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Two receptor-like kinases required together for the establishment of Arabidopsis cotyledon primordia

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Abstract

Inter-regional signaling coordinates pattern formation in *Arabidopsis thaliana* embryos. However, little is known regarding the cells and molecules involved in inter-regional communication. We have characterized two related leucine-rich repeat receptor-like kinases (LRR-RLKs), *RECEPTOR-LIKE PROTEIN KINASE1* (*RPK1*) and *TOADSTOOL2* (*TOAD2*), which are required together for patterning the apical embryonic domain cell types that generate cotyledon primordia. Central domain protoderm patterning defects were always observed subjacent to the defective cotyledon primordia cell types in mutant embryos. In addition, RPK1-GFP and TOAD2-GFP translational fusions were both localized to the central domain protodermal cells when cotyledon primordia were first recognizable. We propose that *RPK1* and *TOAD2* are primarily required to maintain central domain protoderm cell fate and that the loss of this key embryonic cell type in mutant embryos results in patterning defects in other regions of the embryo including the failure to initiate cotyledon primordia.

Keywords: Embryogenesis; Arabidopsis; Receptor-like kinases; Signaling; Protoderm

Introduction

The coordination of cellular differentiation along the apical–basal and radial axes during Arabidopsis embryogenesis establishes the basic adult body plan. At the octant stage, the Arabidopsis embryo is partitioned along its apical–basal axis into the apical, central and basal domains (Fig. 1A). The derivatives of these domains will produce characteristic seedling structures (Jurgens et al., 1994) (Fig. 1A). Although communication between the clonally-distinct apical, central and basal domain derivatives is required for embryonic pattern formation (Laux et al., 2004; Mayer and Jurgens, 1998; Weijers et al., 2006), the cells and molecules involved in inter-regional signaling remain to be fully characterized.

Patterning along the central domain radial axis generates the outer-most protoderm, the middle ground tissue and the inner vascular primordium layers during early embryogenesis (Mansfield and Briarty, 1991) (Fig. 1A). Radial patterning in the apical domain of globular embryos establishes a cylinder of cells at the core of the apical domain (the central or inner region) and a surrounding group of cells referred to as the peripheral region (Long and Barton, 1998) (Fig. 1A). After the late globular stage, the embryo transforms from a radially symmetric structure into a bilaterally symmetric heart-shaped structure with two developing cotyledon primordia (Fig. 1A). During this transition stage, the apical domain is subdivided into a medial region and two flanking lateral regions (Aida et al., 1999; Long and Barton, 1998; Prigge et al., 2005) (Fig. 1A). One model proposes that medial/lateral regional identities are superimposed onto radial identities of late globular/transition stage embryos to pattern the apical embryonic domain (Aida et al., 1999; Long and Barton, 1998; Prigge et al., 2005). For instance, cells in the peripheral/lateral, peripheral/medial and central/medial regions will generate cotyledon primordia, boundaries between the cotyledon primordia margins and the presumptive shoot meristem precursors, respectively (Fig. 1A).

The plant hormone auxin plays an important role in patterning the apical embryonic domain. Polar auxin transport

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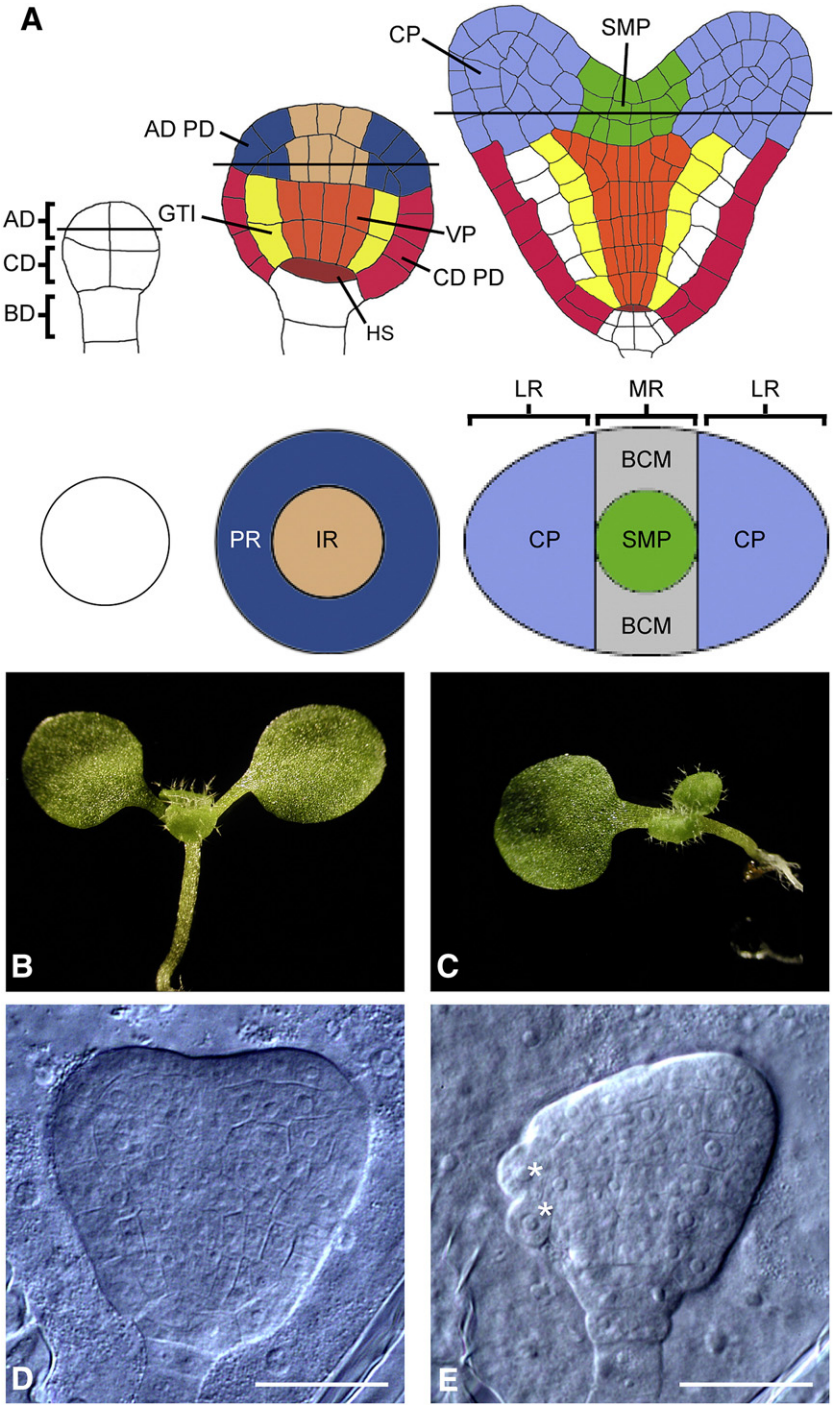

Fig. 1. Seedlings and embryos from self-pollinated *rpk1-1 toad2-1/+* plants have cotyledon development defects. (A) Schematic of pattern formation from the 8-cell (left) to the late globular (middle) and heart (right) stages of Arabidopsis embryogenesis. Top: Schematics of frontal longitudinal sections; Bottom: Schematics of cross sections through the apical domains indicated by bold horizontal lines in the top illustrations. AD, apical domain; AD PD, apical domain protoderm; BD, basal domain; BCM, boundary between cotyledon primordia margins (gray); CD, central domain; CD PD, central domain protoderm (red); CP, cotyledon primordia (light blue); GTI, ground tissue initials (yellow); HS, hypophysis (brown); IR, inner region (light brown); LR, lateral region; MR, medial region; PR, peripheral region (dark blue); SMP, presumptive shoot meristem precursors (green); VP, vascular primordium (orange). (B) Wild-type (Col-0) seedling 7 days after germination (dag). (C) Seedling from self-pollinated *rpk1-1 toad2-1/+* plant with missing cotyledon 7 dag. (D) Representative early heart stage embryo from self-pollinated *rpk1-1 toad2-1/+* plant with correctly formed cotyledon primordia. (E) Representative transition/early heart stage Defective half embryo from self-pollinated *rpk1-1 toad2-1/+* plant with a malformed cotyledon primordium. Enlarged central domain protodermal cells are indicated by asterisks. Scale bars represent 25 μm.

through the PIN1 putative auxin efflux carrier is thought to establish groups of cells with increased auxin signaling, or auxin maxima, at the apices of cotyledon primordia (Benkova et al., 2003; Friml et al., 2003), and many studies indicate that auxin response is required to properly pattern the apical domain (Aida et al., 2002; Berleth and Juergens, 1993; Furutani et al.,