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Nodine, Michael D.

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Plant development: Suspensors as a battlefield for parental tug-of-war?

Michael D. Nodine
Laboratory of Molecular Biology, Wageningen University and Research, 6700 AP Wageningen, The Netherlands
Correspondence: michael.nodine@wur.nl
https://doi.org/10.1016/j.cub.2021.09.081

Parental contributions to zygotes can influence early embryogenesis and may regulate the distribution of maternal resources to progeny. A new study in *Arabidopsis thaliana* has demonstrated that signaling components from maternal sporophytic tissues and paternal gametes converge in zygotes to promote elongation of the extraembryonic suspensor, which supports the developing embryo proper.

The transcriptional activation of genes shortly after fertilization is required for early embryogenesis in plants[1,2]. While it is clear that maternal and paternal factors can also influence embryo morphogenesis[3–8], the mechanisms and interplay of such parental signaling components are not yet known in most cases. In this issue of *Current Biology*, a paper from Martin Bayer and colleagues sheds light on how maternal and paternal cues converge to regulate the earliest steps of plant embryogenesis[9].

At the beginning of *Arabidopsis thaliana* embryogenesis, the zygote divides asymmetrically to produce a smaller apical cell and larger basal cell. The apical cell lineage gives rise to the proembryo that consists of precursors to post-embryonic tissues. By contrast, the basal cell lineage produces the suspensor, which supports the developing embryo proper before undergoing programmed cell death[10] (Figure 1A). Previously, it was demonstrated that maternally derived molecules can travel through suspensors before being delivered to the embryo proper[6,7,11,12]. However, suspensors are not just passive conduits for maternal factors: increasing evidence supports the notion that parental and zygotic signaling pathways are integrated in suspensors to regulate embryo development. Genes preferentially expressed in suspensors are rapidly evolving[13,14], which is consistent with conflicts between siblings for maternal resources being especially prevalent in this terminally differentiated cell lineage[13]. In addition to competition among siblings for maternal resources, competition between parents may differentially regulate suspensor growth.

Mothers are equally related to all of their offspring and, based on parent–offspring conflict theory[15], it would be expected that mothers equalize progeny suspensor growth to distribute resources evenly across their offspring. On the other hand, embryos from different fathers are competing for maternal resources and thus fathers may maximize suspensor growth of their progeny at the expense of genetically unrelated embryos. Recently published data in *Arabidopsis* suggest that mothers have a greater influence on suspensor development than fathers[3]. Perhaps this is not surprising because *Arabidopsis* typically reproduces by self-fertilization, and it is rare that embryos from different fathers develop on the same mother. Therefore, competition between fathers is reduced in *Arabidopsis*. However, fathers still retain some control in this autogamous (self-fertile) species. In fact, the first gene products demonstrated to be transmitted from parents to offspring in *Arabidopsis* were transcripts encoding the sperm-derived SHORT SUSPENSOR (SSP) signaling protein[5] (Figure 1B). Paternal SSP transcripts are delivered to the zygote where they are translated and activate the YODA (YDA) mitogen-activated protein kinase (MAPK) pathway to regulate suspensor elongation. Moreover, the SSP–YDA–MAPK signaling pathway activates the WRKY DNA-BINDING PROTEIN 2 (WRKY2) transcription factor[4]. Both WRKY2 and the maternally provided HOMEODOMAIN GLABROUS 11 and 12 (HDG11, HDG12) transcription factors activate the expression of *WUSCHEL-RELATED HOMEOBOX 8* (*WOX8*), which in turn promotes suspensor growth[4] (Figure 1B). The *EMBRYO-SURROUNDING FACTOR 1* (*ESF1*) family encodes short cysteine-rich peptides that originate outside of embryos and function upstream of YDA to regulate suspensor development[16], but it is not clear how these ligands are perceived by the embryo to control suspensor growth. Based on these observations, it can be speculated that a parental tug-of-war occurs in suspensors that moderates the dispersal of maternal resources to developing embryos.

In the new study, Wang *et al.*[9] found that members of the ERECTA family (ERf) of receptor kinases, including ER and its paralogs ER-LIKE 1 (ERL1) and ERL2, are maternally required for suspensor elongation. Based on the maternal sporophytic effects of the *er erl* mutants on reducing zygote and suspensor lengths, the authors suggested that ERf gene products are generated prior to meiosis in female reproductive tissues and subsequently delivered to zygotes via haploid gametophytic tissues. These results are consistent with previous findings from a large-scale genetic screen[17] and together indicate that premeiotic gene products can influence early embryogenesis. Wang *et al.*[9] then used a brilliant genetic approach to demonstrate that ERf proteins were cell-autonomously required in zygotes for their growth. Transgenic anti-GFP nanobodies fused to ubiquitin ligases are an effective way to specifically target GFP/YFP-tagged proteins for degradation[18]. Wang *et al.*[9] first rescued the mutant phenotypes of *er erl1 erl2* embryos with a transgene encoding a YFP-tagged version of ER under the control of its

endogenous promoter (ER_{pro}:*ER–YPET*). To reduce ER–YPET protein abundance specifically in eggs and zygotes, the authors then introduced transgenes encoding anti-GFP nanobodies fused to ubiquitin ligases and under the control of an egg-cell-specific promoter into plants expressing ER_{pro}:*ER–YPET* in the *er erl1 erl2* mutant background. Reduction of ER–YPET restored the embryonic phenotypes observed in *er erl1 erl2* mutants, indicating that ER activity in eggs or zygotes is required for zygote elongation.

BRASSINOSTEROID SIGNALING KINASEs 1 and 2 (BSK1, BSK2) were previously shown to function upstream of YDA and likely connect ERf signaling with YDA activation[19]. As with the ERf gene products, Wang *et al.*[9] found that *BSK1* and *BSK2* were also maternally required for suspensor elongation. Maternal effects of additional YDA–MAPK signaling components have been recently reported[4,20]. Therefore, several components of the YDA–MAPK signaling cascade are maternally derived. By contrast, the paternally contributed SSP resembles a constitutively active version of a BSK[19] and is specifically expressed in sperm. This raised the interesting possibility that maternal ERf–BSK1/2 and paternal SSP pathways converge on YDA and thus serve as independent inputs to control zygote and suspensor elongation. To test this possibility, Wang *et al.*[9] then assessed the relationships of these two pathways using transgenic approaches. Ectopic expression of SSP in seedlings resulted in the activation of the YDA pathway and consequential loss of stomata in wild-type seedlings[19], but not in *er erl1 erl2* mutant seedlings[9]. Moreover, paternal *ssp* mutants and maternal *er erl2* mutants had additive effects on reducing zygote and suspensor lengths.

Altogether, Wang *et al.*[9] demonstrated that maternal ER–BSK1/2 and paternal SSP pathways converge to activate the YDA–MAPK signaling cascade in zygotes, which in turn promotes zygote and suspensor growth. This research adds another layer to the growing support for the suspensor being a battlefield where parents are vying for control of resource allocation to their progeny. For instance, the ER–BSK1/2 branch, as well as other downstream components, are under maternal sporophytic control. Wang *et al.*[9] propose that this allows mothers to evenly regulate the development of progeny suspensors. In contrast to *ERf* and *BSK1/2*, which are evolutionarily conserved across flowering plants, *SSP* is only found in the Brassicaceae family. Therefore, it is possible that the relatively recent evolutionary innovation of *SSP* circumvents the need for maternal ERf to activate YDA and consequently allows paternal control of suspensor growth. Because pathways involved in conflict over parental resource allocation to offspring are expected to evolve rapidly, it would be interesting to survey how maternal and paternal signaling pathways converge to regulate suspensor

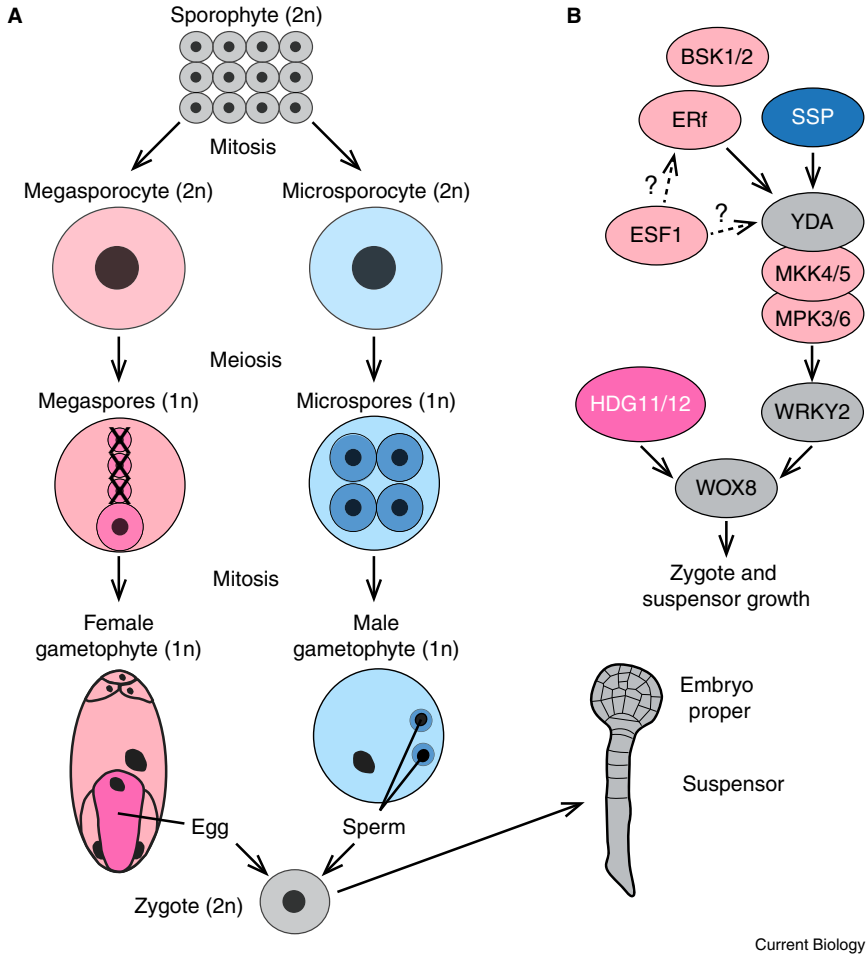

Figure 1. Parental contributions to early *Arabidopsis* embryogenesis.
(A) Illustration of female and male reproduction in *Arabidopsis*. Diploid (2n) sporophytic tissues divide mitotically to produce megasporocytes and microsporocytes, which will then undergo meiosis to produce haploid (1n) megaspores and microspores, respectively. One of the megaspores survives and undergoes mitosis to form a multicellular female gametophyte containing an egg. In contrast, all four microspores undergo mitosis to generate male gametophytes containing two sperms. One of the sperm will fertilize the egg to produce a diploid zygote, which marks the beginning of sporophytic development. Sporophytic and maternal and paternal reproductive tissues are shown in grey, pink and blue, respectively. (B) Schematic of maternal (pink), paternal (blue) and zygotic (grey) contributions to the YODA pathway controlling zygote and suspensor growth. Maternally contributed ERf and BSK12 and paternally contributed SSP converge to activate the zygotically produced YDA MAP3K. Central-cell-derived ESF peptides also act upstream of YDA. Downstream components of the YDA-MAPK pathway (i.e. MKK4/5 and MPK3/6) are maternally contributed and together with egg-cell-derived HDG11/12 activate WOX8 to promote zygote and suspensor growth. BSK1/2, BRASSINOSTEROID SIGNALING KINASEs 1 and 2; ERf, ERECTA family of receptor kinases; ESF1, EMBRYO-SURROUNDING FACTOR 1; HDG11/12, HOMEODOMAIN GLABROUS 11 and 12; MKK4/5, MAP2Ks 4 and 5; MPK3/6, MAPKs 3 and 6; SSP, SHORT SUSPENSOR; WOX8, WUSCHEL-RELATED HOMEOBOX 8; WRKY2, WRKY DNA-BINDING PROTEIN 2; YDA, YODA MAP3K.

development in other plant species. The research by Wang *et al.*[9] has helped pave the way for future investigation of how the integration of maternal, paternal and zygotic factors in plant embryos enable competition among progeny for the limited maternal resources available.

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Neuromodulation: A model for dopamine in salience encoding

Jingyi Chen[1,2] **and Michael Bruchas**[1,2,3,4,*]
[1]Center for the Neurobiology of Addiction, Pain, and Emotion, University of Washington, Seattle, WA 98195, USA
[2]Departments of Anesthesiology and Pain Medicine, University of Washington, Seattle, WA 98195, USA
[3]Department of Pharmacology, University of Washington, Seattle, WA 98195, USA
[4]Department of Bioengineering, University of Washington, Seattle, WA 98195, USA
*Correspondence: mbruchas@uw.edu
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The neurotransmitter dopamine has well-known roles in reward-seeking behaviors: a new study with mice has now revealed that dopamine signaling in the nucleus accumbens core, a region of the basal forebrain, encodes saliency during reinforcement learning.

Neuromodulation is a critical aspect of brain function. Neuromodulatory chemicals create a responsive network to integrate a variety of information sources guiding animal responses and their engagement with the environment. Dopamine, one of the first discovered neuromodulators, has drawn a long-term interest in the field of neuroscience since the 1950s. Early reports demonstrated dopamine's role in reward-seeking behaviors and resulted in dopamine being known in lay terms as 'the pleasure chemical'. Following this initial work, research has further identified the critical