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Molecular basis of self-incompatibility in vegetable crops

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Abstract
Molecular basis of self incompatibility system in vegetable crops Self incompatibility is an important out breeding mechanism results due to morphological, genetic, physiological and bio chemical causes. So far it has been reported in about 70 families of angiosperms including several crop species. The common way of plants to avoid self fertilization is by self incompatibility. It is a physiological barrier making the flower difficult to fertilize itself even though it may be abundantly pollinated with its own pollen. There are two forms of self incompatibility system includes sporophytic self incompatibility and gametophytic self incompatibility. Sporophytic self Incompatibility system is a feature of crucifer family (Brassicaceae). In this review, we discuss the self incompatibility system in molecular level, its practical application and suppression and its impact in vegetable crops.

Keywords: Self incompatibility, pollination, crucifers, vegetable crops

Introduction
Self - incompatibility is the inability of a plant with hermaphrodite flowers producing developmentally functional male and female gametes to set seeds on self – pollination. This is, in effect, achieved by interposing a novel physiological barrier at any stage between pollination and fertilization. The regulation of mating among- self – gametes is generally operative in the stylar region which act as a highly effective biological sieve of diploid tissues arresting the pollen tube growth and thereby preventing haploid gametes (male and female) from uniting and affecting fertilization. Thus, in self-incompatibility nature has evolved one of the most efficient mechanisms to promote out breeding and consequent heterozygosity in angiosperms. The term self incompatibility was originally coined by Stout in 1917. Koelreuter, in the middle of 18th century, first reported self incompatibility in *Verbascum phoeniceum* plants.

Main features of self incompatibility
- Self incompatibility is an important outbreeding mechanism which prevents autogamy and promotes allogamy.
- Self incompatible species do not produce seed on self pollination but leads to normal seed set on cross pollination.
- It maintains high degree of heterozygosity in a species due to outbreeding and reduces homozygosity due to elimination of inbreeding or selfing.
- Self incompatibility results due to morphological, genetic, physiological and biochemical causes. It is not under simple genetic control.
- Self incompatibility reaction can operate at any stage between pollination and fertilization.
- Self incompatibility has been reported in about 70 families of angiosperms including several crop species.

Mechanisms of self incompatibility
There are two different types of events which are considered to constitute the self incompatibility system: (1) the stimulation of unlike genotypes and (2) inhibition of like genotypes. Thus two hypotheses have been proposed to explain the mechanism of self incompatibility in plants.

Complementary hypothesis
This hypothesis was proposed by Bateman in 1952. According to this hypothesis

incompatibility results due to absence of stimulation by the pistil on pollen growth in the like genotypes ($S_1 S_2$ X $S_1 S_2$). In other words, self incompatibility results due to absence of substances in the pistil or pollen which are essential for pollen tube penetration on selfing, the pollen and /or the pistil fail to produce the substance which is essential for pollen germinate or pollen tube growth in the style and the ovary. Complementary system depends on the combination of unlike alleles in the pollen and style. Such combination of alleles leads to production of either a stimulant for pollen tube growth or an antidote to the inhibition already present in the style.

Oppositional hypothesis

This hypothesis states that interaction between like alleles ($S_1 S_2$ X $S_1 S_2$) 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: (1) it may inhibit an enzyme or auxin necessary for pollen tube growth, (2) may block pollen tube membrane, and (3) may inhibit an enzyme necessary for the penetration of style.

Classification of self incompatibility

Self incompatibility can be classified on the basis of (1) flower morophology, (2) genes involved, (3) site of expression of self incompatibility reaction, and (4) pollen cytology.

Table 1: Classification of self incompatibility

Basis of classification	Types of self incompatibility	Brief Description
1. Flower Morphology	(a) Heteromorphic	SI is associated with differences in flower morphology.
	(i) Distyly	Styles and stamens are of two types, *i.e.*, short and long.
	(ii) Tristyly	Styles and stamens have three positions, *i.e.*, short, medium and long.
	(b) Homomorphic	The flowers do not differ in Morphology.
	(i) Sporophytic	SI is governed by genotype of pollen producing plant.
	(ii) Gametophytic	SI is governed by the genetic constitution of gametes.
2. Genes Involved	(a) Monoallelic	SI is controlled by a single gene
	(b) Diallelic	SI is governed by two genes.
	(c) Polyallelic	SI is governed by several genes
3. Site of Expression	(a) Stigmatic	SI genes express on the stigma.
	(b) Stylar	SI genes express in the style.
	(c) Ovarian	SI genes express in the ovary.
4. Pollen Cytology	(a) Binucleate	The pollen grains have two nuclei
	(b) Trinucleate	The pollen grains have three nuclei

SI = Self incompatibility

Based on flower morphology, self incompatibility system is of two types: *viz.*, (1) heteromorphic system, and (2) homomorphic system.

Heteromorphic system

When self incompatibility is associated with differences in floral morphology, it is known as heteromorphic system. In this system self incompatibility results due to differences in the length of style and stamen. This system is again of two types, *viz.*, (a) Distyly, and (b) Tristyly.

Distyly. It refers to two types of styles (short and long) and stamens (low and high). This system operates in the family Primulaceae. In Primula, there are two types of flowers: *viz.*, (1) thrum type which has short style and high anthers, and (2) pin type with long style and low anthers. The crosses are compatible only between the style and stamens of matching length. In other words, crosses are compatible between pin x thrum or thrum x pin but not between pin x pin and thrum x thrum flowers.

Fig 1: Flowers of *Primula veris*: thrum flower (left) & pin flower (right)

Table 2: Differences between thrum and pin flowers of *primula*

Particulars	Thrum (Ss)	Pin (ss)
Incompatibility reaction of style	Thrum type (L_1)	Pin type (l_1)
Incompatibility reaction of pollen	Thrum type (L_2)	Pin type (l_2)
Length of style	Short (G)	Long (g)
Size of stigmatic cells	Small (S)	Large (s)
Height of anthers	High (A)	Low (a)
Size of pollens	Large (P)	Small (p)

Tristyly

When style has three different positions, it is referred to as Tristyly. In Tristyly anthers and style have three positions in the flowers, *viz.*, short, medium and long. Tristyly is common in the family Lythraceae. Tristyly is found in *Lythrum salicaria*. Three position of style are genetically controlled by two genes (Ss and mm.) The S gives rise to short style, s and M to medium style and s and m to long style. Short style may have SSMM, SSMM or SSMM genotypes; medium style has SSMM or SSMM genotypes; and long style has SSMM genotype.

Homomorphic system

In homomorphic system, self incompatibility results due to physiological causes rather than differences in flower morphology. In this system, the plants do not have differences in the length of style and stamens or other floral parts. This system is very much important in crop plants. It can operate in various ways as given below;

- The pollen grains do not germinate on the stigma of same flower. If they germinate the pollen tube fails to penetrate the stigma as in Rye, Cabbage and Radish.
- The pollen grains may germinate but there is retardation of pollen tube growth
- In some cases, there is slow rate of pollen tube growth and it rarely reaches the ovary in time to effect self fertilization.

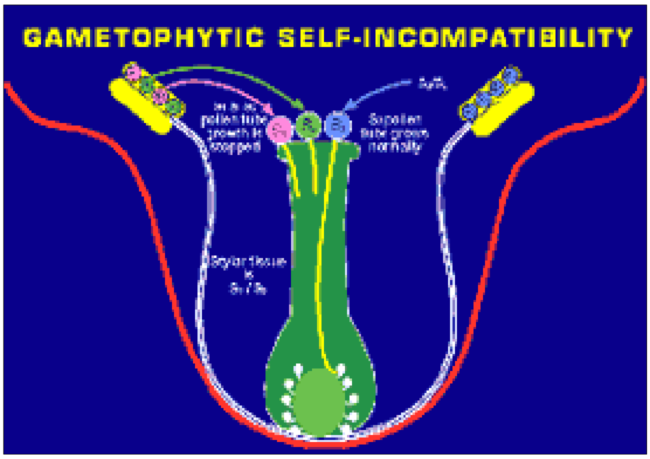

Fig 2: Homomorphic system is of two types, *viz.*, (1) Gametophytic system, and (2) Sporophytic system.

(1) Gametophytic system

When the self incompatibility is controlled by the genetic constitution of gametes, it is known as Gametophytic self incompatibility system.

This system was first discovered by East and Mangelsdorf (1925) in *Nicotiana sanderae*. Now this system has been reported in rye, red clover, white clover, potato, tomato and several other crop plants.

Main features of this system are

1. Self incompatibility in majority of species is governed by a single gene S which has large number of multiple alleles. However, in rye self incompatibility reaction is governed by two loci (Sobotka, 2000) [23].
2. In this system alleles have individual action in the style without interaction.
3. Pollen grains are unable to germinate or function on a pistil having similar alleles as that of pollen. The pollen tube growth is usually inhibited in the style or ovary.
4. This system gives rise to three types of pollinations, *viz.*, (1) fully incompatible ($S_1 S_2$ x $S_1 S_2$) in which both allele are common in the pollen and ovule, (2) half the pollen is compatible ($S_1 S_2$ x $S_1 S_3$) in which one allele is different, and (3) fully fertile ($S_1 S_2$ x $S_3 S_4$) when both alleles differ in pollen and ovule.
5. Gametophytic system permits recovery of male parent only in the partially fertile crosses which are obtained when one allele differs in the cross, *viz.*, $S_1 S_2$ x $S_1 S_3$. This cross would give rise to $S_1 S_3$ and $S_2 S_3$ progeny.
6. Plant species belonging to gametophytic self incompatibility system have Binucleate pollen.
7. All gametophytic systems (except in Gramineae) operate with wet stigma surfaces and there is no direct interaction between one pollen grain and one surface cell because germination takes place in a common fluid medium (Heslop-Harrison, 1975).
8. The biochemical substance which is associated with the incompatibility response of the pollen develops very late, *i.e.*, during pollen formation in gametophytic system.

(2) Sporophytic system

When the self incompatibility is governed by the genotypes of pollen producing plant (Sporophyte), it is called Sporophytic system. This system was first discovered by Hughes and Babcock (1950) in *Crepis foetida* and Gerstel (1950) in *Parthenium argentatum* (Guayule). Now this system has been reported in Radish, Cabbage, Cauliflower, Sunflower, Cosmos and several other crop plants.

Main features of this system are

- In this system also self incompatibility is controlled by a single gene S which has multiple alleles.
- The alleles may show dominance, individual action or interaction in either pollen or style as per the allelic combinations involved.
- This system exhibits inhibition of pollen germination or pollen tube growth on the stigma of same flower.
- The Sporophytic system contains a form of dominance in which $S_1$is dominant over all other alleles, S_2 is dominant over all except S_1 and so on ($S_1 > S_2 > S_3 > S_4$). In this system, crosses between different genotypes are either fully fertile or completely sterile.
- Pollen grains from both heterozygous or homozygous plants react in a similar fashion due to dominance effect of male parent.
- The system permits recovery of parental genotypes in some crosses
- This system of self incompatibility generally have tri nucleate pollen and operate with a dry stigma
- The biochemical substance which is associated with the incompatibility develops very early in Sporophtic system that is before pollen development. (Nasrallah, 1993) [15].

Table 3: Characteristics associated with the two main classes of homomorphic SI

Characters	Monofactorial GSI	Bifactorial GSI
Pollen phenotype	Haploid	Haploid
Controlled by	Pollen genotype	Pollen genotype
No. of genes	1	2
Allelic state	Multiallelic (Often 50 or more)	Multiallelic (Usually < 20)
Stigma type	Wet	Dry
Inhibition site	Style	Stigma
Pollen nuclei	Binucleate	Trinucleate
Pollen germination	Slow	Fast

Table 4: 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

SI in Brassicaceae
- SRK, the female determinant spans the plasma membrane of the stigma papilla cell.
- SP-11 male determinant expression occurs in anther tapetum.
- Upon pollination SP-11 binds SRK in an S- haplotype specific manner.
- Binding induces auto- phosphorylation of SRK, triggering a signal cascade resulting in rejection of self pollen
- SLG enhances the SI reaction in some S -haplotypes
- Positive effectors MLPK, ARC-1.
- Proteasomal degradation.

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
- Transgenic gain of function mutation experiments showed that SRK alone determine SI specificity and its ability is enhanced by SLG

SLG (S-locus glycoprotein) gene
- The first S-linked gene identified in Brassica
- Encodes a stigma specific glycoprotein localized to cell wall of papilla cells
- It shares as much as 98% nucleotide sequence identity with SRK
- Loss of function experiments showed that SLG is not essential for haploid specific pollen recognition even though presence of SLG enhance SRK response

Self Incompatibility in Cruciferae
In controlling pollination, self-incompatibility (SI) has been used in the family Cruciferae. These include many important kinds of vegetables, such as cabbage, radish, Chinese cabbage, turnip and broccoli. The study of SI in crucifer crops began in Japan. In 1949, a Chinese cabbage F_1 hybrid variety, "Nagaoka Kohai I Go", was produced by Shojiro Ito, and in 1961 a radish F_1 hybrid variety, "Harumaki Minowase", was produced by a commercial seed company.
There are genetic variations in the reaction level of self-incompatibility (RLSI) to a 4% CO_2 gas treatment. Thus, the parental lines in the parental seed production in a single cross have to show a marked reaction to CO_2. In F_1 seed production on both a single and a double cross, the parental lines have to show a high LSI. It is therefore important to know the genetic relationship between these characteristics.

Practical application
- Basic method of utilizing heterosis is to cross two inbred lines together to produce an F_1 hybrids.

For this purpose
- Two SI, but cross compatible, lines are interplanted; seed obtained from both the lines would be hybrid seed.
- Alternatively, a SI line may be interplanted with a self compatible line. From this scheme, seed from only the self incompatible line would be hybrid.
- Schemes for the production of double cross hybrids (DCH) and triple cross hybrids (TCH) have been proposed their feasibility demonstrated in brassicas

Problems in use of self incompatibility in hybrid seed production
Production and maintenance of inbred lines by hand pollination is tedious and costly.
- This raises the cost of hybrid seed
- Continued Selfing leads to a depression in self-incompatibility, and it unintentionally, but unavoidably, selects for self-fertility.
- In the gametophytic systems, continued inbreeding gives rise to new incompatibility reactions, which may limit the usefulness of such inbreds as parents.
- Environmental factors eg. High temperature and high humidity etc. reduce or even totally overcome self incompatibility reaction leading to a high (30% or more) proportion of selfed seed.
- Bees often prefer to stay within the parental line, particularly when the parental line differ morphologically. This in turn, increase the proportion of selfed seed.
- Transfer of S alleles from one variety or more particularly species to another variety to species is tedious and complicated. This has prevented the use of self incompatibility in hybrid seed production in Solanaceae and Compositae

Easy, reliable and economical methods for multiplication of inbred lines may become available in the near future. Some of the promising approaches are briefly outlined below.
- Inbreds could be multiplied in greenhouses, self incompatibility is produced by a temperature of $30^{O}C$ or above
- Inbreds could be multiplied in suitable polyethylene tunnels. The CO_2 level of the tunnels could be elevated e.g. by placing in them CO_2 tablets. Pollination could be effected by hand or by a suitable insect pollinator e.g. blow flies
- Field multiplication of inbreds can be done using a 5-10% sodium chloride spray or 3-5 days. This method has been successful with *B. napus*, *B. oleraceae* and *B. campestris*. This is the only approach applicable at the field level

Temporary suppression of self incompatibility
Following measures are used for maintenance of inbred lines:
- Bud Pollination.
- Surgical Techniques – *Brassica* spp.
- End of Season Pollination.
- High Temperature – *Trifolium* spp., *Solanum* spp.
- Increased CO_2 concentration.
- High Humidity.
- Salt (NaCl) sprays
- Irradiation (Solanaceae)
- Double pollination
- Grafting (*Trifolium pratense*)

Conclusion

1. Self-incompatibility (SI) signaling represents a unique mechanism for self/non self recognition between pollen and pistil. As a result, the self or genetically related pollen is unable to germinate or grow in the style to complete fertilization. Recent studies have shown that proteolytic events play important roles in both self-pollen rejection and compatible pollen growth during SI signaling.
2. In Brassicaceae-type SI, a U-box protein ARM-repeat-containing1 (ARC1) participates in the SI response as a functional E3 ligase after the specific recognition between pollen and pistil. In addition, its likely substrate, Exo70A, which acts as a potential pollen compatibility factor, has been identified.
3. In Papaveraceae-type SI, the pistil *S* selectively interacts with self pollen, which in turn triggers a signaling cascade that culminates in the programmed cell death (PCD) of the self-pollen tube.
4. In Solanaceae-type SI, which represents the most Phylogenetic ally widespread form of SI, both the ubiquitin-proteasome pathway and the vacuole pathway appear to take active parts in SI responses.

References

1. Arasu NT. Self incompatibility in Angiosperms – A review, Genetica. 1968; 39:1-24
2. Brugiere N, Yuhai Cui, Steven Rothstein. Molecular mechanism of self recognition in Brassica self incompatibility. Trends in plant science. 2000; 5(10):432-438
3. Dixit R, June Nasrallah B. Recognizing self in the self-incompatibility response. Plant Physiology. 2001; 125:105-108.
4. Edh K, Bjorn Widen, Alf Ceplitis. Molecular population genetics of the SRK and SCR self incompatibility genes in the wild plant species *Brassica cretica* (Brassicaceae). Genetics. 2008; 181:985-995.
5. Gupta SK. Practical plant Breeding published by Agrobios (India), Jodhpur, 2005.
6. Hiscock JS, David Tabah A. The different mechanisms of Sporophytic self incompatibility, 2003, 1037-1045
7. Hiscock JS, Stephanio McInnis M. Pollen recognition and rejection during the Sporophytic self incompatibility response. Brassica and beyond. Trends in plant science. 2003; 8:12.
8. June Nasrallah B. Recognizing self in the self incompatibility response. Plant Phy. 1987; 125:105-108.
9. June Nasrallah B. Cell Cell signaling in the self incompatibility response. Current Opinion in Plant Biology. 2000; 3:368-373.
10. Kachroo A, Mikhail Nasrallah E, June Nasrallah B. Self incompatibility in Brassicaceae. Receptor-Ligand signaling and cell to cell communication. The plant cell, 2002, S227-S238.
11. Kao The-Hui, Tatsuya Tsukamoto. The Molecular and Genetic Bases of S R Nase Based self incompatibility. The plant cell. 2004; 16:S72-S83
12. Matton PD. Oliver Mass Genevieve Laublin, Qin Xike, Charles Bertrand, David Morse and Mario Cappadocia. The Plant Cell. 1997; 9:1757-1766.
13. McClure B. New views of S-R Nase based self incompatibility. Current Opinion in Plant Biology, 2006, 639-646
14. McCubbin, G.A and Tech-hui Kao. 2000. Annu. Rev. Cell. Dev. Biol. 16: 333-364
15. Nasrallah BJ, Mikhail Nasrallah E. Pollen stigma signaling in the sporophytic self incompatibility response. The plant cell. 1993; 5:1325-1335.
16. Nasrallah BJ, Mikhail Nasrallah E. The self incompatibility Locus of Brassica. Biotechnology in Plant Science, 1985, 259-263.
17. Piotr Waligorski, Maciej Szaleniec. Prediction of white cabbage (*Brassica oleracea* var. *capitata*) self-incompatibility based on neural network and discriminant analysis of complex electrophoretic patterns. Computational Biology and Chemistry. 2010; 34:115-121.
18. Roggen HPJR. Scanning electron microscopic observations on compatible and incompatible pollen stigma interaction in Brassica. Euphytica. 1972; 21:1-10.
19. Schopfer CR, Nasrallah ME, Nasrallah JB. The Male determinant of self incompatibility in *Brassica*. Science. 1999; 286:1697-1700.
20. Sharma JR. Principles and practices of plant breeding, published by Tata Mc Graw – Hill publishing company limited New Delhi, 1996.
21. Simon Hiscock J, Stephanie McInnis M. Pollen recognition and rejection during the sporophytic self-incompatibility response: Brassica and beyond. Trends in plant science. 2003; 8(12):606-613.
22. Singh P. Essential of plant Breeding, Kalyani publishers; Rajendranagar, Ludhiana, 1996.
23. Sobotka R, Lenka Sakova, Vladislav Curn. Molecular Mechanisms of self-incompatiblity in Brassica. Current Issues. Mol. Biol. 2000; 2(4):103-112.
24. Tantikanjana T, Nasrallah EM, June Nasrallah B. Complex networks of self-incompatibility signaling in the Brassicaceae. Current Opinion in Plant Biology. 2010; 13:520-526.