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Feeling the pressure: a mechanical tale of the pollen tube journey through the pistil

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Abstract: The pollen tube grows inside the pistil to carry the male gametes to the ovule. During this journey, it invades diverse tissues and must sense and adapt to abrupt changes in its mechanical environment (mechanical transitions). In this issue, a study presents a Receptor-like-kinase/Rho-GTPase module that regulates such transition.

The pollen tube is a tip growing cell that navigates through the female tissues of the pistil to deliver the immobile sperm cells to the ovules. The pistil is a source of diffusible chemical attractants for the pollen tube (Mizuta and Higashiyama, 2018). Mechanical cues also contribute to the proper pollen tube growth and guidance (Reimann et al., 2020; Riglet et al., 2020; Sanati Nezhad et al., 2013). In *Arabidopsis*, the pollen tube has to invade a series of tissues with different mechanical properties on its path to the ovule (Figure 1). It thus encounters several sharp “mechanical transitions”, which correspond to boundary areas where the local mechanical environment of the pollen tube change drastically. For example, it first germinates on the open surface of stigmatic cells, but then penetrates the stigmatic cell walls to grow within this rigid layer, which provides guidance cues to the pollen tube (Riglet et al., 2020) (Figure 1). The pollen tube then progresses within the intercellular space of the transmitting tract (Mizuta and Higashiyama, 2018). Whereas the style transmitting tract is a compact tissue, the ovary transmitting tract is much more open as it undergoes program cell death to facilitate pollen tube passage (Crawford et al., 2007) (Figure 1). Other mechanical transitions include the pollen tube emergence from the transmitting tract into the septum, its growth on the funiculus surface (which is open on the ovary cavity), and ultimately its entrance in the narrow micropyle (Figure 1). It remains unclear how the pollen tubes sense and adapt to these drastic variations in their surrounding mechanical environment. In this issue of *Developmental Cell*, Zhou et al. (2021) describe a Receptor-Like-Kinase (RLK)/Rho-GTPase module, which allows the pollen tube of *Arabidopsis thaliana* to respond to the sharp mechanical transition encountered at the style/ovary boundary.

BUDDHA’S PAPER SEAL-1 (BUPS1) encodes a pollen-expressed RLK from the *Catharanthus roseus* RLK1L-like (CrRLK1L) subfamily, which is required for the transmission of the male gamete in *Arabidopsis thaliana* (Ge et al., 2017). The tips of *bups1*

pollen tubes rupture when enter the ovary (Zhou et al., 2021). The style/ovary boundary corresponds to a sharp mechanical transition (Figure 1), which suggests that BUPS1 might be involved in sensing or responding to changes in the pollen tube local mechanical environment. To test this hypothesis, the authors used a semi-*in-vitro* assay where wild-type pollen tubes grow within pistils cut after the style, and then elongate in a culture medium. In this system, *bups1* pollen tube tips ruptured when emerging from the cut. They also used three in planta situations (immature pistil, the pistil of *Thellungiella salsuginea*, and the pistil of the *no transmitting tract (ntt)* mutant) in which the transmitting tract of the ovary remains compact, similar to the style. Using these systems, they selectively removed the mechanical transition at the style/ovary boundary, which allowed the *bups1* pollens to elongate much deeper within these pistils. Taken together, these data suggest that *bups1* pollen tubes are fully functional in a mechanically stable environment but fail to maintain their integrity when their mechanical environment is changing.

To simulate the mechanical transition encountered by the pollen tube at the style/ovary boundary, Zhou et al. (2021) used an elegant microfluidic system with microchannels of varying diameters. This device recapitulates the mechanical situation of (i) the mature pistil (a narrow region that mimic the style followed by a wider microchannel that mimic the ovary), (ii) the immature, *Thellungiella salsuginea* or *ntt* pistils (a long narrow region) and (iii) a pressure-free control. When compared to the wild type, the *bups1* tubes elongated longer in the long narrow region and exhibited a much higher rupture frequency when emerging from a narrow region into a wider microchannel. Importantly, in a constant mechanical environment, the *bups1* and wild-type pollen tubes were identical (i.e. similar cell wall strength and composition, turgor pressure). However, only the wild-type but not *bups1* pollen tubes were able to adjust their cell wall composition upon increased tensions/decreased compression. Indeed, in the microfluidic chips, demethyl-esterified pectins accumulate at the tip of Arabidopsis wild-type pollen tubes when emerging from a narrow channel. This is thought to enhance wall rigidity thereby allowing the tip to resist to mechanical changes (Bidhendi and Geitmann, 2016). By contrast, in *bups1* pollen tubes, this accumulation is not detected, suggesting that BUPS1 might regulate demethyl-esterified pectin polar secretion and hence cell wall rigidity during this mechanical transition (Zhou et al., 2021).

Rho-of-plant-1 (ROP1) integrates tip-localized polar secretion of wall polymers and mechanics of the pollen tube (Luo et al., 2017). Zhou et al. (2021), found that the kinase domain of BUPS1 interacts with all pollen-expressed ROP Guanidine Exchange Factors (GEF), which are direct ROP1 activators. Accordingly, ROP1 activity is rapidly induced, in a BUPS1-dependent manner, upon acute tensile stress at the pollen tube tips (e.g. induced by pectinase treatment or emergence of the tube from the narrow region of the microchannel). Furthermore, when a constitutive active ROP1 is expressed in *bups1* pollen tube, it partially restored pollen tube growth and fertility. Together, these results show that BUPS1 acts upstream of GEFs/ROP1 to regulate pollen tip rigidity and support tube growth at the style/ovary boundary.

BUPS1/ROP1 not only induce local pectin secretion, but also the polar exocytosis of RAPID ALKALINISATION FACTOR-4 and -19 (RALF4/19), which are required for pollen tube

integrity during the style-to-ovary transition (Zhou et al., 2021). RALF4/19 are extracellular ligands that bind to and activate BUPS1 (Ge et al., 2017). Thus, stimulating RALF4/19 polar secretion triggers a positive feedback loop that self-amplifies BUPS1-dependent signaling at the pollen tube tips. The RALFs/BUPS1/ROP1 module could work downstream of a yet uncharacterized tensile stress sensor, such as for example RLKs, stretch-activated channels or cytoskeleton components (Bacete and Hamann, 2020). In this scenario, such unknown mechanosensor would initiate the feedback loop within the RALFs/BUPS1/ROP1 module and the self-amplifying properties of this module would then be used to execute rapid and local cell wall rearrangements. Moreover, because both RALFs and CrRLK1L receptors directly interact with cell wall components (Bacete and Hamann, 2020), it is also tempting to speculate that they could directly act as mechanosensors at the pollen tip. However, in this case, the molecular mechanisms that would enable to physically sense the mechanical stimuli within the pollen cell wall remain to be determined.

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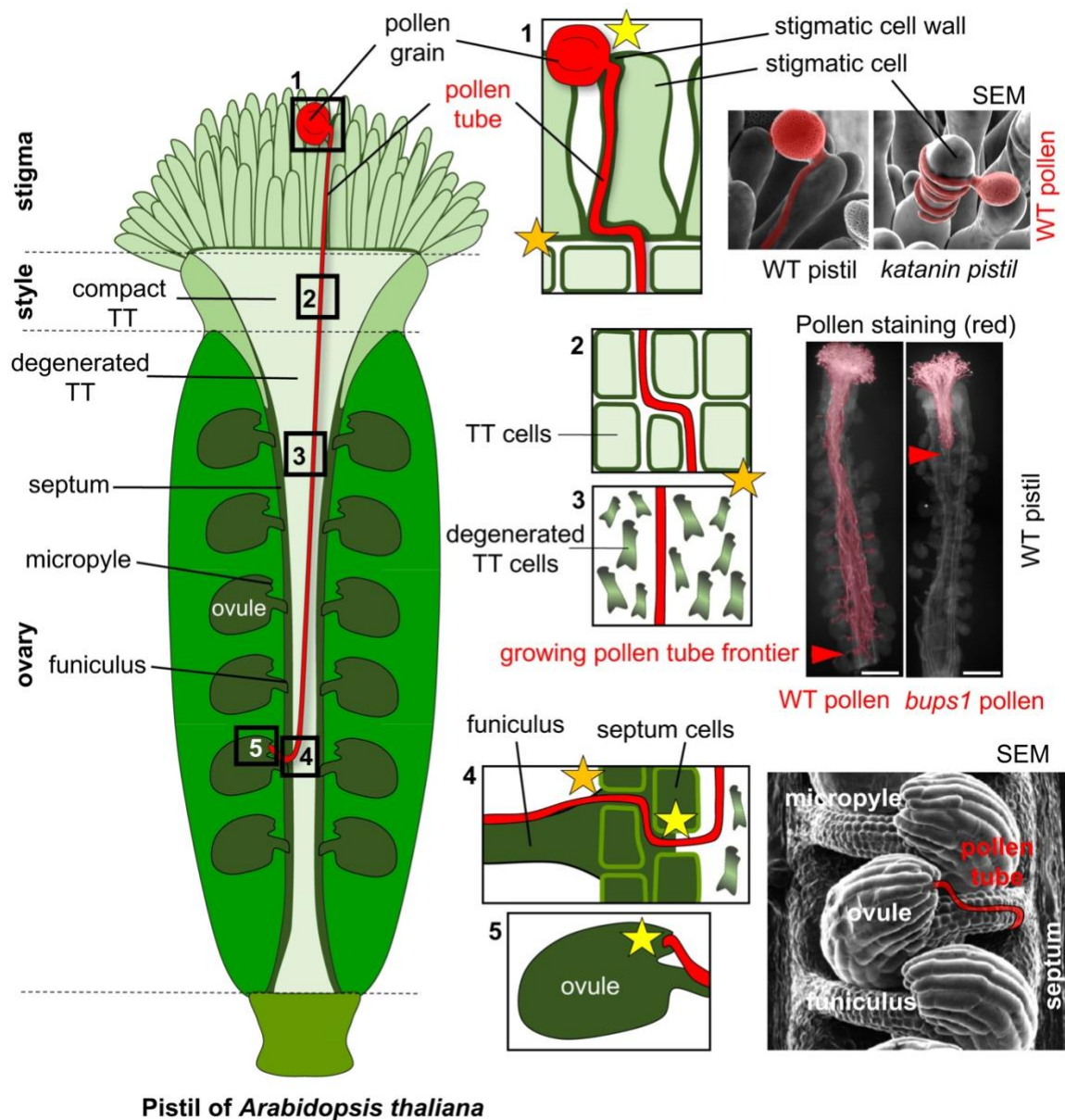


Figure 1: Mechanical transition encountered by the pollen tube on its way to the ovule. Schematic representation of an *Arabidopsis* pistil, highlighting boundary regions with “mechanical transition” (i.e. abrupt changes in mechanical environment). Yellow stars represent transition toward a higher compressive environment, orange stars represent the reverse situation. Micrographs on the right represent pollen tube growth in wild type and/or mechanically challenged mutants: *katanin* pistil or *bups1* pollens (images modified from Riglet et al., 2020; Zhou et al., 2021; Mizuta and Higashiyama, 2018). SEM: scanning electron microscopy, TT: transmitting tract.