PLANT SCIENCES

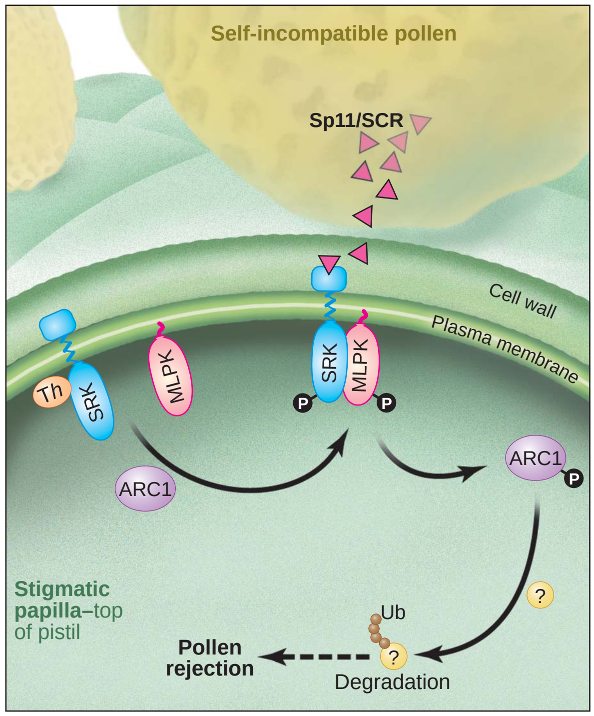
Self-Rejection—a New Kinase Connection

Daphne R. Goring and John C. Walker

Self-incompatibility is a strategy adopted by many flowering plants to reject "self" pollen, thus promoting mating between unrelated individuals. When the pollen and stigma recognize each other as being related, pollen-tube growth is inhibited and fertilization is prevented. Extensive research has unraveled the molecular and cellular pathways of pollen rejection in plants that exhibit self-incompatibility. In *Brassica*, a member of the cabbage family, self-incompatibility depends on recognition between an S receptor kinase (SRK) expressed by stigma cells and its ligand (SP11; also called SCR) present on the surface of pollen grains (*1*). This initial recognition step activates an SRK-mediated signaling pathway in the pistil that results in rejection of self pollen (see the figure). The only component identified in this pathway so far is ARC1, an E3 ubiquitin ligase (*2*, *3*). Enter Murase *et al*. (*4*) on page 1516 of this issue with their report of a new player—the *M* locus protein kinase (MLPK)—in the self-incompatibility signaling pathway of *Brassica*. Their discovery raises an intriguing new aspect of plant signaling in which a receptor kinase may work with a nonreceptor kinase to activate the signaling pathway.

The recessive *modifier* (*m*) locus in the *Brassica rapa* variety Yellow Sarson causes a complete breakdown of the self-incompatibility response in *m/m* plants (*5*). However, the *m* locus segregates independently of the self-incompatibility *S* locus (containing the tightly linked *SP11/SCR* and *SRK* genes) (*5*). Originally, the *m* locus was thought to encode an aquaporin-like protein, MIP-MOD, but this turned out not to be the case (*6*, *7*). Using map-based cloning, Murase *et al.* identified *MLPK* as the *m* gene candidate and demonstrated that mutations in this gene are responsible for the *modifier* phenotype. They identified a mutation in the *MLPK* gene that results in a loss of kinase activity in vitro as well as a complete absence of the protein in *m/m* plants. Using an innovative transient expression assay in stigmatic papillae (the receptive pistil surface for pollen grains), the authors demonstrated that expression of the wild-type *MLPK* gene restored the rejection of self pollen in the *m/m* plants.

MLPK belongs to a group of protein kinases called the receptor-like cytoplasmic kinases (RLCKs). In the model plant *Arabidopsis*, these kinases cluster phylogenetically with receptor-like kinases (RLKs) but do not contain an extracellular domain or transmembrane domain (*8*). Very little is known about the RLCKs, and MLPK is the first member of this group to be linked to a receptor kinase signaling pathway.



The self-incompatibility response in *Brassica*. In the absence of its allele-specific SP11/SCR ligand, SRK is inhibited by thioredoxin *h* (T*h*). After pollination with self-incompatible pollen, the allele-specific SP11/SCR ligand binds to SRK, resulting in recruitment of MLPK to the activated complex. Activation and phosphorylation of the SRK and MLPK domains lead to the activation of one or more intracellular signaling pathways. The signaling component ARC1, an E3 ubiquitin ligase, may be recruited to the kinase complex and activated. ARC1 then targets unknown substrates for ubiquitination (Ub) and degradation by the proteasome. The degradation of these substrates could cause pollen rejection and prevent fertilization (*1*–*4*).

Where does MLPK fit into the SRK signaling pathway? MLPK is enriched in the plasma membrane fraction derived from pistil cells. When transiently expressed in tobacco cells, it has a predicted myristoylation site required for plasma membrane localization. The complete breakdown of self-incompatibility in *m/m* *Brassica* plants indicates that MLPK is required for all SRK-mediated signaling pathways (assuming that there are multiple pathways) leading to pollen rejection. This raises the possibility that MLPK forms a signaling complex with SRK to mediate the rejection response. Typically, phosphorylation of these signaling complexes can lead to activation of the kinase partner and establishment of binding sites for downstream signaling components. In this model, ARC1 may operate downstream of the SRK-MLPK complex (see the figure). Suppression of ARC1 activity with the expression of an antisense cDNA causes a partial breakdown in the self-incompatibility response (*2*). The incomplete breakdown of this response implies that there may be a branch in the signaling pathway after the SRK-MLPK complex. However, it is also very likely that the incomplete breakdown phenotype is due to partial RNA suppression in the antisense transgenic plants or to some functional redundancy with other related E3 ubiquitin ligases. Interestingly, the introduction of related *Arabidopsis lyrata SP11/SCR* and *SRK* genes into *A. thaliana* elicits a self-pollen rejection response for a brief period after flowering (*9*). *A. thaliana* has an MLPK ortholog that is closely related to the *Brassica* MLPK (*4*), and has more distantly related ARC1 orthologs (*10*) that may participate in SRK-mediated signaling.

D. R. Goring is in the Department of Botany, University of Toronto, Toronto, M5S 3B2, Canada. J. C. Walker is in the Division of Biological Sciences, University of Missouri–Columbia, Columbia, MO 65211, USA. E-mail: goring@botany.utoronto.ca

CREDIT: KATHARINE SUTLIFF/*SCIENCE*

The notion of plant receptor kinases working with nonreceptor kinases in heteromeric complexes has emerged in other systems. The kinases in the heteromeric complexes can both be receptor kinases. For example, the BRI1 leucine-rich repeat receptor kinase detects the plant hormone brassinosteroid (*11*). Recently, an activation-tagging screen (*12*) and a yeast two-hybrid analysis (*13*) in *Arabidopsis* identified the receptor kinase BAK1 as a BRI1-interacting protein. Genetic and biochemical analyses suggest that the formation of BRI1-BAK1 heterodimers is required for brassinosteroid signaling (*12*, *13*). Another example is provided by the NFR1 and NFR5 LysM receptor kinases identified in a screen for legume mutants with defects in rhizobial symbiosis and nodulation (*14*). To recognize Nod factors, NFR1 is proposed to form a heterodimer with NFR5, which is missing the activation loop in the kinase domain (*14*).

The Murase *et al.* work presents a new scenario in which receptor kinases cooperate with plasma membrane–localized RLCKs. Perhaps this will become a common theme in plant receptor kinase signaling and certainly would account for the large number of RLCKs and RLKs found in plant genomes (*8*). Future studies will need to address the precise biochemical and cellular relationships among SRK, MLPK, and ARC1 in the plant self-incompatibility response.

References
1. S. J. Hiscock, S. M. McInnis, *Trends Plant Sci.* **8**, 606 (2003).
2. S. L. Stone, M. Arnoldo, D. R. Goring, *Science* **286**, 1729 (1999).
3. S. L. Stone, E. M. Anderson, R. T. Mullen, D. R. Goring, *Plant Cell* **15**, 885 (2003).
4. K. Murase *et al.*, *Science* **303**, 1516 (2004).
5. K. Hinata, K. Okazaki, T. Nishio, *Proc. 6th Int. Rapeseed Conf.* **1**, 354 (1983).
6. S. Ikeda, J. B. Nasrallah, R. Dixit, S. Preiss, M. E. Nasrallah, *Science* **276**, 1564 (1997).
7. E. Fukai, T. Nishio, M. E. Nasrallah. *Mol. Genet. Genomics* **265**, 519 (2001).
8. S. H. Shiu, A. B. Bleecker, *Proc. Natl. Acad. Sci. U.S.A.* **98**, 10763 (2001).
9. M. E. Nasrallah, P. Liu, J. B. Nasrallah, *Science* **297**, 247 (2002).
10. Y. Mudgil, S. H. Shiu, S. L. Stone, J. N. Salt, D. R. Goring, *Plant Physiol.* **134**, 59 (2004).
11. J. Li, J. Chory, *Cell* **90**, 929 (1997).
12. J. Li, J. Wen, K.A. Lease, J. T. Doke, F. E. Tax, J. C. Walker, *Cell* **110**, 213 (2002).
13. K. H. Nam, J. Li, *Cell* **110**, 203 (2002).
14. S. Radutoiu *et al.*, *Nature* **425**, 585 (2003).

PHYSICS

The Cup of the Hand

R. B. Laughlin

There is a memorable scene in the Japanese animé classic *Akira* in which two young protagonists are in a jail cell discussing the nature of the universe (*1*). They have a good excuse for doing so, for one of their school chums is at that very moment gleefully laying waste to Tokyo just by thinking about it, a victim of a powerful overdose of akirahood administered by reckless military surgeons. Amid the peeling paint and dripping water of their prison they come to grips with their friend's terrible fate and the incomprehensible violence they have just witnessed—and will shortly witness redoubled and redoubled again—through an existential discussion of worlds within worlds not so different from what one might overhear late at night in a freshman dormitory. Their conversation reveals that the horror outside was made possible by a government research project into the ultimate power animating all things, which subsequently escaped and was rapidly leading to destructive rebirth of the universe. The latter actually comes to pass in the film, but a brave intervention by three other victims of the program at the last minute causes the new universe thus created to consolidate itself into a tiny luminous marble, which then drifts into the cup of the hero's hands and vanishes.

In discussing cosmic matters it is impossible not to draw analogies with science fiction art from time to time, for the issues are as large as those depicted in such films and equally mysterious, despite being experimentally constrained. Our knowledge of the cosmos is still very primitive, and much of our thinking about it correspondingly speculative, more along the lines of what might plausibly have been than what is so. Plausibility is an interesting concept in theoretical physics, usually amounting to either a physical analogy with something observed to occur elsewhere in nature or a mathematical extrapolation of microscopic law. The latter, however, is actually a shibboleth, for the things that matter are nearly always collective organizational phenomena that cannot be reliably predicted from microscopics. The shapes of galaxies and the behavior of cosmic jets are simple cases in point, but the observation also applies to the grandest issues of modern cosmology: inflationary expansion and the hierarchical consolidation of matter after the big bang (*2*–*4*) . The absence of predictive power is actually self-evident, because there would be no point in measuring these things if one could calculate them. As a practical matter, all plausibility arguments that count are analogies.

It may seem shocking to speak of the vacuum of space-time as an organizational phenomenon, but this is actually just a matter of semantics. The idea behind the words is mainstream and fully consistent with the facts. It has been known since the 1950s, and routinely verified by accelerator experiments since then, that empty space is a kind of matter quantum-mechanically similar to a rock (*5*). The standard model of elementary particles is grounded firmly on the idea of space as a phase. A multiplicity of such phases and a complex sequence of transitions among them in the early universe are cornerstones of modern particle cosmology. The existence of such phases is implicated in the structure one sees on intergalactic scales, and the heat released in the transition between two of them is the ostensible power source of inflation. Inflation itself is partly motivated by these phases, because they make the observed uniformity of the universe unnatural and something requiring explanation.

The semantic incongruity, however, like the sublimated worries about modern life that give us science fiction nightmares, belies something important—unfinished business of the 1970s that has been slowly and systematically tearing physics apart (*6*, *7*). Stripped of their confusing mathematical descriptions, the phases of the vacuum boil down to physical analogies with phases of ordinary matter, natural phenomena observed to exhibit universality. That means that their properties at long length and time scales, where we normally do experiments, do not depend on microscopic details at all, and thus do not constrain them when measured. A simple example of emergent universality would be sound propagation in fluids and solids, an effect perfectly well accounted for as the motion of atoms, but also a generic property of the phases not requiring atoms to make sense. Sound is an especially pertinent example because it has a second identity at low temperatures as an emergent elementary particle with properties identical to those of particles of light. In-sensitivity to microscopic detail thus

The author is in the Department of Physics, Stanford University, Stanford, CA 94305, USA. E-mail: rbl@large.stanford.edu