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Self-Incompatibility in Fruit Crops

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Self-incompatibility was the first documented by Koelreuter in 1761, a term later introduced by Stout in 1917. It refers to the inability of hermaphrodite flowers, despite having functional male and female gametes, to produce seeds after self-pollination. This self-recognition mechanism between pollen and pistil prevents inbreeding in plants with self-incompatibility systems and is controlled genetically by one or more highly polymorphic loci. Among these, the S-locus is the most extensively studied, as it occurs in species of Rosaceae, Solanaceae and Gramineae. Depending on whether the S-haplotype expressed by a pollen grain is determined by the pollen parent's genotype or by the pollen grain's own genotype, S-locus interactions are classified as Sporophytic Self-Incompatibility (SSI) or Gametophytic Self-Incompatibility (GSI) (De Nettancourt, 2001).

General characteristics of self-incompatibility

- Promotes cross-pollination and helps to maintain a high level of heterozygosity
- It can act at any stage between pollination and fertilization
- It prevents self-fertilization and promotes outbreeding, enhancing the possibility of new genetic combinations
- Morphological, physiological, genetic and biochemical factors may all influence this mechanism
- Cross-pollination leads to normal seed development
- In plants, self-incompatibility is often controlled by a single S gene with multiple alleles

Classification of self in compatibility

Bateman in 1952 categorized self-incompatibility into complementary and oppositional systems, based on the nature of interactions between pollen grains and the pistil.

a. Complementary system of self-incompatibility

Complementary system of self-incompatibility is also known as the stimulatory type of self-incompatibility, this system allows successful fertilization when pollen from one SI group lands on the stigma of a different SI group. In such case, both produce specific substances that stimulate pollen germination and pollen tube growth. However, if the pollen and stigma belong to the same SI group, these stimulatory chemicals are not produced, leading to inhibition of pollen germination and subsequent growth

b. Oppositional system of self-incompatibility

Oppositional system of self-incompatibility is also referred as inhibitory type of self-incompatibility. When the pollen and pistil belong to the same SI group, they generate specific substances that block pollen germination and growth. In compatible interactions,

such inhibitory substances are absent, allowing normal pollen growth and development, which leads to successful fertilization.

Lewis in 1954 divided self-incompatibility (SI) into homomorphic and heteromorphic self-incompatibility systems on floral shape. Homomorphic SI is further classified into gametophytic self-incompatibility (GSI), where compatibility is determined by the genotype of the gametes and sporophytic self-incompatibility (SSI), where it is determined by the plant's genotype. Molecular research after the 1980s revealed that at least two genes within the S-locus regulate SI, with one acting as the male determinant and the other as the female determinant.

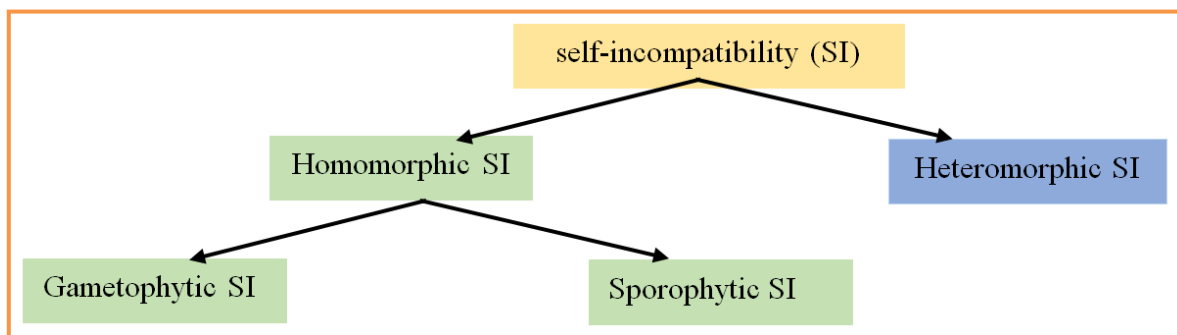


Fig. 1: Lewis (1954) classification of self-incompatibility (SI)

A: Heteromorphic self-incompatibility

In this system, flowers belonging to different incompatibility groups show distinct morphological differences. For instance, pin flowers have long styles and short stamens, as seen in litchi, pomegranate, and sapota. Pollen from pin flowers carries only the *s* genotype and expresses the same incompatibility reaction. Thrum flowers have short styles and long stamens seen in almond and walnut, in carambola heterodistyly is observed. The incompatibility response of pollen is determined by the genotype of the plant that produces it, with the *S* allele being dominant over *s*. Hence, this incompatibility mechanism is classified as heteromorphic-sporophytic. This feature is controlled by a single gene *s*, where *Ss* results in thrum flowers and *ss* produces pin flowers. Thrum flowers produce two types of pollen genotypically (*S* and *s*), but all are *S* phenotypically due to dominance. When a pin plant is crossed with a thrum plant, the offspring will segregate into *Ss* and *ss* genotypes in equal proportions. The only compatible crossing occurs between Pin × Thrum flowers, or vice versa. This trait is governed by a single *S* locus that involves six genes: *L1*, *L2*, *G*, *S*, *A* and *P*. In tristily, styles and stamens occur in three different lengths: short, medium and long. This is controlled by two genes, *S* and *M*, each with two alleles. The *S* gene masks the expression of gene *M*. Short styles are determined by the dominant *S* allele (genotypes: *Ssmm*, *SsMm*, or *SsMM*). Medium styles result from the *M* allele when *s* is present (genotypes: *ssMm* or *ssMM*). Long styles are produced by the recessive combination (genotype: *ssmm*). Examples of tristily include pomegranate varieties like Ganesh and Kandhari, as well as *Prunus* fruit crops.

Table 1: Heteromorphic sporophytic self-incompatibility (Singh B.D., 2014).

Mating		Progeny	
Phenotype	Genotype	Genotype	Phenotype
Pin x Pin	<i>ss</i> x <i>ss</i>	Incompatible	
Pin x Thrum	<i>ss</i> x <i>Ss</i>	<i>Ss</i> : <i>ss</i> (1:1)	Thrum : Pin
Thrum x Pin	<i>Ss</i> x <i>ss</i>	<i>Ss</i> : <i>ss</i> (1:1)	Thrum : Pin
Thrum x Thrum	<i>Ss</i> x <i>Ss</i>	Incompatible	

B: Homomorphic self-incompatibility

In this system flower morphology does not influence the incompatibility reaction, it is determined either by the genotype of the gamete (gametophytic self-incompatibility) or by

the genotype of the pollen producing plant (sporophytic self-incompatibility). East and Mangelsdorf (1925) further classified the gametophytic self-incompatibility system based on the number of genes controlling the reaction. When the incompatibility is governed by a single gene, it is called monofactorial and when it is controlled by two or more genes bifactorial.

1. Gametophytic self-incompatibility

This type of incompatibility arises due to the genetic makeup of the gametes (pollen) themselves. It was first discovered by East and Mangelsdorf (1925) in *Nicotiana sanderae*. In this system, both alleles are expressed in the style and show co-dominance. Key features of gametophytic SI include: pollen is binucleate, pollen behaviour is determined by its own S allele, not by the genotype of the plant that produced it, the stigma is of wet type, incompatibility is controlled by a single gene with multiple alleles and in polyploid pollen, pollen is rejected in the style and incompatibility may be lost due to competition between two S alleles. Examples of gametophytic SI include almond, apple, apricot, ber, cherry, citrus, coffee, loquat, pear, pineapple and plum. For example, if a pollen parent has the genotype S1S2, it produces two types of gametes, S1 and S2. In the female parent, both alleles are codominant and expressed in the stigma. Pollen with S1 or S2 cannot germinate on a stigma with S1S2 because of incompatibility. If the stigma has S1S3, then S2 pollen can germinate, leading to partial incompatibility. If the stigma has S3S4, both S1 and S2 pollen can germinate, resulting in complete compatibility (Hughes and Babcock, 1950).

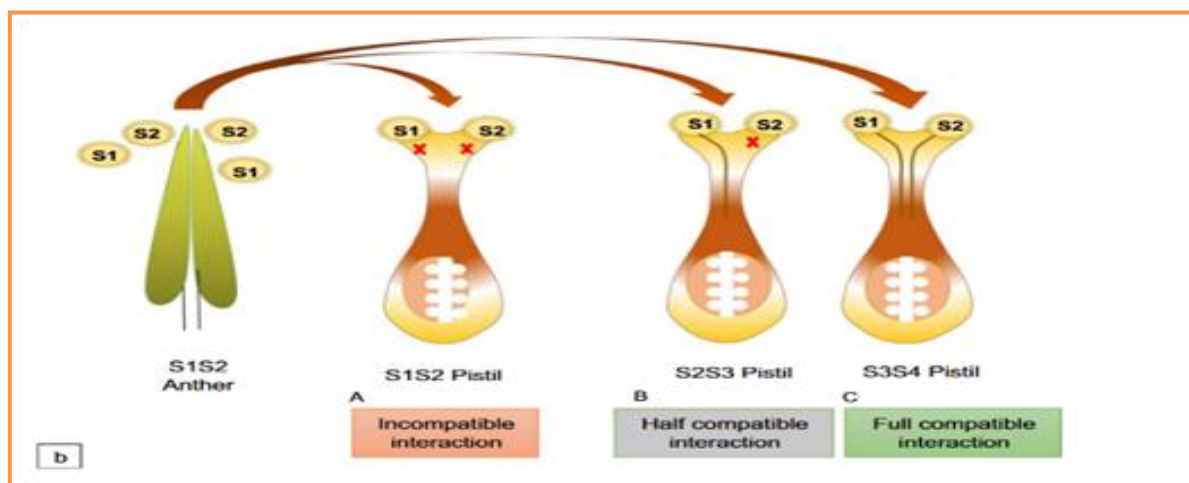


Fig. 2: Diagrams of incompatible, partially compatible and compatible gametophytic interactions (Chakraborty et al, 2022)

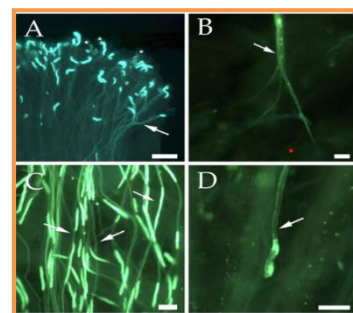
Fruits that exhibit gametophytic self-incompatibility

- a. **Apple:** The great majority of apple cultivars are self-incompatible (Broothaerts & Van Nerum, 2003). Apple (*Malus x domestica* Borkh.) is one of the most important fruit crops showing ribonuclease-mediated self-incompatibility. (Hegedus, 2006). The fruit set mechanism is governed gametophytically by an S-locus on chromosome 17 which is a multigene complex, encoding the pollen (male) factor S-locus F-box Brothers (*SFBB*) and the pistil (female) factor *S-RNase*. (Lopez et al., 2021) (Sheick et al., 2018). The most effective pollinators for the Early Shanburry cultivar were Fanny (54.5%), Winter Banana (60.4%) and Rome Beauty (54.25%). Jonathan produced the highest fruit set in Red Delicious (87.50%). Under self-pollination, cultivars like McIntosh, Rymer, Jonathan and Rome Beauty yield a moderate harvest. However, Delicious is self-incompatible and requires cross-pollination for fruit production.
- b. **Pear:** According to Sassa et al. (2007), European pear (*Pyrus communis*) has a gametophytic self-incompatibility (GSI) system controlled by the S-locus, which contains tightly linked polymorphic genes: a pistil-expressed S-RNase gene that degrades RNA in the style and multiple pollen-expressed *SFBB* (S-locus F-box Brothers) genes. The S-

locus haplotypes show high genetic variation due to the diverse alleles expressed in both pollen and pistil.

- c. **Plums:** Most Japanese plums are self-incompatible, so they need cross-pollination with other compatible varieties during flowering to produce fruit. Sordum (SaSb) was the first S-genotyped cultivar by cloning the cDNA of the S-RNases in the style (Yamane *et al.*, 1999)
- d. **Apricot:** In apricots, gametophytic self-incompatibility is controlled by a single gene with many different forms (alleles). Some cultivars, like *Goldrich* and *Lambert*, are also cross-incompatible, meaning they cannot pollinate each other. In apricot, 33 S-alleles (S1 to S20, S22 to S30, S52, S53, Sv, and Sx) have been identified so far, including one allele linked to self-compatibility (Sc)

Fig.3: (A) Pollen grains, germinating at the stigma surface with pollen tubes emerging towards the style (arrow) in the self-compatible cultivar Water. (B) Pollen tubes (arrow) reaching the base of the style (down) in the self-compatible cultivar Water. (C) Pollen tubes (arrows) growing along the style in the self-compatible cultivar Water. (D) Pollen tube (arrow) arrested in the middle part of the style in the self-incompatible cultivar Samourai (Herrera *et al.*, 2022).

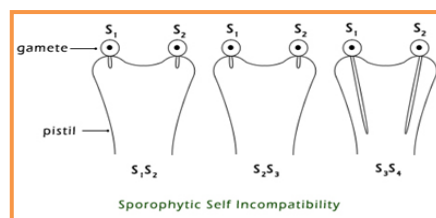


- e. **Almond:** Gametophytic self-incompatibility (GSI) in almond is controlled by a multigene S-locus expressed in both male and female organs. In the pistil, S-RNases, which are stylar glycoproteins (~30 kDa), act as key regulators. These S-RNases, located in the pistil, have ribonuclease activity and show allele-specific variation. When incompatible pollen lands on the stigma, S-RNases enter the pollen tube and block its growth by acting as cytotoxins, preventing fertilization. Only compatible pollen with different S-alleles can grow normally and fertilize the ovules, ensuring cross-pollination and genetic diversity.
- f. **Cherry:** Many cherry varieties self-incompatible. To ensure good fruiting, compatible varieties from different groups should be planted together. However, universal donor varieties like *Stella*, *Vista*, *Vic*, *Seneca* and *Vega* can pollinate any cherry variety, improving fruit set. The cultivars *Kordia*(S3S6), *Regina* (S1S3) and *Summit* (S1S2) are self-incompatible, as most of their pollen tubes stop growing in the middle section of the style, resulting in no fruit set. In contrast, *Karina* (S3S4) is self-compatible, with its pollen tubes successfully reaching the base of the style and ovary, even penetrating the nucellus. Consequently, 'Karina' showed fruit set consistently over three years, with rates of 40.26 %, 18.79 % and 21.81 %, respectively. (Sanja *et al.*, 2013)
- g. **Ber:** Self-incompatibility has been reported in several cultivars of ber: *Gola*, *Seb*, *Jogia*, *Aliganj*, *Ponda*, *Illaichi*, *Mundia*, *Banarasi Karaka*, *Karkrola Gola*, *Kaithli*, *Kathaphal*, *Murhara*, *Reshmi*, *Sandhura*, *Narnaul*, *Safeda Selected* and *Umran*. ZG-2 and *Sanaur-2* (Mehrotra and Gupta, 1985).
- h. **Loquat:** Varieties such as *Late Yellow*, *Golden Yellow*, *Tanaka* and *California Advance* show self-incompatibility.
- i. **Citrus:** Many citrus types, including lemon, grapefruit, pummelo, sweet lime and mandarins, are considered incompatible. For example, the lemon varieties *Kagzi Kalan* and *Pant Lemon* show self-incompatibility (SI). Hybrids produced from SI cultivars also tend to remain self-incompatible and some may also be cross-incompatible (CI).
- j. **Pineapple:** Most commercial pineapple clones are self-incompatible, so their fruits develop parthenocarpically, resulting in seedless fruits.

2. Sporophytic self-incompatibility:

In sporophytic self-incompatibility, the pollen producing plant genotype, determines the incompatibility. Since all pollen from the same plant shows identical responses, it reflects maternal control. Incompatibility prevents pollen germination at the stigma surface. Crops like mango (*Mangifera indica*) and Indian gooseberry (*Emblica officinalis*) shows

sporophytic self-incompatibility and have trinucleate pollen and dry stigma surface. For example, Pollen from S1S2 plant is incompatible with stigmas having S1 or S2, pollen from S1S2 plant is partially compatible with stigmas having S2 or S3 and pollens from S1S2 plant is compatible with stigmas having S3 or S4.



Fruits that exhibit sporophytic self-incompatibility

- a. **Mango:** Singh *et al.* (1962) reported self-incompatibility (SI) in Dashehari, later confirmed in Dashehari, Langra, Chausa and Bombay Green (Mukherjee *et al.*, 1968; Sharma & Singh, 1970). Bombay Green is the best pollinizer for Dashehari, while Dashehari suits Chausa (Ram & Sirohi, 1979). Embryological studies showed that after self-pollination, fertilization occurs but endosperm degenerates within 15 days, indicating a post-zygotic sporophytic SI mechanism in mango (Mukherjee *et al.*, 1968). Pusa Arunima and Pusa Surya are self-compatible. SI has been utilized in mango breeding to develop hybrids like Arka Puneet, Arka Neelkiran and Arka Anmol.
- b. **Aonla:** Singh *et al.* (2001) reported self-incompatibility in aonla cultivar NA-7, with only 2.35% fruit set under self-pollination (bagged) compared to 61.43% under open pollination. For better fruit set and retention, NA-6 and Krishna were identified as suitable pollinizers for NA-7. It was further recommended to use NA-6 and Chakaiya as pollinizers for NA-7 and Chakaiya for Banarasi. Chakaiya × Francis, NA-7 × Krishna, Banarasi × NA-6 and Kanchan × NA-6 showed improved fruit retention, making them suitable for commercial cultivation.

Mechanism of Self-Incompatibility (SI)

SI can be grouped into three stages based on where the incompatibility occurs:

1. **Pollen- Stigma Interaction**
 - In the gametophytic SI system, the stigma is wet (plumose with elongated receptive cells). Pollen usually germinates on the stigma and incompatibility occurs later
 - In sporophytic SI, the stigma is dry (papillate) with a protein pellicle involved in the rejection process, rejection occurs at the stigma surface.
 - Pollen exudates (proteins/glycoproteins) induce callose formation in incompatible pollen tubes, preventing further germination.
 - Pollen exine also carries rejection signals from the anther tapetum.
2. **Pollen Tube- Style Interaction**
 - In many gametophytic systems, pollen tubes germinate but growth slows or stops in the style when incompatible.
3. **Pollen Tube- Ovule Interaction**
 - The pollen tube reaches the ovule and affects fertilization. Due to incompatible combinations which leads to embryo degeneration in early stages of development.

Advantages of self-incompatibility

Self-incompatibility effectively prevents self-pollination, which plays a crucial role in shaping plant breeding approaches and objectives. To ensure proper fruit set in self-incompatible fruit trees, it is necessary to plant two or more mutually compatible varieties.

- In hybrid seed production, self-incompatibility can be advantageously utilized
- Self-incompatibility promotes outbreeding, enhancing heterozygosity and genetic variation through cross-pollination, which can lead to new gene combinations and the evolution of improved crop varieties
- This system eliminates the need for manual emasculation or the use of male sterility to produce hybrids
- Through cross-pollination, desirable genes from different parents can be combined into a single genotype

- Self-incompatibility can be used to establish clonal orchards, where superior self-incompatible clones serve as parents to produce hybrid seeds, though the exact male parent remains unidentified, it is the main drawback.
- In crops like pineapple, parthenocarpy combined with self-incompatibility leads to seedless fruits, as all commercial pineapple cultivars are naturally self-incompatible

Limitations of Self-Incompatibility

- In self-incompatible species, it is challenging to develop homozygous inbred lines.
- Bud pollination is often necessary to maintain parental lines.
- Environmental factors such as temperature and humidity influence the expression of self-incompatibility (high temperature or humidity can weaken or even overcome the incompatibility barrier).
- Due to the complexity and high cost of maintaining inbred lines through manual pollination, the use of self-incompatibility in breeding is restricted in specific cases.
- Mixed planting of different cross-compatible cultivars may lead to variation in fruit quality.

Conclusion

Self-incompatibility is a genetic mechanism that prevents self-pollination, controlled by at least two genes located at the S-locus, which are multi-allelic in nature. The methods used to assess self-incompatibility differ depending on the type of incompatibility and the crop species. It serves as an effective tool for hybrid seed production and offers several advantages over male sterility. However, its major drawback lies in the difficulty of producing and maintaining inbred lines, though various techniques exist to overcome this challenge.

Future line of work

It is essential to identify and utilize strong S-alleles to develop stable self-incompatible parents, enabling the transfer of related genes and efficient exploitation of heterosis through hybrid seed production.

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