewed by Staehelin and Hepler, 1996[204]), the cell plate transforms into a cell division wall by its acquisition of cellulose microfibrils. At much the same time, the callose rapidly degrades (Samuels et al., 1995[186]). If synthesis of cellulose is inhibited, or if fusion of the cell plate with the parental cell wall is blocked, the cell plate disperses and a binucleate cell is formed (Gunning, 1982[77]; Vaughn et al., 1996[218]). Interestingly, stubs of an abortive division wall were sometimes found; their mode of formation is unclear but their presence suggests that division walls can be elaborated from the pre-existing parental walls (Barlow and Baluška, 2000[19]). Vaughn et al. (1996[218]) showed that inhibition of the cellulose synthesis by dichlobenil prevented the maturation of cell plates into cellulosic division walls and that the amount of callose increased 20-fold in these abnormal cell plates. A similar cellular phenotype was described for the *cyt1* mutant of *Arabidopsis* (Nickle and Meinke, 1998[153]) whose walls were enriched with callose. However, the excess callose in *cyt1* meristems was not the result of inhibited cytokinesis; this was indicated by the observation that other mutants showing this defect of division had normal callose distributions.

Interestingly, newly formed PM portions of the cell plate are depleted of cortical MTs but they are enriched with plant unconventional myosin VIII (Reichelt et al., 1999[180]; Baluška et al., 2000[17]). As plasmodesmata are formed within callosic cell plates by entrapment of ER elements during coalescence of Golgi vesicles (Hepler, 1982[93]), it might turn out that the myosin VIII is somehow involved in the process of plasmodesmata formation, especially since myosin VIII localizes to plasmodesmata (Reichelt et al., 1999[180]; Baluška, Šamaj, Volkmann, in preparation). F-actin is also present at the callosic cell plate but in smaller amounts (e.g., Endlé et al., 1998[59]; Schmit, 2000[189]). The change-over of synthetic pathways at the cell plate/division wall from callose to cellulose formation during the earliest steps of interphase may have to do with the re-establishment of cortical MTs beneath the associated PM. There are no cortical MTs beneath the PMs of newly assembled division walls until cellulose begins to be deposited here. Extensive myosin VIII accumulation at callosic cell plates also suggests further possible roles for this interesting molecule, namely a mechanical stabilization during cytokinesis of the newly assembled PM portions. This might be important in the developmental switch from callose synthesis into cellulose synthesis and might also be essential for the completion of cytokinesis *via* structural consolidation and straightening of the delicate cell plate (Mineyuki and Gunning, 1990[141]).

The origin of the cellulose-synthesizing enzymes is unknown. They may have been present in the vesicles that were imported into the maturing cell plate during the final stage of cytokinesis and may require the presence of cortical MTs to become active. Because MTs are required to orient the products of glucan synthesis (Hirai et al., 1998[94]), this suggests that the cortical MTs themselves may be responsible for the switch between β, $1 \rightarrow 3$ and β, $1 \rightarrow 4$ glucan synthesis. Callose synthesis, the alternative to cellulose synthesis (Jacob and Northcote, 1985[99]; Northcote, 1991[155]; Kauss, 1996[108]), can be rapidly induced in response to a wide range of physical and environmental factors that affect MT–PM stability (glutaraldehyde fixation: Hughes and Gunning, 1980[96]; detergents: Li et al., 1997[123]; mechanical stress: Takahashi and Jaffe, 1984[208]; plasmolysis: Baluška et al., 1999[15]; wounding: Galway and McCully, 1987[67]; temperature: Smith and McCully, 1977[203]; pathogen attack: Aist, 1976[1]; Hussey et al., 1992[97]; Škalamera and Heath, 1995[199], 1996[200]; Škalamera et al., 1997[202], aluminium toxicity: Sivaguru and Horst, 1998[196]; Sivaguru et al., 1999 a[197], 1999 b[198]).

For aluminium toxicity, for instance, a relationship was demonstrated between the depolymerization of cortical MTs and the induction of callose synthesis at the PM (Sivaguru and Horst, 1998[196]; Sivaguru et al., 1999 a[197], 1999 b[198]). Callose synthesis may thus be regarded as a default system associated with the enforced absence of cortical MTs and/or nascent cellulose microfibrils. However, other factors impinging on the PM and apoplast are also involved because mere depolymerization of MTs with tubulin drugs is not enough to induce callose formation. In this regard, isolated protoplasts stripped of their cellulosic wall are of particular interest. Upon isolation, their PM immediately synthesize callose (Klein et al., 1981[112]; Van Amstel and Kengen, 1996[216]) but later cellulose predominates (Hasezawa and Nozaki, 1999[86]; Nedukha, 1998[152]). It is also known that cellulose wall regeneration of protoplasts is accompanied by the reformation of a complement of cortical

MTs. Some data indicate that the transient callose acts as a temporary stabilizer of the newly formed PM at the division wall (Van Amstel and Kengen, 1996[216]).

Endoplasmic Perinuclear MTs as a Part of the Default Type of Plant Cell Organization

As already discussed, the cortical MTs underlying the PM polarize the growth of higher plant cells by means of a control over the orientation of the nascent cellulosic microfibrils. By contrast, the interior of the cell is sparsely populated by MTs. However, there are a few situations in which the stage of plant cell development seems to require the assembly of an endoplasmic MT population and the dismantling of cortical MTs at the cell cortex. An extreme but well known example is shown by mitosis and cytokinesis when all MTs are organized around mitotic chromosomes and post-mitotic nuclei (e.g., Nagata et al., 1994[151]; Baluška et al., 1996[9]). These MTs form part of the mitotic "cell body" and its immediately post-mitotic structure (Baluška et al., 1998 b[14]). A similar depletion of cortical MTs and their exclusive re-assembly as endoplasmic MTs radiating from nuclear surfaces occurs during sporogenesis (Dickinson and Sheldon, 1984[49]). These arrays, where they meet and interdigitate during cytokinesis, define the limits of the cytoplasmic domains of the future spore cells (e.g., Brown and Lemmon, 1988[30]). Developing endosperm is another situation where, in certain species, cortical MTs are absent and cellular behaviour is determined by nucleus-associated, radiating arrays of endoplasmic MTs (e.g., Brown et al., 1994[31], 1996[32]; Bajer and Smirnova 1999[6]). As in the previous examples, the absence of cellulose synthesis at this free nuclear stage suggests a phylogenetically more primitive organization, this time within endosperm (Friedman, 1992[65]). All this closely resembles the situation during cytokinesis when cortical MTs are still absent and the endoplasmic MTs continue to radiate from nuclear surfaces forming the phragmoplast (Nagata et al., 1994[151]; Baluška et al., 1996[9]; Hasezawa et al., 1997[87]). For late phragmoplasts, this feature is usually overlooked by most authors (but see Figs. 2i–p in Baluška et al., 1996[9]). These endoplasmic MTs, which radiate from nuclear surfaces and interdigitate within the division plane, may also define a limit upon the size of meristematic cells (Baluška et al., 1997 b[11]).

Higher plant cells also develop an extensive set of radiating perinuclear MTs whenever the cortical MTs fail to be maintained, for example during experimentally induced inhibition of protein synthesis (Mineyuki et al., 1994[143]; Baluška et al., 1995 b[8]). Inhibitors of protein kinases and phosphatases also have the same general effect (Baskin and Wilson, 1997[21]). Depletion of cortical MTs with concomitant assembly of perinuclear radiating MTs was described for root cortex cells of alfalfa seedlings infected with *Rhizobium* during formation of preinfection threads (Timmers et al., 1999[212]). There are also numerous examples of cells of mutant plants which fail to organize cortical MTs but which contain abundant endoplasmic MTs. Although these mutants show defects in both cell growth polarity and morphogenesis (e.g., Hauser et al., 1995[88]; Traas et al., 1995[213]; McClinton and Sung, 1997[136]), the tip growth of their root hairs, and presumably of their pollen tubes too, is unaffected (Hauser et al., 1995[88]; McClinton and Sung, 1997[136]). Importantly, in tip-growing higher plant cells (see below for more extensive discussion) all MTs are distributed

longitudinally throughout the cytoplasm and interconnect subapical nuclei with F-actin-enriched extending apices (for root hairs see Lloyd et al., 1987[127]; Sato et al., 1995[188]; Baluška, 1999[16]). On the other hand, tip growth of higher plant cells does not require abundant cortical MTs associated with the PM and organized transversely with respect to the direction of cell growth. Moreover, tip growth is a typical mode of growth in lower plants or fungi, and exists even in prokaryotic organisms such as streptomycetes (Prosser, 1990[175]). All this strengthens the case that whenever the absence of cortical MTs and the presence of endoplasmic MTs is seen in higher plant cells it represents the primary form of MT organization.

A conclusion from all the above data is that the maintenance of cortical MTs is an active process, requiring a number of different proteins. Since a depletion of cortical MTs, either forced or accomplished naturally, is invariably associated with a concomitant increase of endoplasmic MTs, it would then seem that endoplasmic MTs are assembled as a default state of "cell body" organization. The minimum requirement for this state is a nuclear surface since it is here that the primary MT organizing centres are located (reviewed by Baluška et al., 1997 b[11]).

Growth Polarity of Tip-Growing Plant Cells Depends on Actin-Enriched Cell Cortex Domains

In higher plants there are two examples where growth of a spheroidal or cuboidal cell is focussed to a localized peripheral domain. These are pollen tubes and root hairs which emerge from pollen grains and root epidermal cells (trichoblasts), respectively. Both are convenient for experimental studies (see Sievers and Schnepf, 1981[194]). Their tip growth is evidence of motility of at least some higher plant cells. This is critical for the delivery of sperm cells to ovules located deep in maternal tissues (pollen tubes) or for the effective exploitation of soil regions distant from the root surface (root hairs). Tip-growing pollen tubes interact with specific pistil tissues (e.g., Zinkl et al., 1998[237]) while root hairs interact with soil organisms, for instance, *Rhizobium* bacteria (de Ruijter et al., 1998[184]; Miller et al., 1999[140]).

Tip-growing cells recruit the whole exocytotic machinery towards their dome-shaped tip domain. As a consequence, growing apices of pollen tubes and root hairs contain abundant ER elements (Lancelle and Hepler, 1992[120]; Derksen et al., 1995[47]). The significance of this may go beyond just the supply of precursors for cell growth but may be the very basis for the shape of the cell itself (e.g., Bartnicki-Garcia et al., 1989[20]). Typically, tip-growing plant cells are dependent on intact AF meshworks and their disintegration invariably stops the tip growth (see below). Cessation of growth may be due to impaired translocation of Golgi vesicles and their subsequent accumulation under the tip as was reported following treatments with cytochalasins (e.g., Mollenhauer and Morré, 1976[146]; Pope et al., 1979[174]: Shannon et al., 1984[192]; Phillips et al., 1988[169]). But the situation is obviously more complex as indicated by findings showing that low concentrations of cytochalasin D and latrunculin B, which do not affect cytoplasmic streaming, stop tip growth both in root hairs and pollen tubes (Miller et al., 1999[140]; Gibbon et al., 1999[69]). Gibbon et al., 1999[69] postulated that a latrunculin-B-sensitive dynamic population of F-actin is critical for the tip growth of pollen tubes. Intriguing in this respect is that treatment of extending
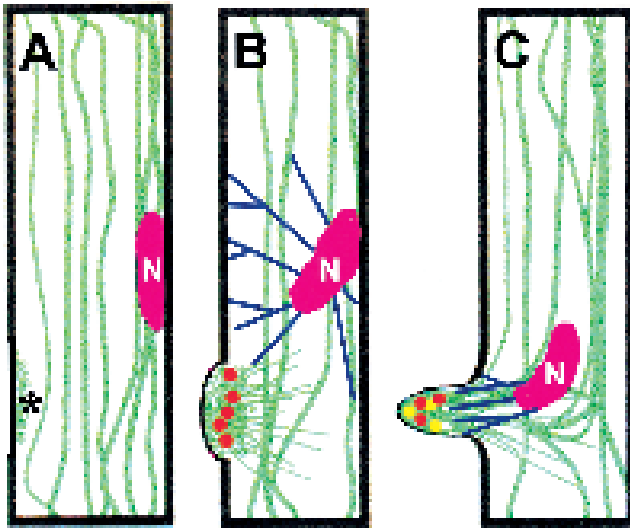
Fig. 1 Schematic view of root hair initiation in idealized root hair trichoblasts. (**A**) The first event is accumulation of vesicles containing hypothetical cell wall loosening factors at a distinct cell cortex domain (asterisk). After thinning of the cell wall, a bulge arises due to a lower cell wall resistance against internal turgor pressure. The inactive nucleus (N) is still settled at the cell wall and it is devoid of endoplasmic MTs. F-actin is organized as longitudinal bundles (green strings). (**B**) The bulged domain recruits dynamic actin (finely-meshed meshworks) due to a local accumulation of profilins (red marks). Endoplasmic MTs (blue bars) are already organized around the nuclear surface. This is the first sign of "cell body" activation. (**C**) The bulged domain transforms into a root hair tip and it then accumulates dense F-actin meshworks, G-actin, profilin, and actin depolymerizing factor (yellow marks). This actin-rich cell cortex domain polarizes the active "cell body" *via* selective attraction and stabilization of nucleus-associated endoplasmic MTs. The nucleus is enclosed within a cytoskeletal basket which obviously allows its "dragging" behind the protrusive root hair tip. Nucleus-associated cytoskeletal baskets and dense cortical MTs are not depicted in this highly simplified scheme which is based on the following papers: Lloyd et al. (1987[127]); Jiang et al. (1997[102]); Braun et al. (1999[29]); Miller et al. (1999[140]); Baluška et al. (1997b[11], 1998a[13], 2000[17]). For corresponding *in vivo* DIC images, taken from a video tape sequence, see Fig. 3 in Baluška et al. (1998a[13]).

lily pollen tube apices with Yariv phenylglycoside stops their tip growth while exocytosis continues (Roy et al., 1999[183]). This suggests that the importance of dynamic F-actin for tip growth goes beyond its support of vectorial exocytosis.

Preliminary data indicate that tip growth might turn out to represent a plant-specific form of protrusive growth driven by actin polymerization (for a model see Fig. 1 in Welch et al., 1997[227]). For instance, the tip growth of lower and higher plant cells does not correlate tightly with turgor pressure (e.g., Money and Harold, 1993[147]; Benkert et al., 1997[24]) but resembles rather an amoeboid type of cell growth (Lord and Sanders, 1992[128]; Sanders and Lord, 1992[187]; Lord et al., 1996[129]; Harold et al., 1996[84]; Harold, 1997[83]; Pickett-Heaps and Klein, 1998[171]). In hyphae of *Saprolegnia ferax,* tip growth not only continues in the absence of turgor pressure but is even more sensitive towards the anti-F-actin drug, latrunculin B (Gupta and Heath, 1997[79]). This is a strong case for the existence of F-actin-dependent protrusive growth in plants and accords with our concept that the actin-enriched cell cortex

domains represent a more primitive plant cell periphery organization.

F-actin-dependence of tip growth applies both to pollen tubes (Pierson and Cresti, 1992[173]; Taylor and Hepler, 1997[211]; Staiger, 2000[205]) and to root hairs (Miller et al., 1999[140]; Volkmann and Baluška, 1999[222]; Baluška, 1999[16]; Ovečka et al., 2000[159]). In the latter cells cytochalasin D treatments induce branching of hair apices, suggesting that F-actin normally determines the integrity of their growing tips (Ridge, 1990[181]; Ovečka et al., 2000[159]; for more general discussion see Steer, 1990[207]). Similar mechanical stabilization of the "cell periphery complex" by the actin-based cytoskeleton was inferred for trichomes of *Arabidopsis* where the disruption of F-actin caused aberrant cell shapes (Mathur et al., 1999[135]). Moreover, dense F-actin meshworks at tips of growing root hairs (Baluška, 1999[16]; Baluška et al., 2000[17]) might structurally support the apical "clear zone" which lacks larger organelles and bundles of AFs (de Ruijter et al., 1998[184]; Miller et al., 1999[140]).

Cytochalasin D and latrunculin B inhibit root hair formation after the bulge stage has been completed (Miller et al., 1999[140]; Baluška, 1999[16]). Obviously, the morphogenic switch from the bulge outgrowth into tip growth is F-actin dependent. This process is associated with enrichment of dense F-actin meshworks at assembling root hair tips (Baluška, 1999[16]; Braun et al., 1999[29]; Baluška et al., 2000[17]; for a schematic overview see Fig. 1). In addition, two plant actin-binding proteins critical for assembly of dynamic AFs, actin-depolymerizing factor and profilin (e.g., Didry et al., 1998[50]), are localized specifically at the tips of emerging and growing root hairs (Jiang et al., 1997[102]; Baluška, 1999[16]; Braun et al., 1999[29]). Their role is to facilitate, in a synergistic fashion (e.g., Didry et al., 1998[50]), high dynamism of the actin cytoskeleton (e.g., Staiger, 2000[205]; Staiger et al., 1997[206]).

The polarity of tip growth does not directly depend upon MTs (e.g., Heath, 1990[89]). In this respect there is a sharp contrast with the strict dependence of diffuse plant cell growth upon distribution of cortical MTs. Recent observations of Bibikova et al. (1999[25]) indicate, nevertheless, that both AFs and MTs contribute to the directionality of *Arabidopsis* root hair growth. A conclusion from their studies is that longitudinal MTs are responsible for maintenance of growth polarity since their disruption leads to wavy, and even bifurcating, hair apices. Longitudinal MTs may provide a scaffold for AFs, and loss of MTs may destabilize the AF system.

The actively growing actin-enriched apices of tip-growing cells are strongly attractive to nucleus-associated endoplasmic MTs (for a schematic overview of situation in trichoblast see Fig. 1). This occurs not only in pollen tubes (e.g., Taylor and Hepler, 1997[211]) and root hairs (e.g., Lloyd et al., 1987[127]; Sato et al., 1995[188]) but also in the protonemata and rhizoids of lower plants (e.g., Kadota and Wada, 1995[103]; Braun and Wasteneys, 1998[28]). It is a characteristic of tip-growing cells that their nuclei are located at a well-defined distance from the tip in each corresponding cell type (protonema - Jensen, 1981[101]; root hairs - Lloyd et al., 1987[127]; Sato et al., 1995[188]; pollen tubes - Pierson and Cresti, 1992[173]) and that disruption of the MTs increases this distance (Lloyd et al., 1987[127]; Sato et al., 1995[188]). This relationship is a manifestation of a polarized plant "cell body" (Baluška et al., 1998a[13]) with the actin-en-

riched apical PM domain playing a crucial role in maintaining the position of the "cell body" represented by the MT-nucleus complex (Baluška et al., 1997 b[11]). It is this principle of tip–nucleus interaction which allows the efficient translocation of the male germ unit (an inactive plant "cell body") from growing pollen grains to ovules during fertilization. Extending, actin-rich apices seem to attract longitudinal MTs *via* selective stabilization and capture of their plus ends. This mechanism is well accepted for motile animal cells where actin-rich PM-associated domains selectively stabilize and attract MTs (Gundersen and Bulinski, 1988[76]; Lin and Forschner, 1993[124]; Koonce, 1996[116]; Kaverina et al., 1998 c[107]). It is also critical for nuclear migration which invariably follows the leading edges of crawling animal cells (e.g., Vega and Solomon, 1997[219]; Wessels et al., 1998[228]).

Plasmodesmata and Pit Fields as Actomyosin-Supported Microdomains of Callosic "Cell Periphery Complex"

Single plasmodesmata as well as pit fields composed of clustered plasmodesmata are further examples of sites at the cell cortex which are depleted of cortical MTs (e.g., Mueller and Brown, 1982[149]). The structure of both the plasmodesmata and the pits which accommodate them includes both callose and actomyosin in addition to pectins (Casero and Knox, 1995[35]; Morvan et al., 1998[148]; Radford and White, 1998[176]; Blackman and Overall, 1998[26]; Reichelt et al., 1999[180]; Chaffey and Barlow, unpublished). The development of primary plasmodesmata is intimately related to cytokinesis, whereas secondary plasmodesmata form in already established postmitotic cells. A key event during the formation of primary plasmodesmata is the entrapment of ER elements within the developing cell plate (Hepler, 1982[93]). Their traversal of the plate precludes the complete cytoplasmic separation of postmitotic daughter cells. The callose of the cell plate is retained at these ER-associated domains, and it is here that plasmodesmatal structures between daughter cells become fully elaborated (Northcote et al., 1989[156]; Delmer et al., 1993[46]; Turner et al., 1994[214]). Significantly, cortical MTs are excluded from these domains of the new division wall thus providing, as proposed earlier, the conditions for the default pathway of callose synthesis.

In both primary and secondary tissues pit formation is revealed by the exclusion of cortical MTs from small elliptical areas on the cell cortex (Chaffey et al., 1999[36]). Pit field development probably commences with the redifferentiation of corresponding elliptical areas of the PM which, as a consequence, no longer support the presence of cortical MTs and the attendant cellulose synthesis. In the absence of cortical MTs, AFs become resident around or within the pit (depending on the cell type – observations on secondary xylem development in poplar – Chaffey and Barlow, 2000[37]; Chaffey, Barlow and Sundberg, in preparation), again suggesting the return to the ontogenetically more primitive, actin-based type of cell cortex organization.

In addition to actin (White et al., 1994[229]), plant myosin as well as other myosin-like proteins have been localized to plasmodesmata (Radford and White, 1998[176]; Blackman and Overall, 1998[26]; Reichelt et al., 1999[180]). These features, which contribute to the "juvenile" nature of the callosic domains at the cell periphery, seem to be critical for intercellular trafficking *via* plasmodesmata by means of an actomyosin control over their permeability (Overall and Blackman, 1996[160]; Ding, 1997[51]). Supporting evidence for this attractive concept is provided by experimental depolymerization of F-actin, either by cytochalasin D treatment or by microinjection of profilins. Both these treatments resulted in the increased permeability of tobacco mesophyll plasmodesmata. By contrast, stabilization of AFs following the microinjection of phalloidin had an opposite effect (Ding et al., 1996[54]). Intriguingly, inhibition of myosin activity by 2,3-butanedione monoxime resulted in plasmodesmata having constricted neck regions (Radford and White, 1998[176]). Moreover, the same myosin inhibitor also alters organization of ER elements at plasmodesmata (Šamaj et al., 2000[185]). Actomyosin activities are regulated by cytoplasmic calcium levels (for review see Nakamura and Kohama, 1999[150]; for plant myosin see Yokota et al., 1999[239]), and recent studies reveal that ER-resident calreticulin (Baluška et al., 1999[15]) and calcium-dependent protein kinase (Yahalom et al., 1998[238]; Baluška et al., in preparation) are further components of plasmodesmata. Moreover, calcium-sensitive, contractile centrin could also be a component of plasmodesmata; antibodies raised against centrin locate to plasmodesmata of onion root tips and cauliflower florets (Blackman et al., 1999[27]).

On the other hand, plasmodesmata may have relevance for the F-actin organization of plant cells. As already mentioned, pit fields can often act as AF-attracting domains (Baluška et al., 2000[17]; Chaffey and Barlow, 2000[37]; Chaffey, Barlow and Sundberg, in preparation for poplar secondary xylem development). The fact that plasmodesmata are most frequent on the transverse walls of root apex cells may account for abundance of AFs at cross walls and the predominance of longitudinally-oriented AF bundles running from end to end of stele cells, as shown for maize root apices (Baluška et al., 1997 a[10]). This latter feature may even assist in the axial transport of solutes and the plant hormone auxin.

Callose seems to perform a structural role in plasmodesmata because when it is depleted by exposure to 2-deoxy-D-glucose, the necks of the plasmodesmata become enlarged (Radford et al., 1998[177]). Similar effects on plasmodesmatal structure were also reported following cytochalasin treatment (White et al., 1994[229]). As already mentioned, inhibition of myosin-based forces induces constriction at plasmodesmata neck regions in root cells of *Allium* and *Zea* (Radford and White, 1998[176]). All these findings are in agreement with our hypothesis that callose and the actomyosin cytoskeleton are inherently interrelated. In certain cells this relationship may also involve ER. For example, close contacts between cortical ER elements and callose have been reported for the sieve plates of developing phloem elements (Esau and Thorsch, 1985[62]; Eleftheriou, 1995[60]). The presence of the ER cisternae, enriched with calreticulin (Baluška et al., 1999[15]), may contribute both to the widening of the plasmodesmatal channels *via* their impact on actomyosin activity as well as to their developmental transformation into sieve plate pores (Esau and Thorsch, 1985[62]).

Secondary plasmodesmata represent another group of important cytoplasmic channels. As the term suggests, they form in already established walls and usually possess a more complex branched structure than do primary plasmodesmata (for a re-

view see Ding and Lucas, 1996[52]). They appear to form from primary plasmodesmata (Itaya et al., 1998[98]) but the mechanism is poorly understood. The prelude to the formation of secondary plasmodesmata is the digestion of material within an existing cell wall. Golgi vesicles and ER participate in this process as they also do in sieve pore formation. Our preliminary data indicate that secondary plasmodesmata of maize root cells contain more actin and myosin VIII than primary plasmodesmata (Baluška and Volkmann, in preparation). Intriguingly in this respect the secondary plasmodesmata are preferentially targeted by viral movement proteins (Ding et al., 1992[53]; Itaya et al., 1998[98]) and they can also be expected to be targeted by putative components of endogenous gating mechanisms (Reichel et al., 1999[179]; Oparka et al., 1999[158]). Viral movement proteins, which seem to hijack the endogenous plasmodesmata gating machinery, do not accumulate in primary plasmodesmata which, at least in developing tobacco leaves, seem to be only poorly gateable (Oparka et al., 1999[158]; Pickard and Beachy, 1999[170]).

In principle, the process of secondary plasmodesmata formation is much the same as that which is responsible for cellular tip growth, except that the site on the cell cortex to which the actin and its exocytotic machinery is directed is, by comparison, much smaller. In support of this notion, movement proteins induce tubulation of plant protoplasts (e.g., Perbal et al., 1993[167]; Kasteel et al., 1996[106]; Ward et al., 1997[224]; Zheng et al., 1997[235]; Heinlein et al., 1998[92]; Huang and Zhang, 1999[95]). This is reminiscent of actin polymerization-driven protrusions of the PM induced by the bacterial pathogen, *Listeria monocytogenes,* in support of its spread from cell to cell in human hosts (e.g., Robbins et al., 1999[182]). Movement protein of tobacco mosaic virus behaves as an integral ER protein exposed to the cytoplasm (Reichel and Beachy, 1998[178]; Huang and Zhang, 1999[95]) and it also interacts with actin (McLean et al., 1995[137]). Therefore, movement protein-induced tubulation of protoplast surfaces might be structurally supported, as are plasmodesmata, *via* interactions of F-actin with ER elements. In fact, movement protein-induced tubules are BiP positive, confirming their ER-like nature (Ward et al., 1997[224]; Huang and Zhang, 1999[95]). Actin cytoskeleton is implicated in interaction between ER movement protein during targeting, gating, as well as during *de novo* formation of new plasmodesmata (for hypothetical model see Fig. 5 in Reichel et al., 1999[179]). Whereas apices of root hairs or pollen tubes may utilize the entire complement of PM-directed cytoskeletal actin strands emanating from the active "cell bodies", each secondary plasmodesmata is produced by a minimal set of F-actin elements.

The connections between the actin cytoskeleton and the primary plasmodesmata are probably constantly monitored and responded to by the "cell body" in accordance with the circumstances of the moment. In support of this attractive notion MTs are known to serve as tracks for viral movements between the nucleus and plasmodesmata (reviewed by Reichel et al., 1999[179]). This could account for the conversion of plasmodesmata from simple (primary) channels to branched (secondary) networks, such as was found in division walls in cells regenerating from protoplasts of *Solanum nigrum* by Ehlers and Kollmann (1996[57]). We suggest that the conversion of plasmodesmata from primary to secondary within a given wall, as well as the formation of pit fields, is related to the loss of MT-associat-

ed cell cortex domains and the consequent gain, by a default mechanism, of actin-based and callose-enriched cell cortex domains organized at the PM.

In some circumstances plasmodesmata and pit fields become sealed and hence the walls which bear them become imperforate (e.g., Lachaud and Maurousset, 1996[119]; Ehlers et al., 1996[58]). If, as we propose, plasmodesmata rely on an acto-myosin–callose complex for their maintenance, then loss of actin may allow cortical MTs to become re-established at these sites. Cellulose would then form and the plasmodesmatal orifices would become occluded by new secondary wall. Interestingly, Fig. 2 F in the paper by Lachaud and Maurousset (1996[119]) shows abundant cortical MTs in the vicinity of a pit field at a stage just prior to its occlusion. Furthermore, the general inhibitor of myosin activity, 2,3-butanedione monoxime, not only constricts plasmodesmal neck regions (Radford and White, 1998[176]) but its action also induces accumulation of cortical MTs at pit fields (Šamaj et al., 2000[185]).

Pathogen Attack Induces Assembly of Callose–Actomyosin Enriched Domains of the "Cell Periphery Complex"

Among the earliest responses of plant cells to a pathogen attack is the accumulation of AFs and cortical ER elements at the cell cortex, close to sites where the pathogen has attempted an entry (Gross et al., 1993[74]; Kobayashi et al., 1994[114], 1997[115]; Škalamera and Heath, 1995[199]; for a review see Staiger, 2000[205]). Callose is then immediately deposited beneath those PM domains which have been perturbed by the infection attempt. It is thought that the callose is necessary for a successful defence against the pathogen (Bayles et al., 1990[22]; Beffa et al., 1996[23]) because it was found that inhibition of callose deposition and application of F-actin depolymerizing drugs enabled *Uromyces* fungal penetration of a resistant cowpea cultivar (Škalamera and Heath, 1995[199], 1996[200]; Škalamera et al., 1997[202]). Similar phenomena were reported for cytochalasin D and *Phytophthora* infection of potato (Takemoto et al., 1999[210]). Other work also suggests that the actin cytoskeleton is organized preferentially under penetration sites and that it is implicated in development of the resistance response (Kobayashi et al., 1997[115]; Škalamera et al., 1997[202]; Škalamera and Heath, 1998[201]; Takemoto et al., 1997[209]; Xu et al., 1998[234]; McLusky et al., 1999[138]).

Another characteristic feature of fungal infections is nuclear migration towards the penetration site (Pappelis et al., 1974[165]; Gross et al., 1993[74]; Heath et al., 1997[90]). A similar migration occurs if the wall is partially digested with hemicellulase (Heath et al., 1997[90]), a step analogous to the creation of a partial protoplast. One possible interpretation of this migration phenomenon might be that cortical MTs are disassembled at the penetration sites and this calls into play both the actin-based cytoskeleton at the PM and the default callose synthesis system. The activated, actin-based domains at the PM then become involved in exocytosis which culminates in the assembly of protective papillae (Aist, 1976[1]; Baluška et al., 1995 a[7]; Heath et al., 1997[90]). The domains at which exocytosis occur also stabilize the endoplasmic MTs which radiate towards papillae (Baluška et al., 1995 a[7]) and are, in turn, connected with the nucleus (Baluška et al., 1995 a[7], 1998 a[13]; Kobayashi et al., 1994[114], 1997[115]). This situation resembles that which occurs during cytokinesis and tip growth. The presence of active "cell

bodies" near fungal penetration sites indicates a close communicative relationship between them and the actin-enriched cell cortex domains.

In the light of statements in the Introduction about the proposed origin of eukaryotic cells, it is intriguing to find that the sites for the entry of pathogens and of potential endosymbionts co-localize with actin-enriched cell cortex domains. For example, root hairs are sites of entry for nodulating rhizobia and vesicular/arbuscular mycorrhizal fungus penetration, whereas plasmodesmata, especially those that are secondarily induced, are targets for viruses which then utilize the associated cytoskeleton for their intercellular transmission (Heinlein et al., 1995[91]; Reichel et al., 1999[179]). Moreover, rhizobia are able to induce their entry into the host by endocytosis (Verma, 1992[220]). This process may require different forms of actin from those which are usually associated with root cells, and these actins have, in fact, been found in developing nodules on bean roots (Pérez et al., 1994[168]).

More recently rhizobial *Nod* factors, which are essential for infection and nodulation, have been shown to rearrange the actin cytoskeleton of root hairs (Cárdenas et al., 1998[34]; Miller et al., 1999[140]; for a review see Staiger, 2000[205]). F-actin rearrangements as a result of *Nod* factor-induced changes in the hair periphery (de Ruijter et al., 1998[184]; Miller et al., 1999[140]) may be instrumental in the formation of the inwardly-growing infection thread. The root hair tip is drawn inwards by the actin and the PM domain working "in reverse" rather than extending forwards. Interestingly, nodule cells have more endoplasmic MTs but fewer cortical MTs (Whitehead et al., 1998[230]). A corollary to these observations is that, although cortical MTs and their associated extracellular matrix normally erect a barrier around the cell, any relaxation of this system permits the development of the more primitive actin-supported PM system. This event lays the cell open to penetration by prospective symbionts which can then make further use of the actin-based cytoskeleton for their intercellular translocation. Whether or not the remodelling of the cell periphery in response to the rhizobia results in the resistance to or the facilitation of penetration is clearly a critical point in the evolution of such response mechanisms. Remodelling of the cytoskeleton occurs in cells involved in endomycorrhizal associations: host cell AFs envelop the fungal hyphal masses whereas endoplasmic MTs bridge the individual fungal branches (Uetake et al., 1997[215]; Genre and Bonfante, 1998[68]).

Conclusions

Cells of higher plants and animals share some previously unnoticed similarities with respect to the involvement of actomyosin in the assembly of their cell peripheries. These similarities go so far as to suggest that both types of cells are inherently mobile though the mobility of plant cells is usually held in check by their tubulin-based "cell periphery apparatus" which assembles a rigid extracellular matrix based on cellulose microfibrils. Most higher plant cells exhibit diffuse growth, the direction of which is MT-dependent. This feature allows plant cells to perform the ultimate control of cell division/growth polarities by activities related to tubulin-based "cell bodies". However, two unique plant cell types, root hairs and pollen tubes, are exceptional in this respect. They express the potential for F-actin-dependent protrusive growth in order

to perform the highly motile processes critical for their specialized functions. Obviously, actin-rich cell cortex domains polarize the "cell bodies" within tip-growing root hairs, and the same feature seems to also operate in pollen tubes. The unconventional plant myosin VIII localizes at those portions of the PMs which support the synthesis of callose. Importantly, the myosin VIII–callose-enriched PM sites which mark specialized domains of the "cell periphery complex" are depleted of cortical MTs. The myosin VIII–callose-enriched cytokinetic cell plates represent "juvenile" forms of the plant "cell periphery complex". Within the resulting division walls, plasmodesmata are unique microdomains of the "cell periphery complex" which retain this "juvenile" quality favouring direct interactions among individual "cell bodies" within plant organs.

Acknowledgements

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Section Editor: T. Nagata