Review Article

# Self- and cross-incompatibilities in sweetpotato and their implications on breeding

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**Abstract**

Sweetpotato [*Ipomoea batatas* (L.) Lam.] is an important food security crop for many rural households in Africa, largely providing calories, together with some protein, minerals and vitamins. In Africa, sweetpotato yields range from 3-6 tons ha$^{-1}$ relative to a maximum achievable yield of 40-50 tons ha$^{-1}$, due to biotic and abiotic stresses, and to socio-economic constraints affecting agricultural inputs. Genetic improvement of the crop is essential to boost productivity. However, the inherent nature of sweetpotato including self- and cross-incompatibility, polyploidy, heterozygosity and a large chromosome number (2n=6x=90) complicate its genetic improvement. In the breeding of the crop, self- and cross-incompatibilities limit combining of desirable traits from candidate parents if they belong to the same incompatibility group. The objectives of this review are three-fold. The first section focuses on highlighting the effects of incompatibility on sweetpotato breeding. The second part focuses on describing the types of incompatibilities and methods to determine and distinguish between incompatibility and sterility. The third part of the review examines techniques that can be used to overcome incompatibilities. The information outlined in the review may assist sweetpotato breeders to manage the detrimental effects of incompatibilities, and for the strategic genetic conservation of the crop.

**Keywords**: genetic improvement; incompatibility; *Ipomoea batatas;* polyploidy; *S* locus.
**Abbreviations:** AGRA, Alliance for a Green Revolution in Africa; BA, 6-benzylaminopurine; CIP, International Potato Center: GA$_3$, gibberellic acid; IITA, International Institute of Tropical Agriculture; ISTRC, International Society for Tropical Root Crops: NAA, naphthaleneacetic acid; QTL, Quantitative Trait Locus; RAPD, random amplified polymorphic DNA; SARI, Southern Agricultural Research Institute; 2,4-D, 2,4-dichlorophenoxyacetic acid.

## Introduction

Sweetpotato [*Ipomoea batatas* (L.) Lam.] is an important food security crop for the millions of people in Africa. It is an autopolyploid (2n=6x=90) crop with a basic chromosome number of 15 (Jones, 1965; Bassett, 1986; Huaman, 1999; Lebot, 2010). Polyploidy and the large chromosome number, coupled with self- and cross-incompatibilities among different genotypes limit the genetic improvement of the crop. In addition, the flowering prolificacy in sweetpotato is variety dependent, where some varieties may not flower at all and others produce very few flowers. Self- and cross-incompatibilities provide a major challenge to sexual recombination, seed production and genetic improvement in sweetpotato (Vimala and Hariprakash, 2011). Martin (1967) and Martin and Cabanillas (1968) noted that the improvement of sweetpotato through breeding was universally hindered by two factors. These are poor flowering in temperate environments, and a limited seed set after open or controlled crosses or selfing in all environments. The second factor is largely attributed to genetic incompatibility. While the problem of poor flowering in temperate environments can be reduced by applying various flower induction techniques, incompatibility remains a global barrier for the genetic improvement and conservation of the crop. Self- or cross-incompatibility in sweetpotato inhibits breeding progress because parents with desirable traits may belong to the same

incompatibility group (Wang, 1964; Charles et al., 1973; Vimala, 1989).

Vimala and Hariprakash (2011) reported that most sweetpotato varieties used in their study were self- and cross-incompatible and therefore these varieties were not able to produce viable seeds when hybridized through both self- and cross-pollinations. In the genus *Ipomoea,* Nishiyama (1971) reported two compatibility groups. The first group consists of *I. lacunosa*, *I. triloba*, *I. trichocarpa*, *I. tiliacea* and *I. gracilis*, which are self-compatible. The second group consists of *I. batatas*, *I. trifida* and *I. litoralis* which are self-incompatible. Sweetpotato (*I. batatas)* is generally regarded as a highly self-incompatible. However, there are varietal differences within this species for incompatibility (Warme and Cruzado, 1949; Montelaro and Miller, 1951; Wang, 1968) and some varieties are reported to be self-compatible (Togari, 1942; Fujise, 1964; Tarumoto et al., 1992 cited by Young-Sup et al., 2004). The objectives of this review are three-fold. The first section focuses on highlighting the effects of incompatibility on the breeding of the crop. The second section focuses on describing the various types of incompatibility, and methods to determine and distinguish incompatibility and sterility. The third section of the review examines techniques that may be used to overcome incompatibility when breeding the crop. The information outlined in the review may assist sweetpotato breeders to

manage the difficulties created by genetic incompatibilities in sweetpotato, and in the genetic conservation of incompatible types of the crop.

**The effect of incompatibility on sweetpotato improvement**

The major barriers to genetic improvement of sweetpotato include its polyploidy, high level of heterozygosity, self- and cross-incompatibility and large chromosome numbers (Cervantes-Flores, 2006; Chang et al., 2009). Mcharo and LaBonte (2007) indicated that the hexaploid, self-incompatible and heterozygous nature of the sweetpotato hinder its genetic studies. The success of breeding and selection responses of sweetpotato for yield and other important quantitative traits is greatly affected by genetic incompatibility within the crop. This has slowed down the progress in genetic advances that can be attained within sweetpotato breeding programs (Mcharo and LaBonte, 2007). The current yield of sweetpotato in developing countries is very low, nearly 3-6 tons ha$^{-1}$, while the potential yield is reported to be in the range of 40-50 tons ha$^{-1}$ (Oswald et al., 2009). Cervantes-Flores et al. (2010) noted that most traits of economic importance in sweetpotatoes show quantitative inheritance which is significantly affected by its polyploidy. This can slow down genetic improvement of quantitative traits. Gasura et al. (2008) posited that self- and cross-incompatibilities in sweetpotato have remained the major challenges in the breeding and genetic mapping of the crop. This is because it is not often possible to produce the expected segregating populations from specific crosses. The self-incompatibility system in sweetpotato leads to a total collapse of pollen germination on the stigma after self-pollination. As a result, even if self-pollination has taken place, there will be no pollen germination, fertilization and subsequently no seed set. On the other hand, if cross-pollination has taken place, and the cross is compatible, then pollen germination occurs on the stigma in about 10-20 minutes after pollination (Kowyama et al., 2000). Cross-incompatibility among different varieties hinders targeted breeding especially when the parents with desirable traits of interest, such as disease resistance, drought tolerance, enhanced levels of protein, vitamins, macro- and micro-nutrients and dry matter, belong to the same incompatibility group (Wang, 1964; Charles et al., 1973; Vimala, 1989). Self-incompatibility can sometimes be an advantageous for hybrid development in crops that are not easily amenable to hand crossing (Sleper and Poehlman, 2006). It can be utilized as a means of hybrid seed production in crops such as *Brassica* vegetables where many commercial hybrid varieties have been produced using this technique since 1950's (Hinata et al., 1994). In vegetatively reproducing crops such as sweetpotato, desired clones that are self-incompatible but cross-compatible can be planted in isolated fields and crossed successfully via natural pollinators, resulting in random polycrosses (Tysdal et al., 1942; Schaepman, 1952; Olesen and Olesen, 1973; Nguyen and Sleper, 1983; Bassett, 1986; Schoen and Cheliak, 1987; Morgan, 1988; Saladaga, 1989; Aastveit and Aastveit, 1990).

**Types of incompatibilities in sweetpotato**

In most cases, there are two types of self-incompatibilities in plants: heteromorphic and homomorphic (Acquaah, 2011). Heteromorphic self-incompatibility arises due to the difference in the length of stamens and style, which is referred to as heterostyly. Heterostyly in turn has two forms. The first is where the style is longer than the anthers while in the second the style is shorter than the anthers. In homomorphic self-incompatibility there is no difference in the floral morphology between mating genotypes. Homomorphic self-incompatibility is of two types: gametophytic and sporophytic. In gametophytic self-incompatibility, the ability of the pollen to function is determined by genes in the pollen itself and not by the plant that produces the pollen. A series of multiple incompatibility alleles designated as $S_1$, $S_2$, $S_3$, etc. control the rate of pollen tube growth. The pollen nucleus contains only one of the incompatibility allele because it is haploid. However, the stylar tissue of the mother plant is diploid and contains two incompatibility alleles (Sleper and Poehlman, 2006). In the case of sporophytic self-incompatibility, the incompatibility of the pollen is determined by the plant (sporophyte) that produces the pollen. It is controlled by a one locus system with a large number of multiple *S* alleles (Sleper and Poehlman, 2006). According to Sleper and Poehlman (2006), if the pollen nucleus and either of the stylar tissue possess identical alleles, then the growth of the pollen tube in the style will be slowed and fertilization will rarely occur. However, if the incompatibility allele in the pollen nucleus differs from the alleles in the stylar tissue, the pollen tube will grow at a normal rate and fertilization will occur normally. For example, if a plant with the genotype $S_1S_2$ is self-pollinated or crosspollinated from another plant with the same $S_1S_2$ genotype, then the pollen nucleus will contain either an $S_1$ or $S_2$ allele that match an allele in the stylar tissue and therefore the pollen tube will rarely penetrate the style to reach the ovule at the time of fertilization. On the other hand, if a plant with the $S_1S_2$ genotype is pollinated with an $S_1S_3$ genotype, only the pollen tubes containing the $S_3$ alleles will fertilize the ovule. Similarly, if a plant with $S_1S_2$ is pollinated with pollen from a plant with an $S_3S_4$ genotype, the pollen tubes contacting either the $S_3$ or $S_4$ allele may penetrate the style normally and result in fertilization. In sporophytic self-incompatibility, the *S* alleles exhibit dominance. Gametophytic self-incompatibility is more widespread than sporophytic incompatibility. The genus *Ipomoea* expresses clear-cut incompatibility reactions that are not affected by environmental manipulation, chemical treatment and bud-pollination. These characteristic features of *Ipomoea* indicate that its self-incompatibility reactions are qualitative genetic traits (Fujise, 1964, cited by Kowyama et al., 2000). Kowyama et al. (1994) identified 49 different *S*-alleles in the wild populations of *I. trifida*, a close relative of sweetpotato, in a genetic analysis of segregants in F$_1$ families derived from cross-pollination with the most recessive homozygote. The authors explained that analysis of *S*-allelic interactions in heterozygous plants showed a linear dominance-recessive hierarchy with six levels of co-dominance among the *S*-alleles. Several plant families such as *Brassicaceae, Asteraceae, Sterculiaceae and Convolvulaceae* are known to have the homomorphic sporophytic type of self-incompatibility (de Nettancourt, 1977). Self-incompatibility in plants from these families is under the genetic control of a single multiallelic locus, the *S*-locus (Kowyama et al., 2000). *Ipomoea* species belonging to the second group, including sweetpotato (Nishiyama, 1971), have a homomorphic sporophytic type of self-incompatibility system (Martin, 1965; Martin and Cabanillas, 1968; Kowyama et al., 2000).

Heterostyly also occurs in sweetpotato (Poole, 1952; Van Schreven, 1953; Yen, 1961). However, it is not associated with the expression of incompatibility in the sweetpotato (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 sweetpotato (Martin, 1965; Venkateswarlu, 1980). In sweetpotato, 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. Williams and Cope (1967) also observed unilateral incompatibility in the sweetpotato cultivars. In their study, cultivars of Group I crossed as female to cultivars of Group II were more fertile than their reciprocals. Matings compatible in one direction were incompatible in the other direction. Williams and Cope (1967) observed a similar phenomenon with interspecific hybridization as well. In inter-specific crosses between *I. trichocarpa* as the female and *I. gracilis* as the male, there was no seed set. However, in the reciprocal crosses, seed set ranged from 2 to 13%. Similar results were reported by other workers (Hernandez and Miller, 1962; Martin and Cabanillas, 1966). The presence of unilateral incompatibilities also suggest the existence of dominance relations among alleles involved in the control of self-incompatibility, as reported by Kowyama et al. (1994). Martin (1967) 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. In other words, each genotype is incompatible with genotypes of the same genetic constitution. In addition, the cross-compatibility or incompatibility between genotypes is determined by the dominant genes present. Therefore, all crosses are fertile except those that have even one dominant gene in common. There is general agreement that the incompatibility in the sweetpotato is controlled by the *S* locus with multiple allelic series in a dominant-recessive relationship (Kowyama et al., 1994).

### Incompatibility versus sterility in sweetpotato

Incompatibility and sterility are sometimes used interchangeably. However, there is a distinction between the two forms. In the case of incompatibility, all sexual processes are normal and viable gametes are produced. Gametes from the same or genetically distinct plants may function perfectly (Martin, 1967). Incompatibility is caused by the failure of plants with normal pollen and ovules to set seed due to a physiological hindrance that prevents fertilization (Sleper and Poehlman, 2006). It has been reported that the incompatibility reaction occurs at the stigmatic surface. This may be due to interactions of substances in the pollen and in stigmatic exudate (Martin and Ortiz, 1967). 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 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. Martin (1967) suggested that the cause of the sterility problem lies in the nature of the floral biology of

sweetpotato. The crop is hexaploid with 90 chromosomes. Although chromosomes pair normally, considerable secondary association occurs, indicating that partial homology exists among the genomes of the crop. Thus gametes may not always carry a well-balanced set of chromosomal material. Poor germination of seeds and weakness of seedlings may be caused by such chromosomal imbalances. 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, 1966). 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 mechanically more difficult (Martin and Ortiz, 1966). Martin (1965) hypothesized that self-fertility is the extreme case of pseudo-compatibility. Both self-fertility and pseudo-compatibility constitute a continuous series of low fertility crosses that probably demonstrate the failure of the incompatibility mechanism in some cases. The author further explained that the failures can be due to modification or reduction of incompatibility by genes other than the *S* allele system, or temporary mutations of *S* alleles, or environmental effects. The hypothesis of pseudo-compatibility was also reported by Fujise (1964; cited in Martin, 1965), explaining that pseudo-compatibility resulted from partial dominance of self-fertility alleles of *S* and *Z* genes. Sleper and Poehlman (2006) suggested that incompatibility alleles are not strong enough to prevent self-fertilization entirely and hence most species may set seed in the presence of incompatibility genes. These authors further hypothesized the existence of self-fertility alleles ($S_f$), which would make the alleles for incompatibility ineffective. However, the hypothesis of pseudo-compatibility instead of self-fertility is not well defined, and many authors have reported that some sweetpotato varieties are self-fertile. Therefore, whether the self-fertility in sweetpotato is due to pseudo-compatibility conditioned by different factors, or it is a true self-fertility that depends on varietal differences, needs further investigation.

### Techniques to determine incompatibilities

Williams and Cope (1967) suggested two methods of determining incompatible matings in sweetpotato. These are: 1) the number of seeds set per capsule after self- or cross-fertilization; and 2) *in vivo* tests of pollen germination on stigma and pollen tube penetration into the style at intervals ranging from 3 to 24 hours after pollination. To understand the genetic control of incompatibility, it is necessary to make several crosses among selected cross-fertile individuals, test the compatibilities of parents and offspring, undertake further back-crosses and second generation crosses, and finally, to draw up an explanatory model of gene number and gene action based on seed set (Martin, 1967). Similarly, to understand the physiological control, it is essential to study pollen behavior in fertile and incompatible matings during the process of germination, pollen tube growth, fertilization, and sometimes also the processes of ovule and embryo development. According to Reynoso et al. (1999), aceto-carmine glycerol solution (2%) can be used to stain pollen grains to estimate male fertility microscopically. Their technique involves a sample of a minimum of four flowers from each parent. Then anthers are removed and placed with a drop of the solution on a slide. A cover-slide is placed immediately, avoiding the formation of air bubbles. A single slide can accommodate two samples from the same parent. After four hours, stained and unstained pollen grains are

counted using a standard optical microscope with 40X magnification. The level of male fertility is estimated by dividing the number of stained pollen grains by the total number of pollen grains counted. Similarly, female fertility can be estimated by examining the number of ovules per ovaries. Ten flower buds per clone can be collected on the day of anthesis, or the afternoon before sepals and corolla are removed. The pistil may be detached from the basal yellow glands or the ovary cut transversely. Ovules are then squeezed out of the ovary and counted. The level of female fertility can be estimated from the mean number of ovules per ovary by dividing by four (Reynoso et al., 1999). Incompatibility can be identified by observing the development of the pollen tube using a fluorescence microscope, as suggested by Martin and Ortiz (1966) and Reynoso et al. (1999). In their approach, flowers are emasculated the afternoon before anthesis and covered with a small hood made of glassine paper. Pollination is carried out by rubbing the anthers over the stigma on the day of anthesis. After pollination, the flower is covered again with the small hood, and labeled with the name of the parents and the date of crossing. Anthers from the same male can be placed in a Petri-dish to facilitate their use and avoid contamination. Four hours after pollination, pistils are carefully removed. Aniline-blue or Schreiter-Tiemann solution staining techniques can then be used to determine incompatibility. In the case of compatible matings, pollen grains germinate over the stigma and pollen tube growth is normal. In incompatible matings, pollen grains do not germinate over the stigma (Martin and Ortiz, 1966; Reynoso et al., 1999).

## Methods to overcome incompatibilities

There are different strategies suggested to overcome incompatibilities in sweetpotato and other crops such as:
- Stigma conditioning by rubbing (Hinata et al., 1994).
- Spraying plants with chemicals such as 2,4-D, $GA_3$, sodium chloride, organic solvents, acids, $CO_2$ gas, naphthaleneacetic acid (NAA), or 6-benzylaminopurine (BA) (Martin, 1965; Hinata et al., 1994; Shu-yun et al., 1994).
- Growing plants at relatively high temperatures (Hinata et al., 1994).
- Embryo rescue (Charles et al., 1973). This techniques has successfully been used in *Gossypium* species where 10-15 day old embryos were cultured on different combinations of nutrient media to obtain interspecific hybrids (Mehetre and Aher, 2004)
- Identification of compatible parents through several well-designed and controlled crosses (Hernandez and Miller, 1962; Martin, 1965; Vimala, 1989).
- Use of random polycrosses with diverse genotypes (Saladaga, 1989).
- Making many controlled cross combinations (Martin, 1965).
- Manipulation of the *S* gene; i.e., modifying the *S* gene or replacing it with another *S* gene through genetic engineering (Hinata et al., 1994).
- The use of molecular markers for assigning varieties into self- and cross-incompatible groups and for the efficient crossing (Young-Sup et al., 2004).
- High relative humidity at pollination also enhances pollen germination on the stigma and reduces incompatibility (Hinata et al., 1994).
These strategies can be used alone or in combinations to overcome incompatibility issues and to improve the success of crosses in sweetpotato.

## Conclusion

Sweetpotato is an important crop for food security in Africa, as a highly productive source of carbohydrates for human nutrition. However, its genetic improvement is hampered by complex factors among which incompatibility is the most serious problem. This paper outlines the effects of incompatibility in the breeding of the crop, the various types of incompatibilities, methods to determine and distinguish incompatibility and sterility, and various techniques that can be used to overcome incompatibility, to enhance the genetic improvement of the crop. The information outlined in the review may assist sweetpotato breeders to devise methods in reducing incompatibilities and in the genetic conservation of sweetpotato.

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