3.4.2 Inheritance of Male Sterility

Three categories of inheritance of male sterility are suggested by the genetic data in the literature: Mendelian (genic), maternal (cytoplasmic), and a combination of the two (gene-cytoplasmic). Table 3.27 details inheritance of the three categories in its simplest form, as follows:

With *genic male sterility* only one plasmatype (S) exists, interacting with a recessive plasmon-sensitive (ms) and a dominant fertility-restoring (Ms) allele.

With *cytoplasmic male sterility*, normal (N) and male-sterility-inducing (S) plasmatypes exist, but only recessive plasmon-sensitive alleles are present in the population.

With *gene-cytoplasmic male sterility*, normal (N) and male-sterility-inducing (S) plasmatypes exist, the latter interacting with a recessive plasmon-sensitive (ms) and a dominant fertility-restoring (Ms) allele.

Table 3.27. Mode of inheritance of genic, cytoplasmic, and gene-cytoplasmic male sterility (simplest model featuring two plasmatypes and one recessive plasmon sensitive allele—see text for details)

Plasmatype	Genic male sterility (GMS)		Cytoplasmic male sterility (CMS)		Gene-cytoplasmic male sterility (GCMS)	
	Fertile genotypes	Male sterile genotype	Fertile genotype	Male sterile genotype	Fertile genotypes	Male sterile genotype
Normal (N)	—	—	ms ms	—	Ms Ms Ms ms ms ms	—
"Sterile" (S)	Ms Ms Ms ms	ms ms	—	ms ms	Ms Ms Ms ms	ms ms

3.4.4 Utilization of Male Sterility in Plant Breeding

Superiority of F_1 hybrids over the better of their two parents is a common phenomenon in both cross- and self-pollinated crops. Such superiority may be expressed in the heterotic phenotype by increased growth, height, leaf area, dry mytter accumulation, early flowering and higher total yields (see SINHA and KHANNA, 1975), as well as in uniformity and agricultural homeostasis of the cultivar population. In addition to the superiority of the hybrids per se, there are advantages in breeding F_1 hybrids over open-pollinated cultivars in speeding up programs (by parallel assembling desirable dominant traits in either of the two parents of the hybrid) and reducing problems of inbreeding depression and undesirable linkages of recessive genes in parents.

Economic benefits for the seed producers (based on proprietory monopoly, novelty value, etc.) no doubt contributed to the promotion of F_1 hybrid cultivars. Commercial F_1 hybrid cultivars become increasingly important for food, fiber and ornamental crops (see WITTWER, 1974; GABELMAN, 1974; HORN, 1974)

In cross-fertilized species the naturally imposed breeding system assures cross-fertilization, whereas in self-fertilized species selfing is favored by floral morphology. Hence, in cross-pollinated species problems arise particularly in the *inbreeding phase* providing suitable parents for the hybrid, whereas in self-pollinated species, they arise in the *crossing phase* of hybrid seed production. The particular problems in the inbreeding phase will not be dealt with here: these problems are related to natural mechanisms of incompatibility (making inbreeding difficult) and to inbreeding depression. To produce hybrid seed economically, the restrictions of controlled cross-fertilization caused by flower morphology, especially of perfect (hermaphrodite) flowers, must be overcome. The female parent should be prevented from self- or intraline fertilization. Moreover, pollen of the male line must effectively pollinate the female line, which requires an efficient natural pollen dispersal mechanism in the male, or artificial pollination. Elimination of self- or intraline fertilization of the female line requires andro-self sterility.

Such sterility can be produced by hand emasculation (castration), chemical emasculation, or manipulation of genetic male sterility or self-incompatibility.

Large-scale production of hybrid corn is done by detasselling the female parent, but large-scale emasculation of species with perfect flowers such as tomato, sorghum, etc., is usually economically unfeasible. Factors influencing the economics of hybrid production by hand emasculations are ease of emasculation, number of seeds produced per flower (per pollination), number of seeds sown per unit area and the upper limit of seed price in relation to crop production costs.

Chemical emasculation has been shown to be unreliable, so far. Therefore, genetic male sterility is of special interest for hybridizing crop plants having perfect flowers with few seeds per flower and where seed prices cannot cover the cost of extra expenses involved in hand emasculation. Thus, it happened that onion was the first crop in which genetic male sterility was clearly defined (JONES and EMSWELLER, 1937) and developed for production of hybrid cultivars (JONES and CLARKE, 1943; JONES and DAVIS, 1944). The crop to follow was field corn (JONES and EVERETT, 1949), and at present genic-cytoplasmic male sterility (GCMS) serves in the production of hybrid seed of field corn, sweet corn, sorghum, pearl millet, sugar beet, alfalfa, onion, carrot, and radish, and may become useful in the production of hybrid wheat, rice, orchard grass sunflower, flax, cotton, soybean, field bean, *Crotolaria*, tobacco, garden beet, pepper, petunia, tuberous rooted begonia, columbine and other plants (GABELMAN, 1956, 1974; DUVICK, 1959, 1966; REIMANN-PHILIPP, 1964, 1974; HORN, 1974). Genic male sterility is used today for hybrid seed production of barley, tomato, pepper, marigold, zinnia, snapdragon, begonia and *Ageratum*, and is potentially useful in the production of hybrid cotton, lettuce, bicolor sweet corn and other crops.

from: Frankel + Galun. 1977. Pollination Mechanisms, Reproduction and Plant Breeding. Springer-Verlag.

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fm: Frankel + Galun 1977. Springer-Verlag

3.4.4.1 Comparison of Hybrid Production Using Genic, Cytoplasmic and Gene-Cytoplasmic Male Sterility

The following lines are involved in hybrid seed production (FRANKEL, 1973):

A line (female parent). The female parent line which has to be male sterile in the seed production plots.

B line (maintainer). The function of this line is to maintain the A line, and with the exception of the male sterility factor, it should be isogenic.

C line (male parent). The male parent line, must also contribute (when required) fertility restoration factors to the offspring.

3.4.4.1.1 Genic Male Sterility GMS

Genic male sterility is usually recessive and monogenic. Hence, fertility restoration in the hybrid and the crossing scheme are relatively easy.

The scheme shown in Fig. 3.50 indicates that removal (roguing) of fertile (heterozygous) segregates (Ms ms) is required in seed production plots and that pure-breeding male-sterile lines can not be maintained, unless fertility is restored

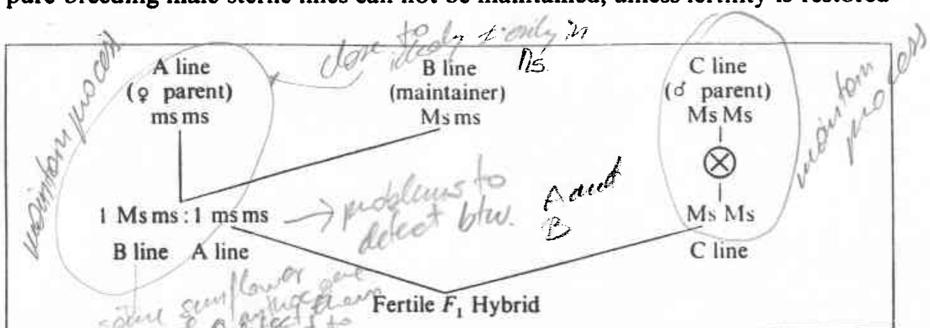

Fig. 3.50. A scheme for maintenance of parent lines and hybrid seed production using genetic male sterility

by a modified environment. Since the environmental conditions for fertility restoration in the A line are difficult to define, the hybrid is likely to contain many plants resulting from selfing. When the A line (but not the C line) is homozygous for an appropriate recessive marker gene, non-hybrid plants can be removed in the nursery before transplantation (in crops where this is feasible). Maintenance of the A line requires identification and removal of the heterozygotes before anthesis; this could be achieved by marker genes closely linked to the male sterility locus. However, insufficient linkage would result in recombination between marker and male sterility genes and thus contaminate the line.

When reproductive parts serve as the agricultural product, we have to be sure that recessive male sterility genes are not present in the C line. Fortunately, the frequency of male sterility genes is low and virtually all F_1 hybrid plants are fertile.

* Also - see Fehr, ch. 16 pages 199–203

3.4.4.1.2 Cytoplasmic Male Sterility CMS

Cytoplasmic male sterility is based solely on plasmagenes transmitted maternally. Thus, fertility in the hybrid cannot be restored. Consequently, the system is useful only in plants where seed production is not important. Production of the hybrid seeds and maintenance of the parent lines are shown in Fig. 3.51.

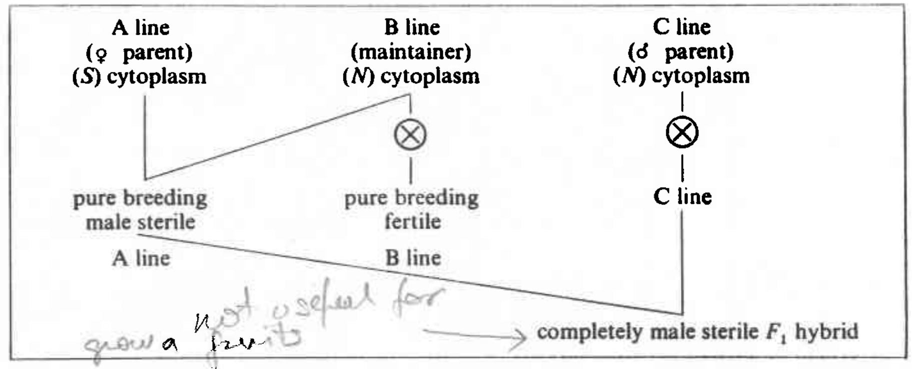

Fig. 3.51. A scheme for maintenance of parent lines and hybrid seed production using cytoplasmic male sterility

3.4.4.1.3 Gene-Cytoplasmic Male Sterility GCMS

Here the interaction between the sterile plasmatype and fertility restoration genes permits utilization of a breeding system most favorable for hybrid seed production. On the one hand, pure breeding male sterile A lines can be maintained and on the other hand, fertility in the final hybrid can be restored. Figure 3.52 outlines a scheme for the maintenance of parent lines and the production of hybrid seed utilizing gene-cytoplasmic male sterility.

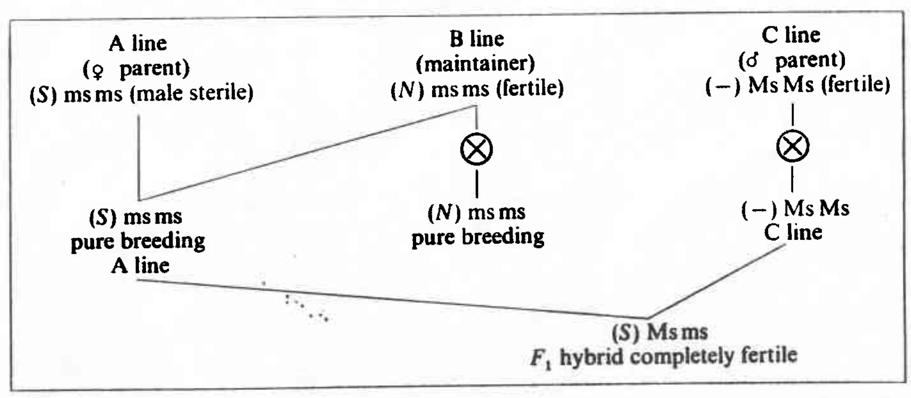

Fig. 3.52. A scheme for maintenance of parent lines and hybrid seed production using gene cytoplasmic male sterility

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and a dominant fertility-restoring (Ms) allele; also referred to as rf anf Rf, respectively

[redacted]

a) msms + (S) cytoplasm = male sterile
b) msms + (N) cytoplasm = male fertile
c) Ms-- + N or S cytoplasm = male fertile
d) msms S X msms N = msms S [sterile]
X MsMs N or S = Msms S [fertile]
X Msms N or S = 1 Msms S: 1 msms S

5) nuclear-cytoplasmic interaction usually makes expression susceptible to instability and can be sensitive to environmental conditions

6) many species have genic-cytoplasmic ms (> 150 spp)

4. Use of Male Sterility in Seed Production: important in breeding and hybrid seed production. (More on seed production later in course). The three systems of male sterility and how they are used are diagrammed in Frankel & Galun (1977), Figures 3.50-3.52. In each system is the A line (female parent), B line (the maintainer, or the line used to propagate the A line), and the C line (male parent)
   a. GMS: the A line segregates 1:1 for sterility and fertility (rogue out fertiles); F1 hybrid is fully fertile
   b. CMS: F1 hybrid is sterile, useful in forage crops where we are not interested in utilizing reproductive parts
   c. GCMS: A line is pure breeding sterile (no need to rogue), F1 hybrid fully fertile.

E. Self-incompatibility (Frankel & Galun, 1977; Fehr, ch. 2)

1. Self-incompatibility (SI) is the inability of a plant producing functional gametes to produce functional zygotes/set seed when self-pollinated

2. Self-incompatibility results from an interaction of pollen/pistil (i.e. stigmas/style/ovary and pollen/pollen tubes); it has been likened to an antibody-antigen reaction (although that is not accurate, it is an anology).

3. There are two main types of SI:
   a. **gametophytic SI** = GSI = pollen/pistil interaction genetically controlled by the **haploid genome of each pollen grain** and the diploid genome of the pistil tissue
   b. **sporophytic SI** = SSI = pollen/pistil interaction genetically controlled by the **genome of the sporophyte in which the pollen developed** and the diploid genome of the pistil tissue

4. What is the difference between the two SI ?
   a. If we look at a pollen grain, it consists of an interior protoplast with haploid sperm nuclei containing genes, and an exterior made up of a fairly complex wall (from exterior inwards, can delineate spines, sexine, cavus, nexine, intine, protoplast).
   b. This pollen grain develops inside the anther, surrounded by paternal tissue. Proteins and carbohydrates from the anther sac diffuse into the wall of the pollen grains and lodge in the spines, sexine and cavus. When the pollen hydrates and germinates on a stigma, these proteins diffuse out onto the stigmatic surface.

c. In **sporophytic SI**, it is these proteins from the walls of the pollen that determine the pollen/pistil reaction. Essentially, the nuclear genes of the pollen do not matter because it is the genes expressed in the sporophyte in which the pollen developed that determine the reaction.

d. In **gametophytic SI**, it is the proteins encoded by the genes in the pollen sperm nuclei that determine the pollen/pistil interaction and not these wall proteins.

5. Gametophytic SI (GSI)

a. Often controlled by a single "s" locus with multiple alleles

b. **Pollen grain genotype determines its phenotype**, and unlike alleles are compatible; e.g. male s1s3 plant makes both s1 and s3 pollen (i.e. two different genotypes and phenotypes) during meiosis

c. Example: (Note: the female parent is always designated first in breeding notation).

parents genotype	pollen geno/pheno	egg cells geno/pheno	progeny geno/pheno	reaction
♀ x ♂ s1s2 x s1s2	s1, s2	s1, s2	none	incompatible
s1s2 x s2s3	s2, s3	s1, s2	s1s3, s2s3	half compatible
s1s2 x s3s4	s3, s4	s1, s2	s1s3, s1s4, s2s3, s2s4	fully compatible

Frankel & Galun (1977) Table 3.24 (on handout) illustrates other examples and indicates whether the reaction is incompatible, half- or fully compatible.

d. This type of SI is not usually important in hybrid seed development since occurs sporadically, but does affect breeding methods/procedures by hampering self-pollination and crosses between parents with similar "s" alleles

e. GSI occurs in many genera, e.g. *Beta, Festuca, Hordeum, Lycopersicon, Medicago, Nicotiana, Prunus, Pyrus, Secale, Solanum, Trifolium*

6. Sporophytic SI (SSI)

a. Often controlled by a single locus with multiple "s" alleles. Alleles can have complex dominance relationships with each other; dominance/independence relationships in the pollen and the pistil may differ.

b. **Genotype of paternal anther tissue determines the phenotype of ALL the pollen produced by that plant**; e.g. male s1s3 plant makes phenotypically s1s3 pollen only

c. Dominance patterns can be different in the maternal (pistil) and paternal (anther) tissues; allelic series of dominance e.g. s2 > s3 > s1 or no dominance (i.e. independent)

d. Examples from Frankel & Galun (1977): if cross s1s3 (female) x s1s2 (male), and dominance patterns vary (examples 1-9), the following results would be observed:

ex.	anther	phenotype pollen	pistil	phenotype pistil	reaction
1	independent	s1 + s2	independent	s1 + s3	Incompatible (I)
2	s1 > s2	s1	independent	s1 + s3	I
3	s2 > s1	s2	independent	s1 + s3	Compatible (C)
4	independent	s1 + s2	s1 > s3	s1	I
5	independent	s1 + s2	s3 > s1	s3	C
6	s1 > s2	s1	s1 > s3	s1	I
7	s1 > s2	s1	s3 > s1	s3	C
8	s2 > s-	s2	s1 > s3	s1	C
9	s2 > s-	s2	s3 > s-	s3	C

e. SSI occurs in some genera, e.g. *Brassica*, *Helianthus*, *Linum*, *Pyrethrum*, *Raphanus*

f. Use of sporophytic SI important in hybrid development

e.g. brassica; single cross hybrids = develop inbred homozygous lines by bud pollination (to circumvent self-incompatibility),

s1s1 -> s1s1 -> s1s1 -> line A

s2s2 -> s2s2 -> s2s2 -> line B

then interplant lines A and B and let bees cross-pollinate, harvest seeds from female plants, obtain hybrid s1s2 seed

e.g. double cross hybrids = (s1s1 x s2s2 = s1s2), (s3s3 x s4s4 = s3s4), then cross s1s2 x s3s4 = the commercial hybrid

7. Comparison of gametophytic and sporophytic SI: Frankel & Galun (1977) Fig. 3.35 compares the two systems in diploids. In gametophytic, crosses are either not compatible, partially compatible or completely compatible; with sporophytic, not compatible or completely compatible.

8. Overcoming or inhibiting SI

a. Genetic

1) Mutation (spontaneous or induced by X-ray): creates another S allele or a self-fertile (i.e., non-functional S) allele

2) Induction of polyploidy overcomes gametophytic SI (but not SSI)

b. Environmental

1) Temperature extremes (hot and cold)

2) Mutagens (X-rays)

3) Time: floral aging, bud pollinations (e.g., *Brassica*, *Raphanus*) → stigma is receptive before the flower opens and is not receptive to the incomp.

4) Surgical: apply pollen to cut style (may work, but rare)

5) "Mentor" pollen: mix compatible and incompatible pollen and pollinate the flowers; the compatible pollen grows and may permit the incompatible pollen to also grow and fertilize the ovules

9. Problems in using SI in breeding

a. New incompatiblity alleles can arise e.g. forced selfing in *Lycopersicon peruvianum*

b. Inbreeding depression by continuous selfing to maintain inbred lines

c. Pseudo-incompatibility can arise: incompatibility reaction affected by genes other than S locus (i.e. epistatic interactions)

5. Gametophytic Incompatibility

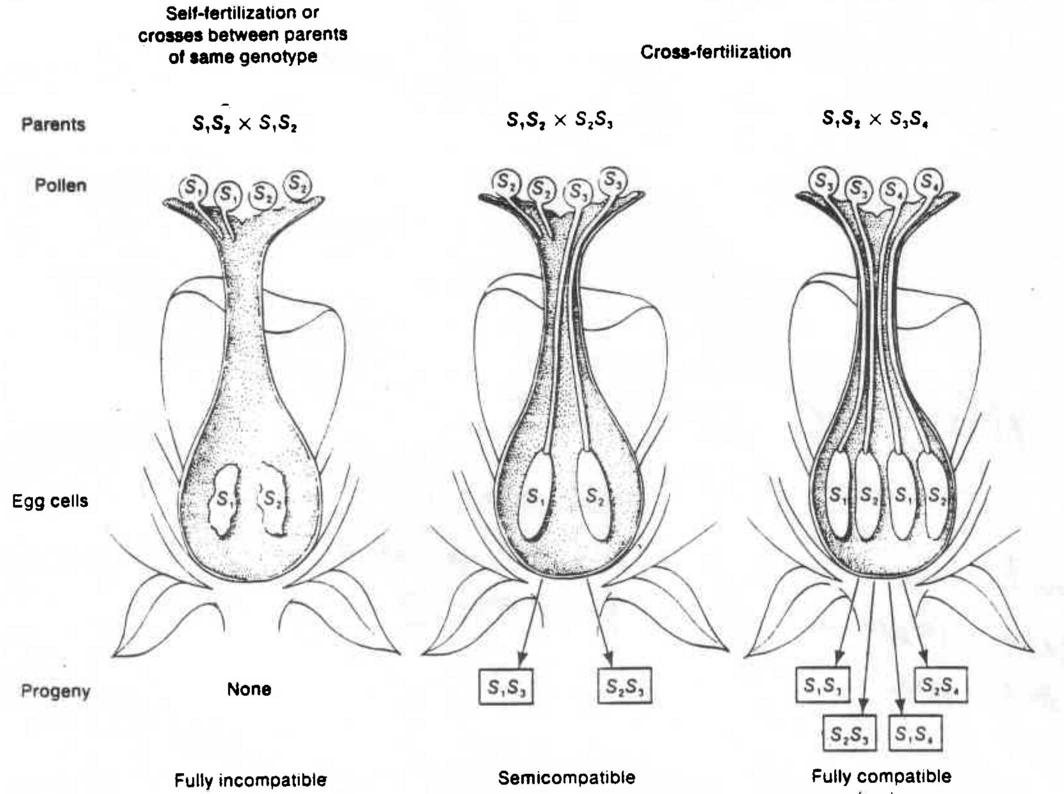

Figure 4-5. Diagram showing how multiple alleles control gametophytic *incompatibility in certain plants. A pollen tube will not grow if the* S *allele that it contains is present in the female parent. This diagram shows only four multiple alleles, but many plant incompatibility systems use far larger numbers of alleles. Such systems act to promote exchange of genes between plants by making selfing impossible and crosses between near relations very unlikely. (From A. M. Srb, R. D. Owen, and R. S. Edgar,* General Genetics, *2nd ed. Copyright © 1965, W. H. Freeman and Company.)*

from: Suzuki, D.T., A.J.F. Griffiths, R.C. Lewontin. 1981. An Introduction to Genetic Analysis. W.H. Freeman + Co.

Table 3.24. Compatible and incompatible combinations among all possible reciprocal cross- and self-pollinations in populations having the one multiallelic S locus, gametophytic incompatibility system. The populations contain either three S alleles (A—plants are S_{12}, S_{13} or S_{23}) or four alleles (A + B—plants are S_{12}, S_{13}, S_{23}, S_{14}, S_{24}, or S_{34}). Numbers in parentheses represent fractions of compatible pollen grains in each cross-pollination (zero (–), ½ or full (1))

♂ plant / ♀ plant		A			B		
		S_{12}	S_{13}	S_{23}	S_{14}	S_{24}	S_{34}
A	S_{12}	—	(1/2)	(1/2)	(1/2)	(1/2)	(1)
	S_{13}	(1/2)	—	(1/2)	(1/2)	(1)	(1/2)
	S_{23}	(1/2)	(1/2)	—	(1)	(1/2)	(1/2)
B	S_{14}	(1/2)	(1/2)	(1)	—	(1/2)	(1/2)
	S_{24}	(1/2)	(1)	(1/2)	(1/2)	—	(1/2)
	S_{34}	(1)	(1/2)	(1/2)	(1/2)	(1/2)	—

ref: Frankel + Galun 1977 Springer-Verlag.

* Also - see Fehr, ch. 2 pages 20 - 22.

6. Sporophytic Incompatibility

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3.3.1.2.2 Homomorphic Incompatibility

Sporophytic control of pollen incompatibility was suggested already in 1912 by CORRENS for *Cardamine pratensis* (Cruciferae), but a satisfactory explanation of the experimental results was delayed for 38 years. Only then was the genetic control in this system fully explained for the two composite species *Crepis foetida* and *Parthenium argentatum* by HUGHES and BABCOCK (1950) and GERSTEL (1950), respectively. Since then, this system of incompatibility has been established in numerous species, many of them of great economic value. These belong mainly to the families Cruciferae, Compositae and Convolvulaceae. The genetic details of this incompatibility system were presented by BATEMAN (1952, 1954, 1955) and later information can be obtained from the general review on incompatibility of ARASU (1968). The main genetic features of this system may be summarized in the following:

1. Incompatibility is controlled by one S locus having several alleles; the number of these alleles is usually less than in the one S locus gametophytic incompatibility system, but in some species (e.g. *Brassica oleracea*) over 30 such alleles were revealed.

2. The reaction of the pollen is determined by the genotype of the sporophytic tissue in which it was formed, and thus it is controlled by two S alleles.

3. Resulting from the above type of pollen control, all the pollen of a plant has the same incompatibility reaction.

4. The two S alleles may react independently or they may interact by one being dominant over the other; these relationships may exist in one, both, or neither the pollen or the pistil; the recessive allele has then no activity.

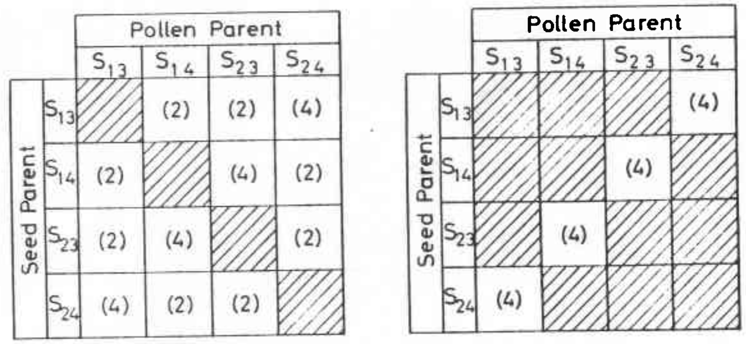
5. Active allele identity in both pollen and pistil leads to incompatibility.

6. The dominance/independence relationships of the S alleles in the pollen and in the pistil may differ.

Such dominance/independence relationships may lead to rather complex incompatibility reactions. This will be demonstrated with an apparently simple cross: $S_{13}(♀) \times S_{12}(♂)$ in which the compatibility is expected to be the following:

Pollen reaction	*Pistil reaction*	*Compatibility*
Independent	Independent	Incompatible
S_1 dominant to S_2	Independent	Incompatible
S_2 dominant to S_1	Independent	Compatible
Independent	S_1 dominant to S_3	Incompatible
Independent	S_3 dominant to S_1	Compatible
S_1 dominant to S_2	S_1 dominant to S_3	Incompatible
S_1 dominant to S_2	S_3 dominant to S_1	Compatible
S_2 dominant to S_1	S_1 dominant to S_3	Compatible
S_2 dominant	S_3 dominant to S_1	Compatible

Figure 3.35 compares the sporophytic incompatibility with the gametophytic one. For simplicity the sporophytic incompatibility is represented by the case of independent activity of the S alleles in both pollen and pistil and the gametophy-



One S locus, multiallelic gametophytic incompatibility
GSI

Homomorphic sporophytic incompatibility with independent S alleles activity in both pollen and pistil
SSI

Fig. 3.35. Comparison between the one multiallelic S locus, gametophytic incompatibility and the homomorphic-sporophytic incompatibility (with independent S allele's activity in both pollen and pistil). The two schemes describe the theoretical results of diallele crosses among the plants of an F_1 progeny of a cross between two unrelated parental plants ($S_{12} \times S_{34}$). *Shaded squares:* incompatibility; *figures in parentheses:* number of zygote genotypes produced by each cross

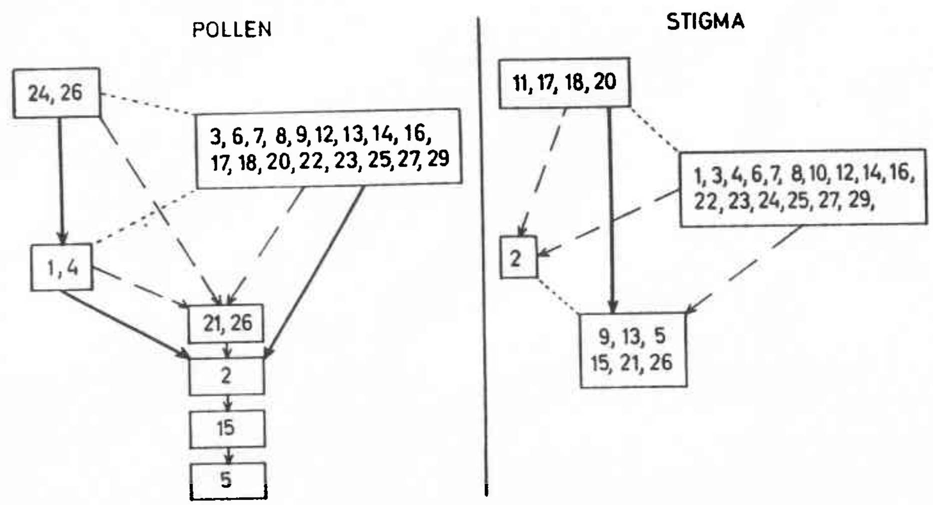


Fig. 3.36. Groups of S alleles arranged spatially in accordance with their dominance relationships in *Brassica oleracea*. *Whole lines with arrow:* dominance of upper over lower group *broken lines with arrow:* S alleles heterozygotes between groups show either activity of both alleles or alleles from upper group dominant over those from lower group *dotted lines:* both alleles active (from THOMPSON, 1968)

from: Frankel, R. and E. Galun. 1977. Pollination Mechanisms, ...