

Asymmetric Cell Division and Cell Determination in Plant Development

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The term "asymmetric cell division" is used here to refer to any cell division in which the two derivatives assume different paths of development and have distinct cell fates. Therefore, the asymmetry does not necessarily lie in the size difference of the derivatives, although the difference in cell size often provides a marker and even has been proposed as a driving force of differentiation (Treinin and Feitelson 1993). Asymmetric cell division provides a mechanism to generate cell diversity in all organisms. Numerous examples of asymmetric cell division exist during the development of a plant. Because plant cells are confined to rigid cell walls and do not undergo morphogenetic movement, the orientation of cell division plane and the direction of cell expansion are key determinants in plant morphogenesis, and thus are tightly regulated. In many cases, differentiation starts from an unequal cell division, in which the small cell forms a specialized structure, either by itself or by further concerted unequal cell divisions in surrounding cells. While in others, the size difference is not as obvious immediately following the cell division, but later, one of the derivatives becomes distinctly larger and is committed to an altered path of development. Here I discuss one example for each type of these asymmetric cell divisions.

Trichome development starts from the small cell delineated by an unequal cell division in the protodermal layer, which then elongates away from the surface into a defined shape. Three classes of mutations in trichome development have been studied in *Arabidopsis* (Marks et al. 1991). Among them, one is devoid of trichomes, and the isolated gene encodes amino acid sequences highly homologous to the protooncogene *myb* (Oppenheimer et al. 1992). Myb protein contains a DNA binding domain and a region participating in protein-protein interactions (Sakura et al. 1989). It does not fit the configuration for a transmembrane

signaling molecule, and therefore could be a downstream molecule in the signaling cascade of cell determination.

Stoma differentiation is similar to trichome development in several aspects but involves concerted asymmetric cell divisions in the neighboring cells. Stomata are surface pores anchored by derivatives of the protodermal layer, resulted from unequal cell divisions, and distributed throughout the epidermis in variable densities, without direct contact of each other. Following an unequal cell division in an epidermal cell, the small cell becomes the guard mother cell (GMC). The nuclei in the surrounding epidermal cells migrate toward the sides of GMC, and further unequal cell divisions occur with precise orientations in these cells and the GMC to produce the stomatal complex, which is highly specialized and distinct from ordinary epidermal cells.

Lateral root initiation in ferns provides evidence for the action of both induction and lateral specification (Greenwald and Rubin 1992). The entire lateral root structure originates from a single cell within the endodermis, which is a single layer of cells surrounding the vascular cylinder along the axis of the main root. The lateral root initial (LRI) is always the distal derivative of a cell division. The asymmetry of the cell division may not be distinct prior to the completion of division, but the cell destined to become LRI expands rapidly. It first enlarges to reach approximately 20-fold the volume of its sister cell or any ordinary endodermal cell, then undergoes a series of cell divisions in precise sequences and orientations within the contour of the cell. Transversely, LRI always arises from the endodermal initial facing the protoxylem of the vascular cylinder. Thus in diarch fern roots, only two longitudinal files of endodermal cells, each facing one protoxylem pole, are potentially capable of generating LRIs through establishing cell polarity and asymmetric cell division.

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