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A Polarity Crossroad in the Transition Growth Zone of Maize Root Apices: Cytoskeletal and Developmental Implications

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Abstract

Due to their simple and regular anatomy, root apices represent a unique model object for studying growth, polarity, and morphogenesis. This advantageous anatomy has been exploited to characterize the developmental changes that occur as root cells progress from their origin in the meristem up to their final nongrowing state at the proximal limit of the elongation region. A new growth region located between the apical meristem and the distal portion of the region of rapid cell elongation was discovered and designated as the 'transition zone.' Cells of this zone accomplish a developmental transition recently from cytoplasmically driven expansion to vacuome-driven elongation. Cells traversing the transition zone use cytoskeletal elements to regulate both growth polarity and the maintenance of cellular growth *per se*. Transition zone cells are also sensitive to diverse endogenous clues and exogenous factors such as auxin, ethylene, extracellular calcium, mechanical pressure, aluminum, and microorganisms. This high sensitivity of transition zone cells, which are not engaged in mitotic divisions, seems to be related to their specific cytoarchitecture whereby postmitotic nuclei occupy a central position within the cell, with their radial perinuclear microtubules extending to the cell periphery. Future studies are challenged to identify genes and proteins that determine the various sensory behaviors of cells in this transitional phase of development, and which, in turn, drive directed growth responses (tropisms) of root apices in response to diverse external stimuli.

Key words: Actin filament; Cell growth; Cytoskeleton; Development; Cytoarchitecture; Maize; Microtubules; Polarity; Root; Apex

Introduction

Due to their large dimensions and structural complexity, eukaryotic cells require a cytoskeleton for internal support and intracellular motility. Microtubules (MTs) and actin filaments (AFs) are cytoskeletal assemblages found in all eukaryotic cells. They are built from the proteins tubulin and actin (Doolittle 1995), each having highly conserved amino acid sequences, which assemble into filamentous polymers that show an inherent polarity and dynamic behavior (Kirschner and Mitchison 1986; Mitchison 1995; Staiger and others 2000). Along

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these polarized cytoskeletal tracks, molecular motors such as myosins, dyneins, and kinesins drag their cargoes of macromolecules and organelles. AFs and MTs are also responsible for the growth of plant cells (Lloyd 1991; Kost and others 1999; Barlow and Baluška 2000; Wasteneys 2000), be it isotropic or anisotropic. Recently, the participation of MTs and AFs in signalling pathways has been discovered in both animal and plant cells (reviewed by Bargmann 1994; Gundersen and Cook 1999; Nick 1999; Volkmann and Baluška 1999; Machesky and Insall 1999; Staiger 2000). The dynamic instability of cytoskeletal assemblages is essential for this sensory role and is influenced by factors as diverse as gravity, light, temperature, moisture, ionic balance, and mechanical stress (for example, see Williamson 1990; Tabony and Job 1992; Baluška and others 1993a; Cleary and Hardham 1993; Zandomeni and Schopfer 1994; Blancaflor and Hasenstein 1995a; Wymer and others 1996; Fisher and Schopfer 1997; Himmelspach and others 1999; Skagen and Iversen 1999; Hejnowicz and others 2000). The participation of MTs in diffuse cell growth, and of AFs in tip cell growth, are known. In both cases, the cytoskeleton dynamically "fixes" the growth response resulting from the previous sensing of the extracellular milieu.

Growing root apices are extremely useful for studies on various aspects of plant cell biology (Barlow and Baluška 2000; Benfey and Scheres 2000). Features such as their simple anatomy, clear developmental zonation, and diversity of cell fates, as well as the absence of a cuticule and easy handling for pharmacological treatments, make root apices ideal for straightforward interpretation of experimental studies on the plant cytoskeleton. For a decade, our focus has been on the cytoskeleton of maize root apices (Baluška and others 1992), concentrating mostly on meristematic cells. But no less important is the cytoskeleton within cells of the transition zone between the meristem and the region of rapid elongation because it is here that the morphogenetic movements of roots are initiated (Barlow and others 1994; Baluška and others 1996b).

Transition Zone: Specific Cytoarchitecture Enables Unique Sensory Status

Before beginning a cytoskeletal characterization, we performed a morphometric study of the cells within maize root apices. Unexpectedly, a unique isotropic growth phase of the cells, beginning immediately after cessation of mitotic divisions and ending at the onset of rapid cell elongation was discovered (Baluška and others 1990, 1994, 1996a; Jacobs 1997; Figure 1). A number of data suggest that this 'transition zone' of the growing root apex is some kind of sensory zone, enabling the growing apex to continuously monitor diverse environmental parameters and to effect appropriate responses (Baluška and others 1994, 1996a). For example, cells of the transition zone are very sensitive to touch and extracellular calcium (Ishikawa and Evans 1992; Baluška and others 1996d), to gravity and auxin (Ishikawa and Evans 1993, 1995; Baluška and others 1996b; Kollmeier and others 2000), water and salt stresses (Sharp and others 1988; Samarajeeva and others 1999; Winch and Pritchard 1999; Wu and Cosgrove 2000), as well as to aluminum (Sivaguru and Horst 1998; Sivaguru and others 1999, 2000; Kollmeier and others 2000). Moreover, root cells acquire architecture of transition zone cells during symbiotic interactions with *Rhizobium* bacteria (Yang and others 1994; Timmers and others 1999) and fungal symbioses Barker and others 1998).

The transition zone is critical with respect to the "steering" of root extension, enabling the advancing root tip to "navigate" towards nutritionally rich areas of soil and to avoid unfavorable areas. This is because the traversal through the transition zone, as well as the subsequent sudden onset of rapid cell elongation (Ivanov and Maximov 1999), can be regulated via external signals and internal cues. Traverse through the transition zone is often accomplished in a differential way across the diameter of the root, for example by accelerated elongation in the upper part relative to the lower part of gravicurving root apices (Barlow and Rathfelder 1985; Ishikawa and others 1991; Zieschang and Sievers 1991; Baluška and others 1996b; Ishikawa and Evans 1995, 1997; Mullen and others 1998). Besides gravity, root growth direction and intensity are modulated by other environmental parameters including moisture, temperature, ion concentrations, soil compactness, as well as biotic factors (reviewed by Baluška and others 1994; Barlow and Baluška 2000). Here again, the speed with which cells traverse the transition zone determines how quickly root apices can pass through regions of soil that might be unfavorable for growth. For instance, salt stress can stimulate the passage of postmitotic root cells towards the elongation region, allowing rapid extension of root apices (Samarajeewa and others 1999). Similar responses can be induced by inhibition of peptidyl-prolyl hydroxylase which supports maturation of cell wall glycoproteins extensins and arabinogalactan-proteins (De Tullio and others 1999). Interestingly, cell walls within the transition zone and the apical part of the elongation region of maize root apices are extremely sensitive to acidification which stimulates cell elongation (Winch and

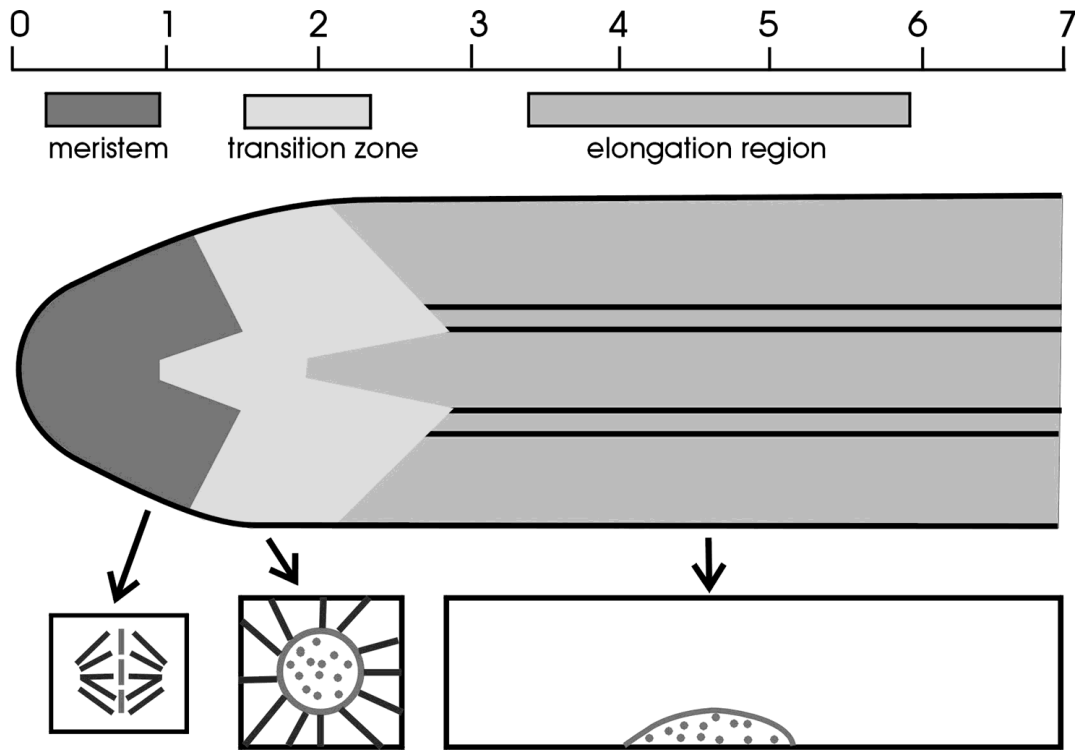

Figure 1. View of the major growth regions of the maize root apex. The apical meristem (dark-shaded field) consists of dividing cells which then first enter the transition zone (light-shaded field) and then the elongation region (medium-shaded field). Note that each of these growth regions is characterized by a unique cytoarchitecture (see arrows): dividing cells assemble mitotic spindles, transition zone cells (defined as all postmitotic cells having their width/length ratio below 1:2) support round nuclei by perinuclear radiating MTs, elongating cells show elongated nuclei (the nuclear form follows the cell form) appressed to side walls. Cortical MTs are not shown in this highly schematized view of cellular architectures. The scale on the top is in mm.

Pritchard 1999; Wu and Cosgrove 2000), and their cells maintain growth even under severe water stress (Sharp and others 1988; Saab and others 1990; Pritchard and others 1993). Moreover, these cells also show the highest activities of xyloglucan endotransglycosylase, which cleaves xyloglucan chains (for maize roots see Pritchard and others 1993; for *Arabidopsis* roots see Vissenberg and others 2000).

How do growing root apices sense these environmental parameters? An attractive possibility is that a specific cytoarchitecture of cells in the transition zone contributes to the monitoring of environmental signals. The unique status of the transition zone cells is characterized by active cell bodies consisting of centered nuclei surrounded by MTs and AFs (Baluška and others 1997a, 1997c, 1998, 2000c, 2001; Figure 1). In contrast to the mitotically active cell bodies of meristematic root cells, which are continually assembling and disassembling mitotic spindles (for example, see Baluška and others 1996c, 1998), centered cell bodies in the transition zone (Figure 1) are not engaged in such activities and hence, are free to pursue new activities, such as environmental sensing (Baluška and others 1998, 2000a,b,c). In fact, cell body MTs are organized between the nuclear surface, which contains MT-organizing centers (Lambert 1995), and the plasma membrane. This organization enables MTs to convey signals between the cell periphery and nucleus (for example, see Albrecht-Buehler 1998). During cell elongation, cells become filled with vacuoles and the metabolically less active nuclei become appressed against the cell walls (Figures 1, 2B). This inactive configuration of the plant cell body (Baluška and others 1998; Figure 1) does not allow efficient interactions with environmental signals and developmental cues. However, if such cells are restored to their meristematic activity as, for example, during lateral root formation (Figure 2C) or after wounding (for maize roots, see Mews and others 1996), then active plant cell bodies form again, manifested by the centering of the nuclei and the resumption of mitosis. Another good example of this feature is activation of root cortex cells in anticipation of receiving infective Rhizobium bacteria (see, for example Yang and others 1994; Timmers and others 1999).

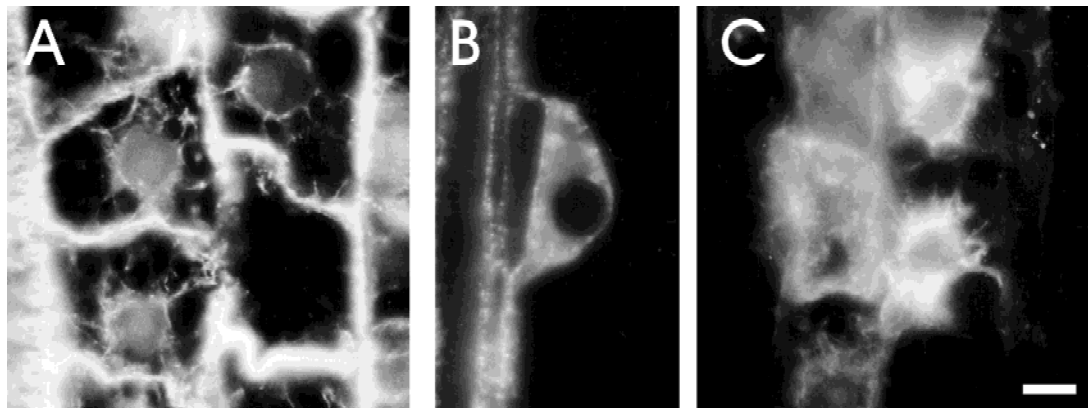

Figure 2. Perinuclear radiating MTs in cortical cells of the transition zone (**A**), metaxylem cells of the elongation region (**B**), and premitotic pericycle cells (**C**) during lateral root primordia initiation in a non-growing root portion behind the elongation region. Bar = 10 μm for **A** and **C;** 15 μm for **B.**

The root cap statocytes are postmitotic cells that represent a special type of sensory tissue whose cytoarchitecture allows effective mechanosensing (Sievers and others 1991; Baluška and Hasenstein 1997; Baluška and others 1997d; Driss-Ecole and others 2000; Volkmann and others 1999; Volkmann and Baluška 2000; Yoder and others 2001). This is the basis for gravity perception by growing root apices (Sack 1991; Blancaflor and others 1998; Tsugeki and Fedoroff 1999; Volkmann and Baluška 2000). The root cap statocytes correspond developmentally, and partially also structurally, to the cells of the transition zone. Therefore, it is not surprising that cells of the transition zone might participate in gravisensing (reviewed by Baluška and others (1994).

Transition Zone: Growth Polarity is Driven by Cortical Microtubules

Maize root cells that have ceased mitotic divisions continue to expand laterally and longitudinally throughout the transition zone. This unique postmitotic cell growth terminates with the onset of rapid cell elongation (Baluška and others 1990, 1994). After passing this critical switch-point, the cellular root-growth machinery is focussed solely on rapid and polarized cell elongation. In fact, the elongation region literally pushes the root apex forward through the soil. MTs densely arranged within the cytoplasmic cortex of the cell are considered to be responsible for determining plant cell growth polarity (Giddings and Staehelin 1988), although the actual mechanism of how the cortical MTs determine the orientation of nascent cellulosic microfibrils, and thus cell growth polarity, remains a mystery. In general there is little, if any, correlation of cellular growth rate with MT density and/or orientation. Nevertheless, data from maize root apices document tight relationships between the progressive realignment of cortical MTs into transverse arrays in the transition zone and the concomitant restriction of cellular expansion into polarized elongation (Baluška and others 1992, 1993b, 1993c; Blancaflor and Hasenstein 1993, 1995b).

Analyses of MTs in root cells deficient in gibberellic acid (Baluška and others 1993b) or in root cells exposed to ethylene (Baluška and others 1993c) have provided good examples that cortical MTs determine the cell growth polarity specifically within the transition zone. In this location, cells of the inner cortex proved to be very sensitive to ethylene to the extent that their MTs became randomized. In contrast, cortical MTs in cells of the outer cortex were much more resistant to ethylene treatments. Morphometric analysis of ethylene-treated root apices revealed that, whereas the inner cortex cells switched to isotropic growth and hence reached larger final cell sizes than usual (Table 1), those of the outer cortex retained their anisotropy (Baluška and others 1993c). These ethylene responses mimic natural growing situations, for example, when extending root apices grow through compacted soil (Atwell 1990; Croser and others 2000) or within rock fissures (Zwieniecki and Newton 1995). Such root apices develop high ethylene levels inducing their cortical cells to expand radially. The swelling of the root apex generates considerable lateral forces that eventually succeed in opening up space within compact soil for further root extension.

Numerous studies, both descriptive and experimental, have documented a close spatial relationship between the orientations of the cortical MTs

Table 1. Effects of Pharmacological and Ethylene Treatments on Final Volumes of Cortical Cells

Treatments	Volumes %
Control	100
Latrunculin B 6h	91
Latrunculin B 2+ 12h	58
Butanedione monoxime 6h	81
Butanedione monoxime 24h	55
Taxol 24h	46
Colchicine 4h	104
Colchicine 8h	129
Colchicine 14h	100
Oryzalin 4h	103
Oryzalin 8h	142
Oryzalin 14h	98
Ethylene 1ppm	140
Ethylene 10ppm	150

Note that the anti-actomyosin drugs, latrunculin B and butanedione monoxime, as well as the stabilization of MTs by taxol, decrease final cell volumes, whereas MT-depolymerizing drugs (oryzalin, colchicine) and long-term ethylene treatments (24 h) increase final cell volumes. For details of treatments, see Baluška and others (1993c, 1995, 1997b, 2000d); Šamaj and others (2000).

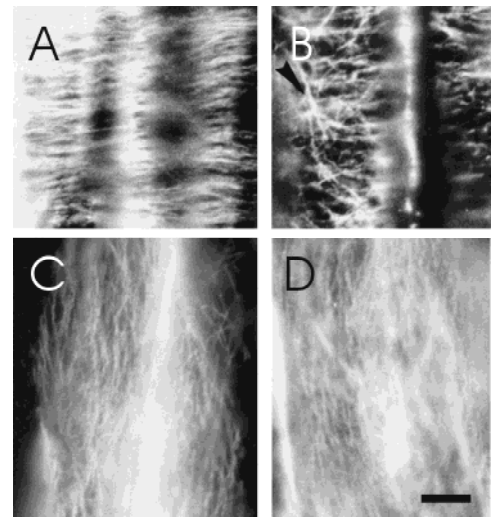

Figure 3. Cortical MTs in cortex cells located in the middle part of the elongation region in control roots (**A**), and in corresponding cells after exposure to an electric field (0.5 V/cm) for 30 (**B**), 60 (**C**), and 120 (**D**) minutes. For the technical details on the application of the electric field, see Stenz and Weisenseel (1993). Bar = 8 µm.

and the nascent cellulosic microfibrils that determine the polarity of plant cell growth. A few other studies have nevertheless suggested that these MT/microfibril relationships may be less tight than was considered previously (for example, see Hauser and others 1995; Baskin and others 1999; Wenzel and others 2000; Wasteneys 2000). Unfortunately, the timescale of responses with respect to the sequential reorientations of cortical MTs, nascent cellulose microfibrils, and growth remains unknown. In line with the observation of a lag between MT reorientation and reoriented cell growth, we have found that, although cortical MTs of elongating cells of maize root apices reorient from transverse to longitudinal arrays within the first hour of an exposure to an electric field (Figure 3), the orientation of cell growth did not change for at least 6 h. A converse situation may also apply where polar growth patterns are apparently reestablished, but MT patterns are still shifting. For example, microsurgical removal of maize root caps resulted in a disturbance to the normal distributions of cortical MTs throughout the apices. The altered arrangements persisted for more than 4 days, even when a new cap had regenerated and the cell growth patterns had returned to normal (Barlow and Parker 1996).

Transition Zone: Actomyosin-Based Forces and Switch Into Rapid Cell Elongation

A switch in cell growth polarity and accelerated root cell elongation are two events accomplished within the transition zone of maize root apices. In contrast to the isotropy of growth in the transition zone, related to the arrangement of cortical MTs and nascent cellulosic microfibrils, the speeding up of cell growth during the change to anisotropy (Kubica and others 1991; Ivanov and Maximov 1999) depends on actomyosin-based forces (Baluška and others 1997c, 2000c, 2001a; Šamaj and others 2000; Volkmann and Baluška 1999). Intriguing in this respect is the finding that cells of the transition zone assemble unique configurations of actin filaments (AFs) that are organized by the surfaces of the still centrally positioned postmitotic nuclei and the actin/myosin VIII-enriched cross-walls (Baluška and others 1997c, 2000c; Figure 4). The AFs are especially prominent in cells of the stele periphery and the cortex/stele interface where they assemble into morphologically unique bundles (Figure 4). Possibly, the cells in these tissues represent some kind of 'plant muscle' which is important for the switch into rapid cell elongation. Root cells made devoid of F-actin for 6 h and longer become effectively locked within the transition zone and do not execute rapid cell elongation, even though mitotic divisions and cytoplasmic expansion continue in the meristem and transition zone (Baluška and others 2001a). As a result, both the transition zone and former elongation region are characterized by small cells whose lengths are similar to their widths. Long-term treatments with latrunculin B even induce seedling dwarfism, which resembles a bonsai effect, or an

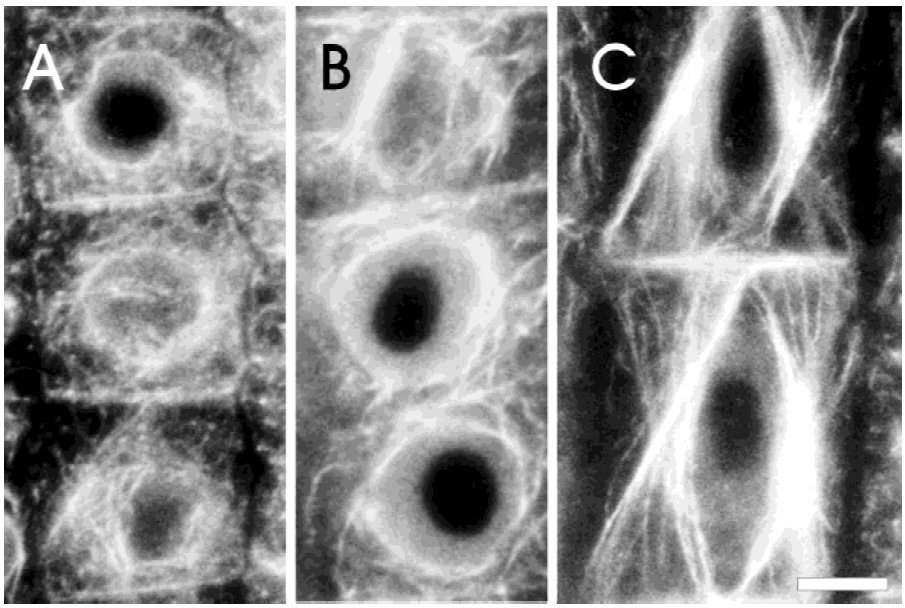

Figure 4. Perinuclear AFs in pericycle cells within the proximal part of meristem (**A**), distal part of the transition zone (**B**), and proximal part of the transition zone (**C**). Bar = 8 μm.

alpine plant form. Interestingly, experimental disturbances to the actin dynamism via underexpression and overexpression of actin-binding profilin (Gibbon and Staiger 2000) inhibits polarized cell elongation in *Arabidopsis* seedlings (Ramachandran and others 2000). Moreover, profilin is strongly expressed in a ring of cells corresponding to the transition zone of *Arabidopsis* root apices (see Figure 6E in Ramachandran and others 2000; Figure 1 in Ishikawa and Evans 1997; and Figure 3 in Mullen and others 1998). All this is in line with the hypothesis that critical F-actin-related events are essential for the onset of rapid cell elongation (Baluška and others 1997c; Volkmann and Baluška 1999; Baluška and others 2000c, 2001a).

Disturbances to the actomyosin cytoskeleton increase the number of cells within the transition zone (Table 2). Similarly, the time spent by cortical cells in the transition zone can be modulated by root cap mucilage and extracellular calcium levels (Baluška and others 1996d). These data support the hypothesis that the passage of cells through the transition zone can be modulated by calcium-related extracellular signals generated in root caps which in turn affect the actin cytoskeleton as well as targets within the cell walls. These data suggest that the transition zone represents some sort of cellular reservoir for the nearby elongation region, a feature that is critical for the control of root growth. In accordance with this concept, recent data obtained from *Arabidopsis* root apices indicate that root growth rate is determined by the rate at which apical root regions supply the elongation region with new cells (Beemster and Baskin 2000). As a consequence, environmentally regulated numbers of cells and their behaviors in the meristem and transition zone could regulate root growth by means of a controlled release of cells to the elongation region. Thus, root extension could be accelerated or delayed according to the impact of environmental conditions on the transition zone cells. Furthermore, if the supply of new elongation-competent cells is asymmetric, as a result of asymmetric environmental signals, then root curvature results, allowing efficient steering of extending root apices towards the source of the asymmetry (for gravitropism see, for example Barlow and Hofer 1982; Baluška and others 1996b; Ishikawa and Evans 1997; Mullen and others 1998). We suggest that the environment-sensitive transitional phase of cellular development, which is ac-

Table 2. Effects of Latrunculin B (10^{-6} M), Cytochalasin D (25 μg ml^{-1}), and Butanedione Monoxime (10^{-3} M) on the Mean Number (±s.e.) of Cortical Cells Along the Length of Cell Files Within the Transition Zone

Treatments	Cells
Control	24 ± 1
Latrunculin B	45 ± 2
Cytochalasin D	41 ± 2
Butanedione monoxime	49 ± 2

Postmitotic cortical cells having their width/length ratio below 1:2 (Form Factor values <7, see Baluška and others 1990, 1994) were considered as cells of the transition zone. All drugs were applied for 6 h. For details of treatments, see Baluška and others (1997c, 2000d); Šamaj and others (2000).

complished within the transition zone, allows growing root apices to monitor the environmental parameters and to navigate their extension towards nutritionally rich and moist soil regions. This 'steering' ability of growing root apices allows them to populate soil in an opportunistic fashion.

The observations mentioned above, based on long-term latrunculin B treatments (Baluška and others 2001a), suggest that F-actin-driven cell elongation is a luxury event performed only in a permissive environment. In accordance with this notion, there is a common response to different stress conditions, such as cold, osmotic and water stress, or ionic imbalances, which involves an inhibition of rapid cell elongation. By contrast, slow cellular growth within the meristem and transition zone is relatively resistant to such stresses (Sharp and others 1988; Pritchard and others 1988, 1990, 1993; Saab and others 1992; Baluška others 1993a, 1996d). Moreover, the progressive dessication of maturing embryos is associated with the locking of cells into a developmental phase that corresponds to that of the transition zone cells of root apices. Mature bean embryos are devoid of actin and regain actin only during embryo germination, in parallel with the onset of rapid cell elongation (Villanueva and others 1999). Again, the mature embryo can be considered to be a reservoir of elongation-competent cells whose complement of F-actin is critical for the switch to rapid cell elongation.

The first response by roots to depolymerization of their MTs is the opposite of that characteristic of the absence of F-actin, that is, the final cell volumes exceed those of untreated root apices (Table 1). This finding indicates that cortical MTs, together with cell walls, might actually restrict root cell growth. On the other hand, long-term absence of cortical MTs in root cells prevents any anisotropic growth and hence morphogenesis, transforming the root apex into a clump of apolarly enlarging cells (see, for example Figure 2 in Hasenstein and others 1999). The mechanisms behind the larger final sizes of cells made devoid of MTs are unclear at present, but it is worth mentioning that depolymerization of MTs activates calcium channels of the plasma membrane (Thion and others 1998). Moreover, depolymerization of MTs induces decondensation of nuclear chromatin and activation of DNA/RNA synthesis (Baluška and Barlow 1993; Baluška and others 1995). On the other hand, taxol-mediated stabilization of MTs has exactly the opposite impact on nuclear structure while cell growth becomes restricted (Baluška and others 1997b) (Table 1).

Transition Zone: Pectins Affect Cellular Shapes and Cytomorphogenesis

Plant organ polarity is closely related to the properties of the cell walls (Fowler and Quatrano 1998; Wojtaszek 2000) and to localized secretion towards certain wall sites (Belanger and Quatrano 2000). The mechanical robustness of the plant cell wall constrains expansion of the cytoplast (Pickett-Heaps and others 1999), and thus cell walls not only set, but also maintain, the growth polarity of plant cells. Intriguingly, root cells of the *lilliputian* mutant of maize (Dolfini and others 1999) show aberrant cell shapes, lack rapid cell elongation, fail in their cell-to-cell adhesion (Dolfini and others 1999), and have lesions in the organization of the actin cytoskeleton (Baluška and others 2001c). These phenotypic features closely resemble those of the *emb30/gnom* mutation of *Arabidopsis* that have been shown to be associated with aberrant distributions of the auxin efflux carrier PIN1 (Steinmann and others 1999) and defects in pectin distributions in cell walls (Shevell and others 2000). Occasionally, rather unusual shapes and impaired cell adhesion are features characteristic of roots growing in aqueous and low oxygen environments, for example, in certain cortical cells participating in aerenchyma formation (Seago and others 2000; Gunawardena and others 2001).

Our preliminary data suggest that cell wall acidic pectins undergo internalization in meristem and transition zone cells of maize root apices (František Baluška, David McCurdy, Jozef Šamaj, submitted). This novel phenomenon might be related to the loosened state of the cell walls in these developmentally plastic regions of the root apex. Loosened cell walls seem to be actively maintained because of the ability of meristematic and transition zone cells to retrieve acidic pectins that would otherwise stiffen the cell walls via cross-links with calcium (McCann and others 1990; Carpita and Gibeaut 1993). In accordance with the importance of cell wall pectins for cell growth and polarity, genetic interference with pectin metabolism results in aberrant cell shapes, chaotic cell division planes, and lesions in cell growth polarity throughout the root apex (Wen and others 1999). Preliminary data suggest that the primary lesion in *emb30/gnom/lilliputian* mutants might be related to the endocytosis/recycling machinery at the plasma membrane affecting auxin flow (Steinmann and others 1999) and cell wall pectin distributions (Shevell and others 2000; František Baluška, David McCurdy, Jozef Šamaj, submitted).

Transition Zone: Changes in Cell Wall Properties and Cytoskeletal Arrangements Drive New Polarity During Root Hair Initiation

Recently, we documented the relevance of cell wall properties for the induction of a new growth polarity during root hair formation (Baluška and others 2000b). In this process, a distinct cell wall domain of specialized root epidermis cells (trichoblasts) becomes thinner. The localized point of weakness in the outward-facing cell wall of the trichoblast is accompanied by randomization of cortical MTs. The challenge of high turgor pressure leads to an outgrowing bulge that precedes the formation and growth of the hair tip (Baluška and others 2000b). Activation and accumulation of cell wall loosening expansins (for example, see Cosgrove 1998) within the bulge appear to participate in this process (Baluška and others 2000b). Maize root trichoblasts are unique in that they form outgrowing bulges while the rest of the trichoblast is still elongating. Therefore, the new polarity of the hair tip growth is perpendicular to the still active polarity of trichoblast elongation. In addition, tubulin-dependent polarity of the cell elongation (diffuse cell growth) is replaced by actin-dependent polarity of the tip growth. One possibility is that the loosened cell wall domain at the bulge, when challenged by internal turgor pressure, is perceived as some kind of wound site and the affected cell then mobilizes all available resources to strengthen this weakened cell periphery domain via dynamic F-actin meshworks and targeted exocytosis (Baluška and others 2000b).

Dynamic F-actin meshworks are critical for the switch from bulge outgrowth to root hair tip growth (for maize see Baluška and others 2000b). On the other hand, local loosening and bulging of the cell periphery domain is independent of F-actin. Later, however, the bulging domain accumulates F-actin as well as the actin-binding proteins, actin depolymerizing factor and profilin, both of which are known to drive cycles of actin polymerization and depolymerization (Jiang and others 1997; Baluška and others 2000b; Gibbon and Staiger 2000). These findings indicate that root hair formation involves not only a change in cell polarity, but also a switch in the state of the cytoskeleton.

A special feature of maize root apices, which clearly distinguishes them from root apices of *Arabidopsis,* is the ability of all epidermis cells to form root hairs. But whether or not root hairs form is dependent upon environmental situations. Therefore, root hair formation in maize necessitates a sensing step preceding molecular switches that initiate bulge formation. That trichoblasts embark upon their trichogenic pathway within the transition zone suggests that the putative sensing step must be localized in this root zone too. This feature is fully in accordance with the proposed sensory status of cells in the transition zone.

Outlook

Although our review has focused on maize root apices, preliminary studies indicate that data obtained from maize roots are applicable to root apices of other plants like *Arabidopsis* (Ishikawa and Evans 1997; Mullen and others 1998; see also Figure 1 in Jacobs 1997). For instance, the *STUNTED PLANT1* gene of *Arabidopsis* seems to be responsible specifically for rapid cell elongation because the first 500 µm of root apices in *Arabidopsis,* representing both meristem and transition zone (see Figure 1 in Ishikawa and Evans 1997), are unaffected by the *stunted plant1* mutation (see Figure 2A in Baskin and others 1995). On the other hand, *ROOT MERISTEMLESS* (*rml*) genes are responsible for the maintenance of apical root meristem during postembryonic development (Cheng and others 1995). Unfortunately, other genes relevant for the control of coordinated growth processes within different zones of root apices still await indentification. Much more is known on shoot apices where the *CLAVATA1,2,3* genes restrict stem cell numbers cooperating with the *WUSCHEL* and *POLTERGEIST* genes which maintain stem cell populations (Clark and Schiefelbein 1997; Mayer and others 1998; Schoof and others 2000; Brand and others 2000, 2001; Yu and others 2000). It is conceivable that, in root apices, similar genes maintain interrelationships between meristem and adjacent growth zones.

We propose that cellular development within the transition zone of the root apex is similar to other apically growing plant organs (see also Jacobs 1997). In this respect, the *NAP* gene of *Arabidopsis* appears relevant because it is essential for cell transition to rapid cell elongation during flower formation (Sablowski and Meyerowitz 1998). *NAPs* belong to a large gene family expressed in all plant organs, suggesting that their putative roles in the developmental transition from slow cytoplasmic cell expansion to rapid vacuome-based cell elongation might be critical for overall plant development and morphogenesis. In accordance with this notion, other genes expressed specifically at the basal boundary of the apical meristem are presently being discovered in shoot apices (Aida and others 1997, 1999; Zondlo and Irish 1999; Vernoux and others 2000).

In maize root apices, cells of some tissues, such as the xylem parenchyma, begin elongation almost immediately after exit from the meristem (Baluška and others 1990). However, adjacent xylem cells perform two or three endocycles before initiating rapid elongation (Barlow 1985; Baluška 1990). Similarly, cortex and epidermis cells show a prominent transition zone composed of around 25 cells in each longitudinal cell file. It is a challenge for future studies to identify other genes that determine unique cellular behaviors within the transition zone of both root and shoot apices, because this zone seems to hold the 'key' for plant development.

Note Added in Proof

Recent report by Schindelman and others (Genes Dev 15: 1115-1127, 2001) shows that root cells of COBRA mutant of Arabidopsis fail in establishing longitudinal, with respect of root axis, polarity in the transition zone and root cells continue in their radial expansion. Interestingly, the COBRA gene is expressed specifically in the transition zone cells (see Fig. 4 in Schindelman and others 2001).

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