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A REVIEW :

Self incompatibility a mechanism for controlled pollination in vegetable crops

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SUMMARY : Self-incompatibility (SI) is a genetically controlled cell to cell recognition system that acts as abarrier to self-pollination in a wide range of vegetable crops like cabbage, cauliflower, tomato etc. Self-incompatibility is a major mechanism by which plants prevent self-fertilization and maintain genetic diversity. SI is estimated to occur in 30-50% of flowering plant species. Several SI systems have now been identified. In all cases incompatible (self-) pollen is recognized by a highly specific genetically controlled mechanism that results in inhibition of the pollen in the stigma or style of the pistil. The use of SI in F_1 hybrid production has major advantage over other methods. Use of SI in cole crops for hybrid seed production is commercialised till date in vegetable crops because availability of cost effective mechanism/method to produce large-scale F1 seeds utilizing selected parental lines is an important factor, which ultimately determines the commercial viability of the hybrid varieties.

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BACKGROUND AND OBJECTIVES

The mating system is one of the most fundamental characteristics of a plant species shaping population level processes such as inbreeding effects, demography (Morgan *et al.*, 2005), and evolutionary trends (Ferrer and Good, 2012). About 40%–60% of all species of flowering plants are thought to be selfincompatible (Igic *et al.*, 2008). Ever since the first discussion on self-incompatibility by Darwin (1877), the phenomenon has extensively studied in several plant families and now significant amount of information is available on genes and gene products involved in the expression of SI trait (Dodds *et al.*, 1997).

Self-incompatibility (SI) is one of the most important systems used by many flowering plants to prevent self-fertilization and thereby generate and maintain genetic diversity within a species. Self incompatibility has been defined as "the prevention of fusion of fertile male and female gametes after self pollination". In case of SI, pollen grains fail to germinate on the stigma of the flower that produced them. If some pollen grains do germinate, pollen tube fails to enter the stigma. In some spp., the pollen tubes enter the style, but they grow too slowly to effect fertilization before the flower drops. Sometimes, fertilization is effected, but the embryos degenerate at a very early stage.

There are two types of SI, *viz.*, gametophytic and sporophytic. In gametophytic system SI reaction of pollen and stigma is determined by the genotype of the mother plant on which pollens are produced (e.g. tomato) while in sporophytic system, pollen phenotype (SI reaction) is determined by the genotype of the mother plant on which pollens are produced (e.g. cole vegetables). In *Brassicacae*, sporophytic self-incompatibility (SSI) has been best characterized and successfully utilized for the development of commercial hybrids (Pearson, 1983; Singh, 2000 and Singh *et al.*, 2001).

Classification of SI:

On the basis of the interaction between pollen grains and pistil, SI is classified into the following two types-

Complementary system of Self-Incompatibility:

This system is also called stimulatory type of SI. In this system pollen and pistil together provide substances, which stimulate pollen germination and growth of pollen tube if the pollen grain differ in SI genotype from that of pistil; the germination and growth of pollen having similar genotype is not stimulated. This type of SI reported in *Dendrobium*.

Oppositional system of self-incompatibility:

This is also known asinhibitory type of SI. In this system pollen and pistil produce such substances which prevent pollen germination and/or pollen tube growth if the pollen has the same SI reaction as the pistil. However, germination and growth of pollen differing in SI reaction is not inhibited. Almost all cases of SI are of this type.

A simpler classification given by Lewis in 1954:

- Heteromorphic System
- Homomorphic System
 - Gametophyticcontrole and
 - -Sporophyticcontrole.

Heteromorphic system :

In this system the flowers of different incompatibility groups are different 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 style and long stamens. This system is known as distyly. Pin and Thrum flowers born on different plants and only compatible mating between pin and thrum flowers. This characteristic is governed by a single locus s; Ss produce thrum, while ssproduce pin flowers. This incompatibility system is also known as Heteromorphic Sporophytic SI because the incompatibility reaction of pollen grain is determined by the genotype of the plant producing them. This system found in sweet potato and buckwheat.

Table 1 : Heteromorphic sporophytic system of incompatibility				
Mating		Progeny		
Phenotype	Genotype	Genotype	Phenotype	
Pin x Pin	SS X SS	Incompatible mating		
Pin x thrum	ss x Ss	1 Ss : 1ss	1 Thrum : 1 Pin	
Thrum x Pin	Ss x ss	1Ss : 1ss	1 Thrum : 1 Pin	
Thrum x Thrum	Ss x Ss	Incompatible mating		

Homomorphic system :

This system found in majority of self-incompatible species, and incompatibility is not associated with morphological differences among flowers. The incompatibility reaction of pollen may be governed by the plant on which it is produced (sporophytic control) or by its own genotype (gametophytic control).

Gametophytic control :

This was first described by East and Mangelsdorf in 1925 in *Nicotiana sanderae*. The incompatibility reaction of pollen is determined by its own genotype because the biochemical substances involved in SI reaction of the pollen is produced after meiosis. The S alleles in style show co-dominance. The incompatibility reaction may be controlled by one or two genes; on this basis the GSI is classified into two groups-

– **Monofactorial** e.g.; *Trifolium*, *Nicotiana*, *Lycopersicon*, *Solanum*, *Petunia*, etc.

- Difactorial system e.g.; In grasses

- While some spp. has more than two genes, e.g.; *Papaver* has three genes, while *Beta vulgaris* has four genes.

Sporophytic control :

In this system the self-incompatibility is governed by a single gene, S, with multiple alleles. The no. of S

Monofactorial gametophytic	Bifactorial sporophytic	Monofactorial
One	Two	One
Multiple alleles (often 50 or more)	Multiple alleles (Usually < 20)	Multiple alleles (often 50 or more)
Pollen genotype	Pollen genotype	Sporophyte genotype
Binucleate	Trinucleate	Trinucleate
Simple	Complex	Complex
Slow	Fast	Fast
Imperforate or Microperforate	Perforate	Perforate or Reticulate
Wet	Dry	Dry
Style	stigma	Stigma
May be eliminated	Unaffected	
	One Multiple alleles (often 50 or more) Pollen genotype Binucleate Simple Slow Imperforate or Microperforate Wet Style	OneTwoMultiple alleles (often 50 or more)Multiple alleles (Usually < 20)

Table 2 : Characteristic feature of different types of homomorphic self-incompatibility. The pollen and stigma morphology and pollen cytology
appear to be correlated with the site of inhibition rather than with the mode of control of SI reaction

alleles is considerably larger in the gametophytic than in the sporophytic system. In this case the incompatibility reaction of pollen is governed by the genotype of plant on which the pollen is produced and not by the genotype of the pollen itself as in the case of gametophytic control. It was first time reported by Hughes and Babcock in 1950 in *Crepisfoetida*, and by Gerstel in *Parthenium argentatum* in the same year.

Brassicaceae type of self-incompatibility :

The SI in the Brassicaceae belongs to SSI and, so far, is the only SSI system in which the mechanism has been characterized at the molecular level. More than 30 and 50 *S*-haplotypes have been identified in *B. rapa*(syn. *campestris*) and in *B. oleracea*, respectively. In the selfincompatible plants of this family, pollen tubes do not develop properly on the stigma that express the same *S*haplotypes as the pollen's parent. Self-pollen rejection results in abrogated pollen hydration, or a rapid arrest of the pollen tube growth at the stigma surface.

Solanaceae type of self-incompatibility :

The Solanaceae, Rosaceae, and Scrophulariaceae families all share a female *S*-determinant, an S-RNase. The S-RNase was first identified in the Solanaceae so we refer to this S-RNase-mediated type of SI as Solanaceae type SI. The Solanaceae-type SI is under gametophytic control (GSI) and the rejection of selfpollen occurs during pollen tube growth in the style. Recently, the genomic sequences around the S-RNase

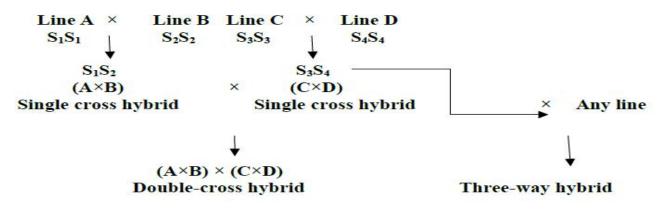


Fig. 1 : Single, double and three way cross hybrid seed production

genes were thoroughly analyzed in these taxa, with the net result of finally identifying the elusive male *S*determinant. The molecular nature of the identified male *S* determinant suggests a new model of how these determinants are involved in the specific rejection of selfpollen.

Uses of SI in cultivar development:

The use of SI in F₁ hybrid production has major advantage over other methods; equal quantities of seed of the two inbred lines can be mixed together for showing, and the whole crop is harvested for seed. For hybrid seed production both the parental inbreds should have two different S alleles for strong self-incompatibility in case of single cross hybrid .One S.I. inbred is used as female parent and a good pollinator (an open pollinated variety) as male to develop top cross hybrid, while four S.I. inbreds having altogether different S alleles are used to produce double cross hybrids (Fig. 1). Among the cole vegetables like cabbage, cauliflower, broccoli etc., sporophytic self-incompatibility mechanism is being utilized for hybrid seed production at several places including India (Singh, 2000). Usually in cauliflower S.I. is weak and S.I. reaction is breaks at high temperature, resulting into selfing and sibling (brother-sister mating) among the plants of female parent, thus deterioration in the genetic make up of F1 seeds.

Conclusion :

Self-incompatibility is a system used by many flowering plant species to prevent self-fertilization and thereby promote outcrossing. Over the years, considerable insight into the mechanisms regulating selfincompatibility has been obtained for the Solanaceae gametophytic self-incompatibility systems as well as for the sporophytic self-incompatibility system of the Brassicaceae in vegetable crops. A combination of genetic and molecular studies has resulted in the identification and characterization of the selfincompatibility genes involved in this response. In addition, careful investigation of the components in the signalling cascades of both the Solanaceae and the Brassicaceae is required for a complete understanding of the selfincompatibility response in these families. A number of mechanisms and methods have not been exploited for the developmentof commercial hybrids in vegetable crops among that SI is of prime importance. In the light of rapid advancement of bio-technology, it may be anticipated that SI systems will be increasingly utilized in near future, in vegetable crops.

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