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Research Highlight

What took you so long? Peptide-receptor kinase signaling mediates reproductive isolation in plants

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The peptide-receptor kinase-based intercellular signaling becomes an important molecular base for various aspects of plant life activities [1], particularly exemplified in the extensive molecular interactions in the journey of pollen tube growth in pistil of flowering plants [2]. Researches in the past two decades demonstrated that peptide-receptor kinase signaling complexes mediate pollen tube promotion, guidance and reception, as well as self-incompatibility and gamete fusion. A recent exciting discovery published on *Science* by Zhong et al. expands the biological functions of peptide-receptor kinase signaling to facilitating formation of a new plant species [3].

This process of pollen tube growth in pistil is known as siphonogamy, a characteristic feature of flowering plants that facilitated them to be the most common type of land plants [4,5]. It starts from the pollen grain landing on the top of pistil, and growing a pollen tube. Then, the pollen tube grows through various tissues of pistil including stigma and transmitting tract, and grows out of the transmitting tract, finally enters ovule to deliver sperm for double fertilization.

In the stage of pollen tube-stigma interaction in tomato, a pollen-specific cysteine-rich peptide LAT52 and a stigma-specific cysteine-rich peptide LeSTIG1 interact with the pollen-specific receptor kinase LePRK2 to facilitate pollen germination and promote pollen tube growth, respectively [6,7]. In the stage of pollen tube-stigma interaction in Brassicaceae, recognition of self S-locus cysteine-rich protein SCR in pollen by the stigma S-receptor kinase SRK leads to self-incompatibility [8]. After arriving at ovules, another group of cysteine-rich proteins, rapid alkalinization factors (RALFs) interact their corresponding receptors of the *Catharanthus roseus* RLK1-LIKE (CrRLK1L) family to play a critical role in controlling pollen tube reception [9,10]. Of particular interests, in the stage of pollen tube guidance in *Arabidopsis*, a group of synergid cell-specific cysteine-rich peptides AtLURE1s are attractive cues from female gametophyte to guide pollen tubes [11]. They can be perceived by pollen tube surface localized LRR receptor kinase PRK6 [12]. Intriguingly, although pollen tubes lacking PRK6 function cannot be attracted by AtLURE1s at all, they still achieve fertilization without apparent defects in fertility.

How come losing such an important function of pollen tube guidance not affecting fertilization at all? AtLURE1 family contains eight genes in Arabidopsis in total [3]. Since it has been reported that down-regulation of AtLURE1 genes did not affect fertility in *A. thaliana* in 2012 [11], people always wondered whether completely deletion of all the AtLURE1 family may show defects in fertility if redundancy was the reason for masking the fertility defects. Since then, Zhong and colleagues took a reasonably long time to successfully knock-out the entire AtLURE1 gene family, i.e., made *atlure1* septuple mutants and verified the gene mutation in the last pseudo gene. The result that the *atlure1* null mutants have no defects in fertility either let Zhong and colleagues to look for other biological defects by AtLUREs-PRK6 deletion. They found that the pollen tubes in *atlure1* null mutant pistils grew normally at early stages but delayed in growing out of transmitting tract to reach ovule. Similar delay in growing out of transmitting tract can be observed when the pollen of *Arabidopsis lyrata*, a relative species of *A. thaliana* [13], were loaded onto the stigma of *A. thaliana*, though they still can achieve fertilization. Zhong and colleagues further identified that AtLURE1s are *A. thaliana* specific. So the AtLURE1-PRK6-mediated signaling can accelerate *A. thaliana* pollen tube reaching fertilization but not pollen tubes from other compatible species such as *A. lyrata*. It took longer for *A. lyrata* pollen tubes to grow to ovule in the pistil of *A. thaliana*, provide a base to favor pollen from the same species, therefore promote reproduction isolation in compatible species. Further studies identified another group of maternal peptide XIUQIUs in *A. thaliana*, which attract pollen tubes of both *A. lyrata* and *A. thaliana*. Finally, hendecuple mutants lacking all the four XIUQIUs and seven functional AtLUREs showed reduced fertility. This concludes that communications between ovule attraction cues, including both conserved and diverse ones, and their corresponding receptors on pollen tubes can differentially accelerate pollen tube growth in the same pistil, therefore underlie reproductive isolation within Brassicaceae species (Fig. 1). Meanwhile, since the deletion of all AtLURE1s and XIUQIUs still caused only ~20% reduction of fertility, there should be other pollen tube attractants and receptors in *Arabidopsis* awaiting to be identified.

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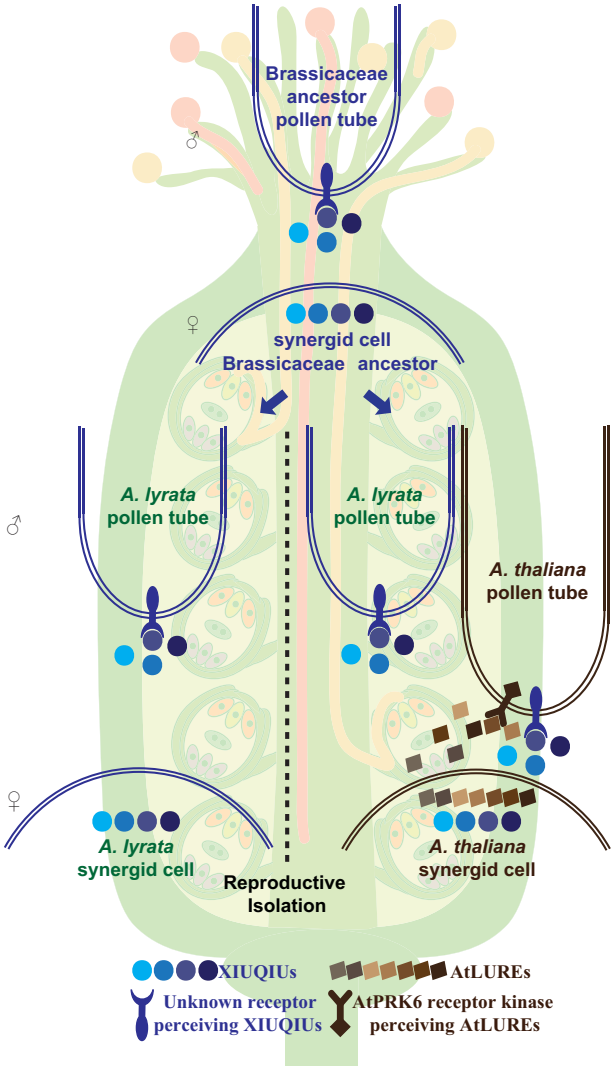

Fig. 1. The interactions of female-derived AtLUREs and their receptor PRK6 on pollen tubes contribute to reproductive isolation between *A. lyrata* and *A. thaliana*.

Reproductive isolation represents a key approach in the new species formation, and flowering plant evolved many reproductive barriers to limit genetic exchange between species [14]. The long journey of pollen tube growth from stigma to ovule has long been thought to provide enriched bases for generating reproductive isolation in flowering plants. The discovery of AtLUREs along with PRK6 promoting interspecific genetic isolation gave a perfect example. Why it took so long for *A. lyrata* pollen tubes to reach ovules in *A. thaliana* pistils? It is because *A. lyrata* pollen tubes insensitive to AtLURE1s cannot be attracted as quickly as *A. thaliana* pollen tubes. It is the speed difference between pollen tubes in growing out of the transmitting tract and reaching ovules that sped up the interspecific genetic isolation in Arabidopsis. Awaiting to see whether the same principle of diverse peptide-receptor kinase signaling promotion of reproductive isolation also apply to other steps in the journey of pollen tube growth from stigma to ovules.

The phenomenon that pollen tubes of one species are not attracted as efficiently as own pollen tubes to the ovules of another species, termed "conspecific pollen precedence", has been proposed to play a pivotal role in the reproductive isolation of closely related plants [15]. The molecular mechanism underlying this phenomenon has not been reported previously. The significant work by Zhong et al. identified AtLURE1s as the firstly-reported factors conferring conspecific pollen precedence, demonstrated that *A. thaliana* facilitating self-pollen tube emergence onto the septa and ovules through the perceiving of female-produced attractant AtLURE1s by pollen tube PRK6. In addition to the pollen species-specific attractant AtLURE1s, the presence of XIUQIUs as general pollen tube attractants might allow compatible fertilization among closely related different species, therefore some genetic exchange can occur among compatible species.

Conflict of interest

The authors declare that they have no conflict of interest.

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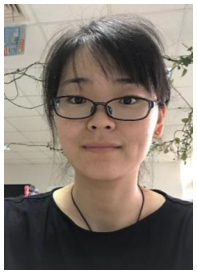

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