Incompatibility in fruit plants — a review

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SELF-INCOMPATIBILITY may be defined as the "inability of a plant producing functional gametes to set seed when self-pollinated" (Brewbaker, 1957). Incompatibility is a mating system in hermaphrodite plants in which gametes are functional but fail to produce zygotes on self and/or cross pollination. Both self and cross incompatibility involve some break in the mechanism between pollination and fertilization. The term "incompatibility" was first used by Stout (1917) but was first discovered by Kolreuter (1764, cited by Darwin, 1876). It is different from sterility which is lack of pollen production or/pollen is unable to function. It is also different from sterility in interspecific hybrids which is due to lack of homology. Most of the early workers (Scott, 1865 to East, 1940) referred to this phenomenon as "self-sterility". This incompatibility phenomenon is widespread in higher plants and is one of the serveral mechanisms which encourage outbreeding.

Incompatibility systems

Incompatibility has been classified in different ways :

1. Flower morphology (Lewis, 1949)
   - (*a*) heteromorphic, and
   - (*b*) homomorphic

2. Genetic control (Mather, 1944)
   - (*a*) Gametophytic, and (pollen control)
   - (*b*) Sporophytic (style control)

1. *Flower Morohology :*

(*a*) *Heteromorphic :* The heteromorophic incompatibility, first described by Darwin in 1877, is associated with differences in the lengths of styles and the levels of the anthers. The two kinds of flowers viz. pin with long style and short anthers and thrum with short style and long anthers are borne on different plants of the same species. Pollinations are compatible only between anthers and stigmas at the same height, i.e. between the pin and thrum and the reciprocal. Apart from heterostyly, the difference between the pin and thrum flowers are also exhibited in incompatibility reaction of style and pollen, size of the pollen grain (small in pin) and size of the stigmatic cells (large in pin). In other words, there is a complex of characters which differentiates the pin and the thrum flowers.

The genetic control of the characters complex in the distylic flowers is by a single S locus with two alleles. The thrum flower is heterozygous (Ss), whereas the pin is homozygous recessive (ss). In thrum x pin matings, the progeny is 1 thrum (Ss) : I pin (ss). In the reciprocal mating of pin x thrum, the pollen behaves as if of S constitution resulting again in equal proportion of pin and thrum flowers in the progeny. The compatibility is thus determined by the sporophyte in which thrum is always dominant to pin. The crosses between the same types of flowers i.e. thrum x thrum or pin x pin are incompatible.

The S locus in distylic systems has been proposed by Lewis in 1954 to comprise three sub units : one unit controlling the stylar characteristics, second the anther height, and third for controlling the size and incompatibility of the pollen. The rare occurrence of homomorphic plants in this group may be explained on the basis of intra-locus crossing over.

A more complex type of heterosyly is found in which the sexual organs grow to three heights, viz. long, intermediate and short. The compatible unions are between the flowers having style and stamen at the same height. This system is controlled by two pairs of alleles : long style (aabb), short style (A—B and A—bb) and mid style (aaBB or aaBb) where A is spistatic to B and b. The anomalous genetic ratios obtained in this system are caused by tetraploidy.

In general, the heteromorphic incompatibility is sporophytic. The common features of the heterostylic species are :

(1) genetic control by small number of alleles,

(2) one allele is dominant to another,

(3) sporophytic incompatibility, and

(4) short style is always dominant to long.

(b) *Homomorphic :* In the homomorphic species, the mating types are of the same kind and can be distinguished only by appropriate breeding tests. The incompatibility systems of *homomorphic* species will be discussed under the second way of classification based on genetic control in pollen or style.

2. *Genetic Control*

The genetic control of incompatbility was independently postulated by Prell (1921), Lehman and Filzer (1926, cited in East, 1929) and East and Mangelsdorf (1925). The basic concent of their hypothesis called the oppositional allele hypothesis is that incompatibility is governed by an allelomorphic series of genes (S1-Sn) such that pollen tubes having a particular S—allele grow slowly (or are inhibited) in styles which carry the same allele and rapidly in those that do not. There are two kinds of genetic control of incompatibility namely gemetophytic and sporophytic.

(*a*) *Gametophytic determination:* The gametophytic control of incompatibility is determined by the genetic constitution of the pollen itself. This system is different from heterostyly in that the alleles have an independent action with dominance in the style. It is the most widespread having been recorded in over sixty Angiosperm families (Growe, 1964) including Solanseae, Onagraeae, Rosaceae, Gramineae, Leguminoseae and Scrophulariaceae.

The main features of this system are:

(1) A large multiple allelic series of one S-locus determine incompatibility (The number of S locus alleles is estimated to be 212 in *Trifollum*, 37 in *Oenothera* and 17 in *Nicotiana*. The high number of S alleles may arise through direct mutation through some balanced changes in the internal structure—an allele giving rise to a new one in several steps or through independent evolution (Pandey, 1957). These multiple alleles assure the perpetuation of a species through outbreeding);

(2) failure of pollen grain to germinate;

(3) growth of pollen tube so slow that it fails to reach the ovule;

(4) growth of pollen tube completely inhibited;

(5) *basic fact*—pollen tube unable to function in style in which the same S allele is present in pollen and style;

(6) control of pollen reaction is gametophytic, and

(7) alleles have individual action in the style without any interaction.

This system has three main types of pollination as follows:

Pollen grain — is haploid and has one S allele

Style — is diploid and has two S alleles.

Matings

Female	*Male*	*Reaction*
$S_1 S_2$	.. $S_1 S_2$	.. Incompatible
$S_1 S_2$	.. $S_1 S_3$	.. $S_1 S_3$ and $S_2 S_3$ (half incompatible)
$S_1 S_2$	.. $S_3 S_4$	.. $S_1 S_3$, $S_2 S_3$, $S_1 S_4$, and $S_2 S_4$ (compatible)

The important point is that the genotype of the female is never recovered in the progeny.

(*b*) *Sporophytic determination.*—In the sporophytic system of incompatibility, the specificity of the pollen is determined by the genotype of the parent (sporophyte). It was first descrbied by Gerstel in *Parthenicum argentatum* and by Hughes and Babcok (1950) in *Crepis foetida.* Since then, a similar system has been reported in many species of the Compositae (Crowe, 1954 ; Habura, 1957 ; Imrie and Knowles, 1971) Cruciferae (Bateman, 1954, 1955 ; Sampson, 1958, 1964 ; Thompson, 1957 ; Adamson, 1965) and Convolvulaceae (Hernandez and Miller, 1962, 1964 ; Martin, 1965).

In the sporophytic system complex relationship may exist among the alleles. The minimm requirement for this system is the presence of one locus with two alleles and dominance interaction (Lundqvist, 1969). The behaviour of S alleles in*Theobroma cacao* has been studied by Cope (1958, 1962) and Knight and Rogers (1955). It was found by Cope that in incompatible pollinations, fusion of the female and male gamete did not take place in 100%, 50% or most commonly, 25% of the ovules—and these degenerated. It appeared that the presence of these degenerating ' non fusion ' ovules led to the shedding of the flowers. Cope suggested that the S—gene acted at two stages : (*a*) the dominane relationship between alleles was imposed before meiosis, and (b) at fertilization, gametes carrying identical alleles which were dominant in the sporophyte (s) failed to fuse. In spite of this element of gametophitic control, Code accepted that *T. cacao* had a sporophytic type of incompatibility. It is evident that in the sporophytic system, the alleles may show independent action, dominance, on more complex action, providing a broad spectrum of genetic action.

The main features of the sporophytic system are as follows :—

(1) Incompatibility is controlled by a series of alleles at a single locus S ;

(2) S-alleles may act independently or show a dominance relationship in determining pollen behaviour. (If the former, the pollen will be inhibited by all styles in which either allele is active ; if the latter, only those in which the dominant allele is active ;

(3) reaction of the pollen is determined by both S-alleles in the sporophyte, all the pollen grains produced having a similar incompatibility reaction ;
(4) S-allele may act independently or show a dominance relationship in the style ;
(5) same alleles may snow different dominance relationships in the style and pollen, leading to reciporcal differences in cross compatibility (Growe, 1954 ; Bateman, 1954) ;
(6) induction of autopolyploidy has no effect on the S-allele action in the sporophytic system. This may be due to the presence of two alleles at the time of S-allele action. In the gametophytic system, there are numerous examples to show that the auto-tetraploidy induces the breakdown of self-pollen creates in a new situation for the operation of monogenic gametophytic control where a competitive interaction between the alleles in the same pollen resulting in the breakdown of the mechanism.

Cytology of incompatibility system :

Scott (1965) was the first to observe slow pollen-tube growth on selfing *Oncidium* (incompatible system). Sears (1937) grouped the incompatible plants into three classes on the basis of the site of inhibition of pollen tubes in the style. These classes are briefly explained as follows :

(i) *Inhibition on the stigma :*

The pollen grains either show poor germination as *Linum grandiflorum* or the tubes fail to penetrate the stigma as in *Notylus.* Many species in the compositae, *cruciferae* and *gramineae* belong to this class.

Removal of a thin layer of stigma or even maceration of the stigmatic surface led to self-fertility in *Brassica oleracea* (Sears, 1937). This showed that the incompatibility barrier resides in the stigma of this species. Heiner and Linskens (1961) showed that in *Cardamine pratensis,* the cuticle of the stigma constitutes the barrier to the penetration by pollen tubes ; compatible pollen tubes enzymatically breakdown the cuticle, while incompatible ones do not produce this enzyme.

(ii) *Inhibition in the style :*

The behaviour of the tubes in the style varies considerably depending on species and environmental conditions. In *Nicotiana* incompatible tubes reach ovary with 7-8 days whereas compatible ones do so in 3-4 days. In Japanese pear, growth is normal to the base of style and then stopped.

(iii) *Inhibition in the ovary or ovules:*

Stout and Ghandler (1933) found that in *Hemerocallis citrina*, inhibition took place at the entrance to, or within the ovary. Cope (1962) reported that in *Theobroma cacao* a proportion of ovules do not fuse with the gametes which results in shedding of flowers. Brewbaker (1957) suggested that intimate contact between pollen tubes and stylar tissue is necessary for inhibition to occur. This view inhibited by the hollow styles of *Anona* and *Gasteria* (Brewbaker and Gorrez, 1967) and Ribes (Arasu, 1967).

The cytological studies on pollen by Brewbaker (1959) and Pandey (1960) have further shown that there is a correlation between pollen cytology and site of inhibition. The species in which the site of inhibition was on the stigma had trinucleate pollen, whereas those in which the site of inhibition was in the style or ovary had binucleate pollen.

Citrus

Nagai and Tanikawa (1928) determined several citrus varieites to be self-incompatible. Self incompatibility as a possible cause of seedlessness in *Citrus grandis* (Linn.) Osbeck had long been discussed (Boyle 1914, Reinking and Groff, 1921, Torres, 1932) but only during the last fifteen years have controlled pollination tests been made (Nuriyal 1952, Aala 1953, Soost 1964). Lararelle and Miedzyzyrzecki (1936) determined that unfruitfulness in 'Clementine' (*C. reticulata* Balnco) was caused by self-incompatibility. Self-incompatibility was demonstrated in 'Minneola' tangelo (*C. paradisi* Macf. x *C. reticulata*) by Mustard *et al.*, 1956 and in 'Orlando' tangelo (*C. paradisi* X *C. reticulata*) by Krezdorn and Robinson, 1958, Soost (1965) reported 'Sukega' orangelo (*C. paradisi* X *C. sinsensis* (Linn.)) Osbeck to be self-incompatible.

The presence of self-incompatibility in several species or interspecific hybirds suggests that incompatibility is determined by a basic gene system of incompatibility alleles as in many other plant genera. In citrus the incompatibility is controlled by a series of S alleles determining gametophytic nature of incompatibility.

Carlos, J. T. & Krezdorn (1968), reported that when Orlando tangelos were self-pollinated at anthesis, the pollen tube growth was slower than when cross-pollinated with Parson Brown Sweet Orange. This indicated that slow pollen tube growth in the style was a major cause of self incompatibility during these investigations. The equal rate of growth of pollen tubes of both selfs and crosses from pollinations made at preanthesis stages, however, suggest the inhibitors present incompatible pistils anthesis at not present in the prenathesis stages.

Self-incompatibility was reported in 'Clementine' (Citrus reticulata Blanco) by Soost (1956) in 'Orlando (*C. paradisi*) Macf. X. *C. reticulate*) by Krezdorn and Robinson (1958) and in 'Minneola' (*C. paradisi* X *C. reticulate*) by Mustard *et al.* (1956).

The U. S. Department of Agriculture developed and named the varieties 'Robinson' 'Lee', Osceoal' and 'Nova' which are hybrids of Clementine × Orlando (Reece *et al.*, 1959, 1964) and 'Page', a hybrid of Minneola X Clementine hybrids might require cross-pollination to obtain good crops of fruit. Reece and Register (1961) reported that Robinson requires cross-pollination.

The results of the studies of controlled pollination of Robinson, Lee, Nova and Page made by C.J. Hearn *et al.* (1969) show that each is self-incompatible ; only Page shows a significant set of parthenocarpic fruit.

Lee and Orlando appeared to be the most effective pollen sources for Robinson, but Temple was nearly as good. The most effective pollens for Lee were Orlando and Page.

Orlando pollen gave the best results on Nova, followed closely by Temple, Lee and Page pollens.

In 1966, Page pollinated by Lee produced the largest fruit and Page by Orlando and Temple were next in size. In 1967 Page open pollinated pollinated by Lee or Orlando produced fruit of the same size. Fruits set from Temple pollen were smaller than those from Orlando pollen. Regardless of pollen source, there was a positive linear relationship between fruit size and number of seeds per fruit. On the basis of large fruit size with fewer seeds, after hand pollination, Lee would be considered the best pollinizer for Page.

Among Page fruits containing equivalent numbers of seeds, fruits set from Lee pollen were larger than those set from other pollen varieties. This is apparently the result of metaxenia, and is one of the first cases of this kind reported. Nova and Robinson were poor pollinizers for Page—perhaps because of cross-incompatibility.

Torres suggested self incompatibility as the cause of the failure of a pummelo variety to set fruit by controlled self-pollination. Nauriyal (1962) reported better fruit set with cross-pollination than with self or open pollination in pummelos and indicated self incompatibility as the reason. The result of the studies made by Soost (1964) indicate that 10 of the pummelo accessions tested are likely to be self incompatible. The accumulating evidence indicates that seedlessness in *C. grandis* may generally be expected only when cross pollination is prevented.

In cross pollination trials of Robinson (1960) the pollen of simple orange induced the highest percentage of fruit set in tangelo. Hensz (1964) reported that both Orlando and Duncan pollen germinated on Orlando stigmas and both produced pollen tubes which grew to the base of the styles and penetrated the upper ovary. Here, however, the Orlando pollen tube growth was inhibited, whereas Duncan pollen tubes penetrated the embryo sets and affected fertilization. A growth substance named Promoter II having an Rf value similar to that of IIA, was isolated from extracts of styles and ovaries. The production of promoter II in the Orlando pistil was stimulated by the presence of pollen tubes. It is suggested that parthenocarpic fruit set in Orlando is controlled by endogenous concentrations of promoter II and that greater fruit set following cross pollination is due to the increased production of promoter II associated with endosperm development. None of the growth substances extracted was considered responsible for self-incompatibility.

Diware (1970) while studying with seedless lemon concluded that the variety is seedless because it is self incompatible. The fruit of this variety sets parthenocarpically.

Mango

Singh (1962) conducted studies on self-incompatibility in Dashehari variety of mango. He reported that self flowers developed fruit only to the pea stage when the fruitlets turned yellow and dropped. They contained small, shrievelled and empty ovules. Open pollinated and cross pollinated flowers produced fruit which ripened normally.

Sharma (1969) reported that all four varieties of mango under study viz. 'Dashehari, Langra, Chausa & Bombay Green' are self unfruitful. Initial fruit set following self pollination is negligible (0.0 to 1.68%) as compared with that after cross pollination (6.40 to 23.4%). From the 15th day after pollination, the selfed fruitlets were invariably the smaller. The majority dropped within about 4 weeks of pollination and none attained even half grown size. An analysis of the causes of this showed that the processes culminating in ovule fertilization were the same as after compatible cross pollination. The differences between self and cross pollination became apparent from the 15th day after pollination when degeneration of the endosperm and the surrounding nucellus was widespread after slefing. Saha & Chonkar (1972) reported that Langra with Gulabkhas and Zardalu & Fazali with Langda gave no initial fruit setting. Landga seems to be cross incompatible with Zardalu & Bulabkhas, when Langda serves the female parent and Fazali has also the character of cross incompatibility with Langda when the same is used as female parent.

Singh *etal.* (1972) undertook studies to find out causes of self incompatibility in Dashehari mango. In their studies the amount of inhibitor was found to be less in cross pollinated fruitlets as compared to self pollinated ones. One of the most important salient features of the finding is that the level of IAA like substances having Rf values from 3 to 4 was always higher in cross pollinated fruitlets as compared to self pollinated ones. With advance age of fruitlets as a result of cross pollination, their amount continued to increase. It showed that endogenous growth regulating substances do play in important role in governing the physiology of developing fruits in mango.

Grape

Studies carried out by Deshmukh (1924) to find out the causes of poor yield in the Pandhari Sahebi grape showed that the variety failed to set fruit properly unless adequate pollination was available from some other variety. Cheema (1928) observed that the variety Pandhari Sahebi is partially incompatible and hence the yields are poor. However, with adequate pollination from the other varieties the variety fruited well

Derman (1954) published papers dealing with hybridization of *Vitis vinifera* into *V. rotindifolia* and the fertility of diploid and allotetraploid hybrids. Using the diploid F_1 hybrids, which exhibited almost complete ovule and pollensterility, he produced allotetraploids by colchicine treatment and described them as " fully fertile hybrids." In reciprocal crosses of auto tetraploid clones of *V. vinifera* and *V. rotundifolia,* he failed to obtain set even when *V. vinifera* was used as a female parent (1964). He concluded that the cross incompatibility reaction between the 2 species is strengthened at the tetraploid level. The cause of the difficulties in obtaining the hybrids at the diploid level and the subsequent sterility he attributed to the different chromosome numbers of the two species.

In regard to crossing behaviour of the tetraploids whenever tetrapoid *V. rotundifolia* is used as female, pollination with *V. vinifera* fails to produce berry set. The reciporcal cross is successful as reported in many experiments by Jelenkovie & Vola (1969). Their results are not consistent with Dermen (1964) who reported complete failure of setting in all crosses at the tetrapliod level. The allotetraploids revaled almost identical crossing pattern as the diploid hybrids reported in earlier papers.

Unilateral failure in crosses is common in species that posses gametophytic or sporphytic incompatibility systems (Martin, 1964). However, this cannot be reconciled to either of these two systems.

. The two species i.e. *V. vinifera* and *V. rotundifolia* are distantly related and taxonomists have classified them into different subgenera : *V. vinifera* with other grape species ($2n = 38$) with the subgenus euritis and *V. rotundifolia* with *V. munsonaiana* ($2n = 40$) in the subgenus muscadinia. The breeding work had indicated that the two sps. hybridize successfully only when *V. vinifera varieties* are used as female parents and *V. rotundifolia* varieties as male parents.

In regard to crossability of P1 hybrid, the P1 hybrids are reciprocally crossable with *V. vinifera* vars. but can only serve as female parents with *V. rotundifolia*. Evidence from breeding tests indicates that incompatibility between *V. rotundifolia.* × *V. vinifera* is not due to cytoplasmic inheritance, but is caused by nuclear factors.

Narasimhan and Mukharjee (1970) made observations on the set of fruit and seed and the occurrence of empty seeds in diploids tetraploids and diploid tetraploid crosses in the vars. Bharat Early, Black Prince, Pearl of Csaba, Maleling Angevine and Nadeline Royal Late abortion of ovules resulting in empty seeds in the tetraploid was related to the shortening of period II of berry growth, to the early and greater accumulation of total soluble solids, to the earlier onset of period III and to the higher rate of ovary growth. The consequent lack of adjustment between the rates of growth of the endosperm and the ovary probably led to somatoplastic sterility.

A study was made of the pollen and pollination of cardinal vines by Lepadatu (1966). The pollen was found to have higher degree of viability and germination capacity. The variety, however, appeared to have vary selective properties in the generative stage, and, although ovules were formed, some of them had imperfections and structural variations resulted in the uneven development of the 60 per cent of the berries.

Observations were made on the effect of supplementary pollination of Bharat Early and Pusa seedless vines with pollen from several different vars. by Uppal and Mukherjee (1968). They found that the bunch wt. and number of grape per bunch of Bharat Early were markedly increased by supplementary pollination with Pearl of Csaba and Pasa Seedless pollen. It may be assumed that the vars. under study may be partialy incompatible and hence with the adequate pollen from other varieties must have induced a satisfactory fruit set.

Guava

Seth (1962) reported that the incompatibility in some guava varieties was due to the inhibition of the growth of pollen tube after it had penetrated into the style.

21 guava clones of different origins were crossed and self-pollinated during several flowering cycles by 1to & Nakasone H (1968). They

did not find any apparent incompability system in the diploid varieties tested, except when Indonesian seedless a triploid was used as male parent. Some crosses yielded few mature fruits, but from those fruits harvested hundred of seeds were viable.

Hirano and Nakasone (1969) undertook the studies of pollen germination and compatibility of some psidium species. They found pollen of different species with high chromosome numbers had poor germination percentages. Pollination studies indicated partial self incompatibility in all the species studied. Reciprocal interspecific crosses showed pronounced differences in compatibility.

Nair *et al.* (1963) reported morphological differences in pollen of guava. However, the differences are restricted to the size of grains, there being big and small ones, the frequency of which varies in the different varieties.

Ber

As reported by Teaotia & Chauhan (1963, Banarasi Pewandi, Ber Thronless and Banarasi Karka were found to be self incompatible for practical purposes. In addition the varieties Ber thronless and Banarasi Karaka are reciprocally cross incompatible.

Loquat

On the basis of the studies of self fruitfulness made by Singh & Rajpur (1962), the loquat variates are classified into two groups:

(*a*) Self incompatible Golden Yellow, Improved Golden Yellow, Pale Yellow and Large Agra ;

(*b*) Partially self-incompatible : Large Bound, Fire Ball, Thames Pride, California Advance and Tanaka.

Self incompatibility in loquat was found to be that of gametophytic nature. It was observed in the varieties Improved Golden Yellow, Pale Yellow and Golden Yellow that pollen tubes penetrated the styler canal upto ¼th to ⅓rd of its length and did not go further even after 72 hours of pollination. This suggested that self-incompatibility in loquat is of a genetophytic nature, because in sporaphytic type of self-incompatibility, only germination of pollen grains is inhibited. In this study California Advance variety was found to be best pollinizer for Improved Golden yellow and Pale Yellow varieties.

Apple

Overholser *et al* (1931) reported that there are appreciable plantings of several red coloured bud mutations of standard named commercial varieties. The growers are interested in knowing the pollination status of these red strains with respect to whether they are self-fertile, inter fertile with other commercial varieties. The work conducted upto 1931, demonstrates that Delicious is self-unfruitful. Bud sport varieties and their parents here studied that seem to be satisfactory pollinizers for the Delicious are Blackjon, King John, Red Rome, Jonathan and Rome. Those varieties that appear to be cross-unfruitful with Delicious are Red Stayman, Richard, Shotwell Delicious, Starking and Winesap.

Whitehouse and Anchter (1926) found that the pollen of Golden Delicious gave a set of only 5.7 per cent upon the Delicious when the normal set was 16.7 per cent.

Since the Delicious is self-unfruitful, it is not inconsistent to find that the Richard, a mutation of the Delicious, is inter-unfruitful with the latter as shown by four year data. Morries and Luce (1928) also reported this to be the case.

Overholster *et al.* (1931) reported that Winesap is self-unfruitful. Those varieties and strains which are good or satisfactory pollinizers for the Winesap are : Delicious, Richard, Starking, Golden Delicious, King John and Red Rome. Red Stayman and Stayman appear cross-unfruitful upon Winesap. The Richard was also self-unfruitful, failed to set satisfactorily with pollen from Delicious, Starking and Shotwell Delicious. The data show Starking Delicious to be self-unfruitful and to be inter-unfruitful with Delicious and Shotwell Delicious. Varieties indicated as satisfactory pollinizers for the Starking are Blackjon, Golden Delicious, and White Winter Pearmain.

Mac Daviels (1928) reported that Northern Spy is self-unfruitful under New York conditions, a fact to be suspected from results obtained elsewhere.

Legasse (1928) found that the Chaplain (Nyack Pippin) and Lily of Kent varieties of apples are self-unfruitful in Delaware. Actual brushing of the pollen upon the stigmatic surface did not increase the set of fruit in the case of the Lily of Kent. Of several varieties tested Rome Beauty is recommended for interplanting with the Chaplain (Nyack Pippin) and Delicious or Griwes Golden with the Lily of Kent.

Vanderacek (1964) studied the pollination relationship. The incompatibility was confirmed in the combination Blenheim x Goldparmane, Boskoop x Crocels, Canada Reinetta x Corncels and Canada Reintette x Goldparmane.

Studies on the floral biology of variety Conventiana apple and of Rosa made by Battalne (1964), have shown that they are incompatible and that each is self-unfruitful.

The trials of Strydom (1962) indicated that in case of Granny Smith, Dunns Seedling x Golden Delicious pollen tubes did not grow more than one third of the way down the style.

Schaldlak (1963) reported that various degrees of self-unfruitfulness can occur, depending on variety and climatic conditions. Fertility in some varital combinations showed an influence of the maternal parent. The cross Biesterfelder x Cox is reported as unfruitful. Only general conclusions could be drawn from studies on pollen tube growth in the style.

Schmallak (1966) reported that the longituudinal growth of apple pollen tubes was influenced by the compatibility of the partners. Combination of Zabergau and Goldparmane and Biesterfelder x Cos and Biesterfelder x Cos Pomona are unfruitful.

Observations of Vondracek (1962) on 33 varieties indicated that apples in general have only a slight tendency to set fruit without cross pollination. The best fruit set and satisfactory fruit size without pollination with pollen of suitable variety was obtained in Ontario, Wagener, Ribston and Laxton's Superb. Boxkoop and Metano nearly always fruited but the fruit size was not satisfactory. Triploid varieties were more prone to set fruit without cross pollination than the deploid varieties. Incompatibility may be broken through polyploidy i.e. triploidy, Polypoidy has thus induced self-compatibility.

Williams (1966) reported that the methods of lengthening the effective pollination period of shy cropping varieties are needed to be investigated. These include the acceleration of pollen tube growth rate and the extension of ovule longivity.

Rome Beauty and Galia are partially cross-fruitful. The combination of Cortland pollinated by Early McIntosh is not sufficiently fruitful. Both are seedlings of McIntosh. Several examples of such cross-incompatibility are : Delicious and all its strains such as Starking, Richard and Shotwell Delicious. Duchess, Dannil's Red Duchess and Van Buren Red Duchess. Cox's Orange Pippin and Laxton's Superb. Jonathan, Jonard and Blackjon. McIntosh lackmack as well as other strains of McIntosh. Northern Spy and Red sp. Ribston Pippin and Cox Pomona.

Pear

Waite (1895) studied the pollination requirements of pears and recorded the first case of incompatibility in fruit trees. He found that plants of the same (clonal) variety were cross-incompatible. De Vries (1906, cited in East, 1929) demonstrated that the individuals in the progeny obtained by crossing two self-incompatible plants consisted of groups—crosses within each group being incompatible and crosses between groups fertile. Crane (1925) showed that the varieties of *Prunus avium* could be divided into a few intra-sterile, inter-feltile groups.

Many workers have reported the existence of self and cross-incompatibility in pear. Even the same variety may behave differently in different localities as Walte (1894) reported Kieffer as self-fruitful in California while Fletcher (1909-10) reported it practically self-unfruitful in Virginia.

Mukherjee and Rana (1966) reported that all the varieties under study started flowering simultaneously within a week's time and showed complete overlapping of full bloom period.

All the pear varieties did not set fruit when selfed. Hand pollination gave 24 per cent fruit set in Leconte. Artificial crosspollination gave higher percentage of fruit than the natural pollination in all the pear varieties. Under Delhi conditions Le Conte was found to be self-fruitful as well as cross compatible with Kieffer and Smith, but Kieffer and Smith were found to be self unfruitful as well as cross-incompatible with each other.

The fruit set under natural conditions was the highest in Le Conte (18. 6 per cent) and the lowest in Smith (5.9 per cent).

Luce and Morris (1928) conducted pollination experiments with Beuree d'Anjou. Evidence as to the variable partial self-fertility of the Beurre d' Anjou was obtained by Tufts and Philp (1923) who reported that when selfed under interior valley conditions in California the per cent set was as follows: (a) 1919, 6.1 (b) 1920, 0.6 (c) 1922, 20.4. In the Sierra Nevada food hills, however, the Beuree d' Anjou was complete self-unfruitful during two seasons. The self unfruitfulness of the Beuree d' Anjou is appreciably influenced by tree vigour. Each of the other varieties tested proved to be satisfactory pollinators for the Beuree d' Anjou. The Bartlett, Flemish, Beauty, Beuree Bose, Winter Nellis and Easter Beuree each gave a set of over 45 per cent when used as pollinizers.

All varieties of European pear and those of hybrid origin such as Keiffer have been found to be self-unfruitful. Pear varieties also fall into two groups and those varieties which are triploid (51 chromosomes) possess non viable pollen and are consequently ineffective in cross-pollination. The varieties Bartlett' Seckel were found to be partially to completely cross and self incompatible in the studies made by Olez (1966). The degree of cross incompatibility in reciprocal crosses and with environmental conditions of which temperature is factor. The incompatibilie reaction occurred after the pollen tubes were half-way down the style and increased in intensity through the basal portion of the style.

Peach

With a few exceptions all important peach varieties have been found to be self-fruitful. The variety J. H. Hale, however has been shown to be self-unfruitful and practically no fruit are borne unless pollen from another variety is available. Likewise June Drop appears to be self-unfruitful for all practical purposes, and the Late Crawford is usually benefitted by cross pollination. Fortunately the pollen of most varieties whose time of blooming synchronise with these varieties cause good fruitset. Varieties such as Elberta and Brackett will no doubt make better pollinizers than others under field conditions because their blooming periods overlap quite well with J. H. Hale. The June Elberta and Late Crawford are also successfully crossed by practically all commercial varieties.

Plum

Self-unfruitfulness is so common in the plum that it generally is accepted as the prevailing condition, though some noteworthy exceptions occur, as in several varieties in *Prunus domestics.* In Minnesota and other states of the upper Mississippi Valley the plums grown are largely hybrids of the oriental species *P. salicina* and *P. simonii* combined in simple and complex hybrids with native species. In addition, there is a considerable number of cultivated varieties representing the native species in the pure form. Both native and hybrid varieities are uniformly self unfruitful even when grown under as nearly optimum conditions as may be provided in a green house.

In trials over 5 seasons carried out by Thiele (1964) no fruit set was obtained from self or inter pollination of the cultivators Golden King, Kelsey & Meriposa. However, all 3 cultivars gave a high per cent of fruit set which combined as male or female parents with a compatible cultivar such as Gaviota & Methley. Histological studies showed that in both compatible and incompatible combinations the pollen grains germinated within 24 hours but in the latter the pollen tubes were confined to the upper half of the styles even 120 hour after the pollination. In incompatible combinations the pollen tube tips appeared to be normal.

The Skopelon clone of Prune d'Agen is completely self incompatible as reported by Raptopoulous (1967), although the original trees imported from France were self compatible. Another clone of Prune de' Agen sets only 15 per cent. of fruit with self pollination, thus needing a pollinator variety to ensure profitable yields. The variety Asvestochorion is completely self incompatible. The variety Imperial prune is also self incompatible, but is a good pollinate for the above types and produces fruit of a good quality as that of Skopelon, Coe's

Golden Drop and Asvestochorion are cross incompatible. High yields resulted from pollination of Skopelon, Prune d'Agen and Asvestochoriaon by Victoria, Harris, Monarch, Golden Gage and Czar.

The trials conducted by Yoshide (1963) showed that hybrids obtained from the same parents were generally incompatible with each other and were often incompatible with one or both parents. Hybrids from different parents were mainly compatible with each other. The hybrid seedlings offered were often tricotyledonous especially when Orei was the female parent.

Fruit set is generally poor in most of the Japanese plums for want of pollination though Beauty, Climex Mathyley and Santa Rosa are partly self unfruitful. These varieties will also be benefitted in fruit set if provision of cross-pollination is made. The degree of self-fruitness of these varieties apparently varies grom place to place depending upon local environmental conditions.

European plums and prunes:

Usually self-fruitful	—	French, Stanely, Sugar.
Partly self-fruitful		Italian prune, Green Gage.
Self-unfruitful	—	Jefferson, President, Tragedy, Denniston's Superb, Warwickshire Dropper.

The partly self-unfruitful varieties should generally not be planted without provision for cross-pollination.

Almond

Since the edible part of the almond is the seed, fertilization of the egg is essential. All commercial varieties of almond are self-unfruitful and required cross pollination by insects to produce a crop. That there is a distinct pollination problem in almond was recognized as early as 1885, when Hatch (1886) pointed out that California Languedoc trees planted near seedlings always produced heavier crops than when planted in solid block. To obtain a maximum crop in the almond, therefore, essentially 100 per cent of the flowers shoud be cross-pollinated.

Criggs (1953) and Gagnaro (1954) reported that all the varieties under cultivation in California and Algeria required cross-pollination for proper fruit set. Tuft (1919) observed self-incompatibility in all the 17 varieties studied at Davis. However, he held that self-incompatibility was not a constant factor in a variety, for it may be barren in one locality and self-fruitful in another and the the degree of adaptation of a variety to soil and climate had much to do with its ability to fruit abundently with its own pollen.

Nauriyal & Rana (1965) reported that all the varieties except Drake gave the evidence of self-incompatibility. Almond varieties, being self-incompatible should not be planted in solid block without provision for pollinizer variety. The variety Non-pareil proved to be the best pollinizer for all the other three varieties tested.

Main Variety		*Polinizer Varieties*
Thin Shelled	..	Out of the three varieties tested only Non-pareil proved to be the best pollinizer. Ne-Plus-Ultra and Drake gave rather poor set.
Drake ..	..	Non-Pareil, Ne-Plus-Ultra & Thin Shelled proved very good pollinizers.
Non-Pareil	..	Thin Shelled & Drake gave good results. Ne-Ulus-Ultra yielded poor fruit set.
Ne-Plus-Ultra	..	None of three varieties provided to be very satisfactory pollinizers, the fruit set less than 11 per cent.

Cherry

All sweet cherries of any commercial importance have satisfactory pollen germinability. But almost all the cherry varieties tested in the United States, England, Germany, Sweden and elsewhere have been found to be self-unfruitful. Practically no fruits whatsoever were obtained from self-pollination.

Not all varietal combinations are fruitful, since there is considerable cross-incompatbility between varieties. More than a dozen groups are now known which contain varieties recprocally incompatible, and the number is being augmented with further research. The varieties within any one group are all closely related, being either seedlings or bud mutations of some parent variety. Such groups are as follows :—

1. Napoleon, Bing, Lambert, Emperor Francia, and Ohio Beauty.
2. Early Purple and Rockport.
3. Advance and Rockport.
4. Windsor and Abundance.
5. Elton, Wood and Stark's Gold.

6. Black Tartarian, Knight's Early Black, Early Rivers, Bedford Prolific, and Black Eagle.
7. Centennial and Napoleon.

Group No. 1 contains several varieites commercially prominent in this country. As has been previously indicated incompatibility within this and the other groups is belived to be governed by a series of multiple allelomorphic genes. The varieties within a group contain the same genes in the style as in the pollen, a fact which results in failure of the pollen tubes to reach the ovary and effect fertilization.

Various strains have been found in Napoleon, Bing, Lambert, Black Republican, and Black Tartarian which do not respond equally to pollination tests. In all likelihood this is due to the fact that seedlings of these varieties which now exist are probably so similar in appearance to the original varieites as to make it difficult to distinguish them from their parents. It has thus become necessory in using Black Tartarian, for instance, as a pollinizer to select trees of strains known to be capable of fertilizing the chosen variety.

Way (1968) identified the specific sterility genes and incomptibility groups of 20 sweet cherry cultivars and seedlings that have not previously been reported. Identification was made of a new incompatibility group, group XIII, S_2 S_4 Compatibility studies showed that venus and vic cannot have the parents that they are reported to have. Incompatibility was used as evidence to show that Buttners Rote Knorpelkirsche and Emperos Francis could be the same clone.

Results of pollination trials in Netherland were compiled to detect groups of inter incompatible cherry varieties by De Vries (1968). In sweet cherry there appeared to be at least 6 groups of inter incompatible varieties, in sour cherry only one such group was found. Moreover, two groups of intercompatible sour and hybrid cherry (*P. arium x P. cerasus*).

Bugbricie (1968) found that the Pandy variety Kereska 1 & 2 and Chese Morello were self unfruitful, the Pandy types were compatible with Chese Morello, Majska, Umbra, Dychouse, Domaca, Rich Morency and Montmorency and the Pandy types were inter compatible.

Rasberry

Zych (1964) reported that red x black & purple x black combinations were completed incompatible. Red x purple, x purple x purple and purple selfed produced fruit usually of normal appearance, but with some irregularity indicating some incompatibility. Pollen tubes in the incompatible crosses did not progress beyond the upper third of the style and exhibited a marked thickening of the wall at the tip.

Zych (1965) made controlled pollination in a green house involving 10 varieties of black rasberry (*Rubus occidentalis*). Three varieties of the red rasberry (*R. idacus* L) and four varieties of the purple rasberry (*R. neglectus*) red x black and purple x black combinations were completely incompatible. Red x purple, purple x purple and purple selfed produced fruit usually of normal appearance, but with some irregularity, indicating some incompatibility. All other combinations were fully compatible. Pollen tubes in the incompatible crosses did not progress beyond the upper third of the style and exhibited a marked thickening of the wall at the tip. Normal pollen tube growth and fertilization occurred in the compatible combinations.

Pineapple

Majumdar *et al.* (1963) reported that the variety Smooth Cayenne was highly self incompatible. Callose fluorescence technique was applied in studies of pollen growth in pineapple styless. The assessment of self and cross incompatibilities by this laboratory technique correlated well with field pollination data.

Brewbaker (1957) pointed out that most species in which incompatible tubes reach the ovary have hollow style ; he suggested that intimate contact between pollen tubes and stylar tissue is necessary for inhibition to occur. The recent findings that incompatible tubes are not inhibited by the hollow styles of *Ananas* (Pineapple) (Brewbaker & Gorrez, 1967), lend support to this view.

Quince

Schanderl (1966) while studying floral biology of different quince varieties reported four out of seven varieties to be self-incompatible and two self-fertile.

Incompatibility and Plant Breeding

Duvick (1966) and Lundqvist (1969) have reported that the occurrence and use of incompatibility, whether genotophytic or sporophytic may be of advantage or disadvantage in the breeding of plants. This mechanism provides a way to produce hybrids between two lines without emasculation. At the same time, it also creates problems in producing inbred lines required for producing the hybrid. The relative advantages or disadvantages of incompatibility are determined by economic value of the part of the crop (whether seed or vegetative portion) and the method of reproduction of the crop (whether sexual or asexual).

Self-incompatibility as an aid

Self-incompatibility is useful :

(i) In the case of seedless varieties where the fruits must not contain seed as in the pineapple.

(ii) In the production of triploids by planting alternate rows of self-incompatible diploids and tetraploids—this is possible where self-incompatibility does not breakdown at the tetraploid level.

(iii) In the production of hybrid varieties where S-homozygotes can occur as in the *Brassica* crops. The inbred lines can be produced in a number of ways. Odland and Noll (1950) proposed developing inbred lines of cabbage through (1) bud pollination, (2) selection of pseudocompatible lines, and (3) asexual reproduction of self-incompatible clones. The inbred lines could be used to produce single-cross and subsequently double-cross hybrid seed. The inbreds lines by using these methods have been produced in cabbage, marrow-stem kale, and Brussels sprouts and are being used to produce commercial F1 hybrid seed (North, 1969) ; Odland, 1965 ; Johnson, 1964). The single cross hybrid is used for commercial production, where the crop is not the seed as in Chinese cabbage. The use of double-cross has to be made, where the crop is for seed.

Self-incompetibility aids but is not essential

When the crop is not raised for seeds, self-incompatibility can be of advantage. In ornamental and leafy and root crops, self-incompatibility, by preventing seed production, will prolong the blooming period of the ornamentals and the vegetative phase in vegetables.

Self-incompatibility as a bottleneck

In grain crops, self-incompatibility is a hindrance because of:

(i) variation in seed set,

(ii) problems of preserving genetic purity of improved varieties, and

(iii) difficulties of producing inbreds and maintaining them.

In the vegetatively propagated plants such as apple self-incompatibility is a hindrance in planting single variations. Two or more cross-compatible varieties have to be grown to induce fruitfulness. It is, therefore desirable to introduce self-fertility alleles into such crops in order to regularize the pollination process and to permit the planting of orchards to single varieties.

Incompatibility is thus of great importance in the breeding of crops, particularly in species in which vegetative plant parts are consumed.

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