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The Molecular Mechanism of Self-Recognition in *Brassica* Self-Incompatibility

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1. Introduction

Many flowering plants have self-incompatibility (SI), the system which prevents self-fertilization. Some species have heteromorphic SI and some have homomorphic SI. The homomorphic SIs of some species are controlled by a single locus, and those of the other species are controlled by multiple loci. In all the homomorphic systems, SI is controlled by a multiallelic locus (loci) and pollen is rejected by pistils having the same alleles. In the single locus system, the locus is designated as *S*. There are two systems of SI: gametophytic SI and sporophytic SI. In gametophytic SI, the *S* genotype of pollen is determined by the *S* genotype of pollen itself. SIs of Solanaceae, Rosaceae, Scrophulariaceae and Papaveraceae are of this type. On the other hand, in sporophytic SI, the *S* genotype of pollen is determined by the *S* genotype of the pollen-donor plant. SIs of Brassicaceae, Asteraceae, and Convolvulaceae are of this type. Interestingly, the molecular mechanisms of SI are different even within the same type. The key molecule in the SI systems of Solanaceae, Rosaceae, and Scrophulariaceae is RNase (Anderson *et al.*, 1986 ; Ai *et al.*, 1990; Xu *et al.*, 1990; Tsai *et al.*, 1992; Broothaerts, *et al.*, 1995; Sassa *et al.*, 1996; Xue *et al.*, 1996; Richman *et al.*, 1996; Ishimizu *et al.*, 1998; Ushijima *et al.*, 1998). On the other hand, that of Papaveraceae is not an RNase (Foote *et al.*, 1994). Similarly, that of *Brassica* is a receptor protein kinase (Stein *et al.*, 1991), but that of Convolvulaceae does not appear to be a receptor protein kinase (Kowyama *et al.*, 1995). It would be interesting to know how these species evolved such diverse SI systems.

Brassica oleracea and *B. rapa* have the same SI system involving a receptor protein kinase (Stein *et al.*, 1991; Goring and Rothstein, 1992; Watanabe *et al.*, 1994; Yamakawa *et al.*, 1995). *Raphanus*, genus relatively close to *Brassica*, also have the same system (Sakamoto *et al.*, 1998), but it has not been demonstrated that this is true for more distantly related species. However, a recent study of mapping around the *S* locus genes of *Brassica* and its homeolog in *Arabidopsis thaliana*, a self-compatible species in Brassicaceae, demonstrated that the *S* locus had been deleted in *Arabidopsis thaliana* (Conner *et al.*, 1998), suggesting that the ancestor of this species had the same SI system as *Brassica*. The receptor protein kinase SI system is thought to be distributed among species in Brassicaceae.

After the isolation of cDNA clones for SLG, *S*-locus glycoprotein, and SRK, *S*-locus receptor kinase (Nasrallah *et al.*, 1985; Stein *et al.*, 1991), which are thought to be the key molecules in the *Brassica* SI, more and more information, especially that obtained by molecular biological/genetical approaches, has been accumulated. In this article, we review the recent reports concerning the molecular mechanism of *Brassica* SI.

2. Findings of SLG and SRK

In *Brassica*, the recognition and rejection of self-pollen occur on the stigma surface: the pollen tube development of self-pollen is specifically inhibited on stigmas (**Fig. 1**). Therefore, the *S* locus product involved in the recognition in SI should be expressed in stigmas. The first molecule found as a possible *S* locus product is SLG (Nishio and Hinata, 1977; Nasrallah *et al.*, 1985). SLG is a soluble glycoprotein of 55-65 kDa. It is synthesized at a high level in stigmas just before flowering. This is consistent with the stage at which stigmas express SI. SLGs have high polymorphism in their pIs and this polymorphism is perfectly co-segrigated with their *S* genotype. The second one is SRK (Stein *et al.*, 1991). SRK is a putative transmembrane receptor kinase with intrinsic serine/threonine kinase activity (Goring and Rothstein, 1992; Stein *et al.*, 1993). The extracellular putative ligand-binding domain (the S domain) shows high homology to SLG and is also highly polymorphic. The polymorphism is also linked to the *S* locus. Since both SLG and SRK proteins are synthesized

predominantly in stigmas, not in pollen (Stein *et al.*, 1996), they have been thought to function in stigmas. Transgenic experiments seem to support this (Shiba *et al.* 1995, Conner *et al.*, 1997). A transgenic line, in which gene expression of both SLG and SRK were suppressed, showed no phenotypic change in pollen although its stigmas became compatible with pollen of original non-transgenic plants. Therefore, a gene distinct from *SLG* and *SRK* is thought to function in pollen (the pollen *S* gene). Consistent with this, a self-compatible pollen-part mutant in *B. oleracea* was reported by Pastuglia *et al.* (1997a). The pollen *S* gene should be located in the *S* locus, because if *SRK* and the pollen *S* gene are not co-segregated, the SI would be broken down. Therefore, the *S* locus is thought to harbor at least three genes, i.e. *SLG*, *SRK*, and the pollen *S* gene. '*S* alleles' of the *S* locus are now termed *S* haplotypes'.

SLG and the S domain of SRK have basically the same structure. They have twelve cysteine residues which are almost completely conserved and three hypervariable regions (**Fig. 2**). The conserved cysteine residues are thought to be important for the structure of SLG and the S domain of SRK. The hypervariable regions are thought to be responsible for the recognition in SI. A recent paper reported that the hypervariable regions of S-RNase, which is the style *S* gene in Solanaceae, is responsible for the determination of the self recognition specificity (Matton *et al.*, 1997).

3. Classification of SLG and SRK

The presence of 50 *S* haplotypes in *Brassica oleracea* and 30 in *B. rapa* has been reported to date. Each *S* haplotype has a different SLG and a different SRK. The *SLG* alleles and *SRK* alleles are classified into two classes, class I and class II, according to their sequence homologies. The homologies of amino acid sequences of class I SLGs to those of class II SLGs are ~70%. The S domains of class I SRKs show high homology to class I SLGs and those of class II SRKs high homology to class II SLGs. The *S* haplotypes with the class I SLGs have class I SRKs, and the *S* haplotypes with the class II SLGs have class II SRKs. Thus, the *S* haplotypes can be classified by the homology of their SLGs and SRKs into class I *S* haplotypes and class II *S* haplotypes. It has been claimed that an *SLG* allele is particularly similar to the *SRK* allele of the same *S* haplotype (Stein *et al.*, 1991). This has been widely accepted, but we observed several exceptions to this rule (Kusaba *et al.*, 1997 ; Kusaba and Nishio, 1999), which will be discussed later.

In *B. oleracea*, most of the *S* haplotypes belong to class I, while only three belong to class II (Okazaki *et al.*, in press). Similarly in *B. rapa* and *Raphanus sativus*, the majority are the class I haplotypes (Hatakeyama *et al.*, 1998b, Sakamoto *et al.*, 1998). The class II haplotypes are basically thought to have weak SI (Nasrallah *et al.*, 1991). All of the class II haplotypes in *B. oleracea* (Thompson and Taylor, 1966) and *B. rapa* (Hatakeyama *et al.*, 1998a) are recessive in pollen to the class I haplotypes. The class II haplotypes are therefore called recessive-type haplotypes. However, it should be noticed that some of the class II haplotypes are co-dominant with the class I *S* haplotypes in stigmas.

The most intensively investigated *S* haplotype of the class II *S* haplotypes is S^2 in *B. oleracea*, which is thought to be a typical class II haplotype. The S^2 haplotype has a unique *SLG*. The class I *SLG* has no intron, while SLG^2 has an intron and a second exon which encodes a transmembrane domain. SLG^2 produces two alternative products: a soluble protein from unspliced mRNA and a membrane-anchored protein from spliced mRNA (Tantikanjana *et al.*, 1993). However, class II SLGs of *B. rapa* do not have transmembrane domains (Hatakeyama *et al.*, 1998b) : the second exons of SLG^{40} and SLG^{44} encode only four amino acid residues and SLG^{29} encodes only eight. The four amino acid residues of SLG^{40} and SLG^{44} are common in SLG^5 of *B. oleracea* (Scutt and Croy, 1992). The only SLG with a transmembrane domain reported so far is SLG^2. This indicates that the S^2 haplotype is not a typical class II haplotype.

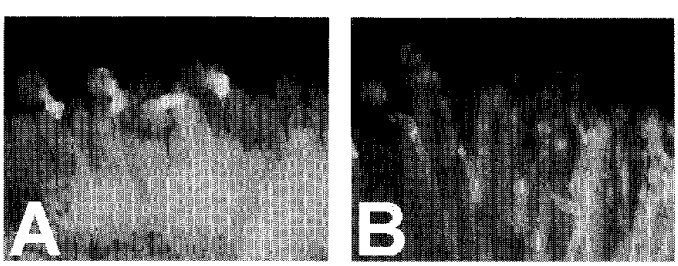

Fig. 1 Pollen tube development 24 hours after pollination in *Brassica*. A; self pollination. B; cross pollination.

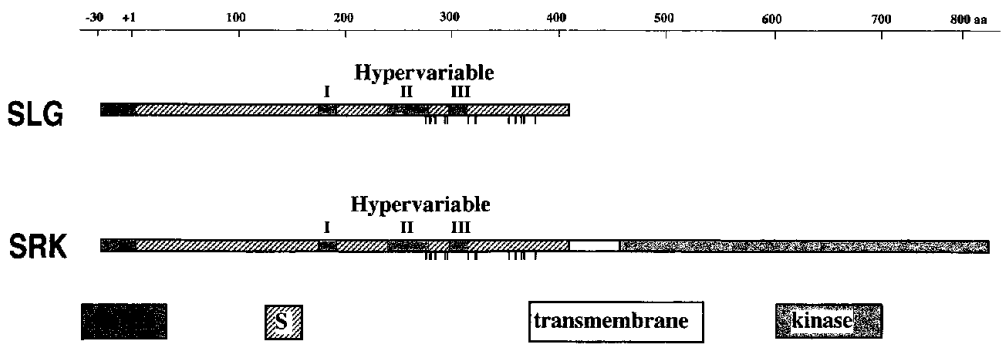

Fig. 2 The structures of class I SLG and SRK. Three hypervariable regions are located in SLG and the S domain of SRK. The short vertical lines under SLG and the S domain of SRK indicate the conserved twelve cysteine residues.

4. Self-Recognition Specificity

4. 1 SLG and SRK

To date only two highly polymorphic genes in the *S* locus complex are known: *SLG* and *SRK*. They are believed to function in the recognition reaction in SI concertedly. The observation that SLG and the S domain of SRK of the same *S* haplotype are especially similar appears to be consistent with this because SLG and the S domain of SRK of the same *S* haplotype are thought to interact with the same pollen *S* product. However, we demonstrated that SLG and the S domain of SRK were not necessarily that similar in some *S* haplotypes and that some *SLG* alleles from different *S* haplotypes show very high similarity and their hypervariable regions are identical, which is thought to be responsible for self-recognition specificity (Kusaba *et al.*, 1997; Kusaba and Nishio, 1999). Initially, we speculated that SLG and the S domain of SRK recognize different sites of the same pollen ligand and that the combination of SLG and SRK defines the self-recognition specificity. However, further observations suggested another possibility. In the S^{24} haplotype of *B. oleracea*, SLG was not detected by protein gel blot analysis and only one band was detected by DNA gel blot analysis using SLG^{12} as a probe in any digestions of three different restriction enzymes (Okazaki *et al.*, in press). Reprobing with a kinase probe revealed that the band is of *SRK*. These findings suggest that this haplotype harbors only *SRK*. *S* haplotypes which do not possess SLG detectable by isoelectric focusing analysis have been reported (Okazaki and Hinata 1984). Gaude *et al.* (1995) observed that the amount of SLG and the strength of SI are not correlated in class II haplotypes. These observations call into question whether SLG has an essential role in SI.

On the other hand, however, some observations appear to indicate that SLG is essential for SI. For example, in a sense-cosuppression experiment (Conner *et al.*, 1997) and an anti-sense experiment (Shiba *et al.*, 1995) using *SLG*, the reduction of the expression of *SLG* seemed to cause self-compatible phenotypes. However, in these transgenic plants, the expression of *SRK* was also reduced because of its high homology to *SLG* (Conner *et al.*, 1997). Another piece of evidence for the function of SLG in SI was forthcoming from the analysis of a self-compatible mutant (Nasrallah *et al.*, 1992). In that mutant (*scf*), the expression of *SLG* was reduced but that of *SRK* was not. *scf* was found not to be linked to the *S* locus, suggesting that it is a trans-acting factor. Consistent with this, the expression of *SLR1* (S Locus Related 1) and *SLR2*, which have similar expression patterns to that of *SLG* but unlinked to the *S* locus (Lalonde *et al.*, 1989; Boyes *et al.*, 1991), was also reduced in the *scf* mutant. The self-compatibility of this mutant could be caused by (an) other genes, whose expression is suppressed by the *scf* mutation. These facts mean that there is no good evidence for the function of SLG in SI.

Findings of transgenic experiments do not necessarily suggest that SLG is involved in SI, but do suggest that (a) genes which have sequences similar to *SLG* are involved in SI. If *SLG* does not function in SI, the most likely candidate for the molecule, the suppression of which caused the self-compatible phenotype in the transgenic experiments, is *SRK*. Unlike SLGs, none of the S domains of SRKs are similar to those in other *S* haplotypes (Nishio *et al.*, in preparation). Transgenic experiments using mutated SRK suggested that SRK is involved in the signal transduction pathway of SI (Stahl *et al.*, 1998). A spontaneous self-compatible mutant has a non-functional SRK, supporting the hypothesis that SRK is involved in SI (Nasrallah *et al.*, 1994). Therefore, it appears very likely that SRK is a determinant of self-recognition specificity.

The S domain of SRK is thought to be responsible for recognition in SI because SRK has a kinase domain very similar to that of another *S* haplotype (Kusaba and Nishio, 1999). The pollen *S* product has not been identified yet, but is thought to be a ligand for

SRK. Therefore, the hypervariable regions could be binding sites for the pollen ligand. It is thought that an *S* haplotype-specific ligand from self-pollen triggers the signal transduction pathway for SI. However, whether SRK is the sole determinant of self-recognition specificity in stigmas should be examined by a gain-of-function transgenic experiment, to determine if SRK donates a new specificity.

4.2 Pollen S product

The pollen *S* gene, which is thought to encode a ligand for SRK, should have at least three properties as follows. First, the gene should be located in the *S* locus as previously discussed. Second, it should be sufficiently polymorphic. Since, basically, each *S* haplotype has evolved independently, the *S* locus genes could slightly vary between the *S* haplotypes even if they are not involved in SI. The pollen ligand genes should be sufficiently variable to represent different specificities. Third, it should be expressed specifically in the anthers. However, based on the sporophytic manner of *Brassica* SI, the exact expression stages of the pollen *S* gene have been debated for a long time. Pandy (1970) suggested that the pollen *S* gene is expressed premiotically. Heslop-Harrison *et al.* (1974) suggested that the pollen *S* gene product is synthesized in the tapetum (diploid cell) and transferred to pollen exin after the degradation of tapetum cells. Doughty *et al.*, (1998) suggested that the pollen *S* gene products are produced in pollen grains gametophytically, are mixed outside the pollen, and accumulate on the surface of the pollen.

To isolate the pollen *S* product, several approaches have been utilized, one of which is the isolation of protein which binds to SLG. Stephanson *et al.* (1997) showed that the application of a pollen coat fraction with a MW less than 10 kDa to the surface of the stigma caused *S*-specific inhibition of pollen hydration, suggesting that the pollen *S* product is in the pollen coat and that it is a small molecule. PCP-A1 (Pollen Coat Protein A1) has been identified as a highly basic 7 kDa protein which binds to SLG (Doughty *et al.*, 1993). The pollen coat fraction mentioned above includes PCP-A1, which is expressed specifically in pollen grains at the binucleate/trinucleate stage and has a little polymorphism between different *S* haplotypes. However, *PCP-A1* is not linked to the *S* locus, indicating that *PCP-A1* is not the pollen *S* gene (Doughty *et al.*, 1998). PCP-A1 shows similarity to defensins and is part of a large multi-gene family with other PCPs (Stanchev *et al.*, 1996). For example, PCP1, which is closely related to PCP-A1, does not bind to SLG. Thus, each PCP appears to have a distinct function, and the possibility that a gene for PCP in the *S* locus functions as the pollen *S* gene cannot be excluded.

From a genetic point of view, positional cloning can be applied to isolate the pollen *S* gene. The size of the *S* locus complex is not known but has been estimated to be ~500 kb in *B. oleracea*, the distance between *SLG* and *SRK* has been reported to be 20-200 kb (Boyes *et al.*, 1993; Yu *et al*, 1996). Boyes *et al.* (1995) reported *SLA* (S Locus Anther gene) to be the first candidate for the pollen *S* gene isolated by positional cloning. *SLA* is located very near *SLG* of the S^2 haplotype, suggesting that it is an *S*-locus gene. Its expression is anther-specific and, interestingly, seems to also be regulated by a natural anti-sense transcript. They could not find any homologous genes in other *S* haplotypes by DNA gel blot analysis, but they speculated that there is great diversity between *S* haplotypes and that the low homology prevents the detection of other *SLA* alleles in the analysis. Thus, according to their claim, *SLA* meets the requirements as a candidate for the pollen *S* gene. However, it has been recently reported (Pastuglia *et al.*, 1997b) that a self-incompatible *B. oleracea* line has a non-functional *SLA*: it is interrupted by a transposon and no detectable expression was observed by RNA gel blot analysis. Kusaba *et al.*, (in preparation) observed that *SLA* was not found even in an S^{2-b} homozygote, which is a line incompatible with S^2. This observation demonstrates that *SLA* is not the pollen *S* gene. Yu *et al.*, (1996) reported that two anther-expressed genes located between *SLG* and *SRK* at the *S* locus, *SLL1* (S Locus Linked Gene 1) and *SLL2*. However, *SLL2* is also expressed in stigmas and *SLL1* has no polymorphism between different *S* haplotypes, suggesting that they are not the pollen *S* gene. Conner *et al.*, (1998) also reported a number of genes closely linked to the *S* locus, but none of them appear to be the pollen *S* gene. On the other hand, these observations clearly demonstrate that the *S* locus complex does not consist of only the genes which are involved in SI.

No good candidate which meets all the requirements as the pollen *S* gene has been reported so far. To evidence that a candidate is the real pollen *S* gene, functional analyses such as loss-of- and gain-of-function transgenic experiments would be indispensable.

5. *S* Gene Superfamily

SLG and *SRK* belong to a large gene family. For example, an SLG-like soluble protein in carrot (van Engelen *et al.*, 1993) and a receptor protein kinase with an S-like domain in maize (Walker and Zhang, 1990) have been reported. In *Arabidopsis*, several SRK-like kinases have been reported (Tobias *et al.*, 1992; Walker, 1993; Dwyer *et al.*, 1994). The physiological function of most of them remains unknown.

In *Brassica*, there are SLG-like proteins SLR1 and SLR2, the genes of which are expressed specifically in stigmas but not linked to the *S* locus. SLR2 is highly similar to the class II SLGs. SLR1 is not involved in SI (Franklin *et al.*, 1996) but is thought to function in pollen adhesion to the stigmatic surface (Luu *et al.*, 1997). An SRK-like kinase is reported to be rapidly induced by wounding and bacterial infection, suggesting its involvement in the defense response (Pastuglia *et al.*, 1997a). What is the general function of the SLG-like motifs? SLG and SLR1 bind to PCPs (Doughty *et al.*, 1993). Therefore, they could be involved in protein-protein interaction. Consistent with this, some members of the gene family are thought to encode receptor protein kinases. If the S domain is really a ligand binding domain, it would appear to be the plant specific motif of the receptor, although it shows a little similarity to the immunoglobulin domain (Glavin, *et al.*, 1994). The elucidation of its crystal structure is of great interest.

6. *Cis* Elements for Expression in Stigmas

Dzelzkalns *et al.* (1993) suggested the possibility that a *cis*-acting element (-339 to -143 region relative to the translation initiation codon) confers stigma/style specific expression. In their experiment, the full length promoter (-3650) and truncated promoter (-411) showed comparable expression in pistils. On the other hand, analysis of the promoter of *SLR1*, whose expression pattern and level are similar to those of *SLG*, suggested that a strong enhancer, in addition to the basal element for pistil specific expression, is located in the -1030 to -1500 region (Hackett *et al.*, 1996). However, it should be noted that tobacco was used as the material for transformation in both experiments. The expression pattern of *SRK* is very similar to that of *SLG*. The promoter of *SRK* has not been analyzed in detail, but it has been shown that a 452 bp promoter is sufficient for the expression in the stigma (Stein *et al.*, 1996). This is similar to the data obtained for the *SLG* promoter. On the other hand, the expression level of *SRK* is much lower than that of *SLG* in RNA gel blot analyses. What causes the difference between them? An interesting case was reported in *B. rapa*. SLG^9 and SRK^9 of *B. rapa* are very similar to each other and their promoter regions are identical up to the -1407 position (Suzuki *et al.*, 1997), suggesting that this region is not involved in the difference of the expression level between *SLG* and *SRK*. According to the data of Dzelzkalns (1993), this region is sufficient for maximum expression. Therefore, the 3' region downstream of *SLG* might modify its expression level. Alternatively, a silencer element might be located in a region further upstream in the *SRK* promoter, introns, or the 3' region. *scf* mutation was reported to modify the expression level of *SLG*, SLR^1, and SLR^2 but not of *SRK* (Nasrallah *et al.*, 1992). Since its effect on their expression is in *trans*, it is possible that SCF is a transcription factor regulating the expression of *SLG*, SLR^1, and SLR^2. If this is the case, SCF would interact with a cis-acting element which regulates the expression of *SLG*, *SLR1*, and *SLR2*, not *SRK*. How *scf* influences the expression of *SLG* and *SRK* in the S^9 haplotype of *B. rapa* is an intriguing question, because it would indicate where the target of SCF is located.

7. Intracellular Signal Transduction Pathway

The central event which occurs after self-pollination is thought to be the activation of SRK (**Fig. 3**). Unlike receptor protein tyrosine kinases, the signal transduction pathway of the receptor protein serine/threonine kinase, except for the transforming growth factor β (TGF-β) receptor family (Heldin *et al.*, 1997), is not well-understood. In plants, the majority of receptor protein kinases including SRK are serine/threonine protein kinases, but it is not known whether they are activated as TGF-β receptors or not. SRK is autophosphorylated and some molecules bind to the autophosphorylated SRK *in vitro* (see below), but it has not been shown yet whether it occurs *in vivo*.

The receptor protein tyrosine kinases form a homodimer and the TGF-β receptors form a heterotetramer in their active states. Do SRKs also form a multimer? A transgenic experiment suggested that SRKs do form a multimer (Stahl *et al.*, 1998). The transgene harboring the mutant SRK deficient in kinase activity caused a partial self-compatible phenotype in a dominant negative manner. The most likely explanation for this is that SRKs form a multimer and that the multimer incorporating the mutant SRK is not functional. In this experiment the transgene did not affect the SI phenotype of another *S* haplotype, suggesting that SRK forms a multimer only with SRK from the same *S* haplotype.

The yeast two-hybrid system using the kinase domain of SRK revealed that several possible molecules are involved in SI signaling. Among the genes isolated by the two-hybrid system, two were thioredoxin genes (Bower *et al.*, 1996). One is designated as *THL-1* and the other as *THL-2*. These thioredoxins bind to the kinase domain of SRK specifically but not to RLK4 (Recepter Like Kinase 4) and RLK5, which are putative receptor protein serine/threonine kinases with S-like domains from *Arabidopsis*. THL-1 was weakly phosphorylated *in vitro* by SRK, confirming that THL-1 binds to SRK, however, the significance of phosphorylation is unclear. Its bind-

ing to SRK does not seem to be phosphorylation dependent. *THL-1* and *THL-2* are expressed in a variety of tissues, suggesting that they may have a more general function than the regulation of SI. Another gene isolated by the two- hybrid system is an arm repeat protein gene, *ARC1* (Gu *et al.*, 1998). *ARC1* is expressed predominantly in stigmas. The binding of ARC1 is specific to the kinase domain of SRK and is phosphorylation dependent. ARC1 was phosphorylated by SRK but only weakly by RLK5. These results suggest that ARC1 is quite possibly a transducer in the SI signaling pathway. Since some arm repeat proteins have been found to be involved in protein-protein interaction, ARC1 is thought to interact with other molecules in the SI signal transduction pathway.

KAPP (kinase-associated protein phosphatase) was first identified as a phosphorylation-dependent protein binding to RLK5 in *Arabidopsis* (Stone *et al.*, 1994). KAPP was found to be a negative regulator of CLV1, which is a putative receptor kinase controlling the size of the apical and young floral meristem (Williams *et al.*, 1997). It was demonstrated that KAPP interacts with the autophosphorylated SRK (Braun *et al.*, 1997). In this context, the KAPP ortholog in *Brassica* might be a negative regulator of SRK. CLV1 phosphorylates KAPP and KAPP dephosphorylates CLV1. The KAPP ortholog in *Brassica* might desensitize SRK by dephosphorylating it.

A spontaneous self-compatible mutation, which is not linked to the *S* locus, has been reported in *B. rapa*. This recessive mutation, *mod*, functions in stigmas but not in pollen. Thus, MOD is thought to be involved in the SRK signaling pathway. The differential display technique revealed that *MOD* encodes aquaporin, which is a membrane protein forming a water channel (Ikeda *et al.*, 1997). *MOD* is expressed in not only stigmas but also in anthers and leaves, suggesting that it has a more general function as well as SI signaling. However, how the loss of function of the aquaporin gene causes a self-compatible phenotype remains unclear.

When self- and nonself pollen are placed on the same stigmatic papillar cell, they behave independently, suggesting that SI occurs as a very regional event (Sarker *et al.*, 1988). SRK signaling appears to be transduced within a very small region in a papillar cell. The main lines of SRK signaling pathways might not be mediated by transcription factors.

8. Future Perspectives

To date, 50 *S* haplotypes have been identified in *Brassica oleracea*. This means that 50 combinations of receptor (SRK)-ligand (pollen *S* product) exist in the SI system of *Brassica*. This appears to be very interesting from both evolutionary and biophysical viewpoints. How did such a number of combinations evolve? How do 50 SRKs, whose basic structures are identical, strictly distinguish each pollen *S* product? Identification of the pollen *S* product or elucidation of its crystal structure is required to answer these questions. Another question is how pollen tube development is inhibited on the stigma in self-pollination. Elucidation of the molecular mechanism of pollen tube development on the stigma and identification of the terminal target(s) of SRK signaling are desired.

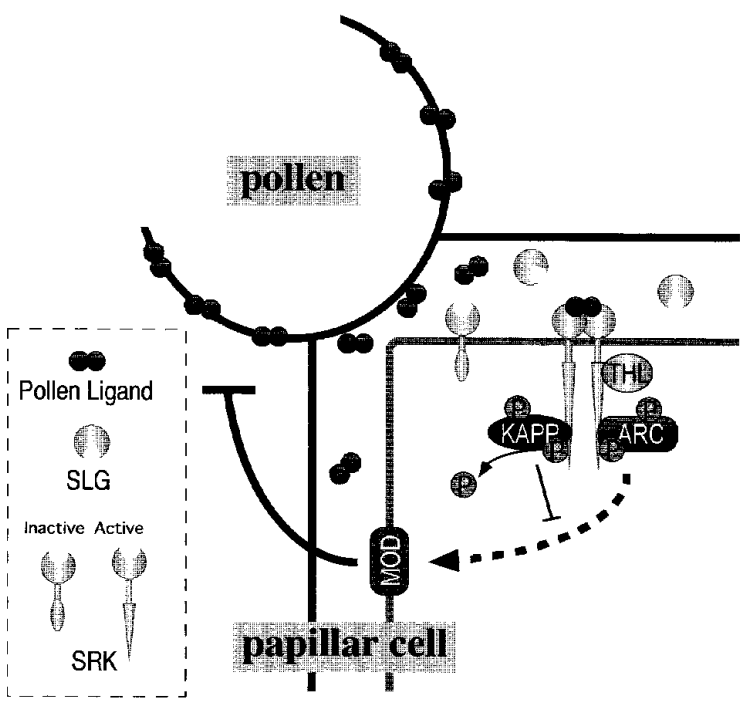

Fig. 3 A model of SRK signaling pathway.

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