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SELF-INCOMPATIBILITY OF SWEET POTATO (*Ipomoea batatas* (L.) Lam.). A REVIEW

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ABSTRACT

The presence of self-incompatibility has been a barrier in crossbreeding of sweet potato due to the limitations in the choice of parental cultivars. Self-incompatibility in this crop has been a topic widely researched by different scientists around the world. *Ipomoea batatas* presents a multi-allelic, sporophytic type self-incompatibility system and there have been identified a total of 49 different S-alleles in the wild populations of *I. trifida*. The objective of this work is to collect, reconstruct and clarify important aspects of self-incompatibility of sweet potato, as well as to define the nature of the genetic control mechanism of incompatibility more precisely and define understanding criteria of accumulated knowledge.

Keywords: incompatibility, *Ipomoea batatas*, multi-allelic, sporophytic

AUTO-INCOMPATIBILIDAD DEL BONIATO (*Ipomoea batatas* (L.) Lam.). UNA REVISIÓN

RESUMEN

La presencia de autoincompatibilidad ha sido una barrera en el mejoramiento del boniato debido a las limitaciones en la selección de progenitores. La auto-incompatibilidad en este cultivo ha sido un tema ampliamente investigado por diferentes científicos de todo el mundo. *Ipomoea batatas* presenta un sistema de auto-incompatibilidad de tipo esporofítico y multi-alélica y se han identificado un total de 49 alelos S diferentes en las poblaciones silvestres de *I. trifida*. El objetivo de este trabajo es recopilar, reconstruir y aclarar aspectos importantes de la auto-incompatibilidad del boniato, así como definir con mayor precisión la naturaleza del mecanismo de control genético de la incompatibilidad y definir los criterios de comprensión del conocimiento acumulado.

Palabras clave: incompatibilidad, *Ipomoea batatas*, multi-alélico, esporofítico

INTRODUCTION

The interaction between plants and their pollinators has been considered key in the evolution of floral characteristics and reproductive systems in angiosperms. One element in the interpretation of the evolution of floral characteristics has been the idea that these promote cross-fertilization and decrease self-fertilization (Darwin 1877). Self-incompatibility (SI) is one of the outcrossing mechanisms extant in flowering plants that leads to a high level of heterozygosity in a population and to a genetical architecture, based on homeostasis and hybrid vigor. But in contrast to other such systems, SI impedes self-pollination rigidly, which is desirable in breeding schemes for the rapid fixation of inherited characteristics, as well as the testing of progeny and the derivation of inbred lines (Martin, 1965).

Nishiyama (1971) posited that section Batatas of the genus *Ipomoea* (Convolvulaceae) consists of two groups of species: Group A and Group B which are sexually isolated from each other and never cross-hybridize. Species in Group A, including *I. lacunosa*, *I. triloba*, *I. trichocarpa*, *I. tiliacea* and *I. gracilis* are self-compatible, whereas species from Group B, *I. trifida*, *I. litoralis* and *I. batatas* are self-incompatible. Cultivars of the hexaploid sweet potato (*Ipomoea batatas*) show several cross-incompatibility groups. The presence of these incompatibility groups has been a barrier in crossbreeding of sweet potato due to the limitations in the choice of parental cultivars (Wang, 1964; Martin and Cabanillas, 1966; Topan, 2002; Susanto *et al*., 2013).

The existence of self-incompatibility and the associated phenomenon of cross-incompatibility in sweet potato has been long recognised (Mendiola, 1921; Tioutine, 1935; Togari *et al*., 1942; Poole, 1952). There are some varietal differences within this species for incompatibility (Montelaro and Miller, 1951; Wang, 1968) and some sweet potato varieties are reported to be self-compatible (Togari, 1942; Fujise, 1964). The major barriers to genetic improvement of sweet potato include its polyploidy, high level of heterozygosity, self and cross-incompatibility and large chromosome numbers (Cervantes, 2006). In a breeding programme, one of the important effects of incompatibility is to reduce the potential genetic base, available for the generation of seedling populations, on which selection for improved types can be practiced. Self-incompatibility also precludes or restricts the use of conventional techniques of parental evaluation narrowly, such as progeny testing and it retards fixation of desirable heritable characters because it limits so severely inbreeding (Williams and Cope, 1967).

The objective of this work is to collect, reconstruct and clarify important aspects of self-incompatibility of sweet potato, as well as to define the nature of the genetic control mechanism of incompatibility more precisely and define understanding criteria of accumulated knowledge. This could help to define strategies in a genetic improvement program.

CRITICAL REVIEW OF THE LITERATURE

Self-incompatibility in sweet potato

The first major reports related to self and cross incompatibility of sweet potato date back to the first decades of the last century. Stout (1924) relayed a report by Vallet de Villeneuve in 1837 that some sweet potato varieties in Java bloomed profusely, but they would set no seed until grown on poor soils for several years. It was not until 1926 that Stout suggested that self-incompatibility might be present in sweet potato, he noted with sweet potato clones at New York Botanical Gardens (Stout, 1926). After Montelaro (1950) in Louisiana State University found no significant difference in compatibility when a clone was used as male or female. He observed a high self-incompatibility in most of the clones studied. In Japan, Kazuma, *et al*. (1955) reported that most American varieties flowered sparsely. They found a complete and high degree of self and cross incompatibility among many clones of sweet potato. And Hernandez (1959) reported that compatibility in sweet potato is apparently determined by genes that form a multiple allelomorphic series S1, S2, S3, etc. Self-incompatibility (SI) may also be a barrier among plants of similar S (incompatibility) alleles, preventing exchange among them of desirable genes (Martin, 1965).

Harmon (1960) conducted a study about the cross compatibility of some sweet potato at Louisiana State University. He found that in most cases the reciprocals of the compatible combinations shown above were also compatible. However, there were some exceptions (0,95 to 2,38 % successful reciprocal pollination vs 0), and he reported clones are highly cross incompatible. For example, he found in the BPR clone 0,44 % of capsules formed from 224 auto-pollinations. Harmon thought that sweet potato clones produced by sexual propagation from the more compatible parents, are usually more compatible than clones that have been propagated asexually for many generations, and probably originated as an asexual or somatic mutation. In clones of this latter type, chromosome aberrations and other irregularities in the genome which cause greater incompatibility and sterility tend to accumulate. In addition, he found about 3,7 % of the observations of inter-group pollinations were exceptions to the general crossing pattern; and, of these exceptions, 21 % were due to pseudo-fertility, where incompatibility was expected, and 79 % were due to incompatibility, where fertility was expected. Martin (1965) explained that the primitive methods of growing sweet potatoes in the tropics lead to frequent crossing and unconscious selection, so that recessive mutations probably do not build up.

There are no simple morphological features to suggest the type of incompatibility in sweet potato. Heterostyly also occurs in sweet potato (Poole, 1952; Poole, 1955 Van Schreven, 1953; Yen, 1961). However, it is not associated with the expression of incompatibility in sweet potato (Van Schreven, 1953). Williams and Cope (1967) made correlation analysis between female fertility and the mean difference between the length of pistil and stamen and found a non-significant association between female fertility and heterostyly. Therefore, heterostyly does not affect fertility in sweet potato (Martin, 1965; Venkateswarlu, 1980).

Neither the presence of SI nor the particular incompatibility phenotype is associated with these lengths (Martin, 1965). The failure of pollen germination on the stigma appears to be the physiological basis of self-incompatibility in sweet potato (Togari and Kawahara, 1942; Van Sehreven, 1953). Van Schreven (1953) found evidence of six incompatibility groups among 61 clones investigated. Martin (1965) said that in sweet potato, the incompatibility is of homomorphic type, as concluded by Van Schrcven failure of pollen germination on the stigma after incompatible matings, the presence of unilateral incompatibilities, and the compatibility reactions among parents and offspring suggest that a sporophytic system is in operation. Kowyama *et al*. (2000) found in *I. trifida* that pollen germination occurs rapidly on the stigmatic papillar cells about 10-20 min after pollination. Self-pollen, on the other hand is rejected at a very early stage of pollination within a few minutes, after making contact with the stigma surface, resulting in complete arrest of pollen germination and no seed set.

Poor seed set in sweet-potato appears to be the product of a complex set of incompatibilities and sterilities (Martin 1965; Martin and Cabanillas, 1966). It appears to depend on inhibition of pollen germination as its principal physiological mechanism (Martin and Ortiz 1966). Williams and Cope (1967) said that the contribution of sterilities associated with unbalanced gametes cannot be completely discredited as a factor related to low seed set in sweet potato. However, the cytological features of pollen tube growth in pistils may possibly point to a unique mode of origination of sterility systems in plants, which could be highly correlated with the operation of the incompatibility system. In the case of sterility, the plant cannot produce normal and viable gametes, and hence it cannot be fertilized, whether it is selfed or crossed to another plant of the same or different species, such as interspecific hybridization. Spores and gametes are absent or abnormal because these individuals fail to produce functional gametes for successful fertilization and seed set. This contrasts with incompatibility systems, where male and female gametes are normal and functional, but progeny are not produced, unless compatible parental genotypes are crossed (Gurmu *et al*., 2013). Martin and Ortiz (1967) suggested that the cause of the sterility problem lies in the nature of the floral biology of sweet potato. Sterility may also be caused by factors, such as chromosomal aberration and gene action (sterility genes), which may also arise due to spontaneous mutation (Martin and Ortiz, 1967). Sterility, on the other hand is caused by pollen tube disorientation or failure at the stigma-style junction and the style-ovary junction, where passage may be more difficult mechanically (Martin and Ortiz, 1967).

Martin and Ortiz (1967) found that the stigma and style of sweet potato probably differ in no fundamental way from those of related fertile species of *Ipomoea.* Within these organs, pollen tube growth restriction occurs between stigma and style, and between style and ovary (Martin and Cabanillas, 1966). These restrictions are probably not related to self-incompatibility system in the species, for the latter is known to be controlled by a system of pollen germination inhibition (Togari and Kawahara, 1942; Martin and Ortiz, 1967). In addition, although not documented here, these restrictions occur in almost if not all fertile sweet potato crosses. Martin and Ortiz (1967) said that the the cause of physiological control of these barriers probably lies in the nature of sweet potato itself. It is a hexaploid with ninety chromosomes. Although chromosomes pair normally, considerable secondary association occurs, indicating that partial homology exists among the genomes constituting sweet potato (Jones, 1965). The specialized structure of the papillate cells of the stigma is indicative of the important role these cells play in the incompatibility reaction. High concentrations of mitochondria and plastid like particles suggest that such cells could be rich in enzymes and inhibitors affecting germination (Martin and Ortiz, 1967).

In sweet potato, three types of crossing compatibilities are distinguished depending on the success of fertility. These are reciprocal fertility (fertility occurs in both directions), reciprocal incompatibility (incompatibility in both directions) and unilateral incompatibility (fertility occurs only when the genotype is used as female and not when used as male or vice versa). These differences are attributed to variation in germinability of the pollen and differences with respect to stimulation of pollen itself and by the style. As reported by Martin (1965), the presence of intermediate compatibility, also known as pseudo-compatibility, increases the difficulty of group classification. The presence of unilateral incompatibilities also suggests the existence of dominance relations among alleles involved in the control of self-incompatibility, as reported by Kowyama *et al*. (1994). Martin (1968) hypothesized that inter-variety incompatibility is controlled by two pairs of genes, where each dominant gene is epistatic to the recessive allele of the other one. In addition, the cross-compatibility or incompatibility between genotypes is determined by the dominant genes present.

Dr. Franklin W. Martin (Federal Experiment Station, U.S. Department of Agriculture, Puerto Rico) was the first researcher in the world to realize that the low production of botanical seed of sweet potato is not only due to self-incompatibility, but also because of self-infertility, and the complex of both phenomena are the most important factors that Martin studied and described in detail. Martin (1968) said the system of sterility is manifested by gametic or zygotic abortion at many different stages of the reproductive process. For the analysis of incompatibility in *Ipomoea*. Martin (1968) used a diploid species (*I. selifera*) from the Convolvulaceae family, free from the sterilities of sweet potato. The survey of crossability among plants taken from five distinct geographical populations revealed 10 incompatibility groups. Since sweet potato is a hexaploid, the incompatibility locus may have been duplicated or even triplicated during its evolution. Because bivalent pairing is the rule in sweet potato, the two loci receive separate letter designations. But the interrelationships between loci (epistatic relationships) are assumed to be comparable to the interrelationships among alleles at one locus (dominance relationships). The model assumes that R1 is dominant over R2, and epistatic to S1 and S2; and that S1 is dominant over S2. Both S1 and S2 are epistatic to R2. The data from *I*. *setifera* are sufficient for the author to suggest that the incompatibility of the Convolvulaceae is of the multi-allelic, sporophytic type. Westwood *et al*. (1997) found the SI system in field bindweed (*Convolvulus arvensis* L.) is of the multiallellc, sporophytic type. They also reported that evidence to support this conclusion is present from both, the pollen-stigma interaction and the pattern of incompatibility in backcrosses of F1 plants to their parents.

Kowyama *et al*. (1980) used three plants, K221-A, K221-B and K221-C, each of which was chosen, respectively, from different incompatibility groups, LA, LB and LC of *Ipomoea leucantha*. He supports the suggestion made by Martin (1968) that the incompatibility of Convolvulaceae is of the same type as mentioned above. According to the opinion of the Japanese researchers Kowyama *et al*. (1980), Martin had only performed Fujise's work in 1964. In our opinion Kowyama and his collaborators were wrong about Martin. Despite previous work, Martin was the first to define accurately the type of self-incompatibility of sweet potato. Currently, he is considered the biggest contributor in this subject related to sweet potato. Van Marrewijk (1977) pointed out that Martin and co-workers were the first to recognize that a more complex system is responsible for poor fruit and seed set, they pointed out that in sweet potato, besides the incompatibility system, there is a sterility complex which acts at different stages in the sexual cycle.

Van Marrewijk (1977) from the Centre for Agricultural Research in Surinam studies the importance of incompatibility and sterility mechanisms in reducing fruit set and seed formation in sweet potato. He evaluated 27 clones of sweet potato using different methods to determine the degree of incompatibility among them, one of the methods was establishing compatibility relations; it was pollen germination on the stigma and pollen tube penetration into the style. Taking into account these two aspects, he classified the cultivars into five groups, he found among various clones a large variation in average number of pollen grains per stigma, germination percentage, style penetration and number of pollen tubes in different regions of the style. The data confirm that poor seed set in sweet potato are due to a complex of incompatibility and sterility mechanisms, in which sterility plays a dominant part.

More recently, Susanto *et al*. (2013) in Malang, concluded that the decreased succeed crosses might be caused by osmotic pressure on stigma. Measurement of sucrose concentration in pistil was conducted to discover the function of sucrose as an essential element that needed in pollination related with incompatibility of sweet potato. It is known that sucrose concentration in compatible crosses (80926,2 ppm) was lower than incompatible crosses (180055 ppm). According to these authors, sporophytic self-incompatibility in sweet potato is influenced by trinucleate pollen and site of inhibition of the pollen that occurs in early pollen growth.

Molecular basis for self-incompatibility in *Ipomoea* species

Kowyama *et al*. (2000) to investigate the genetic and physiological basis of sporophytic self-incompatibility in *Ipomoea* focused on the diploid species, *I. trifida* as the experimental material, because the small genome size makes this species more amenable to genetic analysis than the hexaploid sweet potato. They examined the self-incompatibility genotypes of 224 plants of *I. trifida* collected from six populations in Central America. These authors had previously identified a total of 49 different S-alleles in the wild populations (Kowyama *et al*., 1994). Analysis of S-allelic interactions in heterozygous plants revealed a linear dominance-recessive hierarchy with six levels of codominance among the S-alleles. The linear dominance hierarchy in *Ipomoea* probably respects the sequential generation of new S-alleles from recessive to more dominant alleles (Kowyama *et al*. 2000). Stigma proteins extracted from several S-homozygous plants (subjected to two-dimensional polyacrylamide gel electrophoresis), they detected highly polymorphic protein (S-locus-linked stigma proteins, SSPs), which were associated with particular S-genotypes. They were able to deduce that a high sequence identity (95-98 %) among the four SSP-cDNA clones, and demonstrated that the SSP genes are expressed predominantly in mature papillar cells, and they are developmentally regulated with the highest expression levels at the time of anthesis (Kowyama *et al*. 2000). Despite the excellent work of the previous authors, they were unable to define the exact genes that control incompatibility in sweet potato, as they are not the same as in Brassica.

Kakeda *et al*. (2010) found a spontaneous self-compatible mutant plant of population of *I. trifida* and showed to have loss-of-function mutation(s) in male and/or female *S* gene(s). They suggest that crossing using pollen at early stages after irradiation is effective to obtain mutations affecting SI, and that lower-dose irradiation may help to narrow the deletion region.

Tsuchiya (2014) pointed out that the male *S*-gene is sporophytically expressed in the tapetum of the anther, and the product of the male *S*-gene (*S*-protein) is deposited onto the pollen surface. The male phenotype of the SSI plant is determined by the diploid *S*-haplotypes of the pollen-producing plant; therefore, determination of the male *S*-phenotype is under the control of dominant-recessive relationships. On the other hand, the female *S*-gene is expressed in the papilla cells of the stigma. According to DNA marker analysis, the *S*-locus of *I. trifida* is delimited between 0,23 and 0,57 cM. The physical size of the *S*-locus may be estimated at about 212 kb in the *S 1* haplotype (Kowyama *et al*., 2008). Tsuchiya (2014) comparison of the *S 1* and *S 10* *S*-locus regions found high variability in the *S*-locus region, which was designated the *S-haplotype specific* divergent region. The length of the SDR is about 50 kbp in the *S 10* haplotype, 35 kbp in the *S 1* haplotype, and about 95 kbp in the *S 29* haplotype. The flanking region of the SDR is highly conserved among *S*-haplotypes. This author said that five genes (*AB2*, *AB3*, and three *SE* genes) are currently candidate *S*-genes, based on their localization in the SDR, expression patterns, and copy number cDNA clones of the stigma-specific genes (the *SE* genes), also showed a high level of allelic polymorphism among *S*-haplotypes and were located on the SDR of the *S*-locus.

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