The architecture of polarized cell growth: the unique status of elongating plant cells

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Summary

Polarity is an inherent feature of almost all prokaryotic and eukaryotic cells. In most eukaryotic cells, growth polarity is due to the assembly of actin-based growing domains at particular locations on the cell periphery. A contrasting scenario is that growth polarity results from the establishment of non-growing domains, which are actively maintained at opposite end-poles of the cell. This latter mode of growth is common in rod-shaped bacteria and, surprisingly, also in the majority of plant cells, which elongate along the apical–basal axes of plant organs. The available data indicate that the non-growing end-pole domains of plant cells are sites of intense endocytosis and recycling. These actin-enriched end-poles serve also as signaling platforms, allowing bidirectional exchange of diverse signals along the supracellular domains of longitudinal cell files. It is proposed that these actively remodeled end-poles of elongating plant cells remotely resemble neuronal synapses. *BioEssays* 25:569–576, 2003. © 2003 Wiley Periodicals, Inc.

Introduction

Physical forces shape our world. Hence, a sphere is the default shape for all cells. "Trypsinized" animal cells detached from their substratum, as well as fungal and plant protoplasts released from their surrounding walls, all are almost perfect spheres. However, most living cells do not conform to this apolar state but build some characteristic alternative shape by a process known as cytomorphogenesis.[(1–4)] Although the details of their interactions may vary between different groups of organisms, dynamic arrays of cytoskeletal elements, which are able to read external and internal cues and to interact with membraneous and exocellular matrix (ECM) molecules, are crucial in conferring the property of cellular polarity in all eukaryotic cells. Here, we compare the major regulatory principles and strategies that govern both the establishment and maintenance of cellular polarity in organisms ranging from simple prokaryotes to complex multicellular eukaryotes. The outcome of our comparison indicates that the mode of polarization of most plant cells deviates from that of the eukaryotic mainstream and bears some resemblance to the strategy adopted by rod-shaped bacteria in the polarizing of their cells.

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Polarity is an inherent feature of cellular life

Polarity is understood as the ability of cells to organize their interiors and their external forms so that the physical tendency for spherical symmetry of the cell is broken and, as a first step, a new, cylindrical symmetry is established. Such cells now have the ability to grow differentially, either at their ends or along their sides. However, such a situation, although often loosely referred to as polarity, is really no more than unidirectional growth. A true polarity comes about when one end of the cylindrical cell differs from the other, just as the North and South poles of a bar magnet differ in the polarity of the magnetic flux. For instance, neurons are polarized cells, with dendrites acting as "entry ports" and axons as "output" channels for signaling molecules, specialized for rapid cell-to-cell communication. In higher plants, elongating plant cells are also polarized as one end of their end-poles shows an efflux whereas the opposite end shows an influx of signaling molecules like ions and the phytohormone auxin.[(5)]

Cell polarity is often reinforced by a cytoskeleton that integrates cellular space. Directional or polarized growth is also modulated by biotic and abiotic signals, which lead to the assembly and disassembly of cytoskeletal elements through their altered interactions with membraneous compartments of the cell. Besides having a dynamic cytoskeleton,(for plants see Refs. 6–10) most cells also rely on mechanically stable, yet chemically interactive exocellular matrices for the maintenance of diverse cell shapes. (for plants see Refs. 11,12)

Both cytoskeleton and ECM are dynamic supramolecular structures whose capacity for self-organization[10,12–16] allows signal-mediated self-polarization of the cytoarchitecture.[17] These observations indicate that cytoarchitecture, although dependent upon genomic information, is also inherently endowed with information for its own autoregulated construction.[2,18] Certain studies on bacteria, which suggest that polarity generates polarity,[19] reinforce this idea.

For a long time, the origin of the eukaryotic cytoskeleton has been an evolutionary puzzle. However, recent discoveries of cytoskeletal proteins within the rod-shaped bacteria[20,21] seem to fill one of the major gaps in understanding the evolution of both the cytoskeleton and eukaryotic cells. It is now possible to make informed comparisons of how the diverse ontogenies of cell shaping came into being and how these, in turn, led to diverse cellular and even organ morphologies. It is, however, important to remember that, within the topic of cell theory, the relative contributions of genetic and epigenetic inputs into the shaping of cells remain a controversial issue.[2,14,18,19,22,23]

Acquisition and maintenance of polarity: walled cells versus naked cells

What might be the principal structural elements that govern growth polarity, and how can they contribute to the various types of growth polarity? To answer this, we shall first consider the fundamental difference between walled and naked cells. In walled cells, like those of bacteria, yeast, fungal and almost all plant cells, an ECM is an integral part of the cell.[9,12] In contrast, although animal cells interact dynamically through their ECMs, these structures are associated with localized areas at the cellular surface, usually at focal adhesions. Thus, animal cells are, for the most part, naked. These two major types of cellular organization represent alternative approaches to the problem of maintaining the homeostasis of intracellular chemistry, and have an immediate bearing on cell growth and the acquisition of cellular form (for plants see Ref. 11).

In naked cells, morphogenesis and polarized growth are the result of variable interactions between different types of cytoskeletal structures as well as between cytoskeleton and ECM, operating with and upon a boundary membrane.[4,24] In walled cells, the major driving force for cellular shaping comes from an intracellular turgor pressure. The acquisition of a particular cell shape results ultimately from a precisely defined distribution of the mechanical properties of different wall domains upon which turgor operates to cause differential wall expansion. The growth of walled cells is essentially irreversible[11,12] due to the stiffening of previously expanded areas whereas the growth of naked cells is usually reversible due to the continually dynamic nature of their boundary. Each of these two modes of cell shaping calls for different sets of cytoskeletal interactions. In plants, the cytoskeleton influences growth polarity mainly indirectly, by controling the direction of exocytic and endocytic[25] events, which, in turn, affect the composition and mechanical properties of the surrounding matrix. Crucially, the cytoskeleton also determines the orientation of wall cellulosic components.[9,10,12] It should be remembered, however, that, although the dynamic cytoskeleton integrates cellular organization, the cell also molds the cytoskeleton.[2] A similarly reciprocal relationship exists between cytoskeleton and ECM. For example, the plant ECM can affect the orientation of microtubules within the cell cortex.[12] This ECM–cytoskeleton interrelationship, although less obvious, can also be seen in animal cells.[4]

Growth polarity in diverse groups of organisms: an overview

Polarly growing rod-shaped bacteria define preferentially non-growing domains

Bacteria lack membranous organelles and vesicles and their growth is performed by a localized coincident translation and insertion of proteins into peptidoglycans of their walls.[18,19] Nevertheless, they are able to establish polarized organization of their interior.[18,19,26] An important feature of rod-like bacteria is that new proteins are not inserted into the limiting membrane at the non-growing end-poles[19] (Fig. 1). Recent

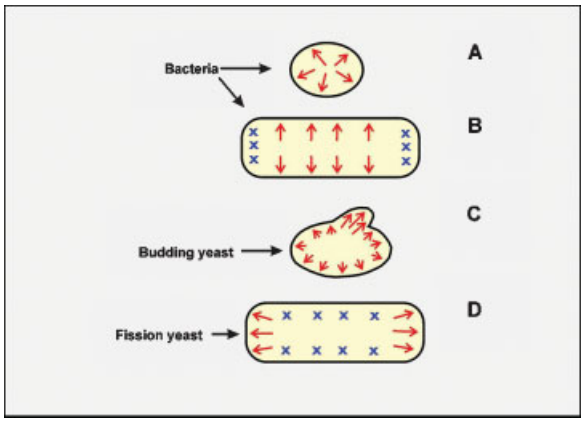

Figure 1. Shaping of cells in prokaryotes and unicellular eukaryotes. **A:** Spherical bacteria grow over their whole surface (as indicated with red arrows). **B:** Rod-like bacteria define non-growing end-poles (blue crosses) while the rest of their periphery grows uniformly. **C:** Budding yeast alternate, in a cell-cycle-dependent manner, between a phase when the whole periphery is growing (interphase) and a phase when a distinct domain is assembled, which recruits exocytic vesicles to produce new bud (mitosis, cytokinesis). **D:** The polarity of fission yeast is just the opposite to bacterial polarity. Only the end-poles grow while the rest of the cell periphery is non-growing. Red arrows indicate the sites (but not necessarily polarity) of growth, blue crosses mark the non-growing sites.

breakthrough data have revealed that these rod-shaped bacteria are equipped with actin-like MreB and Mbl proteins, which form filamentous assemblies under their limiting membrane.[20]

Subcellular localization of MreB protein revealed its accumulation at the non-growing end-poles[20] where their dense submembraneous assembly apparently prevented insertion of new proteins into their limiting membrane, and hence maintained the inert non-growing property of the end-poles.[19] A nonlethal point mutation in *mreB* resulted in the loss of the polarized rod-like shape due to the increased widths of the end-poles.[20] In contrast to rod-shaped bacteria, spherical (coccoid) bacteria lack these actin-like proteins.[20]

These non-growing end-poles of rod-shaped bacteria define the direction, or polarity, of cell growth since it is only between these two ends that membrane material can be inserted (intercalated) resulting in the polar extension of the cell.[2,19] A surprisingly analogous situation occurs in elongating higher plant cells where two non-growing, or only weakly growing, end-poles define and maintain polarized cell growth. However, the non-growing end-poles of elongating plant cells are not inert but perform abundant endocytosis/recycling events (see below) that bring about their continuous remodeling and allow signaling.

Polarly growing yeast cells assemble growing domains

Unlike rod-shaped bacteria, both budding and fission yeast cells polarize their growth by targeting of exocytotic vesicles towards actin-enriched discrete domains,[1,27] while the rest of cell periphery grows slowly or not at all (Fig. 1). A dynamic actin cytoskeleton is essential for this cellular polarization,[1,27] but microtubules are also involved.[28,29] However, considerable incorporation of wall material into the non-growing wall of each budding yeast cell can also be observed, so it cannot be assumed that incorporation always parallels growth. One plausible explanation would be that the non-growing area is a site of intense recycling events. In higher plants there is evidence for this type of wall growth regulation also (see below).

Animal, fungal, lower plant and tip-growing higher plant cells assemble actin-based growing domains

Similar to yeast, almost all eukaryotic cells, with the exception of most elongating higher plant cells, assemble actin-enriched cell periphery domains towards which they recruit a dynamic cytoskeleton and exocytotic vesicles for local growth[30–32] (Fig. 2). This results in a situation whereby pre-existing parts of the cell continue to occupy their original location while the growing regions extend into their immediate surroundings. Intriguingly, such explorative cell growth, remotely resembling navigating neurons,[32] has also been recognized in higher plants. Two specialized cell types, namely pollen tubes and root hairs, have been studied extensively in this respect.(for reviews see Refs. 8,33) An unique feature of this so-called tip growth is that the actin cytoskeleton is essential both for polarity and growth per se.[34,35]

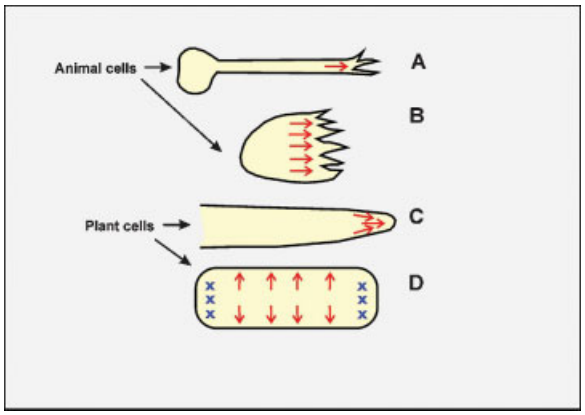

Figure 2. Shaping of cells in multicellular eukaryotes. **A:** One of the most extreme example of polarized animal cells are neurons, which are composed of non-growing cell bodies, harbouring nucleus, and growing cones. **B:** Motile animal cells, like fibroblasts, are highly polarized with growth domains restricted to the advancing edge. **C:** Tip-growing fungal and lower plant cells—root hairs and pollen tubes of higher plants are also included—grow only at their very tips while the rest of these cells is non-growing. This results in the characteristic tubular shapes of these cells. **D:** Elongating higher plant cells are unique among all eukaryotic cells because their polarity is based on defining non-growing end-poles while the rest of their periphery grows uniformly. Consequently, elongating plant cells resemble rod-like bacteria (Fig. 1B) in the shaping of their cells. However, in contrast to end-poles of rod-shaped bacteria, these non-growing end-poles of elongating plant cells are not inert but perform remodeling mediated via abundant endocytosis/recycling events. Red arrows indicate sites (but not necessarily polarity) of growth, blue crosses mark non-growing sites.

Elongating higher plant cells define actin-based non-growing domains

As in other walled cells, axial growth of elongating higher plant cells results from an interplay between internal turgor and mechanical properties of the walls with active participation of cytoskeletal elements.[36] However, most elongating higher plant cells differ fundamentally from all other eukaryotic cells, but superficially resemble prokaryotic bacteria, in that their polarity is marked out by a pair of non-expanding domains at the end-poles of the cell surface (Fig. 2). At the subcellular level, these end-poles are enriched with actin and depleted of microtubules.[37–41] On the contrary, the expanding lateral domains are reinforced by transverse arrays of cortical

microtubules densely underlying the plasma membrane,[9,10] which may or may not be associated with actin. The reciprocal interplay between microtubules and the cellulose-based ECM[12] leads to a transversely oriented set of microfibrils that neither limits the longitudinal turgor-driven expansion nor the further interpolation of new microfibrils into this lateral domain of the cell surface. But what molecular properties define the apical and basal, non-expanding end-poles of these elongating cells? And how are these non-growing domains maintained?

Molecular mechanisms of growth polarization in elongating plant cells: lessons from root apices

Transition growth zone of root apices is interpolated between apical meristem and cell elongation region: progressive cessation of cross-wall expansion at end-poles

Plant root apices are extremely suitable for analysis of factors determining the acquisition and maintenance of their plant-specific type of cell polarity. Root tips show clear zonation of developmental regions(for maize see Ref. 41)—an apical meristem exhibiting highly stereotyped patterns of cell divisions and an elongation region comprised of cells rapidly extending in a direction parallel to the axis of the root.[42] Interpolated between these two regions is a transition zone (Fig. 3) whose cells show a unique cytoarchitecture and which is responsive to many internal signaling systems and external cues.[41] Whereas cells in the meristem and apical part of the transition region grow diffusely around the whole of their perimeter, their end-pole portions of their perimeter (known also as cross-walls or transverse walls) progressively cease to expand in the basal part of the transition zone. In the elongation region, the end-poles do not expand.[41,42] Detailed analysis of cell growth anisotropy in maize root apices revealed that cell expansion in the longitudinal and radial directions can be regulated independently.[43]

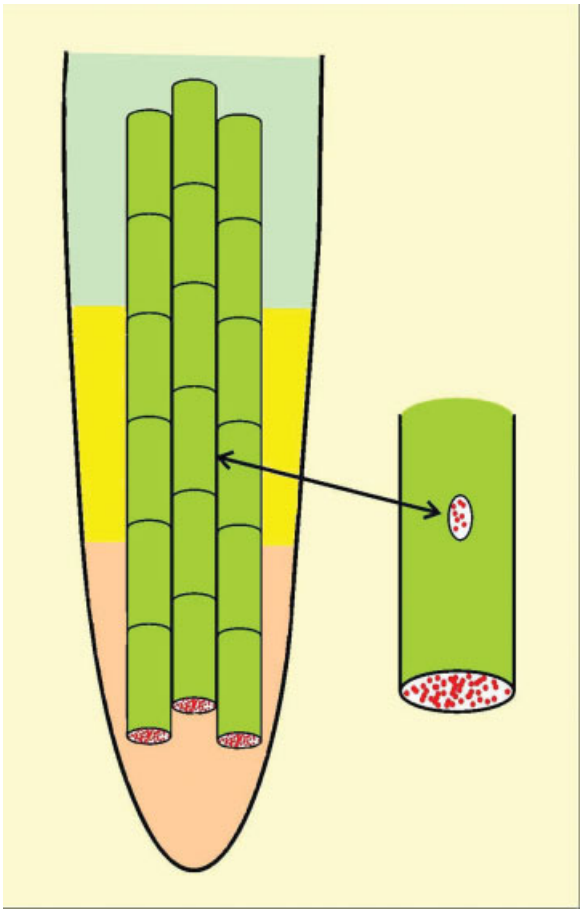

Figure 3. Plant tissues are composed of laterally interacting cell files, as schematically shown here in the example of a root apex. Pit-fields of side-walls enable lateral file-to-file communication. Apical meristem is shown in red colour, the transition zone is yellow, and the elongation region, where the axial cell elongation is accomplished, is depicted in blue colour.

Active maintenance of non-growing end-poles: cortical microtubules

The absence of any expansion of the end-poles of cells in the elongation region of the root enhances the polarization of the cells, and, as if to make certain of this polarity, the non-growing status of the end-poles is actively maintained. Evidence for this is somewhat indirect, being inferred from enlarged end-poles of *Arabidopsis* mutants, such as *fass*, *tonneau*,[44–46] *reb1-1*[47] and *spiral*,[48] all of whose cells lack cortical microtubules, suggesting that these cytoskeletal structures somehow contribute to the non-growing status of the cross-walls. In accordance with this notion, cortical microtubules are becoming depleted and even fragmented at end-poles when their expansion ceases.[39] However, analysis of two other *Arabidopsis* mutants, *rsw4* and *rsw7*, revealed that root cell polarity could be lost without any apparent alterations to the cortical microtubules underlying the side walls.[49] Although not specifically analyzed, the end-poles had obviously lost their non-growing status, as indicated by the enlarged diameters of the mutant cells.(see Fig. 1 in Ref. 49) Thus, the active maintenance of the non-growing status of end-poles in these root cells may not be determined solely by cortical microtubules. In agreement with this, cells of maize root apices can also regulate radial and tangential expansion independently of their cortical microtubules.[50]

Recent evidence suggests that the glycosylphosphatidylinositol (GPI)-anchored protein COBRA appears to be involved in the maintenance of the non-growing status of end-poles.[51]

Curiously, this protein is present specifically at side walls of elongating *Arabidopsis* root cells, but it is missing from their non-growing end-poles.

Active maintenance of non-growing end-poles: actin, myosin VIII and cell wall pectins

Altered actin dynamics, due to underexpression of profilin and overexpression of ADF, resulted not only in shorter cells but also in oblique cross-walls and twisted cell files in transgenic *Arabidopsis* seedlings.[52,53] Our own studies have revealed an extensive actin-based molecular machinery at the non-growing end-poles of elongating root cells,[6,38,41] which also show an enrichment with the plant-specific unconventional myosin of the class VIII[54] and with profilin.[55]

Intact but dynamic F-actin is essential for endocytosis-related internalization of cell wall pectins in cells of maize root apices.[25] Interestingly in this respect, T-DNA insertion into a gene encoding putative membrane-bound glycosyltransferase aberrantly reduces the pectin content in cell walls of *Arabidopsis* seedlings.[56] This is associated with enlarged end-poles and sometimes even with disintegrated cell-to-cell contacts along the cell files.

Plasmodesmata as gateable cytoplasmic channels in the end-poles: supracellular nature of plant cell files

One important feature of plant cell files is that their cells are connected via a large number of cytoplasmic channels, known as plasmodesmata, traversing their non-growing end-poles (Fig. 4). For instance, plasmodesmata are localized abundantly at the cellular end-poles of maize root apices[57] and selectively regulate the transport of proteins and RNA molecules preferentially along the root's apical–basal axis, emphasizing the supracellular nature of individual cell files and whole plants.[58] Although the number of plasmodesmata at side-walls is significantly lower,[57] cells also communicate via plasmodesmata radially. In particular, *SHORT-ROOT* gene controls radial patterning via radial cell-to-cell transport of its transcription factor.[59] Importantly, plant-specific myosin VIII and F-actin also localize to plasmodesmata of maize roots.[54,60] These gateable cell-to-cell channels are unique to plant tissues and the signals that cross them have multiple impacts on development.[58,59]

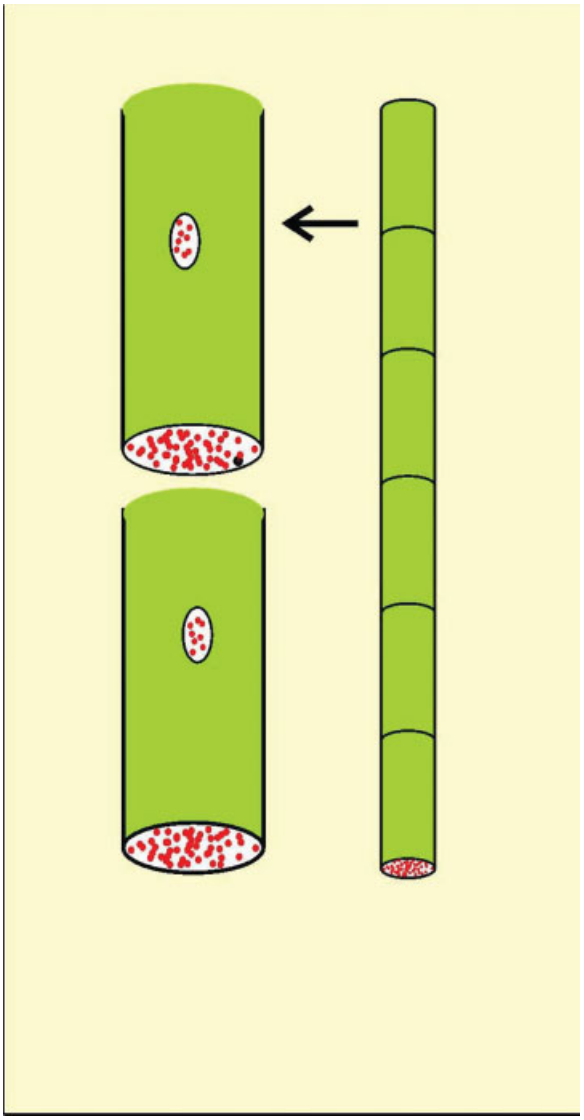

Figure 4. Elongating plant cells assemble into files. Their non-growing end-poles contain abundant cell-to-cell channels known as plasmodesmata (red dots). Growing side-walls harbour fewer plasmodesmata, clustered into pit-fields (oval structures with red dots). All these structures allow lateral file-to-file communication.

Non-growing end-poles of plant cells exhibit rapid recycling of their plasma membrane: do they represent 'plant synapses'?

Two contrasting hypotheses might clarify the non-growing status of end-poles of elongating plant cells. The first is that the plasma membrane of end-poles is not competent to accept exocytotic vesicles and this might preclude new wall assembly. This would resemble situation at the inert end-poles of rod-shaped bacteria.[19,20] However, the finding that F-actin, which is mediator of exocytotic vesicle movements, is localized at these end-poles[38,41,61] weakens this otherwise plausible idea. The second is that the actin-dependent exocytosis at the end-poles could be effectively balanced by endocytotic events, thus resulting in a remodeling of the non-growing cell periphery complex. This is exactly what seems happen at these sites.

Plant cells are equipped with the molecular machinery for performing receptor-mediated endocytosis,[62] a process

often evident at their non-growing end-poles.[63–67] The putative auxin efflux transporter PIN1 and auxin influx transport AUX1 are abundantly located at the plasma membrane of root apical and basal end-poles,[5,63–66] respectively, and are recycled between unidentified endosomal compartments and the plasma membrane.[64–67] Cell wall pectins of maize root cells (see above) seem to use the same endocytosis-based recycling pathway during their cell wall remodeling.[25] Extensive vesicle trafficking was also reported for non-growing end-poles of elongating cells of maize coleoptiles. Interestingly, inhibition of vesicle trafficking with brefeldin A[25,68] is associated with enhanced bundling of actin filaments and increased association of actin with membranes at non-growing cross-walls.[69] This might suggest that vesicle trafficking has some feedback effect upon the abundance of actin at end-poles.

The targeting of PIN1 to the plasma membrane domain at the apical end-pole of root cells is F-actin-dependent.[65,70] Intriguingly, this process also involves the protein BIG,[71,72] which shows similarity to a calmodulin-binding membrane protein involved in the synaptic transmission and phototransduction of animal neuronal tissues.[73] This finding suggests that the non-growing end-poles of elongating plant cells resemble, at least to a certain extent, neuronal synapses, which show dependence for their signal transmission activity upon abundant actin-dependent endocytosis and recycling events.[74,75] In fact, endocytosis is inherently associated with signaling.[76,77] Therefore, end-poles of elongating plant cells might be considered to represent some sort of 'plant synapses' which, via their abundant endocytosis/recycling processes, could process and transfer information along the longitudinal cell files of higher plant organs.[78]

Signaling status of end-poles: transmission of gravity and light signals from root cap to elongation region along cell files?

The signaling status of non-growing end-poles is supported by the localization there of three signaling molecules, profilin,[55] Rops[79] and photoreceptor Phot1.[80] Profilin is an actin-binding protein that integrates the dynamic actin cytoskeleton with diverse signaling cascades.[7] Rops represent a unique subfamily of Rho GTPases that are involved in the developmental transition from slow, approximately isodiametric, cell growth to rapid and strictly polarized cell elongation.[81] Phot1 is a 120 kDa plasma membrane-associated Ser/Thr photoreceptor kinase that undergoes autophosphorylation in response to blue light and is involved in phototropism via a control of differential cell elongation at opposite flanks of growing plant organs.[80,82] In root apices, both gravity and light stimuli are perceived and transduced within specialized cells of root caps[83,84] which are distal to the apical meristem, whereas elongating 'motor' cells located proximal to the meristem accomplish the auxin-mediated tropic bending.[41,42,83,84] The signals are believed to be transmitted along the intervening longitudinal files of cells. Because individual cell files extend from the root cap junction up to the end of elongation region, the non-growing end-poles of their cells might be implicated in rapid signal transmission. Besides the photoreceptor Phot1, which has been localized to cross walls of *Arabidopsis* root apices,[80] the molecules necessary for gravisensing in Characean internodal cells have also been reported to be localized at non-growing end-poles.[85] Moreover, the characteristic organization of the actin cytoskeleton within elongating cells of maize roots[38] and coleoptiles[86] is in the form of longitudinal bundles connected to individual end-poles. Activated phytochrome and auxin stimulate cell elongation and induce unbundling of these longitudinal bundles of actin filaments.[87]

The protein-phosphatase inhibitors okadaic acid and calyculin A induced drastic effects on the actin cytoskeleton (Ref. 88 and discussion there) and compromised gravitropic growth of *Arabidopsis* roots via inhibited polarity and expansion of the end-poles of their cells.[89] Similar effects on cell polarity and end-poles were induced by overexpression of Rac1-like GTPase,[90] a signaling molecule activated by auxin, which mediates auxin-responsive gene expression.

Conclusions and perspectives

One of the most characteristic features of elongating cells in higher plants is the non-growing status of their end-poles, which enables the cells to persist as lengthy files (Fig. 4). Even a single dividing cell will eventually form a cell file in vitro when exposed to a suitable hormonal environment.[91] Plant tissues are composed of many such semi-autonomous cell files (Fig. 3) and these allow the elusive factors of cytodifferentiation to travel from the older, developmentally more advanced cells towards the newly produced cells in the apical region. But conversely, signaling molecules are also transported along the cell files from the root apex towards the root base. Cell-to-cell signaling events both converge upon and emanate from the non-growing end-poles. The high density of the plasmodesmata that traverse these end-poles is no doubt part of a system designed to facilitate the relay of signals along longitudinal cell files.

The number of plant mutants and transgenic seedlings that are defective in organizing their cells into cell files is high and is likely to increase further. This gives us an excellent prospect for a deeper understanding of processes that drive coordinated cell growth polarization in higher plants. For instance, several recently characterized *Arabidopsis* mutants have unexpectedly revealed that, besides proteins, sterols are also critical not only for the organization of plant cells into longitudinal cell files but also for their coordinated elongation.[92]

In conclusion, elongating plant cells are unique amongst eukaryotic cells by localizing almost all of their microtubules at the growing domains of cell periphery, typically under sidewalls, involving them in cell polarity. This then seems to allow

the actin-based cytoskeleton to be concentrated at the non-growing end-poles and to support endocytosis/recycling events related to signal transmission along the cell files. The non-growing signaling nature of end-poles resembles cell-to-cell contacts in animal/human brains. Recently, in his thought-provoking article 'Mindless Mastery', Trewavas[93] stated that the plant 'intelligence' is remarkable despite the lack of any brain-like tissue. Data discussed in this paper allow us to speculate that the signaling end-poles of elongating plant cells can be considered to represent some sort of 'plant synapses' which could be responsible for the 'intelligent' behaviour of higher plants.[78] Indeed, future studies might reveal that higher plants may yet prove to have some degree of neural-like coordination.

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