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Degree programme: Bachelor of Biotechnology

Year: 1st year

Semester: 2nd semester

Course name: Basic Plant Breeding

Course code: PB.101

Topic name:

1. Self-incompatibility

Date: 29/03/2020

Course instructor name: Dr. Nilanjaya; Dr. M.K Singh

SELF-INCOMPATIBILITY

More than 300 species belonging to 20 families of angiosperms show self-incompatibility. Self-incompatible pollen grains fail to germinate on the stigma of the flower that produced them. If some pollen grains do germinate, pollen tubes fail to enter the stigma. In many species, the pollen tubes enter the style, but they grow too slowly to effect fertilization before the flower drops. Sometimes, fertilization is effected, but the embryo degenerates at a very early stage. Self-incompatibility appears to be a biochemical reaction, but the precise nature of these reactions is not clearly understood. The genetic control of incompatibility reactions is relatively simple.

Lewis (1954) has suggested various classifications of self-incompatibility; a relatively simple classification is as follows

1. Heteromorphic System
2. Homomorphic System
   a. Gametophytic Control
   b. Sporophytic Control.

Heteromorphic System.

In this system, 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 styles and short stamens, while thrum flowers have short styles and long stamens. This situation is referred to as distyly. Tristyly is known in some plant species, e.g. *Lythrum* ; in such cases, the style of a flower may be either short, long or of medium length. In the case of distyly, the only compatible mating is between pin and thrum flowers. This characteristic is governed by a single gene s; Ss produces thrum, while ss produces pin flowers. The incompatibility reaction of pollen is determined by the genotype of the plant producing them. Allele S is dominant over s. The incompatibility system, therefore, is heteromorphic-sporophytic. The pollen grains produced by pin flowers, would all be s in genotype as well as incompatibility reaction. The pollen produced in 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; it occurs in sweet potato and buckwheat.

Homomorphic System

In the homomorphic system, incompatibility is not associated with morphological differences among flowers. The incompatibility reaction of pollen may be controlled by the genotype of the plant on which it is produced or by its own genotype.

Gametophytic System

Gametophytic incompatibility was first described by East and Mangelsdorf in 1925 in *Nicotiana sanderae*. The incompatibility reaction of pollen is determined by its own genotype, and not by the genotype of the plant on which it is produced. Generally, incompatibility reaction is determined by a single gene having multiple alleles, e.g., *Trifolium, Nicotiana, Lycoperscion, Solanum, Petunia* etc. If same allele as that of Pollem is present in the stylar tissues, it opposes the growth of pollen tube in the style, so Gametophytic incompatibility is also called as 'oppositional factor system'. Sometimes, Polyploidy may lead to a loss of incompatibility due to a competition between the two S alleles present in diploid pollen. Irradiation of pollen or buds with X-rays or gamma-rays temporarily suppresses the incompatibility reaction, and thus allows the pollen tube to grow through incompatible style. In some species, e.g., *Phalaris, Physalis* etc., two loci (S and Z) govern incompatibility, while in some others, e.g., Beta vulgaris and *Papaver*, three loci are involved. In these cases, Polyploidy does not affect the incompatibility reaction. Pollen tube grows very slowly in the style containing the same S allele as the pollen, and fails to effect fertilization. Therefore, all the plants are heterozygous at the S locus. In a single gene system, there are three types of mating;

1. Fully incompatible, e.g., S1S2 x S1S2
2. Fully compatible, e.g., S1S2 x S3S4
3. Partially (i.e., 50% of the pollen) compatible, e.g., S1S2 x S2S3

In some cases, an allele for self-fertility, S_f, is found (East and Yarnel). Pollen carrying the S_f alleles does not show incompatibility reaction. Thus in a plant with the genotype S_fS1, selfing produces S_fS_f and S_f S1 progeny. Mutations for S_f allele may be induced by irradiating the pollen used for self-pollination. There is another allele, SF, which retards the growth of S*f* pollen tubes, thus enforcing self-incompatibility. The gametophytic system is found in pineapple (2 locus), ryegrass

(2 locus), diploid coffee, diploid clovers (*Trifolium sp.*) etc. In families like *Solanaceae, Rosaseae, Graminae, Leguminoseae, Chenopodiaceae, Ranunculaceae*

Sporophytic System

In the sporophytic system also, the self-incompatibility is governed by a single gene, S, with multiple alleles ; more than 30 alleles are known in *Brassica oleracea*. In general, the number of S alleles is considerably larger in the gametophytic than in the sporophytic system. The incompatibility reaction of pollen is governed by the genotype of the plant on which the pollen is produced, and not by the genotype of the pollen. It was first reported by Hughes and Babcock in 1950 in *Crepis foetida*, and by Gerstel in *Parthenium argentatum* (in the same year). In the sporophytic system, the S alleles may exhibit dominance, individual action (codominance) or competition. Consequently, there may be many complex incompatibility relationships.

Lewis has summarized the following characteristics of this system.

1. There are frequent reciprocal differences
2. Incompatibility can occur with the female parent
3. A family can consist of three incompatibility groups
4. Homozygotes are a normal part of the system
5. An incompatibility group may contain two genotypes

Sporophytic incompatibility is found in radish (*R. sativus*), diploid Brassica crops and *Sinapis*. In many cases, different S alleles vary in their activity leading to varying degrees of self-incompatibility, e.g., *B. oleracea*. Polygenes (modifying genes) are known to increase as well as decrease the activities of S alleles both in the gametophytic as well as sporophytic systems.

Mechanism of Self-Incompatibility

The mechanism of self-incompatibility is quite complex and is poorly understood. The various phenomena observed in self-incompatible matings are grouped into three broad categories: (1) pollen-stigma interaction, (2) pollen tube-style interaction, and (3) pollen tube-ovule interaction.

Pollen-Stigma Interaction

These interactions occur just after the pollen grains reach the stigma and generally prevent pollen germination. At the time they reach stigma, pollen grains generally have two nuclei in the gametophytic system, while they have three nuclei in the sporophytic system. This was once considered to be the basis for the two incompatibility systems, but the available evidence indicates otherwise. However, the structure of stigmatic surface appears to be definitely involved in the differences between the two systems. In the gametophytic system, the stigma surface is plumose having elongated receptive cells and is commonly known as ‘wet’ stigma. Incompatible pollen grains generally germinate on reaching the stigma; the incompatibility reaction occurs at a later stage. There are clear cut serological differences among the pollen grains with different S genotypes; such differences have not been observed in the sporophytic system.

In the sporophytic system, the stigma is papillate and dry, and is covered with a hydrated layer of proteins known as ‘pellicle’. There is evidence that the pellicle is involved in incompatibility reaction. There are striking differences in the stigma antigens related to the S allele composition. Within few minutes of reaching the stigmatic surface, the pollen releases an exine exudates which is either protein or glycoprotein in nature. This exudates induces immediate callose formation in the papillae (which are in direct contact with the pollen) of incompatible stigma. Often callose is also deposited on the young protruding pollen tubes preventing any further germination of the pollen. Thus in the sporophytic system, stigma is the site of incompatibility reaction ; once the pollen tube crosses the stigmatic barrier, there is no further inhibition of pollen tube growth. In the homomorphic sporophytic system, the incompatibility reaction of pollen is probably due to the deposition of some compounds from anther tapetum on to the pollen exine.

Pollen Tube-Style Interaction

In most cases of the gametophytic system, pollen grains germinate and pollen tubes penetrate the stigmatic surface. But in incompatible combinations, the growth of pollen tubes is retarded within the stigma, e.g., in *Oenothera*, or a little later in the style, e.g., in *Petunia, Lycopersicon, Lilium* etc. In the latter case, there is a cessation of protein and polysaccharide synthesis in the pollen tubes, which leads to the degeneration of tube wall and the bursting of pollen tube.

Pollen Tube-Ovule Interaction

In some cases, e.g., *Theobromo cacao*, pollen tubes reach the ovule and effect fertilization. However, in incompatible combinations, embryos degenerate at an early stage of development.

Relevance of Self-Incompatibility

Self-incompatibility effectively prevents self-pollination. As a result, it has a profound effect on breeding approaches and objectives; these are discussed here in some detail

1. In self-incompatible fruit trees, it is necessary to plant two cross-compatible varieties to ensure fruitfulness. Further, cross-pollination may be poor in adverse weather conditions reducing fruit set. Therefore, it would be desirable to develop self-fertile forms in such cases
2. Some breeding schemes, e.g., development of hybrid varieties etc., initially require some degree of inbreeding. Although sibmating leads to inbreeding, but for the same degree of inbreeding it take twice as much time as selfing. Further, for the maintenance of inbred lines selfing would be necessary.
3. Self-incompatibility may be used in hybrid seed production. For this purpose, (1) two self-incompatible, but cross-compatible, lines are interplanted; seed obtained from both the lines would be hybrid seed. (2) Alternatively, a self-incompatible line may be interplanted with a self-compatible line. From this scheme, seed from only the selfincompatible line would be hybrid. (3) Schemes for the production of double cross and triple cross hybrids have also been proposed and their feasibility has been demonstrated in the case of brassicas

The gametophytic system has been used, to a limited extent, for hybrid seed production in clover, *Trifolium* (Leguminosae). In *Solanaceae,* the cultivated species are generally selffertile, and self-incompatibility is confined to wild species. The sporophytic system has been exploited for hybrid seed production in brassicas (Cruciferae), primarily by the Japanese seed companies. In Compositae, another economically important family showing sporophytic self-incompatibility, the cultivated varieties are generally self-fertile.

The use of self-incompatibility in hybrid seed production is hampered by several problems.

1) Production and maintenance of inbred lines by hand pollination is tedium and costly
2) This raises the cost of hybrid seed

3) Continued selfing leads to a depression in self-incompatibility, and it unintentionally, but unavoidably, selects for self-fertility
4) In the gametophytic system, continued inbreeding gives rise to new incompatibility reactions, which may limit the usefulness of such inbreds as parents.
5) Environmental factors, e.g., 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.
6) Bees often prefer to stay within a parental line, particularly when the parental lines differ morphologically. This, in turn, increases the proportion of selfed seed.
7) Transfer of S alleles from one variety or, more particularly, species into another variety or species is tedius and complicated. This has prevented the use of self-incompatibility in hybrid seed production in Solanaceae and Compositae.

Elimination of Self-Incompatibility

In many cases, self-fertile forms will be highly desirable and, in such cases, it would be useful to eliminate self-incompatibility.

(1) In the case of single-locus gametophytic system, incompatibility may be eliminated by doubling the chromosome number, e.g., in potato diploidization leads to self-incompatibility.

(2) Isolation of self-fertile (S_f) mutations is a very useful tool in the elimination of self-incompatibility. Flower buds are generally irradiated at the PMC stages, and pollen from these buds is used to pollinated flowers with known S alleles. Generally, selection for S f alleles is much more complicated in the sporophytic system than in the gametophytic system due to the temporary loss in incompatibility and pseudofertility in the cases of the former. In Oenothera, Sf mutations occur spontaneously at the rate of 10^{-8} and the rate of induction with X-rays is 1.6 x 10^{-8}/r unit. Lastly,

(3) self-compatibility alleles may be transferred from related species or varieties of the same species, if available, through a backcross programme.

Temporary Suppression of Self-Incompatibility

In many situations, e.g., during the production of inbreds for use as parents in hybrid seed production, it is essential that temporary self-fertility is achieved in a manner so that self-incompatibility is fully functional in the selfed progeny. Such self-fertility is known as pseudofertility and is achieved by temporarily suppressing the incompatibility reaction using one of the following techniques.

1. Bud Pollination
2. Surgical Techniques
3. End-of-Season Pollination
4. High Temperature
5. Irradiation
6. Grafting
7. Double Pollination

A number of other techniques have been tried with varying degrees of success, but they are not commonly used. These techniques are : treatment of flowers with carbon monoxide, injecting styles with munosuppressants, application of electrical potential difference of about 100 V between the stigma and pollen grains, treatment of pistil with phytohormones and with protein synthesis inhibitors, and steel brush pollination.