context of general relativity results in a repulsive gravitational force. The measurements of accelerated expansion (*1*) are consistent with the energy density of the vacuum (or the cosmological constant) contributing about 70% of the total cosmic energy density. Current theories cannot explain the value of 70%, but it is consistent with recent measurements of the anisotropy of the cosmic microwave background, which suggest that the matter and vacuum energy together account for an amount close to the critical density that makes the universe geometrically flat (*9*).

One may ask whether the supernovae may somehow fool us into believing that we are observing accelerated expansion. The observed effect is simply that the more distant supernovae are dimmer than expected by about 25%; could this dimming be caused by other effects than accelerated expansion? This is a very relevant question, particularly in view of the fact that the precise progenitor systems of SNe Ia are not known. There is strong evidence that the exploding star is an accreting white dwarf, but the nature of the companion star is not known. The cannibalized star could be another white dwarf that merges with the "hungry" object, or it could be a normal star. Is it conceivable that nearby SNe Ia are formed by one type of system, whereas the more distant supernovae are formed by the other type? This could result in a systematic difference between the nearby and the distant samples, which could provide an alternative interpretation of the data. Recent theoretical work indicates, however, that it is not very likely that the nearby and distant populations of SNe Ia are dominated by different progenitor classes (*10*). Detailed calculations show that dominance by two separate classes would have resulted in a larger diversity in the local sample of SNe Ia than is observed.

Another potential alternative to accelerated expansion could be obscuration by dust. But in that case, one would expect the distant supernovae to appear redder, because dust grains filter blue light more than red, as they do during sunsets on Earth. This is not observed (*1*).

More observations of distant SNe Ia, and more theoretical work on the nature of their progenitors and on other potential evolutionary effects, will be required before one can safely conclude that the cosmic expansion is indeed accelerating (*11*). Observations of SNe Ia at higher redshifts will be particularly important. When the universe was half its present age, gravity in the denser universe must still have had the upper hand over the cosmological constant, and the expansion should have been decelerating at that time. A direct observational confirmation of this transition from slowing down to speeding up would be very difficult to mimic by evolutionary or other systematic effects, and the accelerated expansion would thus be confirmed.

Once the Next Generation Space Telescope (NGST) is launched in 2008, detection and identification of SNe Ia at even higher redshifts will become possible. At these distances, the difference between a universe dominated by matter and one dominated by the cosmological constant will become crystal clear (see the figure).

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PERSPECTIVES: PLANT BIOLOGY

No Stigma Attached to Male Rejection

Hugh Dickinson

Flowering plants are a very successful group thanks to a combination of hermaphrodite flowers and self-incompatibility (SI), that is, the ability to recognize and reject their own pollen (*1*). There are two SI characteristics that are common to all plants: the generation of a male signal by pollen and the growth arrest of self pollen that lands on its own female stigma. However, the mechanisms underlying these characteristics remain unclear. Now, two papers in this issue shed light on SI in members of the *Brassica* (cabbage) family. Schopfer *et al.* on page 1697 (*2*) characterize the male recognition protein produced by pollen (SCR); and Stone and colleagues on page 1729 (*3*) identify one of the earliest components of the self-pollen rejection pathway, ARC1.

When it comes to pollination, plants face a paradox. Individual plants are anchored, relying on wind, insects, and other vectors to deliver pollen to other plants of the same species. Thus, characteristics that maximize the delivery of pollen to the stigmas of other plants have been selected for in evolution. Unfortunately, these same characteristics, combined with hermaphrodite flowers (admittedly an excellent strategy for accelerating gene flow), conspire to promote self-pollination. This in turn leads to restriction of gene flow and inbreeding. Plants have responded to this challenge by developing mechanical devices to prevent self-pollination, by having sex organs arranged far apart or sex organs that mature at different times. Recently, it has become evident that some plants are able to identify and reject their own pollen. This selective pressure on plants to outbreed (that is, not to self-pollinate) is so great that there exist at least five different mechanisms of SI (*4*). Advanced genera, such as the grasses, crucifers, and composites, are able to reject self pollen as soon as it lands on the dry surface of the female stigma; other plant groups allow all pollen to germinate in the stigma's wet secretion, and then identify and reject the self pollen tubes after they have penetrated the tissues of the style.

Many of the SI components in the female part of the flower (the carpel, stigma and style) have been identified, whereas those in the male part (anther) have not. Luckily, the genetics regulating SI are comparatively simple. For example, in the Solanaceae (the family that includes tobacco, potato, and tomato plants), SI is controlled by a single multiallelic (*S*) locus—the haploid pollen carries one allele and the diploid stigma, two. If the pollen and stigma share an allele (of which there are commonly up to 50), the pollen is

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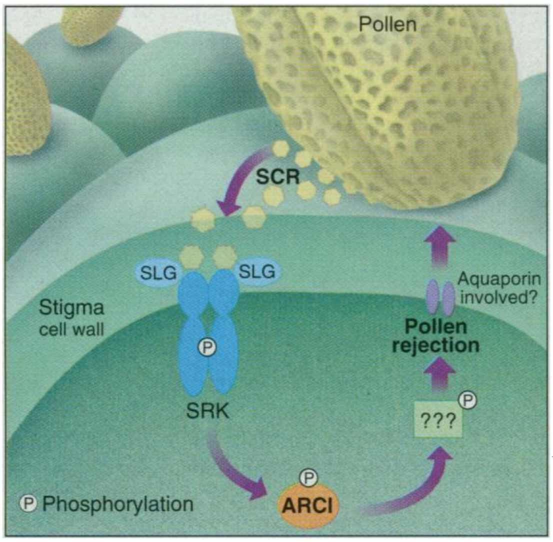
rejected. Conversely, if the pollen has an *S* allele that differs from the *S* alleles of the stigma, the pollen will be accepted. The *S* locus in this group is known to encode an allele-specific ribonuclease that is expressed only in the female tissues of the flower (*5*, *6*). Of course, another gene is required at the *S* locus for male specificity, and this has yet to be identified. Similarly, in the poppy family, the stigma secretes an S protein that binds to an S-binding protein on the surface of the pollen tube. The male S determinant remains elusive as the S-binding protein seems to be a presenting agent and not the determinant itself. Nevertheless, the development of an in vitro assay in poppy has enabled key features of the self-pollen rejection mechanism—the signaling molecules involved, the release of cytosolic calcium ions, and apoptosis of the rejected pollen tube—to be elucidated (*7*).

The SI mechanisms in either the grasses or the composites, have not been identified despite their great commercial importance. But a good deal is known about SI in the crucifers, particularly in the brassicas. Their SI is unusual because, instead of the arrest of pollen tube growth after secretion of a protein by the stigma or style, pollen development is arrested by the stigma cells at a very early stage. (This is reminiscent of the rejection of fungal pathogens by epidermal cells of the plant host) (*8*).

The *S* locus in brassicas is known to encode two key stigma proteins that together form an S receptor complex. These are the S receptor kinase (SRK) in the stigma cell plasma membrane, and the *S* locus glycoprotein (SLG), in the stigma cell wall (*9*). The receptor complex interacts with a factor secreted by pollen that induces autophosphorylation of SRK, phosphorylation of other stigma proteins, and activation of self-pollen rejection (see the figure) (*10*). Schopfer *et al.* (*2*) identify the SCR (*S* locus cysteine-rich) protein as the pollen factor in *Brassica* and suggest that it is a ligand for the S receptor complex.

Genetics suggests that *Brassica* pollen carries two *S* alleles, which it clearly cannot. Of course, it may carry two allelic products, but these would have to be transferred from the parent plant to the pollen grain during development (*11*). Swapping pollen coats (secreted by cells of the parent plant) between pollen grains, and fractionating the coating itself revealed that male specificity in *Brassica* is conferred by a member of a family of highly charged, cysteine-rich pollen coat proteins (PCPs) (*12*). Members of this highly polymorphic family bind specifically to proteins encoded by the female *S* locus (*13*), but none of the *PCP* genes cloned so far either segregate with the *S* locus or are polymorphic between *S* alleles (*13*). Furthermore, all *PCP* genes are expressed from the genome of the pollen grain itself (not that of the parent plant), even though the proteins they encode were isolated from the parentally derived pollen coat.



A little style goes a long way. Recognition and rejection of self pollen in *Brassica*. Male pollen grains that land on the female stigma secrete SCR, a small cysteine-rich protein that passes through the stigma cell wall. If a pollen grain is from the same plant, the protein it secretes is able to bind to the S receptor complex in the stigma cell plasma membrane. This complex is composed of the S receptor kinase (SRK) and the *S* locus glycoprotein (SLG). Binding of SCR results in autophosphorylation of SRK and phosphorylation of ARC1, the first component in the self-pollen rejection pathway.

Adopting an alternative strategy, Schopfer and colleagues mapped the massive *S* locus for a number of *Brassica* alleles and "walked" through it, identifying and characterizing all genes expressed in the male anther. One gene, *SCR*, turned out to have all the assets necessary for encoding a male determinant. It is a close neighbor of *SRK* on the *S* locus, and is highly polymorphic (variable) between *S* alleles. Most conclusively of all, when *SCR* was transferred between plants by genetic engineering, pollen *S* specificity was also transferred.

The *SCR* gene encodes a highly charged pollen coat protein that is similar to the PCPs already identified. Also, like the PCPs, SCR is synthesized by pollen grains. But it is not clear how the pollen coat protein can be the product of two *S* alleles if it is made by the haploid pollen grains. Researchers working on PCPs have proposed a mechanism to explain how two polypeptides encoded by two *S* alleles segregating with pollen grains in a particular anther could be secreted and incorporated onto the pollen surface as a protein mixture (*13*). Such a model might be applicable to SCR production.

A stigma cell is capable of discriminating between two pollen grains, one self and one cross, placed touching each other on its surface. The cross grain will germinate and penetrate the style tissues within 40 minutes, whereas the self pollen barely begins to germinate (*14*). Self-pollen rejection requires protein synthesis in the stigma (*15*), and can be overcome by high humidity, which stimulates rapid pollen germination. Analysis of self-compatible mutants suggests that the self-pollen rejection mechanism may involve the participation of a specific aquaporin (water transport channel) (*16*).

In their study, Stone *et al.* (*3*) investigated the stigma proteins that interact with the kinase domain of SRK. Of three candidate proteins one, ARC1, became phosphorylated on binding SRK (*10*). Encouragingly, ARC1 is expressed in the stigma, but until now evidence for its involvement in SI has been circumstantial. These investigators report the use of antisense oligonucleotides to block expression of ARC1 in *Brassica*. Strikingly, both pollination and seed set studies showed that the SI system broke down in plants that did not express ARC1, confirming ARC1 as a key component of the self-pollen rejection response. Of course, how the activation of ARC1 is linked to the interruption of the stigma's water supply to the pollen grains remains to be determined.

The new work will promote future studies to address many unanswered questions. Which SI mechanisms operate in other species with dry stigmas? What is the perplexing, but commercially important, relationship between self- and interspecific incompatibility? And, perhaps most challenging of all, how did these complex self-recognition and self-rejection mechanisms evolve (*17*).

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