Specialized Zones of Development in Roots

When describing zones of development in roots, it is typical to include the cap, the apical meristem, the cell elongation zone, and the maturation zone. This terminology implies that as soon as a cell leaves the apical meristem, it is part of the elongation zone. (Since cell expansion also takes place in the meristem, the meristem is part of the elongation zone, a region where elongation is accompanied by cell division [Fig. 1].) Accordingly, no distinction (other than relative rate of elongation) is made between elongation zone cells that are closer to the apical meristem (elongating slowly) and cells farther from the meristem (elongating rapidly). Baluška et al. (1990) made a case for the special status of the cap, the apical meristem, and the maturation zone. This commentary we (a) urge replacing the term “postmitotic isodiametric growth zone” with “distal elongation zone” (DEZ), and (b) draw attention to the special physiological properties of the cells in the DEZ and their importance to the response of roots to a variety of environmental signals.

**Terminology**

The expression postmitotic isodiametric growth zone seems inappropriate for the following reasons. (a) The region of the root that includes cells with the special physiological properties described below includes many cells that are still dividing. Erickson and Sax (1956) showed that there is cell division activity as far as 2.5 mm from the tip of the cap in maize roots. This is well into the distal portion of the elongation zone (Fig. 1). Hence, it is inappropriate to restrict this zone to cells that are postmitotic. (b) Most of the cells in this region of the root are not isodiametric. Instead they tend to be wider than they are long except near the point of initiation of rapid elongation as they enter the main elongation zone (Baluška et al., 1990). (c) The pattern of cell expansion in this region of the root varies with position within the region. Cell expansion is not isodiametric except in a very narrow region within this zone (Barlow et al., 1991; Baluška et al., 1994). Consequently, we propose to refer to this region of the root as the DEZ (Fig. 1). This terminology indicates that these cells are near the distal end of the elongation zone but does not categorize them in terms of mitotic activity, shape, or allometric coefficient of expansion. The main distinguishing feature of these cells is their special physiological properties as described below (also see Baluška et al., 1994).

**The DEZ and Responses to Gravi- and Thigmostimulation**

When primary roots of maize are gravistimulated, a major factor causing downward curvature is the induction of very rapid elongation in the DEZ on the top side of the root (Ishikawa et al., 1991). The rate of elongation of these cells prior to gravistimulation is low. In contrast, the rate of elongation of cells in the main cell elongation zone is inhibited by gravistimu-
loration, especially along the lower side of the root (Ishikawa et al., 1991). In roots of Arabidopsis thaliana, gravistimulation causes a similar rapid enhancement of elongation in the DEZ along the top (Ishikawa and Evans, 1994). In mung bean roots, gravistimulation causes a rapid hyperpolarization of cells along the upper side of the DEZ but does not alter intracellular potential within the main elongation zone (Ishikawa and Evans, 1990a). When maize roots are stimulated by touch or mechanical abrasion near the tip, negative thigmotropism results mainly from enhancement of elongation in the DEZ on the stimulated side (Ishikawa and Evans, 1992).

The DEZ and Responses to Mechanical Impedance

When a growing maize root encounters a mild physical resistance to extension, the initial response is an acceleration of the rate of elongation. This occurs within the DEZ (Ishikawa and Evans, 1990b).

The DEZ and Responses to Electrotropic Stimulation

When maize roots are placed in a moderate (<8 V cm⁻¹) electrical field, the electrotropic response is expressed both in the main cell elongation zone and in the DEZ. In the DEZ, curvature is toward the cathode (−) and results from an enhancement of elongation on the side toward the anode (+) and an inhibition on the side toward the cathode. In the main elongation zone, electrotropic curvature occurs in the opposite direction, i.e. toward the anode, and this curvature results from an enhancement of elongation on the side toward the cathode and inhibition on the side toward the anode. Because of the opposite responses to electrotropic stimulation in the main elongation zone and the DEZ, the root assumes an S-shape (Ishikawa and Evans, 1993a).

The DEZ and Responses to Water Stress

When maize roots are grown in vermiculite of low water potential, elongation is inhibited throughout the elongation zone with the exception of the group of cells in the apical-most region, i.e. cells in the DEZ (Sharp et al., 1988). The elongation rate of cells in the DEZ is unaffected even by reducing the water potential of the vermiculite to -1.6 MPa. The rate of elongation in the main elongation zone is inhibited at water potentials as high as -0.2 MPa.

The DEZ and Responses to Auxin

When maize roots are exposed to low concentrations of exogenous IAA, their growth is strongly inhibited. However, after about 1 h, elongation resumes at a rate somewhat lower than the rate prior to exposure to auxin. We have found that the recovery is accounted for by induction of rapid elongation in the DEZ (Ishikawa and Evans, 1993b). Cells in the main cell elongation zone remain inhibited unless the exogenous auxin is removed.

When vertically oriented roots of maize or tomato are treated with a concentration of auxin sufficient to inhibit their growth completely, they are still capable of exhibiting a strong gravitropic response upon re-orientation to the horizontal in the continued presence of IAA (Katekar and Geissler, 1992; Ishikawa and Evans, 1993b; Muday and Haworth, 1994). This is true even when the roots are gravistimulated during the period of complete growth inhibition by auxin (Ishikawa and Evans, 1993b). Under these conditions the entire gravitropic response is accomplished by rapid gravi-induced differential growth in the DEZ. Cells in the main cell elongation zone remain inhibited and do not contribute to the growth response (Ishikawa and Evans, 1993b).

The DEZ and Gene Expression

There are differences in gene expression patterns between cells in the DEZ and cells within the main elongation zone. Masson and co-workers (1993), for example, have examined collections of “promoter-trap” T-DNA insertional mutants of A. thaliana looking for signal transduction mutants and for mutants carrying GUS insertions in genes expressed in various regions of the root. They identified a number of tissue-specific mutations, including examples in which the promoter-trap GUS reporter gene is expressed only in the DEZ and also examples in which the gene is expressed in the extreme root tip and in the main elongation zone but not in the intervening region.

We anticipate that additional examples of differences in gene expression between these regions of the root will surface as attention is drawn to the special properties of the cells in the DEZ. Although variations in the pattern of gene expression at different stages of development are not unexpected, the differences in gene expression in the DEZ and the main cell elongation zone indicate that these zones are distinguished by more than their differing rates of elongation.

The DEZ as a Specialized Region of the Root

According to the observations outlined above, it is clear that the cells in the DEZ respond to a variety of signals differently from the cells in the main elongation zone. In many cases the responses of the two sets of cells are opposite. For example, the elongation of cells in the DEZ is promoted by auxin, whereas elongation in the main cell elongation zone is inhibited. Water stress does not affect the elongation of cells in the DEZ but inhibits elongation in the main elongation zone. Electrotropic stimulation induces opposite bilateral patterns of elongation in the DEZ compared with the main elongation zone. Gravistimulation in-
hibits the elongation of cells in the main elongation zone but promotes the elongation of cells along the upper side of the DEZ. Although it is clear that the physiological properties of the DEZ and the elongation zone differ, this does not imply that the DEZ is composed of a homogeneous population of cells. Cells within the DEZ differ with regard to stage of the cell cycle, degree of commitment to cell development, and time since their final mitotic division. The special physiological properties of the DEZ as described above may be attributable to a particular subpopulation of cells within this region of the root.

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