Review Article

Molecular basis of self-incompatibility in plants: Unraveling nature's genetic check against self-fertilization

Abstract

Self-incompatibility mechanism is critical for the reproductive success of many plant species, as they prevent self-fertilization and promote outcrossing. This review delves into the molecular basis of self-incompatibility in plants, aiming to unravel the intricate genetic and biochemical activities that underlie this essential biological phenomenon. The central focus of this review is on the mechanisms by which plants recognize and reject self-pollen, ultimately ensuring the maintenance of genetic diversity. Key components, including S-alleles, S-RNases, and receptor kinases, are explored in detail to elucidate their roles in self-incompatibility. Furthermore, this review discusses the implications of understanding these molecular mechanisms for both plant breeding and conservation efforts. Despite significant progress that has been accomplished in deciphering the molecular basis of self-incompatibility, there are still numerous unanswered questions and promising avenues for future research. Topics such as the evolution of self-incompatibility systems and the potential applications of manipulating these mechanisms for crop improvement are highlighted. In conclusion, this review provides a comprehensive overview of the molecular intricacies behind self-incompatibility in plants. The insights obtained from this research not only contribute to our understanding of plant reproduction but also endure practical implications for agriculture and the preservation of plant biodiversity.

Keywords: Self-incompatibility; S-RNases; S-haplotypes; Self-pollen.

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1. Introduction

Self-incompatibility is a crucial mechanism in many plant species that prevents self-fertilization. It arises from diverse factors, including morphological, genetic, physiological, and biochemical factors. This plant phenomenon has been observed in approximately 70 plant families, including important crop plants.

Self-incompatibility is the inability of hermaphroditic plants with flowers to produce viable male and female gametes that can result in seed formation through self-pollination. The term "self-incompatibility" was coined by Stout in 1917, but its first documented instance dates back to the 18th century when Koelreuter observed it in *Verbascum phoeniceum* plants.

This mechanism essentially creates a physiological barrier at some point between pollination and fertilization. It most commonly operates within the stylar region, acting as an effective biological sieve composed of diploid tissues. This sieve prevents the growth of pollen tubes and, consequently, the fusion of haploid gametes (both male and female), thus hindering fertilization.

Two fundamental events that constitute the self-incompatibility system in plants (Bateman in 1952) are:

- **Complementary Hypothesis:** According to this hypothesis, self-incompatibility arises from the truancy of stimulation by the pistil on pollen growth in cases of like genotypes (*e.g.*, $S_1S_2 \times S_1S_2$). In simpler terms, self-incompatibility occurs when substances crucial for pollen tube penetration on self-pollination are lacking in either the pistil or the pollen. This means that in selfing situations, the pollen and/or pistil fail to produce the necessary substances for pollen germination and tube growth within the style and ovary. The complementary method depends on a fusion of dissimilar alleles in the pollen and the style.
- **Oppositional Hypothesis:** According to this theory, similar alleles combine to produce an inhibitor that prevents pollen tubes from growing in the pistil (*e.g.*, $S_1S_2 \times S_1S_2$). In essence, when like alleles interact, they generate a substance in pollen and pistil that interferes with the normal metabolic processes of the pollen grain or the pollen tube. This inhibitor can operate in several ways: (1) it may inhibit essential enzymes or auxins necessary for pollen tube growth, (2) it may obstruct the pollen tube membrane, or (3) it may inhibit an enzyme necessary for the penetration of the style.

2. Classification of self-incompatibility

Self-incompatibility can be categorized based on (1) flower morphology, (2) genes involved, (3) site of expression of self-incompatibility reaction, and (4) pollen cytology (Singh, 2012).

2.1. Heteromorphic system

This system is characterized by variances in floral morphology, specifically in terms of stylar length and the position of the stamens. Heteromorphic self-incompatibility can be further divided into two main types namely Distyly and Tristyly.

2.2. Homomorphic system

In homomorphic self-incompatibility, plants prevent self-fertilization based on physiological factors rather than distinct flower morphology (Table 1). This system is crucial in crop plants for controlled breeding, as it relies on specific genes, multiple alleles, and physiological mechanisms to inhibit self-pollination and maintain genetic diversity (Figure 1).

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3. Molecular Basis of Self-Incompatibility

Self-incompatibility (SI) is a crucial mechanism in plants that prevents inbreeding and promotes outcrossing. It is primarily governed by a highly polymorphic locus of genes which is called S-locus (Figure 2). While grasses have two unlinked SI loci, in dicots, SI typically maps to a single genetic locus. Recent molecular studies on various self-incompatible species within plant families like Brassicaceae, Solanaceae, and Papaveraceae have provided insights into the genetic complexity of the S-locus (Table 2).

In these plant families, it's revealed that the S-locus consists of at least two polymorphic genes, with one gene encoding the male compatibility determinant and another encoding the female compatibility determinant. These genes are part of a multi-gene complex at the S-locus, and they are inherited as a single unit, forming what is now known as 'S-haplotypes' (Buchanan *et al.*, 2005). The interaction between the male and female determinants encoded by the same S-haplotype triggers the SI response.

This genetic complexity ensures that plants with the same S-haplotype are self-incompatible, preventing self-fertilization and promoting genetic diversity within populations. SI is a vital mechanism that plays a fundamental role in maintaining the genetic health and adaptability of plant species by encouraging cross-pollination and reducing the risks associated with inbreeding.

4. SI in Brassica

In the Brassicaceae family, S-locus genes play a vital role in self-incompatibility mechanisms. These genes encode two essential components: serine/threonine receptor kinase (SRK) and cysteine-rich (SP11/SCR) proteins (Takasaki *et al.*, 2000). SRK functions as the female S-determinant, while SP11/SCR serves as the male S-determinant. These genes, along with a glycoprotein called SLG that may enhance self-incompatibility expression, are tightly linked and inherited as an S-haplotype (Sehgal and Singh, 2018).

The SRK protein is found on the plasma membrane of papilla stigmatic cells, while the small SP11 polypeptide is secreted from the anther tapetum, deposited onto pollen, and acts as an SRK ligand upon pollination (Iwano and Takayama, 2012). Brassicaceae exhibit various S-haplotypes, each with complex hierarchical dominance relationships regulated by polymorphic small RNAs and their targets (Yasuda *et al.*, 2016).

In simple cases, the interaction between SP11 and SRK from the same S-haplotype triggers the rejection of self-pollen in the stigma papillary cell. Downstream events involve

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additional factors. The M-locus protein kinase (MLPK) interacts with SRK to transmit self-incompatibility signals, and the arm repeat-containing 1U-box type E3-ligase (ARC1) ubiquitinates and degrades the Exo70A1 factor, which is crucial for pollen growth.

Conversely, other factors like thioredoxin h-like 1 (THL1) and kinase-associated protein phosphatase (KAPP) act as negative regulators, inhibiting SRK and suppressing the self-incompatibility response (Cabrillac *et al.*, 2001). While the interaction between SRK and SP11 leads to an increase in cytosolic calcium levels in the papilla cell, the exact mechanism by which this calcium influx prevents self-pollen growth remains unclear (Iwano *et al.*, 2015).

5. SI in Solanaceae

S-RNase-based Gametophytic Self-Incompatibility (GSI) is found in diverse plant families like Rosaceae, Solanaceae, Scrophulariaceae, and Rubiaceae. Despite using similar genes to determine pollen rejection specificity, the mechanisms differ across families. Nonetheless, the S-locus in these families typically contains at least two linked genes.

One gene encodes pistil-expressed glycoproteins known as S-RNases, which act as selective cytotoxins causing pollen rejection when its S-haplotype matches either of the pistil's two S-haplotypes (McClure *et al.*, 1989; Boskovic and Tobutt, 1996; Xue *et al.*, 1996). The other gene is an F-box protein (SLF or SFB, depending on the family) specifically expressed in pollen.

In Solanaceae and the Rosaceae tribe Maleae, multiple SLF genes (16 to 20) collectively contribute to pollen SI functions, while SI Prunus species use a single SFB gene for pollen-side function (Kubo *et al.*, 2010; Kakui *et al.,* 2011; Williams *et al.,* 2015). F-box proteins are known for their roles in the ubiquitin/proteasome pathway, and they interact with self/cross S-RNases, suggesting cross S-RNases may be degraded through this pathway.

In Solanaceae, an array of SLF proteins collectively ubiquitinates and degrades non-self S-RNases, while self-S-RNases evade degradation due to non-recognition. This is known as the collaborative non-self-recognition model (Qiao *et al.*, 2004). However, S-RNases can also be sequestered in the pollen tube endomembrane system, contributing to compatibility.

In contrast, knock-out mutations in Prunus SFB genes lead to self-compatibility, contradicting the collaborative non-self-recognition model. An alternative model proposes that self-SFB protects self-S-RNases from a "general inhibitor" that detoxifies all self/non-self-S-RNases (Matsumoto and Tao, 2016).

6. SI in Papaveraceae

The physiology of Gametophytic Self-compatibility (GSI) in poppy (*Papaver rhoeas*

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L.) stands out as one of the most comprehensively understood systems among all SI mechanisms. The S-locus in this plant comprises two closely linked genes responsible for encoding the female (PrsS) and male (PrpS) S-determinants (Wheeler *et al*., 2009).

PrsS is a small, highly variable protein secreted by the stigmatic papilla cells, and it acts as a signaling ligand. This ligand interacts with the pollen-expressed transmembrane protein PrpS. When self-interaction occurs, it sets off a series of responses within the plant, including an increase in cytosolic free calcium levels, an influx of calcium and potassium ions, and the generation of reactive oxygen species (ROS) and nitric oxide. These processes, in turn, affect downstream targets.

Additionally, the soluble organic pyrophosphatase p26 and the MAP Kinase p56 undergo rapid phosphorylation (Wilkins *et al*., 2015). Concurrently, there is progressive depolymerization of the actin cytoskeleton, leading to programmed cell death (PCD). Other PCD hallmarks, such as DNA fragmentation and caspase-like activity, are also observed as part of the self-incompatibility response.

Furthermore, current research has highlighted that SI-induced acidification of the pollen tube cytosol plays a key role in triggering PCD. This acidification signal influences SI-induced caspase3-like activity, reduces the activity of the p26 pyrophosphatase, promotes the formation of filamentous actin (F-actin) foci, and leads to their colocalization with specific actin-binding proteins (Wang *et al*., 2018). While these findings offer valuable insights, further exploration is still warranted to fully understand the intricacies of this self-incompatibility mechanism in poppies.

7. Practical application

Here are a few different approaches for achieving self-incompatibility (SI):

7.1. Interplanting Two SI, Cross-Compatible Lines: Interplanting two self-incompatible lines, each with distinct S-alleles, in close proximity is a common technique used in crops with self-incompatibility. This method ensures compatibility during pollination, resulting in hybrid seeds due to the cross-compatibility of parental lines' different S-alleles. It's particularly valuable for self-incompatible crops like certain Brassicaceae species.

7.2. Interplanting an SI Line along with a Self-Compatible Line: Interplanting a self-incompatible (SI) line with a self-compatible line involves planting them together. The self-compatible line can produce seeds when self-pollinated, so the seeds acquired from the self-incompatible line become hybrids due to cross-pollination with the self-compatible line. This method exclusively produces hybrid seeds from self-incompatible lines.

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7.3. Production of Double Cross Hybrids (DCH) and Triple Cross Hybrids (TCH): Advanced hybrid schemes like double cross (DCH) and triple cross (TCH) hybrids go beyond simple crossbreeding. In these methods, several inbred lines are strategically utilized to establish a hierarchical cross. For instance, in Brassica crops, specific parental lines are chosen to produce initial F_1 hybrids. Subsequently, these F_1 hybrids are crossed with another set of parental lines to generate DCH or TCH hybrids. These sophisticated approaches are employed to maximize and amplify heterosis, leading to enhanced hybrid vigor.

8. Self-incompatibility as an alternative to male sterility for hybrid seed production

Hybrid vigor, or heterosis, manifests when two parents with distinct genetic backgrounds are bred together. In the case of most cultivated plants, which are self-compatible, a highly efficient pollination control system is essential to prevent the female parent from self-fertilization. It's worth noting that self-incompatibility is generally favored over male sterility in crop species that rely on insect pollination since pollen-gathering bees seldom visit male-sterile plants.

In the Brassicaceae family, self-incompatibility (SI) is extensively employed for hybrid seed production in diploid vegetable species like Brassica oleracea and B. rapa/B. compestris. However, when it comes to the derived amphidiploid oilseed Brassica napus (canola), it naturally exhibits self-compatibility. Consequently, the introduction of SI alleles becomes necessary. An example of this is the work by Goring et al. (1992), who introduced the SI locus from the self-incompatible B. campestris 'W1' line into the self-compatible B. napus cultivar 'Westar,' eventually producing the self-incompatible Westar line through a series of backcrosses.

In the realm of grasses, self-incompatibility also holds promise for developing hybrid breeding schemes. Wheat, for instance, is an entirely self-compatible inbred species, which has faced challenges in hybrid breeding due to difficulties in implementing male sterility. Nevertheless, self-incompatibility exists in related grasses such as rye, offering the possibility of transferring genes from these close self-incompatible relatives to generate self-incompatible wheat strains.

9. Self-incompatibility usage issues with hybrid seed production

Inbred line generation and maintenance via hand pollination can be labour- and financially-intensive, which subsequently increases the overall costs connected with hybrid seed production. Moreover, continuous selfing can give rise to several challenges:

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9.1. Depression in Self-Incompatibility: Over time, continuous selfing can accompany a reduction in self-incompatibility, inadvertently favoring self-fertility in plants. This undermines the efficacy of the self-incompatibility mechanism.

9.2. New Incompatibility Reactions: In gametophytic systems, prolonged inbreeding can lead to the emergence of new incompatibility reactions. These novel reactions can limit the utility of inbred lines as parental contributors in hybrid breeding programs.

9.3. Environmental Factors: Environmental conditions, such as high temperatures and humidity, can diminish or even override self-incompatibility reactions. This can result in a higher proportion of self-pollinated seeds, which is undesirable in hybrid seed production.

9.4. Pollinator Behavior: When the parental lines have noticeable morphological distinctions, pollinators like bees may show a preference for sticking with that particular line of descent. Due to the negative effects of self-pollination on the development of hybrid seeds, this inclination may result in a higher occurrence of it.

9.5. Transfer of S Alleles: It takes a lot of effort and time to transfer S alleles from one variety or species to another. This difficulty has hindered the utilization of self-incompatibility in hybrid seed production in plant families like Solanaceae and Compositae.

9.6. Difficulty in maintaining pure lines: Maintaining homozygous lines is also essential for hybrid breeding. Since SI species inherently favor outcrossing achieving homozygosity may be hindered.

Efforts are being made to develop easier, more reliable, and cost-effective methods for multiplying inbred lines. Some promising approaches include:

i) Greenhouse Multiplication: Inbred lines are multiplied in controlled environments like greenhouses, where self-incompatibility may be induced by maintaining temperatures at or above 30^0 C.

ii) Polyethylene Tunnels: Inbred lines are grown in polyethylene tunnels with elevated levels of carbon dioxide (CO_2) achieved, for example, by using CO_2 tablets. Pollination can be carried out either manually or by suitable insect pollinators, such as blow flies.

iii) Field Multiplication with Sodium Chloride Spray: Field multiplication of inbred lines can be achieved by applying a 5-10% sodium chloride spray over 3-5 days. This method has been successfully used with various Brassica species (*e.g., B. napus, B. oleraceae, B. campestris*) and is practical for field-level applications.

Temporary suppression of self incompatibility

The following measures are being used for the maintenance of inbred lines:

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1) Bud Pollination.
2) Surgical Techniques – *Brassica spp.*
3) End of Season Pollination.
4) High Temperature – *Trifolium spp., Solanum spp.*
5) Increased CO_2 concentration
6) High Humidity.
7) Salt (NaCl) sprays
8) Irradiation (Solanaceae)
9) Double pollination
10) Grafting (*Trifolium pratense*)

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10. Conclusion

The molecular basis of self-incompatibility in plants is a captivating and intricate system that has evolved to ensure outcrossing and maintain genetic diversity within plant populations. This review provides an overview of the fundamental mechanisms underlying self-incompatibility, with a particular focus on the pivotal role of the S-locus and its associated genes. The process of recognizing and rejecting self-pollen involves a complex interplay of genetic, biochemical, and cellular processes. Central to this mechanism is the specific interaction between the S-allele of the stigma and the corresponding S-allele of the pollen. This recognition event initiates a cascade of molecular activities, that ultimately lead to the inhibition of pollen tube growth, effectively preventing self-fertilization.

In essence, self-incompatibility mechanisms in plants are a testament to the intricate ways in which nature has evolved to promote genetic diversity and maintain the health and adaptability of plant populations. The study of these pertaining mechanisms continues to be a fascinating area of research, shedding light on the molecular intricacies that govern plant reproduction and evolution. Moreover, we have explored the various molecular components, such as S-RNases, F-box proteins, and receptor kinases play critical roles in this process. Understanding the molecular mechanisms underlying self-incompatibility not only sheds light on plant reproductive biology but also entails practical implications for plant breeding and agriculture.

While substantial progress has been made in deciphering these molecular mechanisms, many questions and avenues for further research remain. Future studies may delve deep into the regulatory networks governing S-locus expression, and the potential applications of manipulating these systems for crop improvement.

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Table 1: Gametophytic Self-Incompatibility (GSI) vs. Sporophytic Self-Incompatibility (SSI)

Characteristic	**Gametophytic Self-Incompatibility (GSI)**	**Sporophytic Self-Incompatibility (SSI)**
1. Discovery	Discovered by East and Mangelsdorf in *Nicotiana sanderae* in 1925	First recognized by Hughes andBabcock (1950) in *Crepis foetida* and Gerstel (1950) in *Parthenium argentatum*
2. Genetic Control	Controlled by gametic genetics	Controlled by the genotypes of the pollen-producing plant (sporophyte)

3. Gene and Alleles	Both systems involve a single gene denoted as "S" with multiple alleles	Both systems involve a single gene denoted as "S" with multiple alleles
4. Allele Interactions	Alleles have individual actions in the style without interacting with each other	Alleles may display dominance, individual action, or interaction in either pollen or style
5. Pollen-Ovule Interaction	Pollen grains with the same alleles as the pistil result in pollen tube inhibition	Inhibition of pollen germination or tube growth occurs on the stigma of the same flower
6. Compatibility Levels	Results in fully incompatible, half-compatible and fully fertile crosses	Exhibits a dominance hierarchy among alleles (e.g., S1 > S2 > S3 > S4)
7. Recovery of Parental Genotypes	Allows recovery of the male parent's genotype only in partially fertile crosses where one allele differs	Allows some crosses to restore the parental genotypes
8. Pollen Type	Associated with plant species that typically have binucleate pollen	Generally, involves trinucleate pollen
9. Stigma Interaction	Operates with wet stigma surfaces, with no direct interaction between one pollen grain and one surface cell	Operates with a dry stigma where pollen grains react in a similar fashion from both heterozygous and homozygous plants
10. Biochemical Substance	The biochemical substance associated with the incompatibility response of the pollen develops late, during pollen formation	The biochemical substance involved in the incompatibility response develops early, before pollen development

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Table 2: list of the identified female and male determinant genes

Family	**Types of SI**	**Male determinant**	**Female determinant**
Brassicaceae	SSI	SP11/SCR	SRK
Solanaceae, Rosaceae, Scrophulariaceae	GSI	SLF/SFB	S-RNase
Papaveraceae	GSI	unknown	S-protein

Table 3: Achievements using self-incompatibility

Crops	**Hybrids**
Cauliflower	Pusa Hybrid-2, Snow Queen, Snow King, White Contessa.
Cabbage	BRH-5, H-44, H-43, Pusa Synthetic, Meenakshi.
Chinese Cabbage	Hamburg-3

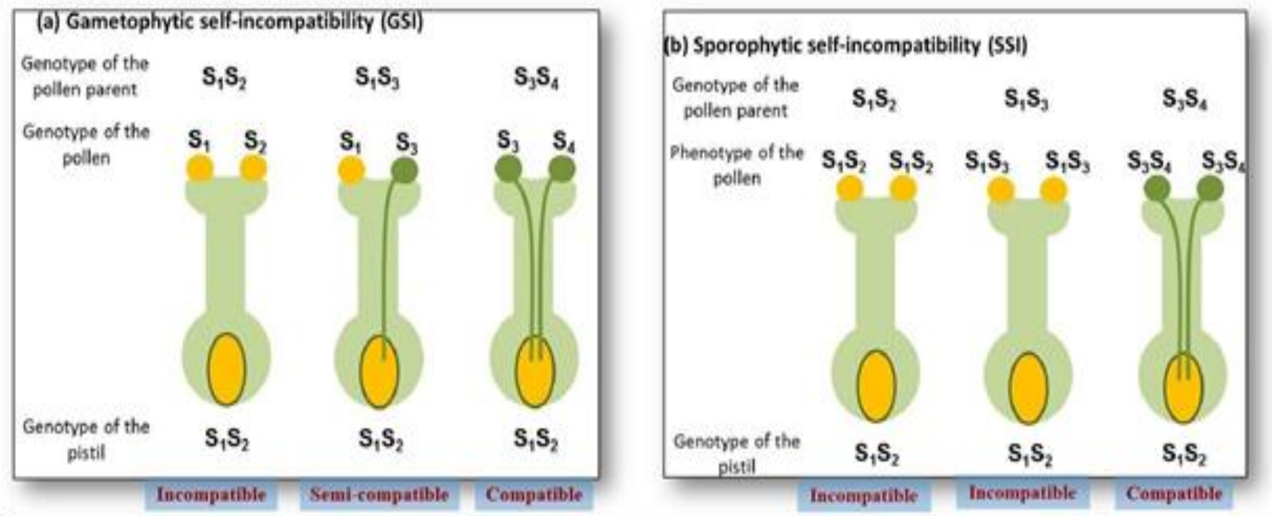

Figure 1. Types of Homomorphic self-incompatibility (Singh, 2012)

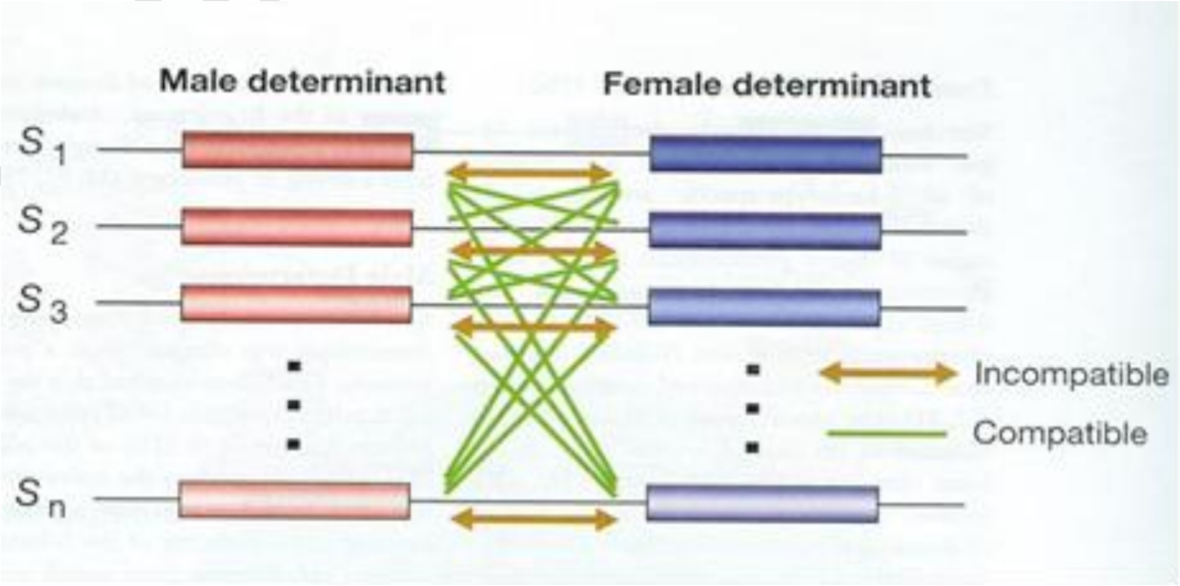

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Figure 2. Schematic Drawing of S-Locus compatibility reaction (Takayama and Isogai, 2005)

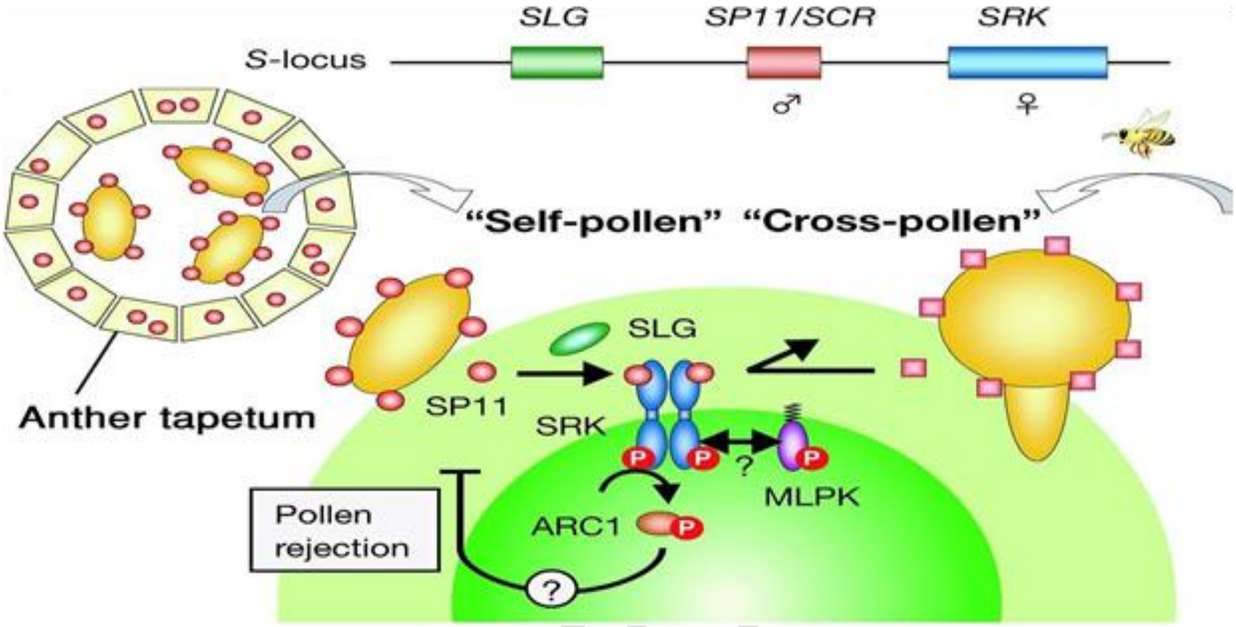

Figure 3: Receptor kinase-mediated signaling in stigma (Takayama *et al*., 2005)

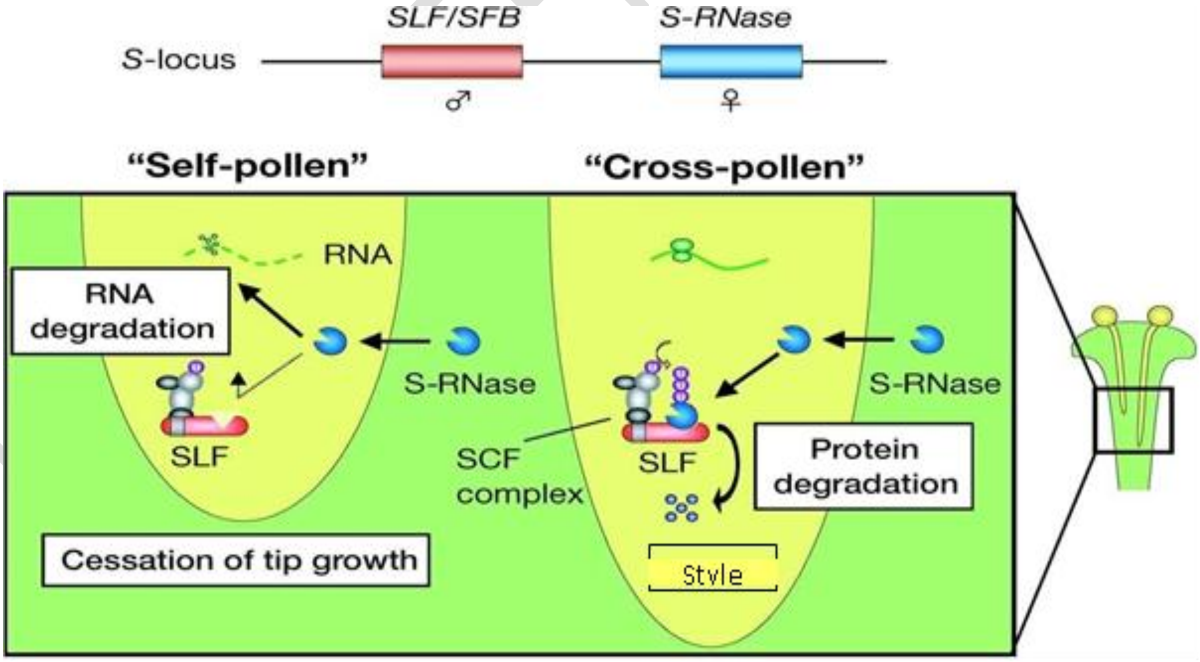

Figure 4: S-RNases mediated degradation of pollen tube RNA (Takayama *et al*., 2005)

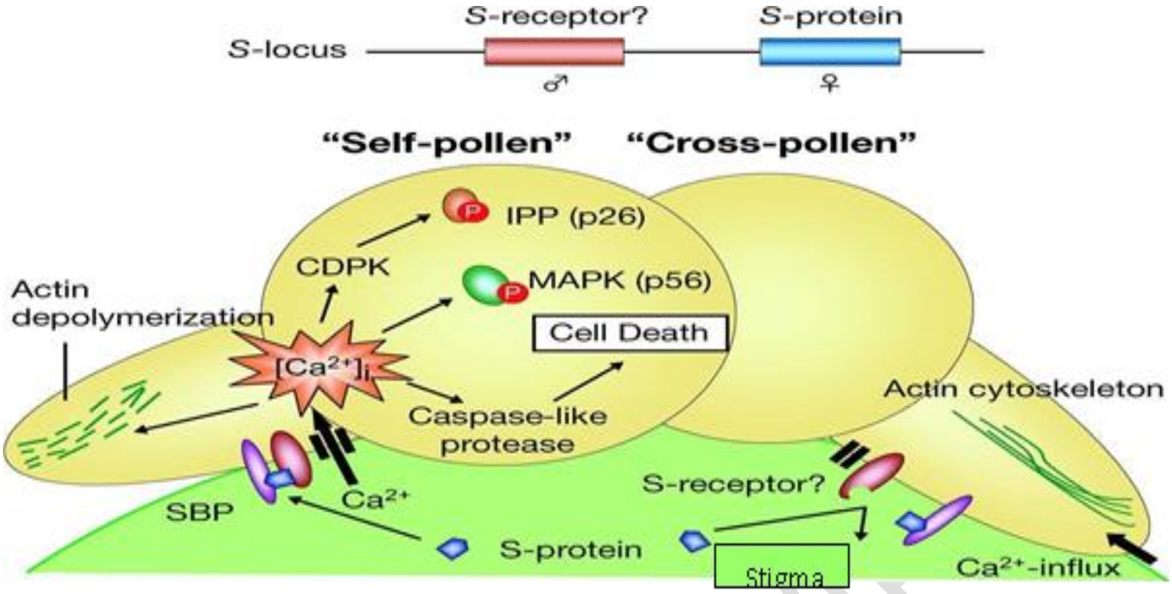

Figure 5: S-protein mediated signaling cascade in pollen (Takayama *et al*., 2005)

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