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# Asymmetric Cell Division in Plant Development

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## Abstract

Plant embryogenesis creates a seedling with a basic body plan. Post-embryonically the seedling elaborates with a lifelong ability to develop new tissues and organs. As a result asymmetric cell divisions serve essential roles during embryonic and post-embryonic development to generate cell diversity. This review highlights selective cases of asymmetric division in the model plant *Arabidopsis thaliana* and describes the current knowledge on fate determinants and mechanisms involved. Common themes that emerge are: 1. role of the plant hormone auxin and its polar transport machinery; 2. a MAP kinase signaling cascade and; 3. asymmetric segregating transcription factors that are involved in several asymmetric cell divisions.

## 1

### Introduction

Asymmetric cell division produces daughter cells with different fates. Distinct fate properties may be morphological or biochemical features or different progeny that cells produce (Horvitz and Herskowitz 1992). Ensuring the asymmetry of divisions at distinct locations and time points provides a commonly exploited solution to the fundamental problem of creating cell diversity in multicellular organisms. This cellular specialization generates the structural and functional cell types that make up tissues and organs during development.

Central to the process of asymmetric cell division is the question how a single cell can produce different daughter cells. A complication to this process is that the daughter cells generated upon division need not be morphologically dissimilar initially. Two distinct mechanisms are employed to generate asymmetric division. First, different daughter cells are generated due to differential inheritance of fate determinants as a consequence of unequal distribution of these factors in the mother cell. In this case, intrinsic factors determine cell fate. This scenario requires the mother cell to be polar at the onset of division leading to the immediate follow up question how the mother cell becomes polarized. Second, identical daughters are produced

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with initially equal developmental potential but fates diverge due to subsequent interaction with their surrounding environment. Now extrinsic cues determine cell fates. Whereas the intrinsic and extrinsic strategies appear very distinct it is easy to envisage how actual development may employ a combination of both. Note for example that in the intrinsic case the polarization of the mother cell before division may be under influence of external spatial information. The central question in both scenarios concerns the factors that cause daughter cells to obtain different fates.

Plant cells are surrounded by a cell wall restricting their movement. To cope with their sessile lifestyle plants evolved a remarkable developmental flexibility to detect and respond to changes in the environment by cell fate changes that ensure their growth and survival. Plant embryogenesis results in the formation of a seedling merely having the basic body plan with the shoot and root stem cell populations at apical and basal ends. A major specialization different from most other multicellular organisms is the lifelong ability of plants to develop new tissues and organs. As a result asymmetric cell divisions serve essential roles during embryonic and post-embryonic development to generate cell diversity. Orientation of cell division is an important aspect of plant asymmetric cell division to determine the position that of a cell in a growing tissue and so the positioning of new walls has significant effects on development. Mutants in which the normal cell division pattern is disturbed still form relatively normal and functional plants with their different tissues in the expected place but growth can be dramatically reduced (Torres-Ruiz and Jurgens 1994; Traas et al. 1995; Smith et al. 1996).

Despite very ordered cell divisions from embryogenesis onwards in some plants species (e.g. the model plant *Arabidopsis thaliana*) it is not lineage but positional information that determines cell fate (Poethig 1987; Furner and Pumfrey 1992; Scheres et al. 1994; van den Berg et al. 1995). This is consistent with the much more randomized division pattern in other species such as cotton, maize and rice (Pollock and Jensen 1964; Schel et al. 1984; Itoh et al. 2005). Nevertheless, the highly regular series of cell divisions during embryogenesis in *Arabidopsis* allows cell lineages to be traced back to their origin which presents a major advantage in developmental research.

The past years we have witnessed an explosion of data on gene and protein expression and auxin hormone accumulation from the initial stages of embryogenesis through to post-embryogenic development in higher plants using in vivo and in vitro systems. This review highlights selective cases of asymmetric division in plants and describes the current knowledge on fate determinants and mechanisms involved. I will focus the discussions on the model plant *Arabidopsis thaliana*. For the processes involved in the physical separation of a single cell into individual daughter cells and the function of the cytoskeleton the reader is referred to several recent reviews (Jurgens 2005; Konopka et al. 2006; Lloyd and Chan 2006).

## 2

### Polarity and Orientation of Cell Division in Plants

Cell polarity is the development of asymmetry within a cell which can be monitored by physical changes in cell shape or localized distribution of molecular components. Cell polarity provides information for axis formation, patterning, growth and asymmetric cell division.

Asymmetric distribution of the plant hormone auxin is instrumental in regulating many polar growth and division responses at the tissue level (summarized in Dhonukshe et al. 2005) but is also implicated in specific cases of asymmetric cell division discussed here. Auxin is actively distributed within the plant by the combined action of AUX1 auxin influx carrier and PIN auxin efflux facilitators whose asymmetric subcellular localization has been correlated with the direction of auxin flow. Binding of auxin to Transport Inhibitor Response 1 (TIR1), an auxin receptor and subunit of an SCF-type ubiquitin ligase, promotes the degradation of a family of transcriptional repressors called Aux/IAA proteins. Aux/IAA proteins bind to Auxin Response Factor (ARF) proteins and inhibit the transcription of specific auxin response genes. Increased nuclear concentrations of auxin promote auxin binding to TIR1, causing the Aux/IAA proteins to associate with TIR1 and leading to their degradation by a proteasome-mediated pathway. The ARF protein is now free to activate transcription from its target promoter (reviewed in Jenik and Barton 2005). Studying the polar localization of PIN protein is aiding significantly in investigations on plant cell polarity and pinpointing the proteins involved (Xu and Scheres 2005).

Certain cell polarization events depend on ADP-Ribosylation Factor (ARF)-mediated vesicle trafficking to polarly localize Rho-related GTPases from plants (ROP). ROPs act as master switches in the transmission of various extracellular and intracellular signals and have classically been linked to the regulation of the cytoskeleton. ROPs control actin assembly and microtubule bundling through ROP-Interactive CRIB-motif (RIC) proteins and Wiskott–Aldrich syndrome protein family verprolin homologous/suppressor of cAMP receptor-actin related protein (WAVE/SCAR–ARP2/3) pathways (Gu et al. 2004; Burridge and Wennerberg 2004; Xu and Scheres 2005). In plants ARFs interact with Guanine nucleotide Exchange Factors (ARF–GEF) like GNOM/EMB30 for polar vesicle transport. *gnom* mutants display aberrant cell shape and abnormal orientation of cell division planes including the first division in the zygote (Sect. 4.1, Mayer U et al. 1993; Shevell et al. 1994; Geldner et al. 2003).

Another way to generate and maintain polarity may be altered sterol composition of the cell membrane which in yeast was shown to interfere with mating and may also be important for animal cell polarity (Bagnat and Simons 2002; Schuck and Simons 2004). A similar case has been made for plants as reported for the *Arabidopsis* mutant *sterol methyltransferase*

*l/orc* (*smt1/orc*), which is disturbed in the biosynthesis of plasma membrane sterols resulting in apolar distribution of cellular markers and aberrant division planes (Willemssen et al. 2003).

Clearly, disturbing the polarity of cells affects the orientation of the cell division plane. But how cell polarity is linked to division orientation in plants remains unclear. In animals the PARtitioning defective (PAR) proteins act downstream of polarization cues to stabilize polarity and they form the connection with the cytoskeleton to control asymmetric mitotic spindle positioning, determine the division plane and localize cell fate determinants to one side of the cell (reviewed in Wodarz 2002; McCarthy and Goldstein 2006). *PAR* genes were originally identified in a screen for mutants affecting the first asymmetric cell division of the *Caenorhabditis elegans* zygote and encode a diverse set of proteins consisting of Ser/Trh-kinases, PDZ-domain proteins and a 14-3-3 protein (Kemphues et al. 1988; Betschinger and Knoblich 2004).

Cell division is distinct in several ways in animals and plants. First, in animals, microtubule nucleation takes place at microtubule-organizing centers (MTOCs) such as the centrosomes associated with the poles of the mitotic spindle that determine the direction of chromosome segregation during mitosis. Higher plant cells lack discrete MTOCs but assemble highly ordered arrays of microtubules from nuclear polar caps that anticipate the mitotic spindle to coordinate cell division. Second, physical cell division or cytokinesis in animal cells involves inward constriction by an actinomyosin contractile ring that pulls in the plasma membrane whereas plant cell cytokinesis occurs at from the center toward the cell periphery. This process involves the “phragmoplast”, the cytokinetic ring of the plant cell, consisting of antiparallel bundles of microtubules and actin that forms from the remains of the spindle between the two sets of chromosomes. The phragmoplast delivers vesicles to the plane of cell division forming the outward growing cell plate. Interestingly, the future site of division in plants is predicted late in G2 by a transient cortical preprophase band (PPB) of co-aligned microtubules and actin filaments encircling the nucleus whereas in animals the site of cytokinesis is selected after chromosome separation. Although on the surface animal and plant division appear very different, the involved mechanisms and protein conservation indicate a common basis to both types of division (Jurgens 2005; Lloyd and Chan 2006 and references therein).

### 3

## Asymmetric Cell Divisions in Plant Development

Plant life starts with the formation of the zygote and its first division is asymmetric generating two daughter cells with different fate: a smaller apical cell and a large basal cell (Sect. 4.1) that will form different cell lineages.

The apical cell next divides vertically and will produce the majority of the embryo. The basal cell divides horizontally forming the extra-embryonic suspensor that connects the embryo to the maternal tissues. At the globular embryo stage of the uppermost cell from the suspensor is recruited to become the hypophysis. This cell then divides asymmetrically generating an apical lens shaped cell (Sect. 4.2) that is the progenitor of the root stem cell organizing cells, the quiescent center. Also embryonic are the oriented periclinal divisions that give rise to the progenitors for the three main tissues, epidermis, ground tissue and vascular tissue (Sect. 4.3). Radial patterning by asymmetric division continues post-embryonically throughout the life of plants in foci of cell division and development called meristems located at the tip of the root and shoot. In the vascular system phloem and procambium are established through asymmetric cell divisions of a set of progenitors. Other examples are the formation of epidermis and lateral root cap tissues and the formation of endodermis and cortex from single progenitor cells whereby the latter is the best-studied example of asymmetric division in plants (Sect. 5.1). All post-embryonic development has its origin in the stem cells located in niches in the heart of the shoot and root meristems. The function of the niche is to provide the microenvironment to keep the stem cells undifferentiated and as a consequence in asymmetric stem cell divisions (Sect. 5.2) to produce a daughter that remains stem cell and a daughter that will differentiate according to position as it moves out of the niche. As the plant develops new organs and specialized cell types are formed needed to deal with the outside world. Asymmetric divisions play a role in root branching (Sect. 5.3) as the root explores the soil in search of nutrient, and in the formation of stomata (Sect. 5.4), cells that regulate gas exchange from the aerial parts of the plant. Finally, when the plant reaches maturity and reproduction becomes an issue, asymmetric divisions are again employed to generate the male gametes completing the life cycle (Sect. 5.5).

## 4

### Asymmetric Divisions in Embryogenesis

As different as the shapes and sizes of higher and lower plants appear, the early steps in embryogenesis show profound similarities. Embryos of higher plants develop deep inside maternal tissues and thus are difficult to use for experimental manipulation. Therefore research on embryogenesis has focused on genetics as an important tool. Lower plants such as the brown alga *Fucus* have free-living zygotes and have provided a valuable system to study asymmetric division (Fowler and Quatrano 1997; Scheres and Benfey 1999). Recently, however, a system has been developed to culture zygotic *Arabidopsis* embryos inside their ovules in vitro (Sauer and Friml 2004), greatly improving experimental accessibility while the normal embryogenesis program proceeds.



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