



# **Incompatibility Systems in Fruit Crops: Applications and Achievements**

**Shikha Jain<sup>a++\*</sup>, Poonam Maurya<sup>a++</sup>, Shubham Jain<sup>b++</sup>,  
Vinay Kumar<sup>a++</sup>, Amulya S.<sup>a++</sup>, Bhargav Kiran<sup>c++</sup>,  
Laya P.<sup>a#</sup>, Subhashree Subhasmita<sup>d</sup>,  
Anju Jayachandran<sup>e++</sup> and Kiran Kothiyal<sup>ft</sup>**

<sup>a</sup> *Division of Fruits and Horticultural Technology, ICAR- Indian Agricultural Research Institute, New Delhi-110012, India.*

<sup>b</sup> *Department of Fruit Science, College of Horticulture and Forestry, ANDUAT, Ayodhya, India.*

<sup>c</sup> *Division of Vegetable Science, ICAR- Indian Agricultural Research Institute, New Delhi-110012, India.*

<sup>d</sup> *Department of Vegetable Science, College of Agriculture, Govind Ballabh Pant University of Agriculture and Technology, Pantnagar, Uttarakhand-263153, India.*

<sup>e</sup> *Department of Fruit Science, College of Agriculture, Kerala Agricultural University, Thrissur- 680656, India.*

<sup>f</sup> *Department of Horticulture (Fruit Science), Govind Ballabh Pant University of Agriculture and Technology, Pantnagar, Uttarakhand-263153, India.*

## **Authors' contributions**

*This work was carried out in collaboration among all authors. All authors read and approved the final manuscript.*

## **Article Information**

DOI: 10.9734/IJECC/2023/v13i92496

## **Open Peer Review History:**

This journal follows the Advanced Open Peer Review policy. Identity of the Reviewers, Editor(s) and additional Reviewers, peer review comments, different versions of the manuscript, comments of the editors, etc are available here:

<https://www.sdiarticle5.com/review-history/103671>

**Review Article**

**Received: 21/05/2023**

**Accepted: 23/07/2023**

**Published: 02/08/2023**

<sup>++</sup> *Ph. D. Research Scholar;*

<sup>#</sup> *M. Sc. Fruit Science;*

<sup>†</sup> *M. Sc. Ag.;*

<sup>\*</sup>*Corresponding author: E-mail: jain64235@gmail.com;*

## ABSTRACT

The method of pollination is crucial for fruit crop breeding since it affects the genetic makeup, type of gene action, ease of pollination control, and stability of varieties after release. There are a number of processes that encourage cross-pollination, but self-incompatibility (SI) is particularly significant since it is exploited in the production of hybrid seeds. SI is the practice of not allowing fertile (functioning) male and female gametes from the same plant to fuse together. Since ancient times, breeders and growers have successfully used SI as a tool to modify domesticated crops. Self-incompatibility may have an array of causes, including those that are physical, physiological, biochemical, and molecular, but on a broader scale, it appears that all of these components interact to regulate it. According to molecular investigations, at least two genes in the S-locus regulate the SI, one of which functions as a male and one as a female determinant. Self-incompatibility has several different uses, including marker-assisted breeding through SI genotyping, agricultural production and quality improvement, and the creation of hybrids to get over intra- and interspecific reproductive obstacles.

*Keywords: Self-incompatibility; cross pollination; S-locus; hybrid development.*

## 1. INTRODUCTION

In flowering plants, sexual incompatibility is a common phenomenon that limits inbreeding within populations and also appears to support speciation by creating unilateral barriers between self-incompatible and self-compatible populations (unilateral incompatibility, or UI). An application of the rule that SI x SC species are cross incompatible would imply that UI operates, on average, in more than one interspecific pollination out of every four, contrary to Darlington and Mather's [1] estimate that half of the species in angiosperms exhibit SI. Outbreeding is forced by the physiological mechanism of incompatibility. It occurs often in all flowering plant families. The inability of functional male and female gametes to effect fertilization in specific combinations is known as incompatibility. Incompatibility plays a crucial role in the interaction between pollen and pistils. Both intraspecific and interspecific incompatibility exist between different species. Incompatibility results from pollen tubes failing to penetrate the entire length of the style in certain species whereas pollen germination failure occurs in others. The interruption of pollen tube growth is caused by a response between the substance in the pollen tube and a complementary component in the style, the pollen and style compounds being reactively different for each allele, according to style-grafting and temperature investigations. The reaction is irreversible and stops a process required for tube growth. There are two main types:

### 1. Cross Incompatibility

According to De Nettancourt [2], cross incompatibility is any association between the

pollen and the pistil that hinders the development of hybrid zygotes in crosses between two viable species. According to Hogenboom [3] and Kermicle and Evans [4], this phenomenon may result from one partner of a given genotypic combination lacking genetic information about the structure or physiology of the other partner, or it may be due to the pistil's inability to recognise pollen from a foreign origin. Depending on whether a certain genotypic combination is, respectively, incompatible in only one direction or in both directions of the cross, CI can be either unilateral or bilateral.

Cross-incompatibility is a term used to describe the relationship between pollen and pistil that prevents the formation of hybrid zygotes in crosses between two fertile species. This definition, provided by De Nettancourt [2], encompasses both the presence or absence of a compatible relationship between the pollen and pistil. The occurrence of cross-incompatibility has been attributed to two main factors. Firstly, it can result from a lack of genetic information in one of the partners regarding the structure or physiology of the other partner, as proposed by Hogenboom [3]. This genetic mismatch can lead to incompatibility and the failure of hybrid zygote formation. Secondly, cross-incompatibility can arise due to the pistil's recognition of pollen with a foreign origin, as suggested by Kermicle and Evans [4]. Cross-incompatibility can exhibit different patterns: unilateral or bilateral. Unilateral incompatibility refers to a situation where a specific genotypic combination is incompatible in only one direction of the cross, while being compatible in the other direction. Bilateral incompatibility occurs when a particular genotypic combination is incompatible in both

directions of the cross. In several members of the Solanaceae family, such as wild potatoes, wild tomatoes, and peppers, cross-incompatibility has been observed [31-33]. In these species, pollen tube growth can be arrested at various sites within the pistil, including the stigma (the receptive surface), the upper, middle, or bottom part of the style (the tube connecting the stigma to the ovary), or even within the ovary itself. This disruption of pollen tube growth prevents successful fertilization and the formation of hybrid offspring [26-28]. Certain fruits, including apples, plums, oranges, cherries, apricots, ber, almonds, and chestnuts, are known to exhibit cross-incompatibility. This means that specific combinations of varieties within these fruit species are unable to produce viable hybrid fruits due to genetic incompatibilities between the pollen and pistil. Overall, cross-incompatibility plays a role in maintaining genetic diversity and promoting outcrossing in plant populations by preventing fertilization between closely related individuals [29,30]. It ensures successful pollination between compatible partners and contributes to genetic mixing and the introduction of new genetic variations.

## 2. Self-incompatibility

The inability of the hermaphrodite flowers' functional male and female gametes to produce seeds by self-pollination is known as self-incompatibility. Self-discrimination between pollen and the pistil, which is genetically controlled by one or more highly polymorphic loci, prevents inbreeding in plants with self-incompatibility systems [2]. Due to its presence in important Rosaceae, Solanaceae, and Gramineae species, the S-locus has been the subject of the most thorough research [2]. Depending on whether the S-haplotype expressed by a pollen grain has been determined, respectively, by the genotype of the pollen parent or by its own genotype, the S-locus reactions are either categorised as sporophytic (SSI) or gametophytic (GSI).

## 2. Early WORK AND IMPORTANCE OF SELF-INCOMPATIBILITY (SI)

Kolreuter first mentioned it in *Verbascum phoeniceum* (Scrophulariaceae). Many workers reviewed observations of the phenomenon made by Darwin and scientists in the late 19th and early 20th century. All of the early definitions

highlighted the role of SI as an outbreeding mechanism, either implicitly or explicitly, but they did not distinguish it from self-sterility or rule out zygote lethality as a result of the process. Since it is now widely accepted that SI is a prezygotic barrier between otherwise fertile pollen and pistil components of the same flower, Lundqvist's definition of SI as "the inability of a fertile hermaphrodite seed-plant to produce zygotes after self-pollination" seems to be the most accurate. SI is found in 50% of angiosperm species [1]. Brewbaker [5], who corroborated this number, discovered that of the 600 he examined, SI operated in more than 70 families and 250 genera. Compiled a list of SI wild species and cultivars that are significant in agriculture or plant-breeding studies.

## 3. CLASSIFICATION OF SELF INCOMPATIBILITY

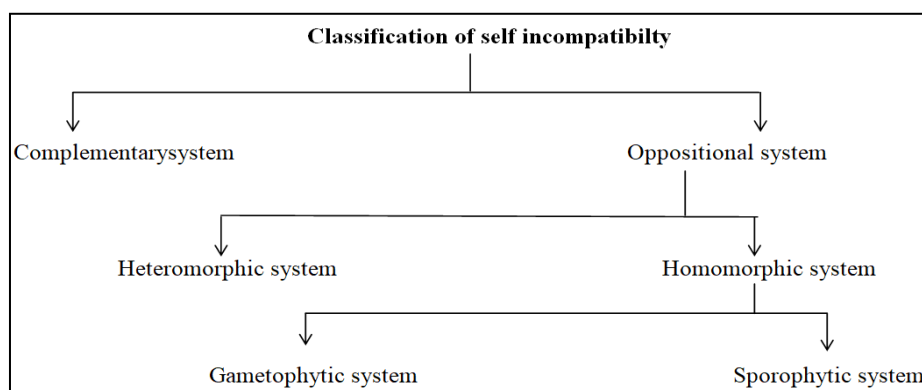
Based upon interaction between pollen grains and pistil, Bateman [6] classified self-incompatibility into complementary and oppositional systems of self-incompatibility.

### 3.1 Complementary System of Self-incompatibility

Another name for this system is stimulatory type self-incompatibility. The germination and development of the pollen tube are stimulated when pollen from one SI group reaches the stigma of another SI group, resulting in successful fertilisation. However, if they are members of the same SI group, no such compounds are produced, inhibiting pollen germination and subsequent growth.

### 3.2 Oppositional System of Incompatibility

This particular kind of self-incompatibility is sometimes referred to as an inhibitory type. Pollen germination and growth are inhibited when the pistil and pollen are members of the same SI. No chemicals are used in a compatible reaction that hinders the pollen's normal growth and development, ensuring successful fertilisation. Lewis divided the SI into two major categories: homomorphic systems and heteromorphic systems. Gametophytic and sporophytic systems are once again subclassified under the homomorphic system of self-incompatibility.



**Chart 1. Classification of self incompatibility**

**A. Heteromorphic self-incompatibility**

In this type of incompatibility same species produce more than one morphological type of flowers. For example, relative length of styles and stamens in flowers of same species. Distyly and tristyly has been reported in *Primula* and Evening primrose respectively. *Primula* has two types of flowers pin and thrum. Pin flowers bear long styles and short stamens, while thrum flowers have short styles and long stamens. The characteristic is governed by single genes, where *Ss* produces thrum and *ss* produces pin flowers. The incompatibility reaction of pollen is controlled by the genotype of the plant producing them *S* dominates over *s*. Incompatibility system thus represents heteromorphic sporophytic type. Such a mechanism has been observed in plants like buck wheat and sweet potatoes. This type of compatibility has not been established for any fruit crop.

**B. Homomorphic self-incompatibility**

Incompatibility in this type is related to floral morphological variations. The incompatibility may result from its own genotype (gametophytic control) or from the genotype of the plant on which it is formed (sporophytic control). Based on the number of genes directing the reaction, East and Mangelsdorf [7] divided the gametophytic system into subcategories. The incompatibility reaction is referred to as monofactorial (regulated

by a single gene) or bifactorial (controlled by more than two genes). It is further divided into two parts:

**i) Gametophytic self-incompatibility**

In this particular form of incompatibility, the stigma is wet type, the pollen is binucleate, and the *S* allele is present in each pollen. That indicates that pollen's incompatibility response is influenced by its own genotypes, not those of the plant on which it is formed. Typically, a single gene with many alleles determines the incompatibility reaction. Sometimes, polyploidy might cause the loss of incompatibility because the two *S* alleles present in diploid pollen compete with one another. The pineapple, loquat, apple, pear, plum, cherry, almond, apricot, certain citrus, and Solanaceae family members are notable examples. Two gametes, *S1* and *S2*, are produced by pollen parents with the genetic makeup *S1* and *S2*, and in female parents, two co-dominant alleles are expressed. As a result, because co-dominance occurs in the stigma, pollen grains with *S1* or *S2* genetic makeup that fall on a plant with *S1 S2* genetic composition will not both germinate. It can germinate and cause partial incompatibility when it falls on the stigma of a female plant with *S1, S3, or S2*; nevertheless, it is entirely compatible when it falls on a female with *S3 or S4*.

**Table 1. Comparison between gametophytic and sporophytic self- incompatibility**

<b>Gametophytic self-incompatibility</b>	<b>Sporophytic self-incompatibility</b>
1. Governed by genotype of the pollen.	1. Governed by the genotype of the plant producing pollen.
2. Stigma is smooth and wet.	2. Stigma is papillate and dry.
3. Growth of the pollen tube arrests in the style.	3. Growth of the pollen tube arrests at the surface of the stigma.
4. Pollens are binucleated.	4. Pollens are trinucleated.

## ii) Sporophytic self-incompatibility

The genotype of the plant on which the pollen is produced, not the genotype of the pollen itself, controls the incompatibility behaviour of the pollen. Due to the fact that all pollen grains from a certain plant exhibit the same behaviour, it indicates that the maternal genotype imposes the incompatibility. Pollen germination is inhibited as a result of incompatibility at the stigmatic surface. Plants like *Mangifera indica* and *Embllica officinalis* have trinucleate pollen and dry stigmatic surface.

## 4. MECHANISM OF SELF-INCOMPATIBILITY

Based on the various phenomenon observed during pollination and fertilization it can be grouped into three types:

- 1) Pollen stigma interaction
- 2) Pollen tube style interaction
- 3) Pollen tube ovule interaction

### 1) Pollen-stigma interaction

This interaction happens right as the pollen grains get to the stigma, and it typically stops pollen germination. Wet stigma is the term used to describe the plumose stigma surface seen in the gametophytic system, which has extended receptive cells. An incompatibility reaction happens afterwards. Clear serological differences exist between pollen grains of various S genotypes, although these differences have not been seen in sporophytic systems. The stigma of a sporophytic plant is papillate, dry, and covered in a pellicle- a layer of hydrated protein. There is proof that the pellicle plays a part in the incompatibility reaction. The chemical composition of the stigma antigens associated to the S allele differs noticeably. The pollen produces exine exudates that are either protein- or glycoprotein-based shortly after it touches the stigmatic surface. Incompatible stigma's papillae, which are in direct touch with the pollen, immediately develop calloses as a result of this exudate. Callose is frequently also deposited on the immature, projecting pollen tubes, preventing the pollen from germination. Therefore, stigma is the location of the incompatibility reaction in the sporophytic system. Pollen incompatibility is most likely caused by the deposition of certain chemicals from one tapetum onto the pollen exine.

### 2) Pollen tube - style interaction

Pollen grains germinate and pollen tubes pierce the stigmatic surface in the majority of gametophytic systems. However, the development of the pollen tube within the stigma is slowed down in incompatible combinations.

### 3) Pollen tube - ovule interaction

In a few instances, the pollen tube reaches to the ovule and interferes with fertilisation. However, an embryo degenerates at an early stage of development when unsuitable combinations are used.

## 5. METHODS OF OVERCOMING SELF INCOMPATIBILITY

One of the following techniques can be used to temporarily inhibit the incompatibility reaction and bring about partial fertility:

- a. **Bud pollination:** 1-2 days before anthesis, mature pollens are applied to immature, non-receptive stigma. By using bud pollination and NaCl treatment in a different study, Wang et al. [8] discovered that the latter was highly important, with a self-incompatibility index value of 2.54.
- b. **Surgical technique:** Removal of stigmatic surface.
- c. **High temperature:** Exposing pistils to temperatures as high as 60 °C.
- d. **Irradiation:** Radiations such as x rays or  $\gamma$  rays for single locus gametophytic incompatibility.
- e. **Double pollination:** Incompatible pollen is mixed with compatible pollen before application. Attempted to overcome self-incompatibility in passion fruit by using bud pollination and double pollination; they discovered that fruit sets of 16.67 and 10%, respectively, were seen in bud selfing and double pollination. However, no fruit set was seen in the control.
- f. **Pollination at the end of season:** According to, methanol killed the mentor pollen in low chilling plum and peach cultivars and was ineffective in removing incompatibility barriers. In contrast, frozen and thawed mentor pollen-one that, if alive, would be completely compatible with the style receiving it-improved fruit set in both intra- and inter-specific incompatibility.

In contrast to gametophytic incompatibility, which begins when the pollen tubes have already travelled 9 to 12 the length of the stylar tissue, the breakdown of the sporophytic incompatibility system is relatively simple because the incompatibility reaction occurs between the stigmatic surface and pollen wall.

## 6. ADVANTAGES OF SELF-INCOMPATIBILITY

- i. Self-incompatibility can instead help with  $F_1$  hybrid development in cases where male sterility is non-existent.
- ii. In clonally propagated orchard species like cherry and apple, self-fertility can be temporarily or permanently encouraged by mutation of S alleles to S1 through artificial irradiation. As parental material, we use superior clones with self-incompatibility and good general combining ability. Each clone will produce hybrid seeds. The biggest drawback is a lack of precise information on the male parent [9].
- iii. If self-incompatibility exists, seedless variants, such as those found in pineapple, grapes, and other fruits, can arise.

## 7. DISADVANTAGES OF SELF-INCOMPATIBILITY

- i. Seed set variations brought on by low fertility.
- ii. Since cross-pollination is not restricted the genetic purity of improved cultivars is poorly preserved.
- iii. Problems with the development and preservation of homozygous lines (inbreds) that can be used for hybridization.
- iv. Fruits of varying quality because of mixed plantings of several types based on their compatibility with one another.

## 8. S LOCUS CONTROLLING SELF-INCOMPATIBILITY

In the past, self-incompatibility was thought to be controlled by a single gene at the "S" locus, according to classical genetics. But thorough molecular analyses conducted after 1987 have revealed that the S locus contains at least two genes. Of which one gene has a male-determining function and the other a female-determining function. This multigene complex is passed down as a single entity. The 'S' haplotype

designates the variations of these genes. They only exhibit themselves temporally (during anthesis) and spatially (in stigma). i.e., they only appear during anthesis and on the stigmatic surface [10].

## 9. POLLINATION PATTERN AND INCOMPATIBILITY

For seed/fruit set, which comprises pollen hydration and germination, pollen tube growth into the style to the ovary, entry into the ovule and embryo sac, and release of sperms, self-incompatible fruit cultivars/species require cross pollination. Failures in pollination could consequently result in barrenness in trees that are otherwise healthy, pest-free, and disease-free. Cross pollination necessitates sensitive discriminations between pollen grains of various genotypes, necessitating the knowledge of each pollen's identification. Pollen grain germination depends on the pistil's selective acceptance before it can penetrate the stylar tissue and reach the embryo sac.

## 10. FRUITS SHOWING SPOROPHYTIC SELF-INCOMPATIBILITY

### 1. Mango

Mango self-incompatibility has been found to be of the sporophytic type [11,12]. It was noted in a number of commercial varieties of Indian mangos (*Mangifera indica*), including the Langra and Dashehri cultivars [13]. The results of the study on self-incompatibility make it abundantly evident that, unlike typical sporophytic self-incompatibility, self-incompatibility in mango is post-zygotic. Mango cultivar Mallika is self-incompatible, but cultivar Amrapali is only partially so. However, Pusa Arunima and Pusa Surya get along well with one another. The house fly is primarily responsible for cross-pollinating the male and perfect flowers that grow on the panicles. Per panicle, there are between 1000 and 6000 perfect flowers.

According to uniform cross pollination of the cultivars Dashehri, Langra, and Bombay Green with the pollen of Totapari and Bombay Green, Langra and Chausa, Dashehari and Totapari, and Bombay Green, in nature, about 50% of perfect flowers remain unpollinated, stigmas are particularly receptive on the day of anthesis, and mixed pollination generally leads to better fruit set. Different hybrids, including Arka Puneet,

Arka Neelkiran, and Arka Anmol, are created in Mango through self-incompatibility.

## 2. Aonla

In aonla, female flowers are found on the upper end of a few branches, whilst male flowers are found in clusters in the axil of leaf all over the branchlet. Male to female ratios of 307.9:1 and 197:1 in two consecutive years were recorded by Bajpai [14], demonstrating a significant variation in sex expression. Between 6 and 7 PM, the majority of male flowers open, and anther dehiscence begins shortly after. The stigma becomes receptive on the third day of anthesis, and the female flowers open in stages over a period of 72 hours. According to Bajpai [14], aonla pollen is light, hence wind serves as a source for wind pollination. Aonla exhibits sporophytic self-incompatibility. Aonla exhibits sporophytic self-incompatibility. A large proportion of staminate flowers may be the cause of poor fruit set.

## 11. FRUITS SHOWING GAMETOPHYTIC SELF-INCOMPATIBILITY

### 1. Apple

A multiallelic single locus known as the S-locus regulates the apple's gametophytic self-incompatibility (GSI) system. S-RNase, the pistil factor, and SFB/SLF, the pollen factor, are the genes that have been cloned to cause apple GSI [15,16]. Both S-RNase and SFB/SLF are found in the S-locus, and because of their close genetic relationships, their combined alleles are known as S-haplotypes. In the GSI system, pollen tube growth in the style terminates if one of the S-haplotypes of the pistil matches that of the pollen. For instance, cross-incompatibility occurs when cultivars S1S2 and S1S2 are crossed. While cross-compatibility occurs from a cross between the cultivars S1S2 and S3S4. Semi compatibility would result from the cross of S1S2 and S2S3, as the pistil's S2 haplotype will reject pollen of the S2 haplotype but not that of the S3 haplotype. These unfavourable fruit deformities, such lopsided fruits, might occasionally result from these incompatibility crossovers. According to Schneider et al. [17], Matsumoto et al. [18]; Matsumoto et al. [19], this may be owing to insufficient seeds in the fruit as a result of insufficient effective pollen at the time of pollination.

Additional knowledge about minor apple species and old cultivars, such crab apples, is particularly crucial in addition to the S-haplotype since stable apple production requires the utilisation of pollinators from old cultivars, wild apple orchards, and minor species. Furthermore, an understanding of the apple S-genotypes is crucial for the breeding of novel cultivars as well as cultivar pairing for consistent apple fruit production. As the apple (*Malus domestica*) exhibits gametophytic self- and cross-incompatibility, stable apple production requires at least two genetically different cultivars. Although there aren't many self-compatible apple cultivars in existence, "Megumi" is one of them. However, given the ratio of fruit set and seed number per fruit of Megumi x Megumi is 24.088.8% and 4.2, respectively, cross-pollination of "Megumi" is also advised here for reliable fruit production [20]. Fanny (54.5%), Winter Banana (60.4%), and Rome Beauty (54.25%) were more effective pollinators for the Early Shanburry cultivar. With regard to Red Delicious, cultivars McIntosh, Rymer, Jonathan, and Rome Beauty produced an acceptable harvest using self-pollination, with Jonathan having the highest fruit set (87.5%).

### 2. Ber

The majority of flowers appear in axillary clusters on growth from the current season. Distinct regions of India have distinct blooming times. According to Godara [21], the cultivars Banarsi, Karaka, Mundia, Murhara, Reshmi, Sandhura, Narnaul, Safeda, Umran, Ilaichi, and kakrola were all incompatible with one another, with Umran emerging as both the best pollen donor and recipient. Due of its stickiness, pollen is mostly spread by honey bees. Due to a short receptivity time, many flowers die because they are not pollinated at crucial gynoecium receptivity phases.

### 3. Pear

According to Sassa et al. [22], the European pear (*Pyrus communis*) has a gametophytic self-incompatibility system based on RNase. The S-locus, which includes at least two tightly linked polymorphic genes: a pistil-expressed gene and one or more pollen-expressed genes, controls this system genetically [23]. The pistil S-gene encodes an S-RNase that catalyses the degradation of RNA and is strongly expressed in the style [22,24]. The pollen S-determinant in *Pyrus* species is thought to be made up of

several F-box genes known as SFBBs (S-locus F-Box Brothers) [25]. The S-locus haplotype of *Pyrus communis* exhibits significant genotype-to-genotype variation, as shown by the allelic diversity of the genes expressed in pollen and pistil.

#### 4. Apricot

A single locus with several allelic variations controls gametophytic self-incompatibility in apricots (*Prunus armeniaca* L.).

#### 5. Plums

Gametophytic self-incompatibility, a prezygotic reproductive barrier, prevents the formation of self-pollen tubes in the style of the Japanese plum (*Prunus salicina* Lindl.), inhibiting self-fertilization. A multiallelic locus (S) is responsible for genetically regulating this incompatibility reaction. The pollen tube stops growing in the style, inhibiting fertilisation, when the S allele in the pollen grain matches one of the two S alleles expressed in the pistil. The majority of Japanese plum-type cultivars require cross-pollination with compatible cultivars that flower at the same time since they are self-incompatible.

#### 6. Loquat

The Rosaceae plant species loquat (*Eriobotrya japonica* Lindl.) possesses the RNase-dependent gametophytic self-incompatibility (GSI) fertilization system. The polymorphic stilar ribonuclease (S-RNase) encoded by the S-locus, which regulates gametophytic self-incompatibility. This enables the female reproductive organ (style) to distinguish and reject pollen from individuals with the same S-alleles while enabling the fertilisation of eggs by pollen from individuals with different S-alleles. The stilar area is where self-incompatibility occurs in self-incompatible cultivars. Examples of cultivars that are incompatible with one another are Tanaka, California Advance, Golden Yellow, and Pale Yellow.

#### 7. Pineapple

Commercial clones of the pineapple are incompatible with one another. As a result, they develop fruits which are parthenocarpic and having no seeds.

#### 8. Cherry

The majority of *Prunus* species have a GSI system based on S-RNase, which makes it difficult to successfully breed and cultivate fruit trees like sweet cherry (*P. avium*) and sour cherry (*P. cerasus*). Possible crossing relationships are determined by S alleles in the style and pollen.

#### 9. Almond

Gametophytic self-incompatibility (GSI) is a mechanism that controls sexual reproduction in almond and is driven by a multigene complex located within the S-locus. This process involves at least two linked genes found inside the S-locus that are expressed in both the female and male reproductive organs. In the pistil, the S-RNases play a crucial role in GSI. S-RNases are stilar glycoproteins with a molecular weight of approximately 30 kDa. They possess ribonuclease activity and display allele-specific polymorphism that is linked to the S-locus. The S-RNases are localized in the extracellular matrix of the transmitting tissue in the pistil. During the process of sexual reproduction, the S-RNases act as cytotoxins. When incompatible pollen grains come into contact with the extracellular matrix of the transmitting tissue, the S-RNases selectively prevent the growth of these incompatible pollen by exerting their cytotoxic effects on the pollen tubes. This mechanism ensures that only compatible pollen tubes, carrying different alleles at the S-locus, are allowed to grow and fertilize the ovules, promoting outcrossing and genetic diversity.

#### 10. Citrus

Gametophytic self-incompatibility (SI), a crucial trait in the creation of citrus cultivars with no seeds. There have been reports of self-incompatibility in mandarin, grapefruit, lemon, sweet lime, and pomelos. Kagzi Kalan variety of lemon exhibits incompatibility.

### 12. FRUITS SHOWING CROSS-INCOMPATIBILITY

#### 1. Apricot

Cross Incompatibility is reported in some cultivars like Goldrich, Hargrand and Lambertin – 1.



## 2. Almond

Cross compatible combinations are Jordanella X Har Pariel, Non Parial X IXL.

## 3. Plum

## 4. Cherry

Many cultivars of sweet cherries are unable to produce a crop through self-pollination. These "self-incompatible" cherry cultivars must be planted with a cherry cultivar that is genetically different from their own (a pollinizer), as this cultivar will supply the "compatible" pollen necessary for fruit set. Some cultivars are self-fertile and don't need a pollinizer. The S locus determines whether cherry pollen can descend the floral style. Each pollen grain contains one of the two S-alleles that are present in each cultivar. Pollen from any source, including its own, that carries any of those two alleles cannot fertilise flowers. Numerous cultivar pairs share the same two S-alleles (identical S-genotypes) as a result of inbreeding in the small gene pool of North America, making them incompatible with one another.

## 5. Citrus

Clementine, Orlando, Minneol, Sukega, Nova, and Robinson are incompatible hybrid cultivars.

## 6. Chestnut

## 7. Apple

Cross-incompatibility is found in many combinations of "Fuji" ( $S_1S_9$ ), "Akifu 1" ( $S_1S_9$ ; sport of "Fuji"), "Akifu 4" ( $S_1S_9$ ; sport of "Fuji"), "Akifu 7" ( $S_1S_9S_{28}$ ), "Alps Otome" ( $S_1S_9$ ), "Akiyo" ( $S_1S_9$ ; "Senshu" × "Fuji"), "Aofu 1" ( $S_1S_9$ ; sport of "Fuji"), "Aori 6 Gou" ( $S_1S_7S_9$ ; "Fuji" × "Jonathan"), "Benishigure" ( $S_1S_9$ ; sport of "Fuji"), "BeniShogun" ( $S_1S_9$ ; sport of "Yataka").

## 13. CONCLUSION

A genetic defence mechanism against self-pollination is self-incompatibility. Self-incompatibility in the S-locus is controlled by at least two genes. Self-incompatibility-causing genes are multiallelic in nature. Depending on the type of self-incompatibility and crop, there are various ways to determine self-incompatibility. Self-incompatibility can be

used to produce hybrids. Compared to male sterility, it offers numerous benefits. The creation and maintenance of inbred is the key restriction on self-incompatibility. There are many ways to produce inbred by overcoming self-incompatibility.

## 14. FUTURE LINE OF WORK

Researchers and breeders can identify and characterize S-alleles, develop stable self-incompatible parents, and exploit heterosis to produce hybrid seeds with improved traits in a controlled and targeted manner.

## COMPETING INTERESTS

Authors have declared that no competing interests exist.

## REFERENCES

1. Darlington CD, Mather K. The elements of genetics, Allen and Unwin Ltd, London; 1949.
2. De Nettancourt D. Incompatibility and incongruity in wild and cultivated plants (Vol. 3). Springer Science & Business Media; 2001.
3. Hogenboom NG. A model for incongruity in intimate partner relationships. *Euphytica*. 1973;22(2):219-233.
4. Kermicle JL, Evans MM. The *Zea mays* sexual compatibility gene *ga2*: Naturally occurring alleles, their distribution, and role in reproductive isolation. *Journal of Heredity*. 2010;101(6): 737-749.
5. Brewbaker JL. Biology of the angiosperm pollen grain. *Indian Journal of Genetics and Plant Breeding*. 1959; 19:121-133.
6. Bateman AJ. Self-incompatibility systems in angiosperms. *Heredity*. 1952;6(3):285-310.
7. E M, Mangelsdorf A. A new interpretation of the hereditary behaviour of self-sterile plants. *Proceedings of the National Academy of Sciences*. 1925;11(2):166-171.
8. Wang L, Hou X, Zhang A, Li Y. Effect of NaCl on overcoming self-incompatibility in non-heading Chinese cabbage (*Brassica campestris* ssp. *chinensis* Makino) studied by fluorescent microscopy. *Acta Horticulturae*. 2012;932:127-132.

9. Minimol JS, Suma B, Mathew M. Importance of polyclonal garden in production of superior materials in cocoa; 2015.
10. Takayama S, Isogai A. Self-incompatibility in plants. Annual Review of Plant Biology. 2005;56: 467-489.
11. Ram S, Bist LD, Lakhanpal SC, Jamwal IS. Search of suitable pollinizers for mango cultivars. In I International Symposium on Tropical and Subtropical Fruits. 1976;57: 253-264.
12. Litz RE. The mango, botany, production and uses. 1<sup>st</sup> Ed. CAB International. New York. 1997;587.
13. Singh RN. Mango indian council of agricultural research, New Delhi, India;1978.
14. Bajpai PN. Studies on flowering and fruit development in aonla (*Emblica officinalis*). Advances in Horticultural Sciences. 1968;7: 38-67.
15. Cheng J, Han Z, Xu X, Li T. Isolation and identification of the pollen-expressed polymorphic F-box genes linked to the S-locus in apple (*Malus domestica*). Sexual Plant Reproduction. 2006;19:175-183.
16. Broothaerts W, Janssens GA, Proost P, Broekaert WF. cDNA cloning and molecular analysis of two self-incompatibility alleles from apple. Plant molecular Biology. 1995;27:499-511.
17. Schneider D, Stern RA, Goldway M. A comparison between semi-and fully compatible apple pollinators grown under suboptimal pollination conditions. HortScience. 2005;40(5):1280-1282.
18. Matsumoto S, Kitahara K, Komatsu H, Abe K. Cross-compatibility of apple cultivars possessing S-RNase alleles of similar sequence. The Journal of Horticultural Science and Biotechnology. 2006;81(6): 934-936.
19. Matsumoto S, Soejima J, Maejima T. Influence of repeated pollination on seed number and fruit shape of 'Fuji' apples. Scientia Horticulturae. 2012;37:131-137.
20. Matsumoto S, Komori S, Kitahara K, Imazu S, Soejima J. S-genotypes of 15 apple cultivars and self-compatibility of 'Megumi'. Journal of the Japanese Society for Horticultural Science. 1999;68(2):236-241.
21. Godara NR. Studies on floral biology and compatibility behaviour in ber (*Zizyphus mauritiana*). Ph. D thesis, Haryana Agricultural University, Hisar (India); 1981.
22. Sassa H, Hirano H, Ikehashi H. Self-incompatibility-related RNases in styles of Japanese pear (*Pyrus serotina*Rehd.). Plant and cell physiology. 1992;33(6): 811-814.
23. Entani T, Iwano M, Shiba H, Che FS, Isogai A, Takayama S. Comparative analysis of the self-incompatibility (S-) locus region of *Prunus mume*: Identification of a pollen-expressed F-box gene with allelic diversity. Genes to Cells. 2003;8(3):203-213.
24. Zhou H, Yin H, Chen J, Liu X, Gao Y, Wu J, Zhang S. Gene-expression profile of developing pollen tube of *Pyrus bretschneideri*. Gene Expression Patterns. 2016;20(1):11-21.
25. Sassa H, Kakui H, Miyamoto M, Suzuki Y, Hanada T, Ushijima K, Koba T. S locus F-box brothers: multiple and pollen-specific F-box genes with S haplotype-specific polymorphisms in apple and Japanese pear. Genetics. 2007;175(4):1869-1881.
26. Baek YS, Covey PA, Petersen JJ, Chetelat RT, McClure B, Bedinger PA. Testing the S1x SC rule: pollen–pistil interactions in interspecific crosses between members of the tomato clade (*Solanum* section *Lycopersicon*, Solanaceae). American Journal of Botany. 2015;102(2):302-311.
27. Camadro EL, Peloquin SJ. Cross-incompatibility between two sympatric polyploid *Solanum* species. Theoretical and Applied Genetics. 1981;60:65-70.
28. Hayes RJ, Dinu II, Thill CA. Unilateral and bilateral hybridization barriers in inter-series crosses of 4x 2EBN *Solanum stoloniferum*, *S. pinnatisectum*, *S. cardiophyllum*, and 2x 2EBN *S. tuberosum* haploids and haploid-species hybrids. Sexual Plant Reproduction. 2005;17: 303-311.
29. Lewis D. Comparative incompatibility in angiosperms. Advances in Genetics. 1954; 6:235-255.
30. Onus AN, Pickersgill B. Unilateral incompatibility in Capsicum (Solanaceae): Occurrence and taxonomic distribution. Annals of Botany. 2004;94(2):289-295.
31. Rêgo MM, Rêgo ER, Bruckner CH, Finger FL, Otoni, W C. Overcoming self-incompatibility in Passion Fruit by double pollination in anthesis stages. In VII International Symposium on New Floricultural Crops 1000. 2011;533-536.

32. Singh Z, Singh L. Increased fruit set and retention in mango with exogenous application of polyamines. Journal of Horticultural Science. 1995;70(2):271-277.
33. Thomas SG, Franklin-Tong VE. Self-incompatibility triggers programmed cell death in Papaver pollen. Nature. 2004; 429(6989):305-309.

---

© 2023 Jain et al.; This is an Open Access article distributed under the terms of the Creative Commons Attribution License (<http://creativecommons.org/licenses/by/4.0>), which permits unrestricted use, distribution, and reproduction in any medium, provided the original work is properly cited.

*Peer-review history:*

*The peer review history for this paper can be accessed here:*  
<https://www.sdiarticle5.com/review-history/103671>