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Molecular Mechanisms of Self Incompatibility

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The term self incompatibility was originally coined by Stout in 1917. Koelreuter in the middle of 18th century, first reported self incompatibility in *Verbscum phoeniceum* plants. Later on, numerous cases of self incompatibility in flowering plants were reported which were reviewed by East (1940). Thus, self incompatibility refers to the inability of a plant with functional pollen to set seeds when self-pollinated. Some authors define self incompatibility as the hindrance to self-fertilization.

Mechanism of Self Incompatibility

There are two different types of events which are considered to constitute the basis of self incompatibility system:

(1) The stimulation of unlike genotypes and

(2) The inhibition of like genotypes.

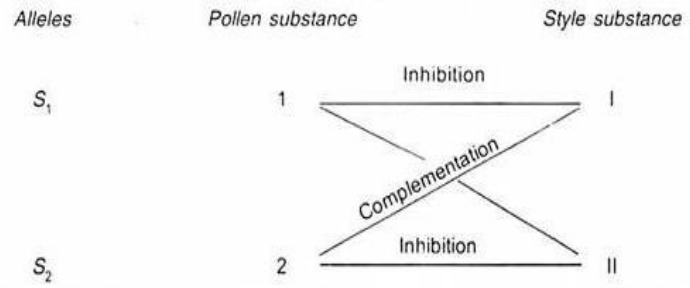
Thus, two hypotheses have been proposed to explain the mechanism of self incompatibility in plants**.** They are:

I. Complementary Hypothesis

This hypothesis was proposed by Bateman in 1952. According to this hypothesis self incompatibility results due to absence of stimulation by the pistil on pollen growth in the like genotypes ($S_1S_2 \times S_1S_2$). In other words, self incompatibility results due to absence of substances in the pistil or pollen which is essential for pollen tube penetration.

Complementary system depends on the combination of unlike alleles in the pollen and style. Such combination of alleles leads to production of either a necessary stimulant for pollen tube growth or an antidote to the inhibition already present in the pollen.

In a gametophytic system, if two alleles S_1S_2 produce two different substances in pollen and style then they behave in the manner as given below:



II. Oppositional Hypothesis

This hypothesis states that interaction between like alleles ($S_1S_2 \times S_1S_2$) leads to production of inhibitor which inhibits the growth of pollen tube in the pistil. In other words, as a result of interaction between like alleles a substance is produced in pollen and pistil which has the property to interfere with the normal metabolism of the pollen grain or the pollen tube.

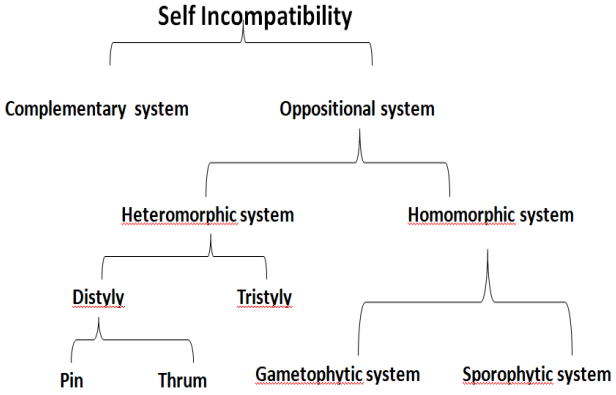
The inhibitor can act in three ways

(a) It may inhibit an enzyme or auxin necessary for pollen tube growth,

(b) May block pollen tube membrane and

(c) May inhibit an enzyme necessary for the penetration of style.

Classification



Gametophytic Self Incompatibility

It was first explained by East and Mengelesdorf (1925) in *Nicotiana sinderae*. Outcome of the interaction between the pollen tube and the style is determined by the genotype of the pollen (gamete). S-locus products are synthesized after completion of meiosis. So, allele may show their individual effect. (Co-dominanace like action). Growth of the pollen tube arrests in the style but sometimes also in stigmatic region. Three types of crosses are produced:

1. Fully Incompatible (S)
2. Partial Compatible (PF)
3. Fully Compatible (F)

Found in**:** Solanaceous, Papavarecea crops, Clove and Rye.

S1=S2=S3=S4…= Sn

Sporophytic Self Incompatability

It was explained by Huges and Babcock (1950) in *Crepis foetida.* Outcome of the interaction between the pollen tube and the style is determined by the genotype of the pollen producing plant. S-locus products are synthesized before completion of meiosis so alleles may not show their individual effect. So that dominant one shows their effect on all. (Dominant effect). Growth of the pollen tube arrests at the surface of the stigma. Two types of crosses are produced:

1. Fully Incompatible (S)
2. Fully Compatible (F).

Found in: **Brassica spp. S1>S2>S3>S4… >Sn**

Molecular Mechanism of Self Incompatibility

1.Brassicaceae-Type Self Incompatibility

Classic genetic studies in the early 1950s unravelled two distinct forms of SI, the gametophytic (GSI) and the sporophytic (SSI), which were distinguished by the genetic behaviour of the pollen's SI phenotype. The pollen SI phenotype in GSI is determined by its own haploid genome, whereas in SSI the pollen SI phenotype is determined by the diploid genome of its parent (sporophyte). According to this classification, the SI in the Brassicaceae belongs to SSI and so far, is the only SSI system in which the mechanism has been characterized at the molecular level. More than 30 and 50 S-haplotypes have been identified in *Brassica rapa* and in *Brassica oleracea,* respectively. In the self-incompatible plants of this family, pollen tubes do not develop properly on the stigma that express the same S-haplotypes as the pollen's parent. Self-pollen rejection results in abrogated pollen hydration or a rapid arrest of the pollen tube growth at the stigma surface.

1. SLG (*S-locus glycoproteins*)

- The first S-linked gene identified in *Brasssica.*
- Soluble cell wall localized protein.
- It shares as much as 98% nucleotide sequence identity with SRK
- SLG is not necessary for SI response, but enhances the activity of SRK

2. SRK (S-locus receptor kinase)

- The female determinant of SSI
- Encodes allelic forms of a receptor serine/ threonine receptor domain
- Expressed in the epidermal cells (papillae) of the stigma
- It directly interacts with pollen ligand/ SCR protein to initiate the SI reaction
- Transgenic gain of function mutation experiments showed that SRK alone determine SI specificity and its ability is enhanced by SLG.

3. SP11/ SCR (*S-locus protein 11/ S-locus Cysteine-Rich protein*)

- Male determinant of SSI (Pollen Ligand)
- Secreted from pollen cell wall and interact directly with SRK protein
- Tightly linked with SLG and SRK protein
- Induces incompatible reactions in stigma papilla cells (SP11/SCR of matching S-locus haplotype induced autophosphorylation of SRK in stigma plasma membrane)

4. Pollen Coat Proteins (PCP)

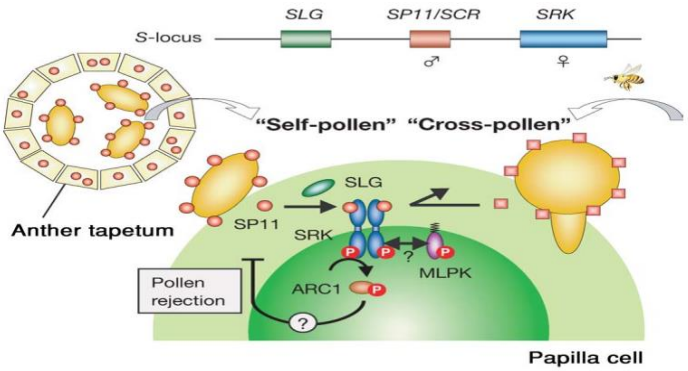
- Small molecules located in the pollen coating i.e. cell wall of pollen
- Have high affinity to bind with SLG protein
- PCP-SLG complex is bind with SRK protein and enhances their affinity with SCR/ S-11.

5. ARC1 (Armadillo Repeat Containing -1)

- Positive effectors molecule
- Helps in signal transduction of SSI
- Specific function is unknown

6. MOD protein/ MLPK protein

- Found in stagmatic cell/ papillar cell
- It is aquaprotein like protein which form a channel in the plasma membrane and transport water into pollen grains for their germination and growth.
- Transport water until the pollen grain become fully turgid.
- This is checkpoint for pollen grain growth and their interaction with stigmatic cell



Molecular model of the SI in *Brassicaceae*

Fig 1: The S-locus consists of three genes, SRK, SP11 and SLG. The SRK receptor kinase is the female determinant and spans the plasma membrane of the stigma papilla cell. SP11 is the male determinant and is predominantly expressed in the anther tapetum and accumulates in the pollen coat during pollen maturation. Upon pollination, SP11 penetrates the papilla cell wall and binds SRK in an S-haplotype-

specific manner. This binding induces the autophosphorylation of SRK, triggering a signalling cascade that results in the rejection of self-pollen. SLG is not essential for the self-/nonself-recognition but localizes in the papilla cell wall and enhances the SI reaction in some S-haplotypes. The signalling cascade downstream of SRK has not yet been characterized but the essential positive effectors include MLPK and ARC1. MLPK localizes papilla cell membrane and may form a signalling complex with SRK. ARC1, an E3 ubiquitin ligase, binds to the kinase domain of SRK in a phosphorylation-dependent manner and may target unknown substrates for ubiquitination. The proteasomal degradation of these substrates could result in pollen rejection

2. Solanaceae-Type Self Incompatibility

- Male Determinant: SLF/SFB (*S* locus F box protein)
- Female determinant: S-RNase (Ribonuclease activity)
- S-RNase is expressed in the pistil and is localized mostly in extracellular matrix in the upper region of style, where its concentration may range from 10 to 50 mg/ml.
- S-RNase are glycoproteins of 30 KDa; which function as highly specific cytotoxin that inhibits the growth of incompatible pollen tubes.
- SLF/SFB are known to function as ubiquitin ligases which degrade the non self S-RNases so that pollen tubes from compatible pollen would grow normally.
- Pollen tube growth is inhibited in stylar region
- S-RNase enters into both compatible and incompatible pollen tubes but they degrade the RNA of only incompatible pollen tubes.
- Tobacco (*Nicotiana*), Petunia, tomato (*Lycopersicon*), roses .

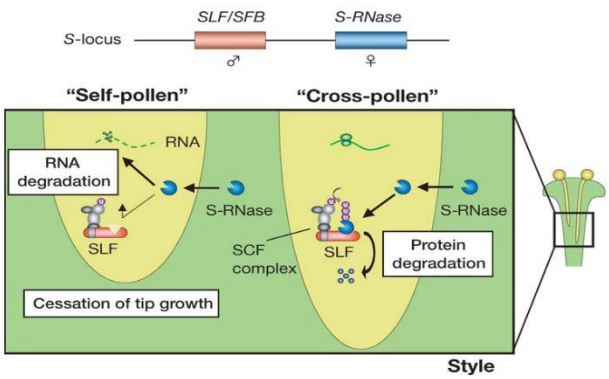


Fig. 2 The S-locus consists of two genes, S-RNase and SLF/SFB. S-RNase is the female determinant and is secreted in large amounts into the extracellular matrix of the style. In a pollinated style, S-RNase is incorporated into the pollen tubes and functions as a cytotoxin that degrades pollen RNA. Although the S-RNase enters the pollen tubes regardless of their S-haplotypes, RNA degradation occurs only in self-pollen tubes. SLF/SFB is the male determinant and is a member of the F-box family of proteins, which generally function as a component of an E3-ubiquitin ligase complex. Thus, SLF/SFB is expected to be involved in ubiquitin-mediated protein degradation of non-self-S-RNases.

3. Papaveraceae-Type Self Incompatibility

- SI under gametophytic control (GSI)
- Pollen germination and pollen tube growth can be inhibited by the recombinant *S*-protein in an *S*-haplotype specific manner in the stigmatic surface.
- *S*- protein acts as female determinant
- Male determinant: is not yet identified
- However, a receptor SBP (S protein binding protein) present in pollen plasma membrane and binds with S- protein.
- In the *Papaveraceae*, the only identified female determinant induces a Ca^{2+}-dependent signaling network that ultimately results in the death of incompatible pollen.
- As the incompatible pollen tube is growing along the stigmatic surface, the stigmatic S protein is predicted to interact with the pollen S protein in an S allele specific manner.
- The unidentified pollen S product is thought to be a membrane receptor in the pollen tube and may in fact be SBP; nevertheless, SBP is involved in the interaction. Binding of the stigmatic S protein to the pollen S receptor then triggers a signal transduction cascade in the pollen tube.
- The signal transduction pathway is thought to involve two phases, a calcium-dependent signaling pathway followed by a calcium-independent signaling pathway.
- In the first step, there is a rapid increase in calcium levels which may be mediated by IP3. This is then followed by an increase in phosphorylation of specific proteins, such as p26, by calcium dependent protein kinases.
- During this early phase, rearrangements of the actin cytoskeleton are also occurring, though it is not known if this is caused by the calcium

signaling (Geitmann *et al.*, 2000). Subsequently, the calcium independent signaling pathway occurs and there is an increase in phosphorylation of other proteins.

- These events may lead to gene activation and ultimately may result in programmed cell death and the inhibition of pollen tube growth.

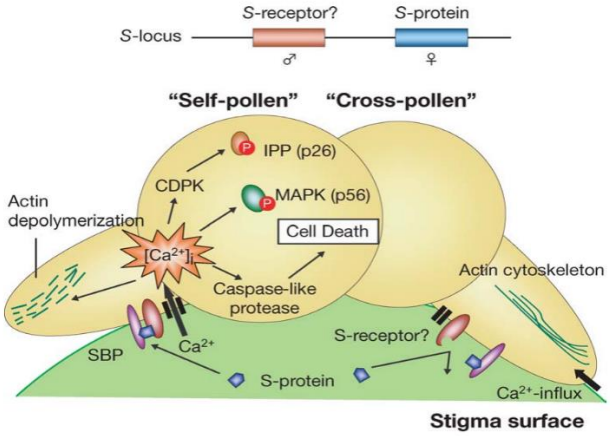


Fig. 3 Only the female determinant gene has been identified, which encodes a secreted stigma protein named S-protein. S-protein interacts with the assumed S-haplotype-specific pollen receptor (the putative male determinant) and induces Ca2+ influx in the shank of the pollen tube. SBP is an integral proteoglycan of the pollen plasma membranes and is expected to function as an accessory receptor. Ca2+-influx stimulates increases in [Ca2+] i, with some contribution from the intracellular stores as well as from extracellular sources. These increases in [Ca2+] i trigger the downstream signalling cascades that result in rapid growth inhibition and ultimately the death of incompatible pollen tubes.

Conclusion

1. In many species, the specificity of the SI response is determined by the haplotypes of the S-locus, which contains at least two separate multiallelic genes, the female and the male determinant genes.
2. SI does not represent one system, but rather a collection of divergent mechanisms, suggesting that SI evolved independently in several lineages.
3. In the Brassicaceae, the determinant genes encode a pollen ligand and its stigmatic receptor kinase and their interaction induces incompatible signaling(s) within the stigma papilla cells.
4. In the Solanaceae, Rosaceae, and Scrophulariaceae, the determinants are a ribonuclease and an F-box protein, suggesting the involvement of RNA degradation and protein degradation within the system.
5. In the Papaveraceae, the only identified female determinant induces a Ca2+-dependent signaling network that ultimately results in the death of incompatible pollen.

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