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A REVIEW

Self-incompatibility: a pollination control mechanism in plants

Vijayakumar B. Narayanapur, B. Suma and J.S. Minimol

SUMMARY

Mode of pollination is very important in plant breeding because it determines the genetic constitution, nature of gene action, ease in pollination control and stability of varieties after release. There are several mechanisms that promote cross pollination, among these self-incompatibility (SI) is of special significance as it is used in hybrid seed production. SI is defined as the prevention of fusion of fertile (functional) male and female gametes of the same plant (Gowers, 1989). SI is a system where self-recognition and rejection is the rule that prevents inbreeding depression. Bateman (1952) classified self-incompatibility based on the interaction between pollen grains and pistil as complementary and oppositional system. Lewis (1954) has classified SI into homomorphic and heteromorphic systems. Homomorphic SI is again subdivided into gametophytic (determined by the genotype of gametes) and sporophytic (determined by the genotype of the plant) systems. Molecular studies after 1980's revealed that at least two genes within S-locus control the SI, among these one unit function as male and the other as female determinant. In Brassicaceae family, the determinant gene encodes a pollen ligand and its stigmatic receptor kinase and their interaction induces incompatible signaling within the stigma papilla cells. In the Solanaceae, Rosaceae, and Scrophulariaceae, the female determinant is ribonuclease and F-box protein, suggesting the involvement of RNA degradation and protein degradation within the system. In the Papaveraceae, the female determinant induces Ca^{2+} dependent signaling network that ultimately results in the death of incompatible pollen (Takayama and Isogai, 2005). Genes controlling the SI is multiallelic in nature and number of alleles varies depending upon the crop. Number of alleles reported are five in *Theobroma cacao* (Knight and Rogers, 1953), 30 in *Brassica campestris* (Singh, 2012), 32 alleles in *Raphanussativus* (Karron *et al.*, 1989). SI is commercially exploited for the production hybrid seeds. Pusa Hybrid-2, Snow Queen and Snow King hybrids of cauliflower, BRH-5, H-44 of cabbage and CCRP8 to CCRP15 (Minimol *et al.*, 2015a) of cocoa are some of the examples. Kucera *et al.* (2006) has compared the quality between SI and male sterility hybrids in cauliflower and it was found that SI hybrids are superior in their performance. Minimol *et al.* (2015b) emphasized the importance of polyclonal garden in cocoa for production of F_1 hybrid seeds by utilizing the self-incompatibility. Rego and Rego (2013) evaluated the efficiency of three methods of overcoming self-incompatibility in passion fruit and found fruit set of 16.67 and 10 per cent in bud and double pollination, respectively. The main limitations in exploiting SI is the maintenance of inbreds, however, it can be overcome by some temporary methods such as bud pollination, salt sprays and irradiation methods.

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The restriction of sexual pairing by a specificity gene is considered to be an ancient development in the plant kingdom. The diversity and general parallelism of incompatibility system seen amongst the phyla at the present time can be rationalized in terms of association of various derived forms of the ancestral specificity unit with differing spectra of accessory factors controlling sexual physiology in the different phyla. Sexual morphogenesis has become divided into phases under the control of complementary genes. These phases are initiated by regulatory system of "coordinator genes" which control the order in which group of morphogenetic genes are expressed during development. The entire sexual cycle will be completed only if all the complementary groups are activated in the appropriate sequence.

Pollination is a very important part of the sexual reproduction process of flowering plants, which results in seeds which grow into new plants. Gymnosperms have similar pollination as all transmit their pollen by wind. In contrast, angiosperm have a wealth of pollination methods involving many different agents to transfer pollen, including insects (entomophily), birds (ornithophily), bats (chirophily), wind (anemophily) and water (hydrophily), dichogamy (male and female reproductive organs mature at different times that lead to the cross pollination) and male sterility (in a bi-sexual flower the stamens are sterile). Self-incompatibility is of special significance as it is used in hybrid seed production. Gowers (1989) has defined self-incompatibility as "the prevention of fusion of fertile (functional) male and female gametes after self-pollination. Self-incompatibility was reported by Koelreuter during 1850's. Self-incompatibility is a genetic mechanism of avoiding self-fertilization that leads to natural out breeding where self-recognition and rejection is the rule. It promotes heterozygocity and prevents inbreeding depression. Self-incompatibility has been classified based on the allele specific interaction between stigma receptor and pollen ligand. This character is distributed in nearly 6000 species belonging to 250 genera from 70 families representing 19 orders from both monocots and dicots (Gowers, 1989).

Classification of self-incompatibility :

On the basis of interaction between pollen grains and pistil, Bateman (1952) classified self-incompatibility into complementary and oppositional systems of self-incompatibility.

Complementary system of self-incompatibility :

This system is also called as stimulatory type of self-incompatibility. When pollen of one SI group fall on the stigma of other SI group, both will produce certain substances which will stimulate germination and growth of pollen tube resulting in successful fertilization. But if they belong to same SI group no such chemicals are produced and thus the germination and further growth of pollen is inhibited.

Oppositional system of incompatibility :

This is also known as inhibitory type of self-incompatibility. When pollen and pistil belong to same SI they produce certain chemicals which will prevent pollen germination and growth. In a compatible reactions no chemicals are inhibiting normal growth and development of pollen will be resulting in a successful fertilization.

The classical classification of self-incompatibility was given by Lewis (1954). He classified SI into two main groups, *i.e.*,homomorphic and heteromorphic system. The homomorphic system of self-incompatibility is again sub classified into gametophytic and sporophytic system.

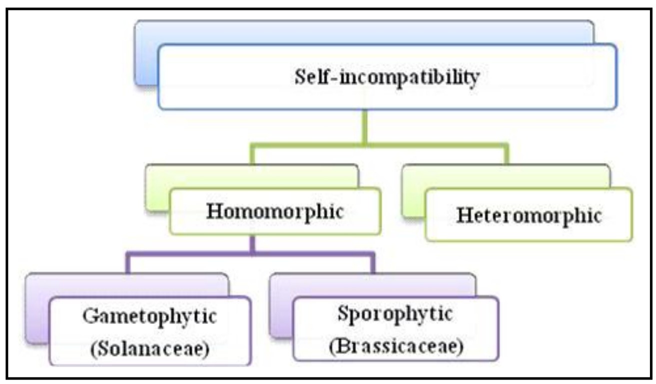


Fig. 1 : Classification of self-incompatibility

In heteromorphic self-incompatibility, flowers of different incompatibility groups are in morphology. For example, in *Primula*, there are two types of flowers, pin and thrum. Pin flowers have long style and short stamens while thrum flowers have short styles and long stamens. This situation is referred as distyly. Pin and thrum flowers are produced on different plants. The only compatible mating is between pin and thrum flowers. This character is governed by a single locus s; Ss produces thrum, while ss produces pin flower. The incompatibility reaction in pollen grainsare determined by the genotype of the plant.The gene governing SI reaction has two alleles S and s; allele 'S' is dominant over 's'. In some species two genes, each having two alleles, control the SI reaction. The incompatibility system is therefore heteromorphic-sporophytic. The pollen grains produced by pin flowers, would be all s in genotypes as well as incompatibility reaction. The pollen produced by thrum flowers would be of two types genotypically, S and s, but all of them would be S phenotypically. The mating between pin and thrum plants would produce Ss and ss progeny in equal frequencies. This system is of little importance in crop plants and it occurs only in sweet potato and buckwheat.

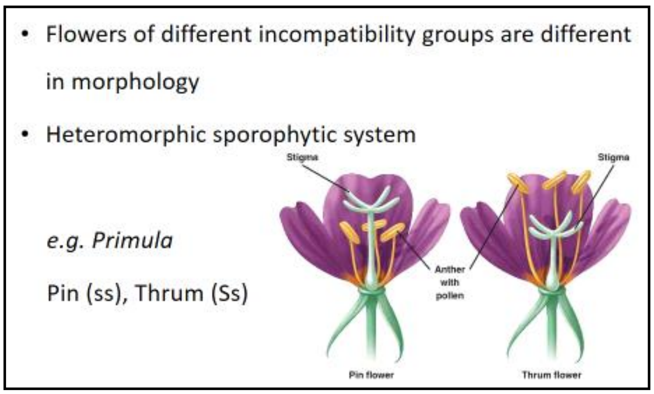


Fig. 2 : Heteromorphic self-incompatibility in *Primula*

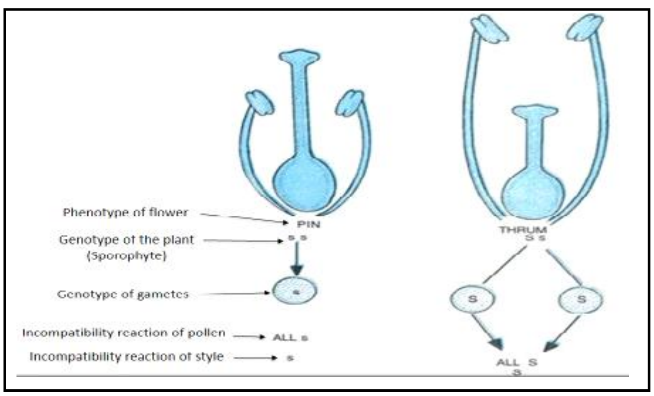


Fig. 3 : Heteromorphic self-incompatibility in *Primula*

Table 1 : Heteromorphic sporophytic self-incompatibility

Mating		Progeny	
Phenotype	Genotype	Genotype	Phenotype
Pin x Pin	ss x ss	Incompatible mating	
Pin x Thrum	ss x Ss	1 Ss : 1 ss	1 Thrum : 1 Pin
Thrum x Pin	Ss x ss	1 Ss : 1 ss	1 Thrum : 1 Pin
Thrum x Thrum	Ss x Ss	Incompatible mating	

Homomorphic self-incompatibility :

The morphology of the flower is nothing to do with incompatibility reaction. The incompatibility reaction is controlled either by genotype of the gamete *i.e.*,gametophytic self-incompatibility or by genotype of the plant *i.e.*, sporophytic self-incompatibility. East and Mangelsdorf (1925) have given a sub classification to gametophytic system based on number of genes controlling the reaction. The incompatibility reaction if controlled by a single gene it is known as monofactorial or more than two genes (bifactorial system).

Gametophytic self-incompatibility :

Pollen parent with genetic constitution S_1 S_2 produce two gametes $S_1$and S_2 and in female parent two alleles are co-dominant and both get expressed. Hence, when pollen grains with S_1 or S_2 genetic makeup fall on a plant with S_1 S_2 both will not germinate since the reaction in stigma is co-dominance. When it fall on the stigma of a female plant with S_1 S_3, S_2 can germinate and partial incompatibility is executed and when it falls on a female with S_3 S_4 it is completely compatible (Hughes and Babcock, 1950).

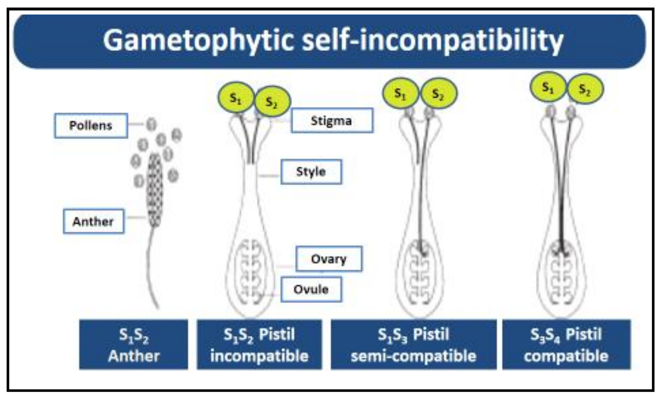


Fig. 4 : Gametophytic self-incompatibility

Sporophytic self-incompatibility :

In sporophytic system it is the genotype of the parent

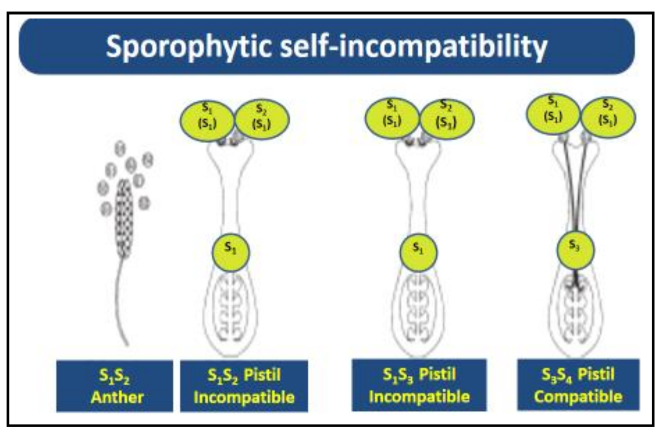


Fig. 5 : Sporophytic self-incompatibility

which is determining the incompatibility reaction and $S_1 > S_2$, $S_2 > S_3$ and $S_3 > S_4$ etc., Male gamete both S_1 and S_2 produced from S_1 S_2 will behave as S_1 and in style of S_1 S_2 will behave as S_1. Hence, a cross between S_1 S_2 x S_1S_2 is incompatible and S_1S_2 x S_1S_3 is also incompatible while S_1 S_2 x S_3 S_4 is compatible.

Sporophytic self-incompatibility was reported in members of brassicaceae like Kale (Thompson, 1957), Radish (Sampson, 1957), Broccoli (Sampson, 1957 and Odland, 1962), Cabbage (Adamson, 1965), Cauliflower (Hoser-Krauze, 1979),Cocoa (Knight and Rogers, 1953), Tea (Thompson, 1957), Mango (Singh *et al.*, 1962).

S. locus controlling self-incompatibility :

Earlier with classical genetics,'S' locus controlling the self-incompatibility was assumed to be a single gene. But after 1987 with detailed molecular studies, it has been identified that at least two genes are there within S locus. Of which one gene function as male determinant while the other as female determinant. This multigene complex is inherited together as one unit. The variants of these genes are known as 'S' haplotypes. Their expression is temporally (only at the time of anthesis) and spatially (in stigma) regulated. *i.e.*, they get expressed only at the time of anthesis and on stigmatic surface (Takayama and Isogai, 2005).

Molecular models of self-incompatibility :

Molecular model of SI in Brassicaceae :

Two genes *SP11/ SCR* is present, *SP11* is male determinant and *SRK* is the female determinant. SLG is promoter of incompatibility reaction. SRK acts in the plasma membrane of papilla cells of stigma while *SP11* get expressed in the anther tapetum during the maturation of pollen grain. In a SI reaction, when pollen grain land on stigma *SP11* will bind with SRK and leads to autophosphorylation resulting in prevention of pollen tube growth. But in a compatible reaction, *SP11* is not get activated and hence, normal pollen germination and fertilization takes place.

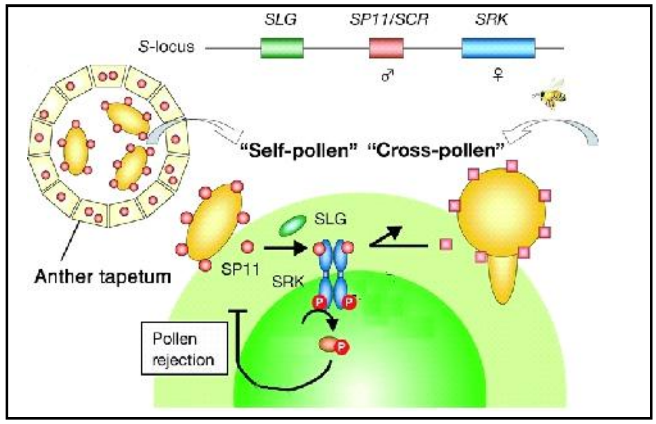
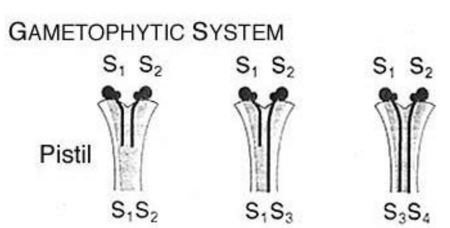


Fig. 6 : Molecular model of self-incompatibility in Brassicaceae

Table 2 : General comparison between gametophytic and sporophytic self-incompatibility

Gametophytic SI	Sporophytic SI
– Stigma is smooth and wet	– Stigma is papillate and dry
– Genotype of the pollen (gamete)	– Genotype of the sporophyte (diploid tissue)
– S-locus products are synthesized after completion of meiosis	– S-locus products are synthesized before completion of meiosis
– Growth of the pollen tube arrests in the style	– Growth of the pollen tube arrests at the surface of the stigma



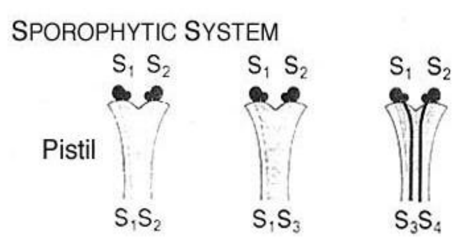


Table 3 : Male and female determinant genes reported in some families

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

SP11- S locus protein 11 *SCR*- S locus cysteine rich protein SRK- S locus receptor kinase
SLF- S locus F-box protein *SFB*-S-haplotype-specific F-box protein

Table 4 : S locus/ S related genes and their function/s in Brassicaceae members

Sr. No.	S-locus related gene	Gene function	Species name	References
1.	*SLG*	Doubtful	*B. oleracea*	Nasrallah, 2000
2.	*SRK*	Female determinant	*B. oleracea*	Stein *et al.*, 1991
3.	*SP11/SCR*	Male determinant	*B. rapa*	Suzuki *et al.*, 1999
4.	*MLPK*	Positive regulator	*B. rapa*	Murase *et al.*, 2004
5.	*ARCI*	Positive regulator	*B. napus*	Stone *et al.*, 2003
6.	*Rdr6*	Positive regulator	*B. thaliana*	Tantikanjana *et al.*,2009
7.	*THLI*	Negative regulator	*B. napus*	Haffani *et al.*, 2004
8.	*KAPP*	Putative SRK interactor	*B. oleracea*	Vanoosthuyse *et al.*, 2003
9.	*SNXI*	Putative SRK interactor	*B. oleracea*	
10.	*Calmodulin*	Putative SRK interactor	*B. oleracea*	Schopfer *et al.*, 1999
11.	*PUB8*	Putative SRK interactor	*A. thaliana*	Liu *et al.*, 2007
12	*sp locus*	Putative suprpressor	*B. napus*	Ma *et al.*, 2009

Molecular model of SI in Solanaceae :

In Solanaceae family, *SLF/ SFB* is the male determinant and *S-RNase* is the female determinant. During SIC reaction, when pollen falls on stigma, *S-RNase* is produced and enter into the stigmatic surface. They will degrade the RNA encoding the enzyme for pollen tube growth and result in death of pollen tube. In incompatible reaction also *RNase* is produced and it enter the stigma but it goes and forms a complex with SLF. Hence, RNA encoding enzyme for pollen tube growth is not disturbed and results in normal pollen tube growth and fertilization.

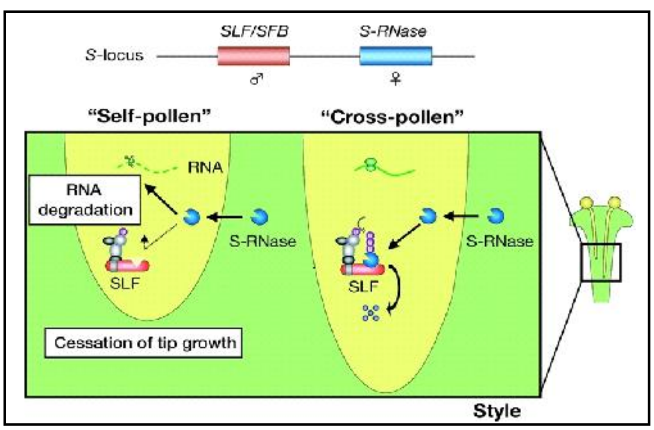


Fig. 7 : Molecular model of self-incompatibility in Solanaceae

Molecular model of self-incompatibility in Papaveraceae :

In Papaveraceae family, only female determinant has been identified and named as S-protein. Male determinant is unknown. In a SIC reaction, S protein will get bind with SBP (S-protein binding protein) and result in increase in concentration of Ca^{++}. This will trigger various reaction mainly actin depolymerisation resulting in death of pollen tube but in compatible reaction, S-protein will not bind with SBP.So no fluctuation in Ca^{++} concentration and hence results in normal growth of pollen tube.

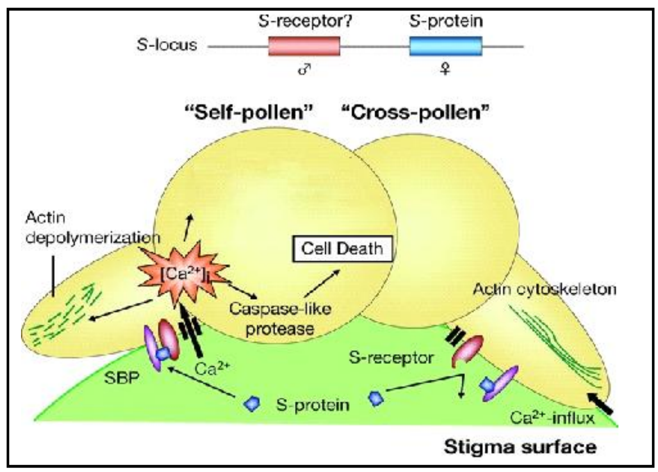


Fig. 8 : Molecular model of self-incompatibility in Papaveraceae

S locus with multiple alleles :

The S-locus is reported to be multiallelic in nature and the following table shows some examples. The number of alleles responsible for self-incompatibility range between five in cocoa to 192 in *Trifoliumpratensea* (Table 5).

Genetic hypothesis of SI in *Theobroma cacao* L.:

A classical work has been done by Knight and Rogers (1953) in cocoa to study the allelic interaction. They have selected three clones Pa-7, Pa-35 and Na-32. Five alleles are reported in cocoa as S_1, S_2, S_3, S_4, and S_5. The interaction of alleles was $S_1>S_2=S_3>S_4>S_5$.

Table 5 : The number of alleles and type of self-incompatibility identified in different plants

Crop	No. of S alleles	Type of SI	Reference
B. oleraceavar. capitata	50	Sporophytic	Bassett (1986)
B. campestris	30	Sporophytic	Singh (2012)
Theobroma cacao	5	Late acting SI	Knight and Rogers (1953)
Raphanusraphanistrum	9	Sporophytic SI	Sampson (1964)
Trifoliumpratensea	192	Gametophytic SI	Paxman (1963)
Trifoliumrepens	71	Gametophytic SI	Samuel *et al.* (2009)
Prunusavium	6	Gametophytic SI	Choi *et al*. (2002)
Raphanussativus	32	Sporophytic SI	Karron *et al*. (1989)
Prioomula vulgaris	50	Sporophytic SI	Choi *et al*. (2002)
Trifoliumpratens	50	Sporophytic SI	Thomson (1985)

They assumed the genetic constitution of Pa-7 as S_1S_5, Pa-35 as S_3S_5 and Na-32 as S_2S_4. Cross combinations were made between them and interaction was studied. In the cross between Pa-7 and Na-32, Pa-7 produced two gametes S_1 and S_5 and Na-32 produced two gametes S_2andS_4. Four type of classes are expected in nature *i.e.*, S_1S_2, S_1S_4, S_2S_5 and S_4S_5. But when progenies were crossed with each other, only three groups were able to identify *i.e.*, individual in group A can be crossed with B and C, B with A and C and C with B. But individuals within group A were cross incompatible *i.e.*, between $S_1S_2XS_1S_4$. This is because all the individuals in this group behave as S_1, Since $S_1>S_2$ and S_4 and reaction is sporophytic self-incompatibility (Fig. 9).

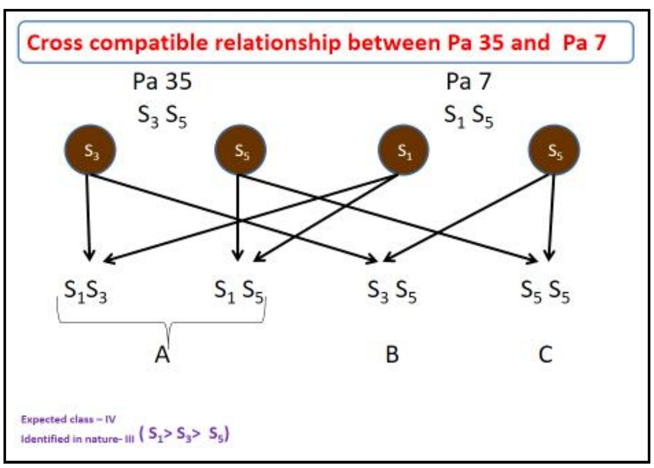


Fig. 9 : Cross compatible relationship between Pa-35 and Pa-7

Similarly in the cross between Pa-35 and Pa-7, the expected classes were four, but in nature only three classes were identified since all individuals in class A S_1S_3 and S_1S_5 behave in the same manner and they cannot cross each other. This is because $S_1>S_3$ and S_5, and the self-incompatibility is sporophytic.

In another cross compatible relationship between Pa-35 and Na-32, four crosses were expected but only two classes were found in nature. All individuals under class A, S_2S_3, S_3S_4 and S_2S_5 have same behavior and are not cross compatible. This is because S_2 is co-dominant to S_3 and S_2 and S_3 are dominant over S_4 and S_5 and reaction is sporophytic (Fig. 10).

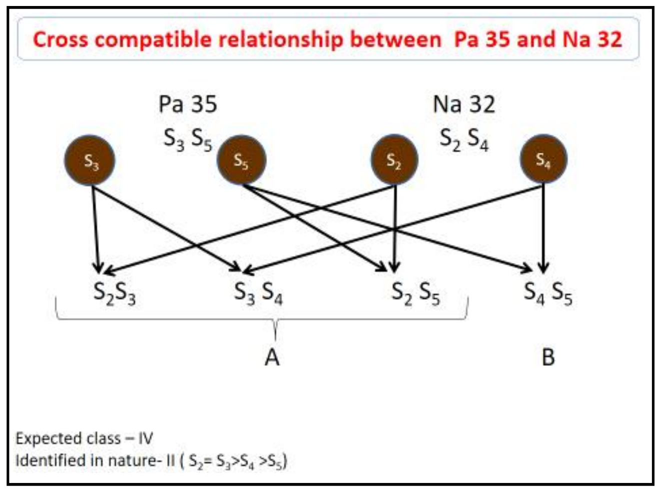


Fig. 10 : Cross compatible relationship between Pa-35 and Na-32

Methods to assess the self-incompatibility :

There are different methods to assess the self-incompatibility in plant like

- Pollination method
- Cytological method
- Molecular method

Pollination method :

Pollination methods varies depending upon the type of self-incompatibility and crop. For example, in cabbage, after selfing, the self-incompatibility is assessed by counting the number of seeds after harvest. After selfing wait for 60 days till the pod maturity and count the number of seed set per pod. If more number of seeds are formed then it is self-compatible, if less seeds are formed then it is incompatible. The disadvantages of this method are it takes long time to assess the self-incompatibility reaction, and the number of seeds formed is also influenced by many other factors such as temperature, humidity, incidence of pests and diseases. Similarly in cocoa selfing is done in 100 flowers per tree and wait for 14 days for cherelle wilt. If cherelle is retained after fourteen days then it is compatible. If cherelle wilt and drop then it is incompatible.

Cytological method :

This method varies with type of self-incompatibility and crop. In cabbage, the self-incompatibility reaction is assessed by number of pollen tube penetration in the style. Stigma and style are squashed on a microscope after 48 hours of pollination. Aniline blue is the stain used. It will get accumulated in the pollen tube and become fluorescent when irradiated with UV light. If there is no or less penetration of pollen tube in the style, then it is incompatible.If penetration of pollen tube is intermediate, then it is semi-compatible and penetration by many pollen tube in the style then it is compatible (Plate 1). But in cocoa, the method followed in cytological study is different since it is late acting self-incompatibility as the growth of pollen tube is similar in compatible and incompatible types. They grow down to the ovule and one male gamete is fused with the endosperm nuclei in both compatible and incompatible reaction. But in self-incompatible type the second male gamete will not fuse with egg and division of zygote is affected resulting in incompatibility. After 24 hours of pollination the pollen tube reaches the synergid cells, two spermatic nuclei can be seen in the synergid, one sperm nuclei fuse with the polar nucleus, development of endosperm nucleus and fusion between egg and sperm has not been affected it will result in formation of irregular ovule (Cope, 1939) (Plate 2).

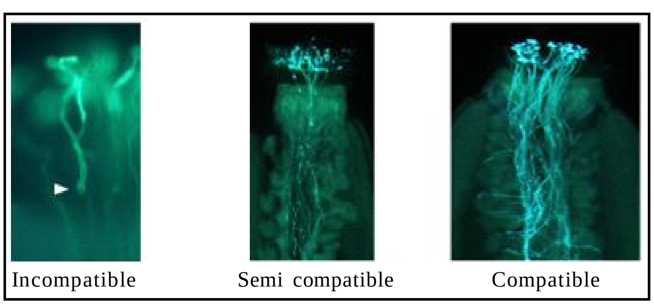


Plate 1 : Assessment of self-incompatibility in cabbage by cytological method

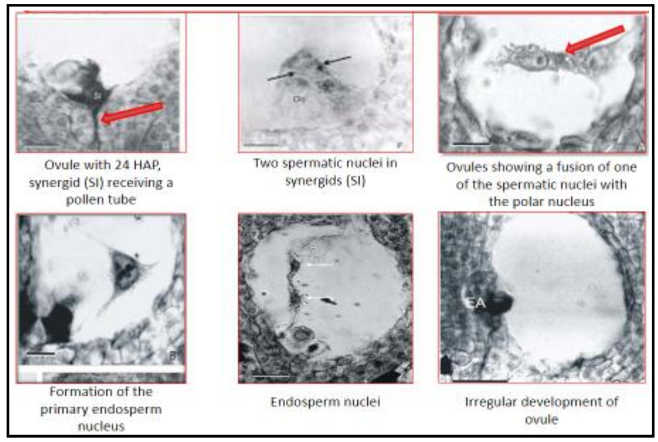


Plate 2 : Assessment of self-incompatibility in cocoa by cytological method

Molecular method :

Pollination and cytological studies can be further validated by molecular studies. Markers associated with self-incompatibility has been reported in many crops. In a study conducted by Valanova *et al*. (2003) in apricot to map the self-incompatibility trait. They found the marker in G6 (Plate 3). The mapping population used was F_2 population derived from a cross between Start early orange and Tryntos.

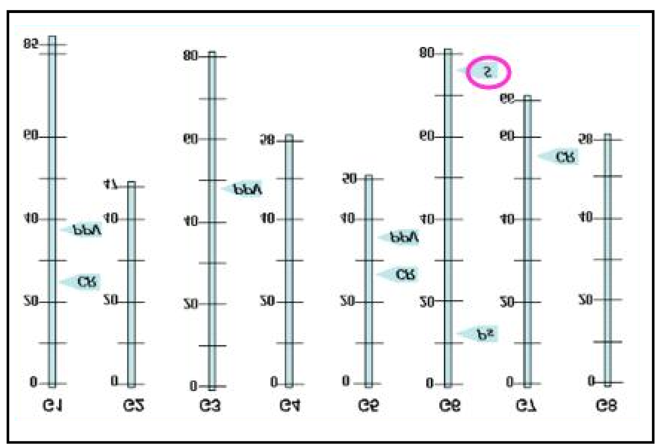


Plate 3 : Molecular mapping of self-incompatibility in apricot

Significance of self-incompatibility :

Self-incompatibility effectively prevents self-pollination. As a result, it has profound effect on breeding approaches and objectives. Some of the significance are discussed here under.

Hybrid production :

Self-incompatibility is primarily exploited for hybrid production. If self-incompatible lines are available tedious process of emasculation can be avoided. If both lines are self-incompatible, they can be utilized for forward and reverse crosses. By using self-incompatibility double cross and three way cross hybrids can be produced.

A case study was conducted by Ma *et al*. (2009) to assess the performance of double hybrids in *Brassica napus*. They have made 44 cross combinations and mid parent heterosis was estimated. Out of 44 crosses, 42 crosses showed high mid parent heterosis. While only two expressed negative heterosis. The averageheterosis value was 28.91 with a maximum value of 115.66 and a minimum value of -3.44.

Establishment of clonal garden :

The second most importance of self-incompatibility is, this mechanism can be exploited for the establishment of clonal gardens. Superior clones with self-incompatibility and good general combining ability are used as parental material. The seeds from each clones will be a hybrid. The main disadvantage is that the information about the exact male parent will be lacking (Minimol *et al.*, 2015b).

A total of nine clonal gardens have been established using 4722 self-incompatible clones (Table 8). The average number of hybrid pods estimated to be produced from these gardens comes to be about 472200 pods. These are used to raise hybrid seedlings which is distributed to the farmers all over India by Kerala Agricultural University and Cadbury India Ltd. (Minimol *et al.*, 2015a).

Parthenocarpy along with self-incompatibility results in seedless fruits :

In certain crops like pine apple parthenocarpy along with self-incompatibility results in seedless fruits. All commercial cultivars of pineapple are self-incompatible in nature. Self-compatible clones would produce fruits

Table 6 : Hybrids developed using self-incompatibility

Crops	Hybrids
Cauliflower	Pusa Hybrid-2, Snow Queen, Snow King, White Contessa, Pusa Kartik Sankar Xiahua 6
Cabbage	BRH-5, H-44, H-43, Pusa Synthetic, Meenakshi, Pusa Cabbage-1
Chinese cabbage	Hamburg-3
Raddish	Pusa Chetaki, Pusa Desi, Half Red, Acc. No. 30205, Acc. No.282, Chinese Pink, BDI-689
Cocoa	CCRP 8, CCRP 9, CCRP 10, CCRP 11, CCRP 12, CCRP 13, CCRP 14, CCRP 15
Mango	Arka Puneet, Arka Neelkiran, Arka Anmol

Table 7 : Performance analysis of double cross hybrids in *Brassica napus*

	Mid parent heterosis (%)
Maximum	115.66
Minimum	-3.45
Average	28.91
No. of combinations with high heterosis	42
No. of combinations with negative heterosis	2

Table 8 : Details of clonal gardens of cocoa in KAU

Sr. No.	Garden	No. of parents	No. of plants	Year of planting	Avg. No. of hybrid pods year^{-1}
1.	Poly clonal garden I	12	120	1989	12000
2.	Polyclonal seed garden II	38	228	1993	22800
3.	Bi-clonal seed garden	6	1243	1996	124300
4.	Polyclonal seed garden III	5	100	2000	10000
5.	Polyclonal seed garden IV	8	1100	2005	110000
6.	Polyclonal seed garden V	7	946	2006	94600
7.	Polyclonal seed garden VI	10	400	2010	40000
8.	Poly clonal seed garden VII	6	286	2010	28600
9.	Polyclonal seed garden VIII	8	299	2014	29900
	Total		4722		472200

containing hundreds of very hard inedible seeds; such fruits would not be acceptable to the consumer. Therefore, at least in one case, *i.e.*, pineapple, commercial success depends on the clones being self-incompatible.

Self-incompatibility plays a key role in evolution :

Since self-incompatibility is a mechanism promoting out breeding, it plays a key role in evolution. Cross pollination will result in increase in heterozygosity and variability. It will promote a new gene combination which may lead to evolution of new crops.

Comparison between self-incompatibility and male sterility :

When self-incompatibility is compared with male sterility,which is another mechanism that promote cross pollination, there are some advantages. If self-incompatible lines are used for hybrid seed production and if both parents are self-incompatible in nature, hybrid seeds can be collected from both parents. But in case of male sterility, hybrid seeds can be collected only from male sterile lines. Maintenance of self-incompatible inbreds are easy when compared to male sterile lines. In male sterility a specific maintainer is required to maintain male sterile lines. In self-incompatibility no specific restorer line is required but to exploit male sterility suitable restorer has to be identified. Self-incompatibility is not having any negative effect of sterile cytoplasm. But in male sterility,there will be linkage drag of sterile cytoplasm with other undesirable characters.

Kucera *et al.* (2006) conducted a study to compare between self-incompatibility and male sterile hybrids of cauliflower. Mean weight of seeds obtained per plant was higher in male sterile line compared to self-incompatible lines. But when the quality was compared, the F_1 produced by SI lines was much uniformwith high curd quality, good covering of curd with inner leaves and satisfactory disease resistance. F_1 produced by utilizing CMS lines produced less uniform curd which are smaller, lighter in size and susceptible to diseases.

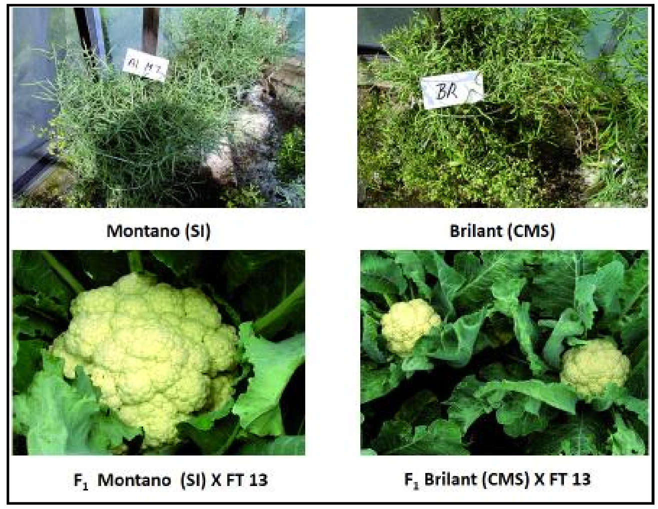


Plate 4: Self-incompatible and male sterile line Montano and Brilant(top), matured cauliflower curd of F_1 hybrids of Montano(SI)XFT13 and Brilant(CMS)XFT13

Limitations in exploiting self-incompatibility :

Continued selfing will lead to inbreeding depression. Continuous inbreeding may lead to complete loss of the inbred lines. Some self-incompatible lines may become self-compatible due to environmental factors *i.e.,* pseudo-incompatibility. The hybrids seeds produced using self-incompatible lines may be expensive if self-incompatible lines are difficult to maintain. Sometime, environmental factors may reduce or totally overcome self-incompatibility. There is possibility of preferential visit of pollinating insects mainly due to the flower structure. The transfer of S allele is tedious and complicated

Table 9 : Comparison of self-incompatibility and male sterility

Self-incompatibility	Male sterility
Hybrid seeds can be collected from both the parents if they are SI	Hybrid seeds can be collected only from MS lines
Maintenance is easy by bud pollination	Specific maintainer line required
No specific restorer line required	Suitable restorer has to be identified
No negative effect of sterile cytoplasm	Linkage drag of sterile cytoplasm with other undesirable character

Table 10 : Comparison between self-incompatible and male sterile hybrids of cauliflower

Sr. No.	Parental genotype	No. of grown plants	No. of harvested plants	Weight of harvested seeds(g)	Mean weight of seeds $plant^{-1}$ (g)
1.	Montano(SI) X Fortuna 13 (SC)	24	22	40	1.8
2.	Brilant (CMS) X Fortuna 13 (SC)	24	20	45	2.3

Table 11 : Overcoming self-incompatibility in passion fruit by bud selfing and double pollination

Sr. No.	Treatments	No. of flowers selfing	Fruit set (%)
1.	Bud selfing	30	16.67
2.	One selfing at anthesis (control)	30	0.00
3.	Double pollination at anthesis	30	10.00

Table 12 : Overcoming self-incompatibility in Chinese cabbage by bud pollination and NaCl treatment

Sr. No.	Lines	Pollination stage	No. of flowers	No. of seeds	SI Index
1.	Self-incompatible	Bud	132	124	0.94
		Anthesis	135	8	0.06
		Anthesis with NaCl treatment	54	157	2.54

Table 13 : Effect of CO_2 treatment on pollen germination and fruit set in a self-incompatible cocoa genotypes

Pollination treatment		Pollen germination	Fruit set
CO_2	Method	(%)	(%)
-	Self	0	0.0
-	Cross	100	45.6
+	Self	95	44.8
+	Cross	100	38.4

process.

Temporary suppression of self-incompatibility :

To maintain the inbred lines, self-incompatibility has to be suppressed temporarily. For this purpose, a number of methods like bud pollination, mixed pollination, surgical techniques (Brassica), end of season pollination, high temperature (*Trifolium, Lycopersicon*), increased CO_2 concentration, high humidity, salt (NaCl) sprays, irradiation (Solanaceae), double pollination, grafting (*Trifolium pratense*) are followed.

In passion fruit, bud pollination and double pollination was attempted to overcome self-incompatibility by Rego and Rego (2013) and they found that fruit set of 16.67 and 10 per cent was observed in bud selfing and double pollination, respectively. But no fruit set was observed in control.

Another study was conducted by Wang *et al.* (2012) in Chinese cabbage by bud pollination and NaCl treatment and it was seen that NaCl treatment was highly significant with self-incompatibility index value of 2.54.

In cocoa, CO_2 treatment was used to overcome self-incompatibility there was an increase in pollen germination and fruit set when the flowers were treated with CO_2 and the percentage of fruit set was at par with that of normal cross pollination (Aneja and Badilla, 1994).

Conclusion :

The self-incompatibility is a genetic mechanism that avoids self-pollination. At least two genes within S-locus control self-incompatibility. The genes responsible for self-incompatibility are multi allelic in nature. The different methods to determine self-incompatibility varies with the type of self-incompatibility and crop. Self-incompatibility is a viable tool for hybrid production. It has many advantages over male sterility. The major limitation of self-incompatibility is production/maintenance of inbred. There are various methods to overcome self-incompatibility for production of inbred.

Future line of work :

There is need to identify and characterize precisely the S-alleles in the germplasm and utilize the strong alleles to develop stable self-incompatible parents. Efforts have to be taken to transfer self-incompatible related gene and subsequent exploitation of heterosis by producing hybrid seeds.

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