DEVELOPMENT

Homeobox kick-off for *Arabidopsis* body plan

The genetic basis of early plant development has proved challenging to dissect: the cells of interest are surrounded by tissue and therefore hard to get at, and functional redundancy makes it hard to link genotypes to phenotypes. A recent study has overcome these problems to provide important new insights into early *Arabidopsis thaliana* embryogenesis, showing that setting up the main body axis involves the differential expression of WUSCHEL-related homeobox (WOX) family genes.

The anterior–posterior (AP) axis of the *A. thaliana* embryo is established when the zygote divides asymmetrically to produce a large basal cell and a small apical cell, which give rise to distinct embryonic lineages.

What are the key differences between the basal and apical cells that establish distinct identities along the AP axis? As multiple transcription factors of the WOX family have recently been shown to be differentially expressed in *A. thaliana* embryonic lineages, Breuninger and colleagues investigated whether distinct expression domains of WOX genes contribute to AP-axis formation.

WOX2 is expressed in the apical cell and the early proembryonic cells that are derived from it. Combinations of mutations in *WOX2* and in other WOX genes that are expressed in the same cells revealed *WOX2* as a key regulator of AP patterning; other WOX genes have overlapping functions, but these are only revealed when *WOX2* expression is absent. Two other genes of this family, *WOX8* and *WOX9*, are specifically expressed in the basal cell. Analysis of single and double mutants for these genes revealed that they are redundantly required for the normal development of both basal and apical lineages. Providing an explanation for their non-autonomous requirement in apical cells, *WOX8* and *WOX9* were shown to be needed for a reporter gene driven by *WOX2* regulatory sequences to recapitulate normal *WOX2* expression.

Disruption of polar distributions of the hormone auxin causes severe AP-patterning defects at various stages of *A. thaliana* embryogenesis. Using an auxin-responsive reporter gene, Breuninger and colleagues showed that *WOX8* and *WOX9* are required for normal auxin distributions in the early embryo, and are

essential for the correct expression of *PIN1* — one of several auxin efflux proteins that enable polar distributions of this hormone to be set up. The effect of WOX genes on auxin distributions seems to be mediated partly through redundant interactions with the *MP* transcription factor, which is known to regulate *PIN1* expression. Disrupting either *WOX2* or *WOX8* function increased the severity of *MP* mutant phenotypes with respect to auxin distribution and morphogenetic defects.

The evidence described above suggests that *WOX2* functions downstream of *WOX8* and *WOX9* in the early embryo. In support of this, the authors showed that ectopically providing *WOX2* in embryos that lack both *WOX8* and *WOX9* function rescues apical cell fates. So, it seems that *WOX8* and *WOX9* expression in the basal cell induces *WOX2* expression in the adjacent apical cell, establishing different transcriptional programmes in the two cell types.

The role of differential expression domains of WOX family transcription factors in setting up the primary body axis in the *A. thaliana* embryo highlights interesting parallels with the key role of HOX genes in establishing animal body plans. Important questions to be addressed now are how the asymmetric localization of *WOX8* and *WOX9* is established, and how these genes induce *WOX2* expression in the apical cell.

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