5. Self-Incompatibility in Crop Improvement

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Abstract:

The mechanisms responsible for self-incompatibility (SI) in angiosperms serve to impede the occurrence of self-fertilization by discerning between self-pollen and non-self-pollen. The trait plays a crucial role in the regulation of sexual plant reproduction by promoting outcrossing and preventing inbreeding, thereby making it a widely utilized strategy. Over the course of history, those involved in agriculture and breeding have adeptly utilized the method of selective breeding to manipulate cultivated plant species.

However, it is important to acknowledge that the exploration of the fundamental molecular characteristics of self-incompatibility (SI) has only commenced in the last three decades. The factors responsible for self-incompatibility (SI) have been identified in the saprophytic system. The deliberate manipulation of transitions between self-incompatibility (SI) and self-compatibility (SC) has been made possible through molecular-level research. Scientific advancements have established a strong foundation for the implementation of novel approaches in agricultural production and plant breeding.

The utilization of self-(in)compatibility spans a diverse range of goals, including the enhancement of agricultural productivity and quality, the facilitation of marker-assisted breeding through self-incompatibility genotyping, and the production of hybrids to overcome reproductive obstacles within and between species. This review centers on the utilization of Self Incompatibility (SI) in crop enhancement and production.

Keywords:

Self-Incompatibility, Heterozygosity, Inbreeding Depression, Genetic Diversity, Crop Production, Plant Breeding.

5.1 Introduction:

The phenomenon of self-pollination in hermaphrodite flowers has been documented to lead to negative consequences such as inbreeding depression and a decline in genetic variation. As a result, plants have evolved numerous methods to inhibit self-pollination.

Self-incompatibility (SI) is an essential mechanism that is observed in a wide range of flowering plants. The term "self-incompatibility" (SI) refers to the reproductive phenomenon observed in sexually mature hermaphroditic seed plants, wherein they are incapable of producing zygotes through self-pollination (Nettancourt, 1977). The genetic mechanism responsible for preventing self-fertilization plays a crucial role in promoting heterozygosity and reducing the detrimental consequences of inbreeding depression. The self-incompatibility phenomena observed in angiosperms is commonly acknowledged as an advantageous adaptation owing to its efficacy in preventing inbreeding and promoting outcrossing. Based on the findings of Igic *et al.* (2008), it may be inferred that approximately 40% to 60% of the overall population of flowering plant species exhibit self-incompatibility. Self-incompatibility (SI) is a crucial mechanism utilized by many plant species to inhibit self-fertilization, hence promoting the preservation and perpetuation of genetic variability. The self-incompatibility (SI) response encompasses a mechanism wherein there is a recognition process between the pollen and pistil, distinguishing self, and non-self, leading to the subsequent prevention of self-pollen tube development. In the present scenario, pollen grains manifest functional attributes, however their capacity to effectively fertilize the egg cell inside the same plant is impeded. In the present situation, the process of pollen grain germination is impeded on the stigma of the flower from whence they originated. Nevertheless, if specific pollen grains initiate germination, they encounter difficulties in effectively penetrating the stigma. In specific cases, there is an occurrence where the pace of growth of pollen tubes in the style is significantly slow, resulting in their subsequent separation from the flower before the process of fertilization occurs. In specific cases, fertilization is obligatory, however, the embryos experience degeneration throughout the early stages. The phenomena of self-incompatibility were first seen and described by Koelreuter in the mid-eighteenth century. Since the inception of Darwin's discourse on self-incompatibility in 1877, extensive scholarly investigations have been undertaken to explore this phenomenon within various plant taxa. The nomenclature "self-incompatibility" was first coined by Stout in the year 1917. In a study undertaken by Bateman (year), an investigation was carried out on three species of brassica plants, namely *Iberis amara* L., *Raphanus sativus* L., and *Brassica campestris* L. The study revealed the presence of incompatibility among these plants. Since then, there have been notable progressions in comprehending the genes and gene products linked to the emergence of the self-incompatibility (SI) characteristic (Dodds *et al*., 1997). The phenomenon of tristyly, which represents an alternate reproductive strategy, has been documented in specific plant species. In this case, the style is classified into three distinct categories based on their respective lengths: short, medium, and long. Tristylic species are characterised by a more limited geographic range, predominantly found within the *Lythraceae* and *Oxalidaceae* botanical groups. The homomorphic system does not demonstrate any discernible association with fluctuations in floral morphology. The regulation of the incompatibility reaction can be regulated by either the diploid genome of the plant that produces pollen (saprophytic control) or the haploid genome of the pollen itself (gametophytic control).

The documentation of gametophytic incompatibility as a phenomenon was first conducted by East and Mangelsdorf in 1925, focusing on the plant species *Nicotiana sanderae*. The determination of the incompatibility reaction of pollen is contingent upon its own genotype rather than the genotype of the plant upon which it is generated. The synthesis of biological substances involved in the self-incompatibility response takes place after the meiotic process.

The control of this response may be subject to the effect of either a single gene or a pair of genes. Within this event, the elongation of the pollen tube comes to a halt within the style. The phenomenon of sporophytic self-incompatibility (SI) was first observed and reported by Hughes and Babcock in *Crepis foetida* and by Grestel in *Parthenium argentatum* in 1950. The determination of the outcome of the interaction between the pollen tube and the style is dependent on the genotype of the sporophyte, which is the diploid tissue. In this situation, the elongation of the pollen tube halts at its arrival to the external layer of the stigma. Different varieties of *Brassica oleracea* display a sporophytic self-incompatibility (SI) mechanism, which demonstrates varied levels of effectiveness in different agricultural varieties. It is worth noting that according to Watts (1963), this system exhibits its highest potency in kale, while its lowest potency is observed in summer cauliflower.

5.2 Genetic Basis of Self-Incompatibility:

The regulation of self-incompatibility is governed by a single genetic locus referred to as S, which comprises a diverse range of alleles. The gametophytic system is characterized by a greater abundance of S-alleles in comparison to the saprophytic system. Within the gametophytic system, the alleles demonstrate co-dominance, leading to offspring that can be categorized as incompatible, somewhat compatible, or totally compatible. In contrast, within the sporophytic system, the alleles exhibit characteristics of dominance, co-dominance, and sporadic instances of competition. Consequently, the offspring that arise can be classified into two distinct groups: those that are compatible and those that are incompatible. The S alleles of brassica have been categorized in a dominance series based on their genetic activity in heterozygous plants, as documented by Thomson and Taylor in 1966. According to traditional genetic research, it has been shown that brassica S alleles can be categorized into two separate groups based on their phenotypic influence on self-incompatibility features. The alleles within the initial population demonstrate a notable self-incompatibility phenotype, which is characterized by an average of 0 to 10 pollen tubes emerging per stigma that undergoes self-pollination. The alleles in question exhibit a relatively high level of dominance. The alleles belonging to the second group are categorized as recessive and have a comparatively diminished phenotypic effect on self-incompatibility. This leads to the production of 10 to 30 pollen tubes per stigma during self-pollination. The stigma in a gametophytic system is characterized by its plumose structure, consisting of elongated receptive cells. It is commonly known as a moist stigma because to its moist nature. The germination of incompatible pollen grains often occurs upon their arrival at the stigma. The occurrence of the incompatibility reaction is delayed, so avoiding the associated social stigma. Pollen grains exhibiting different S genotypes have apparent serological differences. In a sporophytic system, the pollen grain is characterized by the presence of an outer lipidic coating known as the superficial layer (CSL). This thin layer is formed by the tapetum onto the pollen grain shortly before it undergoes drying. Beneath the superficial layer of coating is the primary outer coating of pollen known as tryphine, which encompasses constituents responsible for the maternal regulation of pollen reactivity. The stigma within the saprophytic system exhibits papillate characteristics, with the presence of papillae that are enveloped by a pellicle or sheath. The pellicle is composed of proteins and may have a variable thickness of wax coating. When pollen that is appropriate for fertilization encounters the stigma, the pollen's cellular surface layer (CSL) undergoes fusion with the papillae. When pollen becomes hydrated and undergoes germination on papillae, it releases a cutinase enzyme that facilitates the digestion of the cuticle.

This enzymatic activity allows for the expansion of the pollen tube within the cellular pectin layer of the papillae.

5.3 Self-Incompatibility's Molecular Base:

Extensive research has been conducted on the self-incompatibility mechanism within the Solanaceae and Brassicaceae botanical families, which encompass various vegetable species. The mechanism involves the interaction between two proteins located at the S locus. One variable is linked to those who identify as male, whereas the other determinant is linked to individuals who identify as female. When examining the brassica plant, the self-recognition determinants encompass the S-locus receptor kinase (SRK) located in the stigma, and the S-locus cysteine-rich protein (SP11/SCR) existing in the pollen. Within every species, the determinants exhibit a multitude of alleles and are closely interconnected within the S-locus complex. The structure of the S-locus displays considerable diversity, and this polymorphic nature is thought to be essential in inhibiting recombination between the SRK and SP11 genes. Recombination events possess the capacity to disturb self-incompatibility mechanisms, hence resulting in their failure. Near to SRK, there is an additional protein called S-locus glycoprotein (SLG). According to Thakur and Dhiman (2021), there is a proposition suggesting that self-incompatibility in plants, specifically SLG, can be attributed to a duplication event that involves the S domain of SRK. The augmentation of the SI recognition reaction in transgenic plants is assisted by its enhancement, as evidenced by the study conducted by Takasaki *et al*. (2000). The presence of the SP11 protein has been detected in the tapetum cells situated within the anther locules. During the process of maturity, pollen grains undergo a subsequent accumulation on their surface. The penetration of the papilla by SP11 molecules and their specific interaction with SRK have been observed during cases of self-pollination. Following this, the phenomenon of phosphorylation takes place on SRK, leading to the incorporation of phosphate groups onto several proteins present in the stigma, such as MLPK (M-locus protein kinase). Subsequently, a further phenomenon referred to as signal transduction, whose precise processes remain unidentified, finally leads to the rejection of self-pollen (Watanable *et al*., 2012).

5.4 The Molecular Mechanisms Behind Dominance Relationships Within the Context of Pollen Interactions:

The mediation of dominance relationships in self-incompatibility (SI) is regulated through the transcription of SP-11. The plant SP-11, which possesses heterozygosity for the sporophytic feature, demonstrates typical phenotypic manifestation when derived from the dominant allele. In contrast, the recessive SP-11 allele exhibits suppression and is not detectable in RNA gel blot examination. Moreover, previous studies have demonstrated that the synthesis of small RNA molecules originating from the dominant allele can trigger the methylation process of the recessive allele, leading to the suppression of transcriptional activity of SP-11. The *Solanaceae* family demonstrates a compatibility mechanism referred to as S-RNase-Based Self-Incompatibility (SI). During this biological process, the pollen grains that lack compatibility with the surface of the stigma initiate germination. Subsequently, they go on a process of development inside the transmission pathway of the style.

Nevertheless, the progression of this expansion ceases when the pollen grains have reached a point where they occupy roughly one-third of the overall length of the style. The occurrence of S-locus F Box protein (SFB) has been seen within the pollen tube, where it is hypothesized to serve as the male determinant. The elongation of the pollen tube is hindered when the S-RNase, a protein present in the stigma, infiltrates the pollen tube and subsequently degrades its ribosomal RNA. The development of the SFB complex occurs when the S-RNase interacts with the pollen SFB, which is connected to ubiquitin, in the presence of a suitable pollen grain. The protein ubiquitin is significant in the process of protein degradation in living tissues, particularly in the removal of damaged proteins, as well as in the synthesis of newly formed proteins (Stefanowicz *et al.*, 2015).

5.5 Application of Self-Incompatibility in The Hybridization Breeding of Vegetable Crop:

The process of hybridization is of considerable importance in determining the economic feasibility of various cross-pollinated crops. Nevertheless, the application of this technique in crops that undergo self-pollination is constrained by the relatively higher costs involved in seed production. Self-incompatibility is a method utilised in hybrid breeding to augment productivity, diminish the costs linked to hybrid seed production, expedite the creation of hybrids, and abbreviate the duration of hybrid seed production. The change from cross-fertilized species to self-fertilized species is influenced by multiple causes, while the reverse transition is a rare phenomenon, if it occurs at all. Hence, it is probable to see the occurrence of self-incompatibility in the offspring of self-fertilized crops, such as tomatoes, lettuce, and beans. The manifestation of this hereditary attribute has been documented in multiple untamed tomato species, and its genetic attributes have been comprehensively scrutinised by McGuire and Rick (1954) as well as Martin (1968). Based on the research conducted by Martin in 1968, it was observed that the Tiny Tim cultivar of *Lycopersicon esculentum*, which was originally capable of self-fertilization, underwent effective modifications to develop self-incompatibility. However, in this context, there are several interconnected barriers that hinder its feasibility for commercial applications. Whitaker and Jagger (1939) reported that individuals belonging to the *Lactuca* genus, specifically the species *perennis*, exhibit a high likelihood of self-incompatibility. The chromosomal count of *Lactuca perennis* and the commercially cultivated lettuce *Lactuca sativus* is the same, as both species have a chromosome number of n=9. Nevertheless, while conducting crossbreeding experiments between these two species, it was seen that the resultant seeds exhibited a lack of viability. Considering the possible existence of unilateral incompatibility, it is advisable to facilitate its transfer among different species. Nevertheless, it is important to acknowledge that the manifestation of the principal alleles responsible for incompatibility can be altered by the existence of modifier genes (Martin, 1968; Thompson & Taylor, 1966). In addition, the interplay of alleles in the sporophytic system leads to intricate phenomena (Sampson, 1957; Thompson & Taylor, 1966). To get optimal outcomes, it is advisable to partake in breeding endeavours that span a broad range of genetic variation. Rather than utilizing the backcross methodology, it is recommended to adopt the pedigree selection method. The implementation of sporophytic self-incompatibility mechanism for the purpose of hybrid seed production in Cole crops, such as cabbage, cauliflower, and broccoli, has been observed in several regions, including India (Singh, 2000). The observation of this mechanism was first made by Stout in 1920. In the year 1921, a Japanese enterprise achieved a significant milestone by successfully creating the inaugural hybrid variety of

Chinese cabbage, known as Nagaoka Kohai I Go. Following this, in the year 1961, a further F1 hybrid variant of radish, referred to as 'Harumaki Minowase', was developed. The existence of the self-incompatibility mechanism has been recorded in various cole crops, such as kale (Thompson, 1957), broccoli (Sampson, 1957; Odland, 1962), cabbage (Adamson, 1965), and cauliflower (Hoser-Krauze, 1979).

The first step in the development of hybrid seeds using self-incompatibility is the selection of self-incompatible (SI) plants from a diverse population or several genotypes. The procedure entails the utilization of different pollination methods, including self-pollination in recently bloomed flowers (SP), pollination with unrelated Sallele pollen (CP), and bud pollination. These methods are employed to ascertain the plant's fertility as either male or female, as well as to facilitate self-seeding to obtain offspring. The categorization of plants into self-incompatible or compatible groups is established based on the interplay between self-pollen (SP) and cross-pollen (CP), as elucidated by Watts in 1963. The computation of the Fertility Index (FI) can be employed as a means of assessing self-incompatibility. Nevertheless, this strategy has certain limitations. Firstly, it is necessary to observe a waiting time of sixty days till the point of maturity is attained. Furthermore, the potential yield could be reduced due to a range of environmental factors. When the numerical value surpasses 2, it is referred to as self-incompatibility. On the contrary, if the number decreases to a value less than 1, it is categorized as self-compatibility. The phrase "pseudo-compatibility" is utilized to describe values within the range of 1 to 2.

The technique of pollen tube growth is also utilized in combination with fluorescent microscopy, facilitating the collection of data within a time of 24-48 hours following pollination (Vidyasagar and Chatterjee, 1984). The occurrence in which six to nine pollen tubes pierce the style is considered an incompatible reaction. A more advanced and effective method for identifying the presence of self-incompatibility genes is the application of molecular markers. The methodology produces results during the early phases of plant growth. In their study, Niikura and Matsuura (1998) utilized the Polymerase Chain Reaction-Restriction Fragment Length Polymorphism (PCR-RFLP) technique as a means to identify S-alleles in radish. The amplification of a single DNA fragment, with an approximate length of 1.16 kilobases (kb), was observed as expected, in accordance with the original sequence of *B. oleracea*. After the discovery of self-incompatible plants, the subsequent step entails the production of homozygous self-incompatible plants. The objective is accomplished through the deliberate selection of a minimum of seven plant specimens derived from self-incompatible plants, followed by the implementation of intra-progeny crosses. The process of crossing is executed by pollinating recently blossomed flowers in a comprehensive diallel design, as described by Thakur and Dhiman (2021). Intra-crossings are performed to assess the level of heterozygosity in self-incompatible plant species. Based on the facts, it is possible to classify plants into two distinct categories: compatible and incompatible. Following this, there is a noticeable occurrence of either a homozygous and a heterozygous phenotypic group, or both a homozygous and a heterozygous phenotypic group. Plants are selected from the homozygous population, and successive generations are subjected to breeding to establish homozygous lines within a span of 2-3 generations. After the creation of homozygous self-incompatible lines, the identification of the S-alleles within these lines is carried out. The objective of this study is to evaluate the level of dominance and interactions pertaining to S-alleles. The presence of alleles exhibiting pronounced dominance leads to a notable decrease in progeny production and self-pollination in hybrid seeds. The S-allele interactions seed set technique is utilized in reciprocal pollinations conducted between a heterozygote and its two corresponding homozygotes, with the aid of fluorescence microscopy. Based on available studies, it has been observed that there are four discrete categories of S-allelic interactions. The various types can be classified as follows: type I, characterized by the dominance of a single S-allele in both pollen and stigma; type II, characterized by the dominance of one S-allele in pollen but co-dominance in stigma; type III, characterized by the dominance of one S-allele in stigma but co-dominance in pollen; and type IV, characterized by the co-dominance of both S-alleles in both pollen and stigma. The primary goals of this study include establishing inter-allelic links among S-alleles and identifying the best-combining lines. To achieve heterotic hybrids, it is crucial to determine the most advantageous combination of S-allele lines. The assessment can be carried out by examining research conducted in the domain of SCA (Situational Crisis Communication Theory) and evaluating the entity's performance.

Hybrid seeds can be produced by crossing a self-incompatible line with a self-compatible line. Nevertheless, the number of resultant seeds is somewhat restricted because of their selective acquisition from self-incompatible plants. The third phase entails the maintenance of parental hybrid lines, a procedure that entails considerable financial costs. The commonly used techniques involve manual self-pollination during the bud stage, exposing the plants to a carbon dioxide concentration of 3-5% for a period of 8-24 hours in growth chambers with 100% relative humidity, and utilizing tissue culture methods that utilize the meristem as an explant. Prior research has demonstrated that the application of sodium chloride sprays, containing concentrations ranging from 3% to 5%, has been shown to effectively mitigate self-incompatibility on a temporary basis (Kucera *et al*., 2006). Hybrid seed is produced by employing the single cross, double cross, or triple cross procedure. The experimental design referred to as the single cross involves the cultivation of two lines that possess self-incompatibility but are capable of cross-pollination. These lines are planted in alternating rows inside a distinct and regulated plot. The seed derived from both lineages is categorized as hybrid seed. This methodology produces the utmost level of heterosis and leads to uniform plant traits. The double cross involves the utilization of two distinct crosses. Thompson (1966) proposed the utilization of kale cultivation, a plant species that exhibits sporophytic self-incompatibility (SI), as a viable approach for implementing the triple cross breeding strategy. In the experimental design including a three-way cross, a solitary cross is conducted alongside a self-incompatible line, with the two being planted in alternate rows. The present investigation employed six inbred lines that were characterized by possessing suitable self-incompatibility alleles. The practice of employing top cross is also widely observed in the United States with the aim of producing hybrid seeds. The experiment involved the planting of a self-incompatible line and a pollen-pollinated cultivar in a ratio of 2-3:1. The seeds obtained from the self-incompatible lines are classified as hybrid seeds. The process of generating hybrid seeds via self-incompatibility faces several obstacles, including pseudo-fertility, the suppression of S-alleles resulting from repeated inbreeding, the impact of environmental factors like elevated temperature and humidity on self-incompatibility levels, and an elevated occurrence of siblings due to insufficient synchronization in flowering. This objective can be accomplished by adopting S-allele lines that display resilience in many environmental conditions, implementing vegetative propagation methods, and carefully selecting parental lines that exhibit synchronization in flowering.

5.5.1 The Distinguishing Features of Superior SI Lines:

The presence of stable self-incompatibility is a necessary characteristic. The process of developing and maintaining the system should be relatively uncomplicated. The presence of the trait of desirable combining ability is necessary. It is advisable to establish a significant seed population by the process of self-pollination during the budding phase. The economic aspects ought to demonstrate consistency. Kucera *et al*. (2006) utilized the SI line Montano (MT) in conjunction with SP Fortuna (FT13) in their research. The facilitation of SI line reproduction was achieved by applying a 3% NaCl solution in the evening, followed by the utilization of bumblebees as pollinators. The F1 hybrid, derived from the cross between MT and FT 13, displayed favourable characteristics like uniformity, high-quality curd, sufficient leaf coverage of the curd, and satisfactory disease resistance.

The work conducted by Park *et al.* (2007) centered on the generation of consistent F1 hybrid cultivars of Korean Radish by employing self-incompatibility in double crossing. The present investigation involved the analysis and categorization of a comprehensive set of 45 commercially available radish varieties. This was accomplished using the Polymerase Chain Reaction-Restriction Fragment Length Polymorphism (PCR-RFLP) technology. The objective of this investigation was to ascertain and choose parental materials exhibiting discernible S haplotypes. Two distinct sets of parents were selected from two distinct populations, namely the summer population (population 1) and the autumn population (population 2). A population characterized by the presence of inbreeding was established through a single parental cross and five subsequent generations of inbreeding, originating from two separate parental sets. In each generation, a PCR-based selection process was employed to detect and choose individuals exhibiting heterozygosity for self-incompatibility (SI). The selection of SI heterozygotes was conducted with the objective of generating cross-compatible near-isogenic lines (CCNILs). The researchers utilized a method of reciprocal crossing involving genetically homogeneous inbred lines in order to attain a targeted degree of homogeneity. To improve and establish uniformity in seed production, CCNILs were employed. The NILs derived from self-incompatible (SI) plants had a significantly greater seed output (4.88) per flower pollination when compared to an inbred line (1.5) of radish. The generation of parental seed for double cross can be accomplished by means of bee pollination, employing CCNILs derived from an inbred lineage harbouring discrete S haplotypes. The assessment of self-incompatibility was conducted in cabbage lines I-4-6 and II-12-4-7, which were found to have the S allele.

The seeds were obtained by subjecting them to NaCl solution sprays with concentrations of 3% and 5%, respectively. Subsequently, the procedure of manual self-pollination was conducted on recently bloomed flowers. The seeds that were obtained were sown to assess the effectiveness of seedling establishment. To inhibit outcrossing, the plants were enclosed within cages constructed from nylon netting. The study involved the examination of selfing in open flowers (referred to as OP) and bud pollination (referred to as BP). The plants subjected to the BP treatment exhibited successful seed production, hence providing evidence for the reproductive competence of both male and female gametes within the plant specimens under investigation. Nevertheless, it was observed that there was an absence of seed-set in the OP treatments for both lines possessing the S allele. Singh and Vidya Sagar (2015) conducted an experiment wherein they observed that the utilization of a solution comprising of sodium chloride (NaCl) resulted in a temporary disturbance of self-incompatibility. The discovery holds considerable ramifications for the conservation of S-allele strains utilised in the production of hybrid seeds. Singh and colleagues (2016) did a research investigation on the phenomena of self-incompatibility and its enduring presence in cauliflower plants cultivated in the sub-temperate climate of the western Himalayas. The aim of this study was to exploit the phenomenon known as hybrid vigour. The identification of self-incompatible (SI) plant lines and their progeny is of great importance in attaining this objective.

5.5.2 Applications in Crop Production and Breeding:

The increasing understanding of the molecular mechanisms underlying self-incompatibility (SI) is opening new possibilities for utilizing this trait to improve crops through breeding and biotechnology-based approaches. The utilization of existing information on synthetic intelligence (SI) encompasses a broad spectrum of diverse applications, which can be categorized into three main domains: crop production, with a focus on enhancing yield and quality; marker-assisted breeding; and the creation of hybrids, both within and between different species.

5.5.3 Role of Pollinizers in Orchard Management:

In agricultural contexts where self-incompatibility (SI) is observed, and even in self-compatible (SC) crops, it is common practice to distribute cultivars that function as pollen donors ("pollenizers") evenly among orchards. This is because the successful fertilization and subsequent fruit set in these crops heavily rely on cross-pollination. Pollenizers are frequently employed in the cultivation of several crops, including canola (*Brassica napus* L.), sunflower, strawberry (*Fragaria x anannasa* [Weston] Duchesne), as well as fruit-bearing trees such as apple (*Malus x domestica* L.), European pear (*Pyrus communis*), sweet cherry, and Japanese plum (*Prunus salicina* Lindl) (Woodcock, 2012). The utilization of pollenizers is also advised in olive (*Olea europaea* L.), given the recent identification of homomorphic sporophytic diallelic self-incompatibility (DSI), which is expected to simplify the process of selecting suitable pollenizers (Saumitou-Laprade *et al.*, 2017). In diploid fruit tree species that exhibit gametophytic self-incompatibility (GSI), outcrosses can be categorized into three distinct varieties based on the degree of compatibility between the parents. These types include: incompatible outcrosses, where both parents possess identical S-haplotypes; semi-compatible outcrosses, where one S-haplotype is shared between the parents; and fully compatible outcrosses, where no S-haplotypes are shared between the parents. In crosses that are semi-compatible, approximately 50% of the pollen grains are not accepted, resulting in potential consequences for fruit set and yield, particularly in apple, European pears, and Japanese plums cultivated in sub-optimal regions such as the Mediterranean basin (Schneider *et al*. 2005; Zisovich *et al*. 2005; and Sapir *et al*. 2008).

The increase in honeybee visits has been found to result in higher yields in semi-compatible cultivars, therefore providing evidence that the decrease in yield can be attributed to a shortage of compatible pollen (Sapir *et al.*, 2007). Furthermore, in plant genera characterized by a high number of ovules, such as Malus and Pyrus, a decrease in the process of fertilization can lead to a reduction in the number of seeds produced and a decline in the overall quality of the fruit. In various species, the phenomenon of self-compatibility (SC) has been observed to be associated with favorable fruit set, increased yields, and in some cases, excessive crop production (Goldway *et al*., 2007; Claessen *et al*., 2019). Self-compatibility (SC) may also be advantageous due to its ability to eliminate the requirement for pollenizers, which rely on bloom overlapping. Consequently, SC enables the cultivation of a single cultivar across a contiguous area, resulting in a more consistent crop yield.

The utilization of SC has been regarded as a potential strategy to mitigate the impacts of colony collapse disorder on honeybee pollination, particularly in industries such as the California almond sector. Nevertheless, although self-pollination (SC) may decrease the number of beehives needed, it does not always ensure optimal crop yields. This is because certain crops, such as sunflower, canola, sour cherry (*Prunus cerasus* L.), almond (*Prunus dulcis* {Mill.} D.A.Webb.), apricot (*Prunus armeniaca* L.), and others, rely on cross-pollination for maximum fruit production. For example, many apple and pear cultivars in South Carolina (SC) exhibit reduced fruit set due to impaired expression of the S-RNase gene. However, the issue of low fruit set can be resolved by introducing cross-pollination, which replaces self-pollination (Zhang and Hiratsuka. 2005). Moreover, self-compatibility (SC) may not necessarily guarantee self-fruitfulness due to the potential requirement of insects for efficient self-pollination, which is influenced by the floral structure. On the other hand, honeybee pollination has the potential to cause excessive pollination in stone fruits such as sour cherry, apricot, and peach (*Prunus persica* {L.} Batsch), resulting in an abundance of fruits that are smaller in size and of diminished value (Woodcock, 2012). Furthermore, this phenomenon may potentially manifest in SI cultivars. Hence, it may be inferred that fruit set is influenced not only by the SI/SC phenotype but also by the specific cultivar.

5.6 Diverse Sources of Self Compatibility: A Beneficial Characteristic for Improving Yield Enhancement

In the case of self-incompatible crops, most commercially available self-compatible cultivars are the result of naturally occurring or artificially produced changes in the style or pollen parts. These mutations are found and selected by farmers and breeders. The molecular characterization of these alterations is an ongoing process, but, the utilization of uncharacterized sources of stem cells is still prevalent. Stone fruits, namely those belonging to the Prunus genus such as apricot, Japanese apricot (*Prunus mume* Sieb. Et Zucc.), Japanese plum, and almond, commonly exhibit a connection between self-compatibility (SC) and a specific allele at the self-fertility (S) locus. These alleles are denoted as SC, Sf, Se, and Sf for apricot, Japanese apricot, Japanese plum, and almond, respectively (Yamane and Tao, 2009). Yamane and Tao (2009) have reported that while Prunus SC alleles with loss-of-function S-RNase mutations have been identified, mutations in SFB are more prevalent. In the 1940s, the sweet cherry breeding effort at the John Innes Center employed the technique of pollen x-ray irradiation to deliberately promote self-compatibility in the 'Napoleon' cherry variety. Several self-compatible (SC) commercial cultivars were obtained from the 'Napoleon' cultivar, such 'Stella,' 'Lapins,' 'Newstar,' and 'Sweethart.'

Subsequently, it was discovered that all these self-compatible cultivars shared a common mutant gene, known as SFB4´, which was found to be faulty (Sonneveld *et al*., 2005).

In apricot cultivars, self-compatibility (SC) is primarily determined by the presence of the mutant SFBC allele. However, there is another source of self-compatibility in certain varieties such as 'Canino,' 'Patterson,' 'Trevatt,' and 'Portici,' which is attributed to an unlinked mutation at the M-locus ParMDO gene (Muñoz-Sanz *et al*., 2020).

The sweet cherry cultivar 'Cristobalina' has been shown to exhibit self-compatibility due to a mutation in the M-locus GST gene (Ono *et al.* 2018). In a different instance, the cultivars 'Yellow Sarson' and 'Dahuangyoucai' of SC turnip (*Brassica rapa* L.) were found to possess indels that impact SRK and SP11, along with a knockout point mutation in the non-S-locus gene MLPK (Zhang *et al.* 2013).

The understanding of the molecular and genetic underpinnings of self-incompatibility (SI) has facilitated the deliberate engineering of self-compatibility (SC) in a precise and targeted manner. The researchers Shiba *et al*. (1995) were the pioneers in effectively employing a focused approach to overcome social inhibition. The researchers acquired self-compatible *Brassica rapa* plants by inhibiting the expression of the SLG gene, and it is probable that the expression of the SRK gene was also affected due to their significant sequence similarity. This was achieved by employing an antisense SLG construct. In a similar manner, Stone *et al.* (1999) generated somatic hybrids of *Brassica napus* cv. W1 that exhibited somatic cybridization (SC) through the introduction of an antisense ARC1 cDNA.

In a subsequent study, Jung *et al.* (2012) employed RNA-mediated S-locus gene silencing to create SC *B. rapa.* The RNA interference (RNAi) construct utilized in this study was derived from the S60-allele of the pollen S-determinant, SP11/SCR, specifically from the 'Osome' cultivar. The application of this designed synthetic chromosome (SC) in the commercial Seoulbechhu variety serves as evidence of the effectiveness of this method in breeding. Broothaerts *et al.* (2004) successfully created a self-fertile apple cultivar (US Patent No 20060123514) within the pome fruit category. This was achieved by suppressing the expression of the S-RNase gene in the self-incompatible (SI) cv. 'Elstar' with an S3S5 genotype. The researchers provided a description of two distinct transgenic trees that were engineered to express an S3-RNase antisense construct. The observed trees exhibited typical pollen tube growth and successful fertilization following self-pollination, resulting in the production of fruits and seeds at expected quantities. It is noteworthy that both S3- and S5-RNases were subject to silencing, perhaps because to their sequence homology.

The presence of SC in these plants was maintained for multiple years without any apparent negative consequences. In more recent times, the technique of CRISPR-induced knockouts has been employed to create self-compatible (SC) diploid lines in potato (*Solanum tuberosum* L.) for the aim of breeding (Enciso-Rodriguez *et al*. 2019).

5.7 Instances in Which Self-Incompatibility is Favoured for Crop Cultivation

In situations where the lack of seed or fertilization is deemed advantageous, self-incompatibility (SI) may be the favored state. Seedless fruits are of great importance in certain crops, such as citrus fruits (e.g., orange, mandarin, lemon, etc.). Many citrus cultivars exhibit varying levels of parthenocarpy, resulting in the development of typical fruits that are devoid of seeds due to the absence of fertilization.

Nevertheless, in cases where seedless cultivars are grown near cross-compatible cultivars, it is possible for undesired fruits containing seeds to still develop. Therefore, self-incompatibility (SI) is considered a desirable characteristic for Citrus breeding to be utilized alongside parthenocarpy, resulting in a significant reduction in seed count (Vardi *et al*., 2008). The validity of this approach was confirmed by experimentation using a mutant mandarin (*Citrus reticulata* Blanco) cultivar known as 'Wuzishatangju'. It was determined that the absence of seeds in this cultivar can be attributable to gametophytic self-incompatibility (GSI) (Ye *et al*. 2009).

Additionally, studies have documented the involvement of gametophytic self-incompatibility (GSI) in the development of seedlessness in the mandarin cv. 'Afourer' (Gambetta *et al*., 2013), as well as in the lemon cultivars 'Xiangshui' (Zhang *et al*., 2012) and 'Kagzi kalan' (Kakade *et al*., 2017). Li *et al*. (2015) have shown that the involvement of style-expressed S-like-RNases and SKP1-like genes in the self-incompatibility (SI) response of the mandarin cv. 'Wuzishatangju'. Further investigation into the Citrus SI system is necessary prior to the practical implementation of engineering SI for seedlessness.

5.8 Self-Incompatibility as A Viable Alternative to Andro Sterility for The Development of Hybrid Varieties

Hybrid Vigor, also known as heterosis, manifests when two parents possessing distinct genetic origins, typically characterized as pure lines, undergo crossbreeding. The Heterotic F1 offspring exhibit increased production, along with other agriculturally advantageous characteristics, such as improved resilience to abiotic stressors.

The prevalence of this phenomena is extensive, resulting in the widespread presence of hybrid cultivars in numerous crop species such as maize, sorghum, tomato, and pepper (Kempe and Gils, 2011). Due to the predominance of self-compatible (SC) farmed crops, the production of hybrid seed necessitates the implementation of a proficient pollination control system to avert self-fertilization in the female parent.

Various control methods encompass a spectrum of approaches, including mechanical emasculation, chemical gametocide agents, as well as nuclear or cytoplasmic-encoded male sterility, which can be accompanied by fertility restoration in the F1 hybrid (Kempe and Gils, 2011). According to Kaothien-Nakayama *et al.* (2010), self-incompatibility (SI) has been found to be the more favourable option compared to male sterility in crop species that rely on insect pollination, as male-sterile plants are rarely visited by pollen-collecting bees.

However, it is important to note that self-incompatibility (SI) can also present certain drawbacks. One such drawback is that offspring resulting from the crossbreeding of two SI parents, known as F1 hybrids, also exhibit self-incompatibility. This might be undesirable in the context of crop production. The utilization of self-incompatible (SI) F1 hybrids does not pose a disadvantage for ornamental or vegetable crops. However, it may impede the generation of seeds in crops such as oilseed rape/canola or the development of fruits in stone and pome crops. As a result, breeding programs exhibit a preference for both self-incompatible (SI) female lines and self-compatible (SC) F1 hybrids (Kaothien-Nakayama *et al*, 2010).

5.9 The Phenomenon of Self-Incompatibility in Hybrid Breeding Schemes

The utilization of self-incompatibility (SI) is prevalent in Brassicaceae for the purpose of producing hybrid seeds. This reproductive mechanism is commonly employed in diploid crops such as *Brassica oleracea* and *B. rapa/B. campestris*. Nevertheless, it is worth noting that the amphi-diploid oilseed rape, also known as canola (B. napus), is inherently self-compatible. However, to obtain hybrid seeds, the incorporation of S-alleles from its parental species is necessary. In their study, goring *et al*. (1992) successfully incorporated the S-locus from the self-incompatible (SI) B. campestris 'W1' line into the self-compatible (SC) *B. napus* cv. 'Westar' through introgression. They further refined this process by conducting backcrossing, resulting in the development of a self-incompatible 'Westar' line. In a subsequent study, Rahman (2005) conducted the reconstitution of self-incompatibility (SI) in *Brassica napus* through the hybridization of SI *Brassica oleraceae* (cv. 'Green Duke') and *Brassica rapa* (cv. 'Horizon', 'Colt,' and 'AC Parkland'). The achievement of successfully restoring self-incompatibility (SI) across several species has generated optimism regarding the potential for a more widespread application of SI in hybrid breeding through a more comprehensive comprehension of its molecular genetics. The transfer of cloned S-genes from self-incompatible (SI) *Arabidopsis lyrata* to its self-compatible (SC) relative *A. thaliana* has been observed to lead to effective pollen rejection, as demonstrated by Nasrallah *et al.* (2002). However, there is currently no published evidence of such transfer occurring in distantly related crop species. It is improbable that the endeavour will yield success, given that *Brassica* self-incompatibility necessitates the presence of modifier genes for its optimal functioning, as elucidated in the publication "Molecular Mechanisms of Self-Incompatibility."

However, it has been observed that Papaver S-genes have the potential to facilitate targeted rejection of pollen in numerous species. In contrast to the S-RNase-based systems and the *Brassica* SSI system, the Papaver S-specificity determinants (PrpS and PrsS) demonstrate adequacy in facilitating self-incompatibility (SI) function. In a study conducted by Lin *et al*. (2015), a proof-of-principle experiment was conducted to transfer the PrpS and PrsS genes from P. rhoeas to *A. thaliana.*

The findings indicated that *A. thaliana* had a distinct rejection reaction that bore resemblance to the SI pollen rejection observed in *P. rhoeas*. The findings of this study are quite encouraging, considering the distant relationship between *P. rhoeas* and *A. thaliana*. The potential realization of engineered crop incompatibility through the utilization of Papaver SI genes is a topic of interest, as evidenced by the subsequent discussion over a related patent. The utilization of SI also holds significant potential in the development of hybrid breeding systems in grasses. For example, the plant species *Triticum aestivum* L., commonly known as wheat, is a completely self-compatible (SC) inbred species. However, the utilization of hybrid breeding to take advantage of heterosis in wheat has faced challenges, partly due to the complexities associated with utilizing male-sterility.

Nevertheless, silicon (SI) can be found in other grass species, such as rye. Therefore, it is conceivable that genes from closely related self-incompatible (SI) cousins could be included to produce self-incompatible wheat (Whitford *et al*., 2013). All grass species that have been researched demonstrate a gametophytic self-incompatibility (SI) system that is extensively described. This SI system is regulated by two loci, S and Z, each of which have many alleles. In the plant species *Lolium perenne*, two genes that encode proteins with a DUF247 domain, whose function is currently unclear, exhibit co-segregation with the Z- and S-loci.

These genes have been suggested as potential S-genes based on studies conducted by Shinozuka *et al.* (2010) and Manzanares *et al*. (2016). The present study aims to conduct a detailed mapping of the *L. perenne* Sand Z-loci, which will greatly assist in the discovery of markers peculiar to each haplotype. This will enable the prediction of cross compatibility between different haplotypes. Therefore, the utilization of selection based on S- and Z-loci could prove advantageous in conventional ryegrass breeding. This is particularly relevant in cases where the limited ability to produce a greater number of F1 hybrids has hindered the genetic improvements associated with heterosis. In standard semi-hybrid systems, the final phase of seed production involves the interpollination of two heterotic populations, which are synthetic types. This process typically yields hybrid seed at a rate of 50%.

The utilization of S-genotyping has the potential to enhance the outcome. According to Pembleton *et al.* (2015), simulations indicate that the utilization of two parental populations with limited variety in S-alleles, employing linked markers for selection, has the potential to enhance cross compatibility and yield F1 hybrids up to 83.3%. As an illustration of a theoretical framework, the imposition of limitations on the presence of S-alleles within the parental populations of the forage legume red clover (*Trifolium pratense* L.), which belongs to the *Fabaceae* family, resulted in an enhanced level of hybridization among the generated seeds. In the context of controlled research, multiple populations consisting of only three S-alleles were randomly bred and subsequently compared to a population without any restrictions on S-alleles. The study conducted by Riday and Krohn (2010) revealed that the proportion of hybrid seeds obtained from the unrestricted population was only 48%, whereas the restricted populations yielded a higher percentage of hybrids, specifically 75%.

5.10 Methods for Attaining Self-Compatibility and Its Significance in Hybridization

The preservation of "pure" lines, characterized by a high degree of homozygosity, is necessary for the practice of hybrid breeding. Due to their nature, self-incompatible (SI) species tend to exhibit a preference for outcrossing. Consequently, the attainment of homozygosity may be impeded by the presence of the intra-specific crossing barrier and the resulting negative effects of inbreeding depression.

Ensuring the consistency of attributes in SI parent lines might pose challenges. As a result, breeders have employed or contemplated many methods to overcome self-incompatibility (SI). These methods include mentor pollen, bud and stump pollination, pollination of senescent flowers, irradiation, and high-temperature stress (De Nettancourt, 2001). In addition, chemical therapies have been utilized. As an illustration, the application of sodium chloride (NaCl) or carbon dioxide (CO2) has been found to inhibit self-incompatibility (SI) in self-compatible (SSI) plants, as demonstrated by Kučera *et al*. (2006). According to Kim *et al*. (2001), the inhibition of S-RNases through the combination of divalent zinc and copper ions has been seen in in vitro investigations. This finding suggests that there is a possibility for the suppression of self-incompatibility (SI). In recent times, there has been a proposal for the implementation of a "in vitro nursery" system for self-incompatible (SI) crops. In this hypothetical framework, the fusion of gametes derived from somatic cells is proposed as a means of replicating self-pollination. This process aims to yield homozygous lines, which can then be utilized in the production of single cross hybrids (De La Fuente *et al*., 2013). The sources of self-compatibility (SC) for hybrid breeding can also originate from spontaneous or induced mutations that result in the loss of self-incompatibility (SI) function in pollen, stigmas, or styles. For further information on the various sources of SC and its advantageous role in enhancing crop yield, please refer to the section under "Different Sources of SC: A Favorable Trait for Yield Enhancement." One example that serves to illustrate this point is the utilization of the Sli (S-locus inhibitor) gene, which induces self-compatibility, in diploid potato plants. The discovery of Sli occurred in a specific variant of the wild potato cousin known as *S. chacoense*, which was found in a SC variant. This discovery was made by Hosaka and Hanneman in 1998a and 1998b, who also mapped Sli to the distal end of chromosome 12. Despite lacking molecular characterization, the Sli gene has been observed to function as a dominant pollen component that induces sporophytic inhibition of gametophytic self-incompatibility (GSI) (Hosaka and Hanneman, 1998a). Furthermore, the utilization of Sli was not only recognized for its possible implications in comprehending the GSI mechanism (McClure *et al*., 2011), but it was also acknowledged as a valuable "tool" for the self-fertilization of diploid potato plants, leading to the development of highly homozygous and seed-propagated lines (Phumichai *et al*., 2005). Jansky *et al.* (2014) introduced M6, a robust diploid *Solanum chacoense* line with a high level of homozygosity (including Sli), reaching 90%. The M6 variety exhibits complete fertility, as it can produce viable seeds when subjected to crossbreeding with both cultivated and wild potato species. Furthermore, the utilization of M6 will facilitate the methodical development of inbred diploid lines.

Nevertheless, the process of incorporating the *S. chacoense* Sli gene into different potato varieties is a laborious task that can be time-consuming. Additionally, this process may inadvertently introduce undesired characteristics, such as elongated stolon or elevated levels of tuber glycoalkaloids. The utilization of CRISPR knock-out technique on the S-RNase gene has been demonstrated as a feasible approach for producing self-compatible (SC) potato lines without the undesired transfer of traits linked to Sli. This method has been supported by recent studies conducted by Ye *et al.* (2018) and Enciso-Rodriguez *et al.* (2019). The consequences of this significant milestone are relevant to the potential replacement of the existing tetraploid potato, which is transmitted asexually, with a diploid inbred line-based crop that is propagated by seeds (Jansky *et al*., 2016). Synthetic and hybrid breeding techniques frequently employ self-incompatibility (SI) in perennial grasses. Nevertheless, the utilization of synthetic crosses (SC) offers several benefits to breeders, such as the promotion of uniformity and the efficient replication of parental inbred, as well as the decrease of genetic load. Multiple pathways leading to self-compatibility (SC) have been observed in grasses, encompassing mutations in S- and Z-loci (mostly affecting pollen development), as well as other loci such as T- (Thorogood *et al*., 2005) and SF-loci (Do Canto *et al*., 2018). In practical applications, the process of incorporating self-compatibility (SC) traits into populations of allogamous grasses can be achieved by the technique of backcrossing. According to Do Canto *et al.* (2016), it is possible to select derived inbred lines for heterozygosity at the S-locus using molecular markers. This selection process would enable the restoration of self-incompatibility (SI) in the ultimate synthesized variety.

The introduction of self-compatibility (SC) in Brassica has been achieved through conventional breeding methods as well as through direct manipulation of S-gene expression (see to Different Sources of SC: A Favorable Trait for Yield Enhancement). One instance involved the utilization of marker-assisted selection (MAS) to transfer two SC QTLs from line 87-534 (Xiao *et al*., 2019) into SI cabbage (*B. oleraceae*).

One quantitative trait locus (QTL), namely qSC7.2, exhibited a strong linkage with the S-locus, while the other QTL, qSC9.1, did not demonstrate any association with a known gene related to self-incompatibility (SI).

Therefore, it is important to note that while additional research is required to discover novel stem cell (SC) genes, the current markers already demonstrate use for marker-assisted selection (MAS) of stem cells (Xiao *et al*., 2019). Tantikanjana and Nasrallah (2015) introduced an alternative inducible synthetic biology system. Earlier in the discussion, it was stated that the expression of functional S-genes from *Arabidopsis lyrata* in the pollen and stigmas of SC A. thaliana leads to self-incompatibility (SI). In a study conducted by Tantikanjana and Nasrallah (2015), it was observed that the simultaneous expression of the *A. lyrata* SRK and SCR genes in the stigma epidermal cells of A. thaliana resulted in the ligand-mediated cis-inhibition of SRK. Consequently, this disruption of self-incompatibility (SI) occurred. As a result, they put up two methodologies based on cis-SCR for the creation of hybrid seeds. Both procedures employ a heat-inducible promoter to enable inducible synthetic cytoplasmic male sterility (SC) in self-incompatible (SI) inbred lines, both for the purpose of maintenance and for large-scale seed generation in F1 hybrids.

5.11 Conclusion:

The process of plant reproduction plays a vital role in crop breeding and production, with self-incompatibility (SI) systems being a key focus for manipulating reproductive behaviour. Recent scientific progress in comprehending self-incompatibility (SI) has successfully enabled the surmounting of barriers within and between species, hence promoting the creation of novel plant materials such as cultivars, hybrids, and IL populations. Furthermore, the manipulation of self-incompatibility (SI) has proven to be advantageous in endeavours aimed at enhancing other characteristics of crops, such as seed lessness and fruit set. The utilization of emerging methodologies such as omics and genome editing has contributed to the advancement of sophisticated tools that may be used to analyse the mechanisms involved in cell-cell recognition in the context of self-incompatibility. Future studies on sustainable intensification (SI) will play a crucial role in aiding breeders in tackling the issues associated with agricultural production. These studies will focus on enhancing the utilization of plant genetic resources and finding effective strategies to mitigate the adverse impacts of global warming on crops.

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