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Viewpoints

Specialized Zones of Development in Roots: View from the Cellular Level

Recently, Ishikawa and Evans (1995) focused attention on the immediately postmitotic growth zone of plant roots and indicated its importance in root growth in response to internal and external factors. This previously unrecognized region of the root, intercalated between the apical meristem and the zone of rapid cell elongation, was originally discovered as the result of a morphometric analysis of the breadth:length ratios of cells along the length of the maize root (Baluška et al., 1990). The analysis indicated that as cells are displaced away from the root apex, their growth is adjusted in such a way that, in the immediate postmitotic region, approximately isodiametric (cuboidal) cellular shapes are obtained. Thus, the term "postmitotic 'isodiametric' growth" (or PIG) was coined for this region. In the cortex of maize primary roots the PIG zone was about 450 μm; in cultured tomato roots its length was about 380 μm. The length of this region thus represents about 5.5% of the entire growth zone. Subsequent studies confirmed the uniqueness of the cells located in the PIG zone, not only from a morphometrical point of view, but also on account of their specific cytological and physiological properties (Barlow et al., 1991; Baluška et al., 1992, 1994, 1996a, 1996c; Ishikawa and Evans, 1992, 1993, 1995).

From a cellular point of view, the root tip has (a) a zone of cell division, a zone of more-or-less isotropic cell growth in which the cells both elongate and increase in width at similar rates; and (b) a zone of elongation in which cell growth is distinctly anisotropic and the rate of elongation is much greater than in the PIG zone. In cell-based terminology, therefore, the term "zone of cell elongation" should be reserved for root cells that grow in this strictly polar fashion. Significantly, our morphometric studies at the cellular level showed that an abrupt decline of cellular widening coincided precisely with a prominent increase in the rate of cell lengthening, and this occurred at the base of the PIG region (Baluška et al., 1990, 1994; Barlow et al., 1991). This occurrence provided the first hint that the newly formed postmitotic cells of the root may undergo some kind of preparatory phase wherein they adjust or reorganize their growth from the formerly slow, mitotic mode of growth to a rapid mode of elongation.

Rapid cell elongation in roots is based in part on an extensive uptake of solutes coupled with the formation of a prominent vacuolar compartment. These events accelerate cell expansion, which is channeled with the aid of specific alignments of both the cortical microtubules (CMTs) in the cytoplasm and the cellulose microfibrils in the cell wall, into strictly anisotropic cell enlargement. A significant reorganization of the metabolic machinery is required to achieve this new mode of cell growth. For example, cells of maize root apices increase their volume approximately 10-fold in the 13 h during which they migrate through the elongation region, whereas in the meristem cell volume may only double during this period (Baluška et al., 1996c). Once the rapid acceleration of cell growth has been triggered, it must be supported by a robust synthetic machinery that is obviously not yet operational in cells that are just ceasing their meristematic phase of development. If it were otherwise, root cells would commence their rapid elongation simultaneously with the termination of mitotic division. Not all cells of the root cease to divide at the same distance from the root tip, and it was recently found that the proximal limit of the meristem fluctuates in a rhythmic manner in accordance with a programmed pattern of transverse cell division within its constituent cell files (Lück et al., 1996).

It is probably advantageous, therefore, for the early postmitotic root cells to enter a critical preparatory phase, located in a special transition zone behind the meristem, where they acquire the ability to embark on rapid elongation. Moreover, some supracellular organizing process within this transition zone may ensure the simultaneous commencement of the rapid elongation phase in cells of different tissues (epidermis, cortex, stele, etc.) at a particular distance from the root tip. Root-generated electric fields, for example, may be one way of defining the conditions required for a coordinated program of rapid elongation after cells have completed their preparatory phase within the transition zone. Also, within this zone cells develop the necessary synthetic machinery for the biogenesis of new tonoplast and plasma membranes, cell-wall components, new enzymatic complexes, and cytoplasmic structures that support such rapid growth.

Aside from the basic synthetic machinery for cell growth, individual elements of the cytoskeleton can also be expected to alter their intracellular distribution from those configurations that support mitotic cell growth and division to arrangements that enable rapid cell elongation. In cells of the postmitotic transition zone, the CMTs change from loosely organized transverse arrays to an exclusively transverse orientation with respect to the root axis; the latter orientation is often accompanied by the appearance of

prominently bundled CMT arrays (Baluška et al., 1992). Later experimental studies (reviewed by Baluška et al., 1994), however, have confirmed that although the distribution of CMTs controls cell-growth polarity in maize root apices, the propensity for postmitotic cell growth is actually independent of the detailed arrangement of the CMTs. If all CMTs in postmitotic root cells are disorganized by an ethylene treatment, for example, or if they are destroyed with anti-microtubule agents such as oryzalin or colchicine, the postmitotic cells will still achieve final cell volumes similar to or even greater than those found in control, untreated roots. Furthermore, disintegration of microtubules does not prevent cortical cells of graviresponding maize root apices from undergoing the complex pattern of differential growth that normally appears to drive root bending (Baluška et al., 1996a). All of these findings suggest that ordered CMT arrays are necessary to regulate the polarity of cell growth and, hence, the rectilinear nature of root growth. On the other hand, certain growth processes, such as gravitropism, have no requirement for intact arrays of CMTs. Moreover, there is no evidence that CMTs are involved in the control of cell growth rate or that they are required for cellular growth per se.

A complementary picture emerges from our studies on the actomyosin cytoskeleton of maize root cells. A close relationship can be detected here between the intactness of the actin cytoskeleton, as visualized using actin antibodies applied to sections of root apices, and the degree of postmitotic cell growth (Baluška et al., 1996b). Partial disintegration of the actin cytoskeleton by application of either cytochalasin D or a high concentration of calcium both lead to similar effects on postmitotic cell growth. In particular, the early postmitotic cells in the transition zone are impaired in their ability to accomplish the preparatory phase, which, as a result of a 6-h-long treatment with 10 mM calcium, was extended in duration by 350% (Baluška et al., 1996b, 1996c). The actin cytoskeleton undergoes a dramatic reconstruction precisely in cells of the transition zone. Here, F-actin bundles elongate from perinuclear sites toward the transverse end walls of the cells. When the bundles have reached the end walls they acquire an oblique alignment with respect to the future cell axis and have a straight appearance, suggesting that they could be under tension. When the cells enter the elongation zone, the F-actin cables realign in parallel to the cell axis and assume a wrinkled appearance, as though the tension has now been relaxed. The location within the maize root where these changes occur suggests that the F-actin system is involved in generating a force associated with the transition from a slow, near-isotropic mode of cell growth close to the base of the meristem to the rapid anisotropic growth characteristic of the zone of elongation. Thus, our results support the notion that conformational changes of F-actin are relevant for postmitotic cells during their sojourn within the transition zone, and that they seem to be a prerequisite for the initiation of rapid cell elongation as well as for its progress once this mode of growth has commenced.

In conclusion, we fully agree with Ishikawa and Evans (1995) that cells in the transition zone are more similar to meristematic cells than to cells located in the major portion of the elongation zone (see also Baluška et al., 1994). Root cells obviously continue their cytoplasmic mode of growth after leaving the meristem. The transitional, preparatory phase of root-cell development appears to be essential to enable postmitotic root cells to switch their growth into rapid-elongation mode. At least from the cytological and cell-developmental points of view, the most suitable term for this highly specialized root zone is transition zone. It could also encompass the region termed the differential elongation zone (DEZ) by Ishikawa and Evans (1995). The term DEZ refers to a region of an organ, whereas our original term PIG refers to a region of cellular structure and hence is associated, as we have attempted to show here, with the growth properties of root cells, rather than with the properties that pertain to the root organ as a whole. The term transition zone can refer appropriately to both the organ and cellular levels, and therefore may be preferable to either of the terms DEZ or PIG.

František Baluška*, Dieter Volkmann, and Peter W. Barlow
Botanisches Institut der Universität Bonn, Venusbergweg 22, D-53115 Bonn, Germany (F.B., D.V.); Institute of Botany, Slovak Academy of Sciences, Dúbravská cesta 14, SK-84223 Bratislava, Slovakia (F.B.); and IACR-Long Ashton Research Station, Department of Agricultural Sciences, University of Bristol, Long Ashton, Bristol BS18 9AF, United Kingdom (P.W.B.)
* Corresponding author; e-mail unb110@ibm.rhrz.uni-bonn.de; fax 49–228–732677.

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