Nature Reviews Genetics | AOP, published online 1 April 2009; doi:10.1038/nrg2582

PLANT DEVELOPMENT

Paternal control regulates division

The phenomenon of parent-of-origin effects is well documented in animal embryogenesis. In flowering plants, however, only a few cases of maternal control of embryogenesis have been identified and, until recently, there were no documented cases of paternal control. Bayer and colleagues describe the first paternal effect on plant embryogenesis, and show that the timing of zygote elongation and the first division are mediated by a signal provided by the sperm cells.

In flowering plants, including *Arabidopsis thaliana*, male and female gametophytes each contain two cells. The pollen provides two sperm cells — one fuses with the egg to form the zygote, the other with the central cell to form the endosperm. The zygote elongates and then divides asymmetrically, in a process regulated by YODA (YDA), a mitogen-activated protein kinase (MAPK) kinase kinase. This division forms the apical cell, which develops into the embryo, and the large basal cell, which develops into the suspensor. The endosperm and the suspensor are both involved in nutrient delivery to the developing embryo.

Bayer *et al.* investigated mutations in *SHORT SUSPENSOR* (*SSP*) in *A. thaliana*, which encodes a Pelle-like kinase, and found that the resulting *ssp* phenotypes in embryogenesis closely resembled those of *yda* mutations — zygote elongation fails and basal cells are smaller, and the suspensor fails to develop normally. Double mutant *spp*;*yda* embryos were indistinguishable from *yda* single mutants, indicating that the two genes do not function independently. Hyperactive variants of *YDA* reversed the suspensor phenotype in *spp* mutants, leading the authors to suggest that SSP has a role upstream of YDA. So how might SPP function to activate the YDA pathway?

From reciprocal crosses involving *ssp* mutants, Bayer and colleagues found that the phenotype of the embryo depends on the genotype of the pollen — *ssp* plants crossed with wild-type pollen were normal, but wild-type plants crossed with pollen from *ssp* homozygous plants developed abnormally, indicating that SSP has a paternal effect. Reverse transcription PCR and microarray analysis indicated that *SSP* mRNA accumulates in mature pollen, but tagging of SSP with yellow fluorescent protein showed that this mRNA is only translated after fertilization, in the zygote. The authors suggest that *SSP* mRNA from the sperm is translated in the zygote after fertilization. The SSP protein then activates the YDA MAPK cascade, which in turn promotes zygote elongation and the asymmetric first cell division. Therefore, SSP acts as a temporal cue linking the onset of zygote development to fertilization.

All previously identified parent-of-origin effects in flowering plants are maternal. The most prominent effect arises from a parental conflict in which maternally imprinted genes lead to maternal control over nutrient allocation to the embryo by the endosperm. The findings of Bayer *et al.* provide a way to overcome this maternal regulation by delivering paternal transcripts directly to the seed, and they suggest that paternal control over the suspensor may have evolved as a way to antagonize these maternal influences.

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ORIGINAL RESEARCH PAPER Bayer, M. *et al.* Paternal control of embryonic patterning in *Arabidopsis thaliana*. *Science* **323**, 1485–1488 (2009)

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