

Review Article

Self-incompatibility a Mechanism for Controlled Pollination in Vegetable Crops

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ABSTRACT

Self-incompatibility is a widespread phenomenon in flowering plants that prevents inbreeding and promotes outcrossing. The response of self-incompatibility is genetically controlled by one or more multi-allelic loci, and relies on a series of complex cellular interactions between the self-incompatible pollen and pistil. It is a genetically controlled cell to cell recognition system that acts as a barrier 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 F₁ 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 F₁seeds utilizing selected parental lines is an important factor, which ultimately determines the commercial viability of the hybrid varieties.

Keywords

Self-
incompatibility,
Mechanism for
Controlled
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Vegetable Crops

Introduction

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 self-incompatible (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 *Brassicaceae*, sporophytic self-incompatibility (SSI) has been best characterized and successfully utilized for the development of commercial hybrids (Pearson, 1983; Singh 2000, 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 as inhibitory 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
Gametophytic controle and
Sporophytic controle.

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 *ss* produce 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.

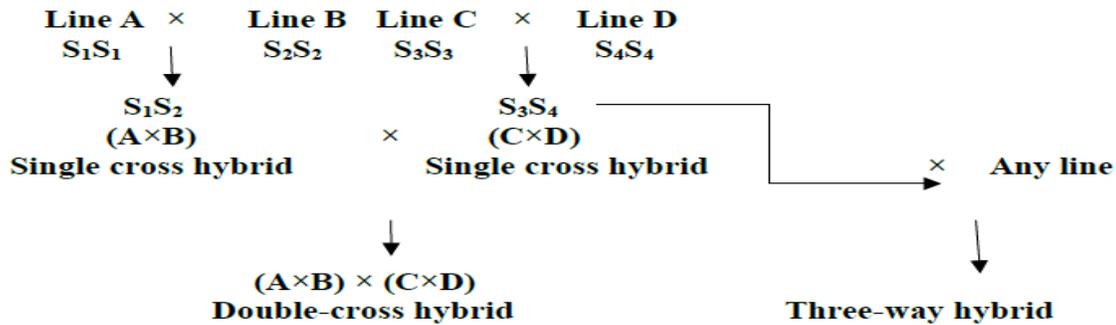
Table.1 Heteromorphic sporophytic system of incompatibility

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	

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

Feature	Type of self-incompatibility		
	Monofactorial gametophytic	Bifactorial gametophytic	Monofactorial sporophytic
Genes governing SI reaction			
Number of genes	One	Two	One
Number of alleles	Multiple alleles (often 50 or more)	Multiple alleles (Usually < 20)	Multiple alleles (often 50 or more)
Pollen grains			
SI reaction controlled by	Pollen genotype	Pollen genotype	Sporophyte genotype
Number of nuclei at the time of pollen shed	Binucleate	Trinucleate	Trinucleate
Pollen coating (exine morphology)	Simple	Complex	Complex
Pollen germination	Slow	Fast	Fast
Exine morphology	Imperforate or Microperforate	perforate	Perforate or Reticulate
Others			
Stigma type	Wet	Dry	Dry
Site of inhibition	Style	stigma	Stigma
Effect of polyploidy on SI reaction	May be eliminated	Unaffected	–

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



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 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 *Crepis foetida*, 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 self-incompatible 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 self-pollen occurs during pollen tube growth in the style. Recently, the genomic sequences around the S-RNase 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 self-pollen.

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 sowing, 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 (Figure 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.

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 self-incompatibility 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 self-incompatibility 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 self-incompatibility response in these families. A number of mechanisms and methods have not been exploited for the development of commercial hybrids in vegetable crops among that SI is of prime importance. In the light of rapid advancement of biotechnology, it may be anticipated that SI systems will be increasingly utilized in near future, in vegetable crops.

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