the other hand, high temperature and high humidity are proper conditions for propagation of parental lines. The climatic conditions should thus be considered in the various steps of hybrid seed production.

5. *Restriction of Pollination within Parental Lines.* In Brussels sprouts hybrid seed production fields, it was found that bees were not visiting the plants at random. Each bee preferred to stay within one parental line. This preference was stronger when the two parental lines differed morphologically. The result was more sib-pollination and less cross-pollination, which led to an unacceptably high percentage of 'sib' seeds in the commercial hybrid. Increasing the morphological similarity between parental lines and using other pollen vectors (e.g. flies) may overcome this problem.

In conclusion, it should be noted that in spite of the problems mentioned above, sporophytic incompatibility can be successfully applied for commercial hybrid seed production. There is probably no better proof of that than the availability of uniform and high-yielding varieties of many cruciferous crops, e.g. from Japanese seed companies.

3.4 Male Sterility

We have discussed the situation in which viable pollen is incapable of effecting self-pollination through the genetic mechanism of self incompatibility. A situation in which viable pollen is unable to reach own and foreign stigmata exists in positional (or functional) male sterile mutants. Male sterility proper is defined as the deviant condition in normally bisexual plants (monoecious or hermaphrodite) when no viable pollen is formed.

3.4.1 Gynodioecy: Male Sterility in Natural and Artificial Populations

The phenomenon of male sterility in bisexual flowering plants was reported as early as the middle of the 18th century by KÖLREUTER (1763), who differentiated correctly between anther abortion within a species and what he called "male contabescens", an abortion resulting from species hybridization. Gynodioecious species feature hermaphrodite and 'female' (male sterile) individuals in one and the same population. Stable proportions of females regulate the degree of outbreeding and, in contrast to conditions in dioecious (and androdioecious species, seed fertility is retained on all plants, thus providing a high reproduction potential (LEWIS, 1942). From 2 to 50% or more male steriles have been reported in gynodioecious populations which tend to stay stable in particular habitats.

3.4.1.1 Male Sterility as an Outbreeding Mechanism in Gynodioecious Species

The first to carry out genetic analysis of male sterility were CORRENS (1904) and BATESON et al. (1908), the former showing gynodioecy to be governed by the maternal cytoplasm, the latter by a recessive monofactorial male sterility gene. The equilibrium proportions of female individuals in the gynodioecious population may be achieved through a gene balance system (genic male sterility) adjusted by relative seed fertility of the male sterile individuals, heterozygote advantage, high mutation rate towards male sterility alleles, and lethality of homozygotes. If gynodioecy is governed by genome-plasmon interaction (gene-cytoplasmic male sterility) and the reproductive potential of the plasmatypes is equal, the proportion of the two plasmatypes in a population will achieve a stable equilibrium of females and hermaphrodites.

Gynodioecy as an outbreeding system has often been considered as a transitional condition in the evolution from bisexuality to dioecy (DARWIN, 1877; CARLQUIST, 1966; ROSS, 1970). The very occurrence of hermaphrodites in small quantities in otherwise dioecious populations (e.g. in carob, *Ceratonia siliqua;* poplar, *Populus alba*) also suggests such a notion. When pollen production and transference are more than sufficient and increased hybridity becomes advantageous, there is nothing preventing the hermaphrodite from becoming progressively female sterile. At the most, when the advantage of seed fertility in all plants of the gynodioecious population is fully offset by heterozygote advantage, the population may become dioecious, i.e., the hermaphrodite becomes male (see VALDERYON, 1972).

Inferior seed fertility of the hermaphrodites in a gynodioecious population has been reported repeatedly since DARWIN'S initial observation in 1877 (e.g. in majoram, *Origanum vulgare:* LEWIS and CROWE, 1956; in sage, *Salvia nemorosa:* LINNERT, 1958). Greater seed fertility of the male steriles in gynodioecious populations is considered to contribute to the maintenance of an equilibrium proportion of genic male steriles (JAIN, 1968) but is not necessary for cytoplasmic male steriles (LEWIS, 1941). If the reproductive output of male steriles and hermaphrodites were equal in a gene balance system, the former would contribute a frequency-dependent fraction of nuclear genes to the next generation (see Section 2.1.3). In a population with equal numbers of male steriles and hermaphrodites, each hermaphrodite contributes three times as many genes as each male sterile, since it supplies its own pollen and egg nuclei and also pollen that fertilizes the male sterile (LEWIS and CROWE, 1956). However, in a population including only 1% of male steriles, any one hermaphrodite contributes only about two times as many genes as one male sterile. The increase in the relative seed fertility required to maintain an equilibrium in the gynodioecious population appears to be independent of the number of genes controlling male sterility. Figure 3.38 gives the relation between the relative seed fertility and equilibrium proportions of the male steriles in gynodioecious populations (ROSS and SHAW, 1971) and shows that male steriles would be lost from the population unless they were at least twice as seed-fertile as the hermaphrodites.

Contrary to maintenance of male steriles by differential seed fertility, the maintenance of low frequencies of male steriles by heterosis appears to be controlled by the mode of inheritance (Fig. 3.39; HO and ROSS, 1973). Heterozygote advantage cannot account for the higher than 30% proportion often found in gynodioecious populations based on genic male sterility. Partial or complete lethality of some homozygotes (LINNERT, 1958; JAIN, 1968; LEWIS and CROWE,

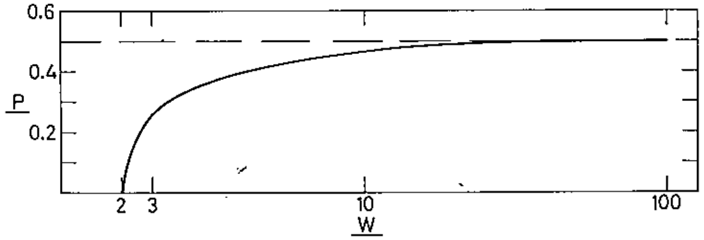


Fig. 3.38. Relationship between relative female fertility of male steriles (W) and their equilibrium proportions (P) (after Ross and Shaw, 1971)

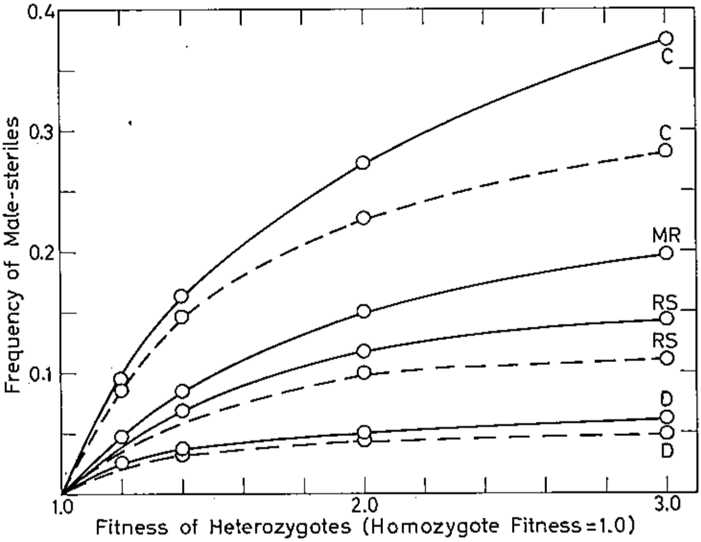


Fig. 3.39. Effect of heterozygote advantage on proportions of male steriles under four modes of inheritance of male sterility. *Continuous lines:* epistatic *broken lines:* non epistatic fitness interactions. C: complementary genes, MR: monogenic recessive, RS: recessive suppressor, D: duplicate genes (after Ho and Ross, 1973)

1956), as well as high mutation rate, may add to differential seed set and heterozygote advantage for maintaining high proportions of genic male steriles.

The combination of self incompatibility and gynodioecy found in rib grass *(Plantago lanceolata)*, sea pink *(Ameria maritima)* and sea lavender *(Limonium vulgare)* indicates that enforced outcrossing of male steriles in these gynodioecious populations may represent secondary outbreeding systems (Ross, 1967; Baker, 1966). Although selfings may be prevented with self incompatibility as with male sterility, each mechanism regulates sib- and outcrossing in different ways such that crosses possible with one system are sometimes prevented by the presence of the other system. Jain (1968) suggested that the very combination of self sterility and gynodioecy may be a means for the gradual evolution of self compatibility from self incompatibility.

Equilibria of more than 0.5 male steriles in gynodioecious populations may be maintained under cytoplasmic inheritance of male sterility. In savory *(Satureia hortensis)*, thistle *(Cirsium oleraceum)*, columbine *(Aquilegia vulgaris)* and *Plantago ovata*, female plasmatypes have been found to yield female progeny only, and hermaphrodites, hermaphrodite progeny only (CORRENS, 1916; 1928; KAPPERT, 1944; PALIWAL and HYDE, 1959). Superimposed upon plasmatype variation, a gene balance system may serve as a sensitive adaptation to changes in hybridity optima. A collaboration of nuclear genes and cytoplasmic condition can adjust equilibrium proportions of females by shifts in gene frequencies (DARLINGTON, 1958), as illustrated by the gynodioecious thyme *(Thymus vulgaris)*. Females pollinated by different hermaphrodite genotypes may produce either all female or a majority of female progeny, whereas hermaphrodites selfed or sib-crossed yield either all hermaphrodite or a majority of hermaphrodite progeny. Such crossing results, and equilibrium proportions of females in populations ranging between 60 and 70 %, can be explained by high frequency presence of a *recessive* "plasmon sensitive" allele, f, and high-frequency presence (80%) of a "sterile" plasmatype (*S*), (see VALDEYRON et al., 1970). A similar situation based on *dominant* "plasmon sensitive" alleles may be present in orchard grass, *Dactylis glomerata* (MYERS, 1946).

3.4.1.2 Nuclear Male Sterility Genes in Cultivars

Gynodioecy in inbreeding cultivars is an outcome of mutation and survival of androsterility alleles in the population. Genic male sterile mutants appear to occur regularly in self-pollinated cultivars. Possible models for the origin of genic male sterility and its maintenance in populations are given in Fig. 3.40. On the average one monogenic recessive male sterile mutant can be found in a population of about 20,000 plants of lima beans (ALLARD, 1953) and tomatoes (RICK, 1945a). The elimination of recessive androsterility mutants from the cultivar population depends on the degree of outcrossing prevailing, but even with little outcrossing, elimination is quite slow. This is in contrast to mutations affecting female gametes and to dominant androsterility mutants which are promptly removed from the population. As a matter of fact, the overwhelming majority of the more than 100 cases of Mendelian male sterility detected and analyzed in cultivated plants show monofactorial recessive inheritance. Furthermore, many non-allelic male sterility genes may be found within the same self-fertilizing species. More than 30 non-allelic recessive male sterility mutants have been found in the tomato (CLAYBERG et al., 1966), more than 20 in barley (HOCKETT and ESLICK, 1971), six in sorghum (DOGGETT, 1970), and a few in rice (CHANDRARATHNA, 1964), cotton (WEAVER, 1968; KOHEL and RICHMOND, 1968), sweet pea (BATESON et al., 1908; PUNNETT, 1932), pea (GOTTSCHALK and JAHN, 1964), soybean (BRIM and YOUNG, 1971), tobacco (BHAT and KRISHNAMOORTHI, 1956), pepper (SHIFRISS, 1973; DASKALOFF, 1973), eggplant (JASMIN, 1954), and lettuce (LINDQUIST, 1966; RYDER, 1967).

Recessive male sterility alleles may also be detected in cross-fertilized cultivars upon artificial inbreeding or subdivision into small populations. Splitting up

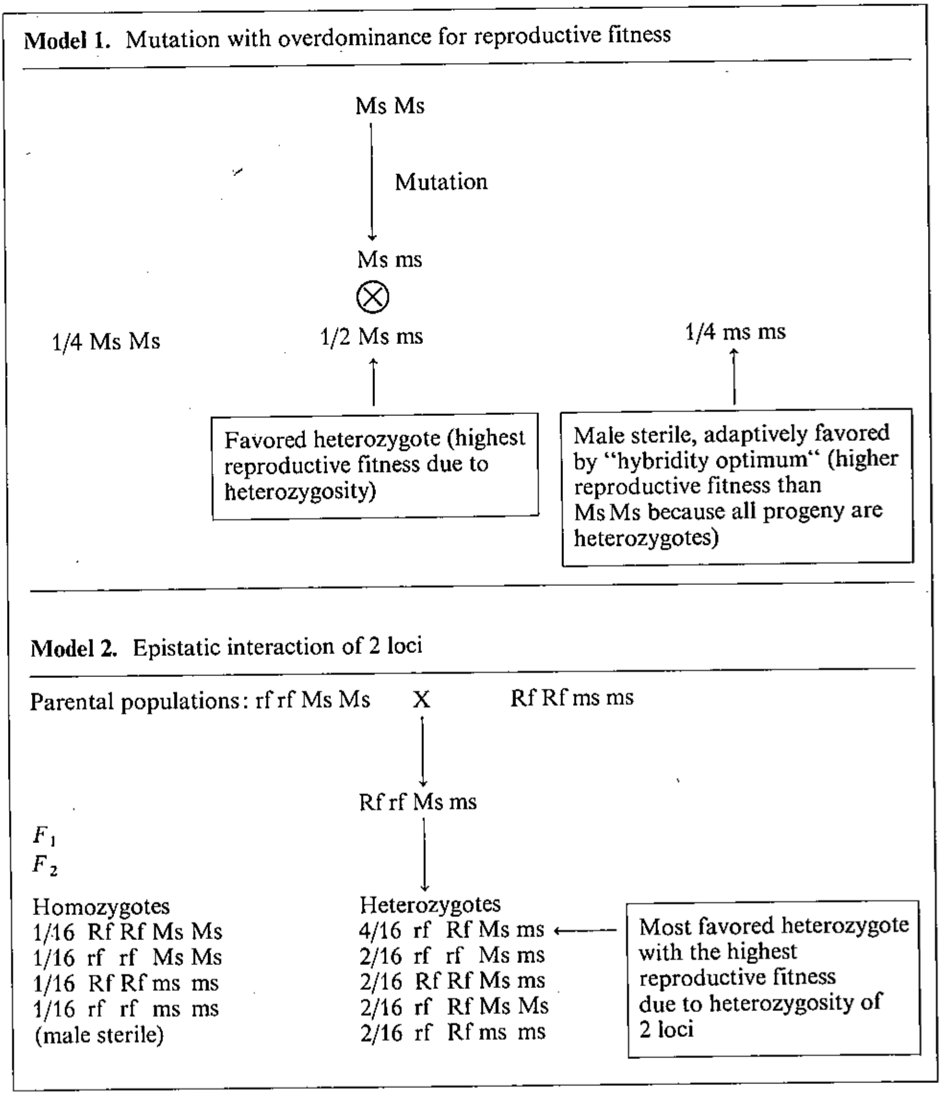


Fig. 3.40. Models for the origin and maintenance of genic male sterility (from FRANKEL, 1973)

cultivars into small subpopulations or artificial inbreeding increases the chances of revealing recessive male sterility genotypes in the homozygous condition (FRANKEL, 1940). Partly inbred populations of maize yielded more than 14 monogenic recessive male sterile mutants (EMERSON et al., 1935). Simple monogenic recessive male sterile mutants have also been uncovered in restricted populations of *Cucurbita pepo* (SHIFRISS, 1945), *Cucurbita maxima* (HUTCHINS, 1944; SCOTT and RINER, 1946) and in *Cucumis* species (ROBINSON and WHITAKER, 1974). The monogenic mutants mentioned condition male sterility independent of plasmatic background and may thus be considered plasmon-sensitive alleles to a universal "sterile" plasmatype (*S*) originating as outlined in Fig. 3.41.

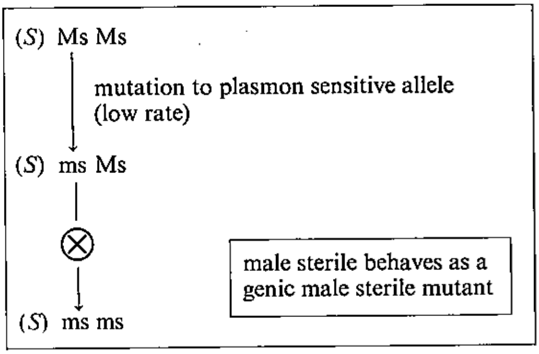


Fig. 3.41. Spontaneous occurrence of male sterility due to mutation to a plasmon sensitive allele

3.4.1.3 Male-Sterility-Inducing Plasmatypes in Cultivated Plants

Diversity of male-sterility-inducing plasmatypes can be identified through the differential disharmony (expressed by male sterility) caused by the presence of interacting nuclear male sterility genes. Male sterility becomes "cytoplasmic" when two or more plasmatypes can be established within the same cultivar. In the most simple and common case two alternative plasmatypes exist, one "normal"—usually designated (*N*) or (*F*), and the other "male sterile"—designated (*S*). The "male sterile" plasmatype interacts with a pair of alleles, one "plasmon sensitive"—if recessive usually designated ms or rf, and the other "fertility restoring"—if dominant usually designated Ms of Rf. In this common case male sterility is produced in the homozygous recessive genotype with "male sterile" cytoplasm only. The diversity of independent sources of "male sterile" plasmatypes has been established in quite a number of cultivated plants. To identify diversity of plasmatypes, GRACEN and GROGAN (1974) produced 38 different plasmatic versions of 28 inbred lines of maize. Differential fertility restoration reaction grouped the plasmatypes into three main groups (C, S and T groups) and five other plasmatypes with different restoration pattern. All these plasmatypes in the outbreeding maize originated apparently spontaneously within the species ("Autoplasmy"). Possible models for the spontaneous origin of male-sterility-inducing plasmatypes and their maintenance in populations are given in Fig. 3.42. The qualitative change of plasmatypes may be induced by chemicals (e.g. Colchicine in sorghum: ERICHSEN and ROSS, 1963; MALINOWSKY et al., 1973) and may or may not be influenced by the nuclear environment. The change may be preceded by a mutation toward a "mutaplasmic allele", followed by a mutation of the plasmatype in the homozygous mutant, as exemplified by the case of the "iojap" mutation in maize (RHOADES, 1950). The male sterile plasmatype may not be stable, and reverse plasmon mutation toward fertile plasmatypes has been reported for maize (SINGH and LAUGHNAN, 1972) and for pearl millet (BURTON, 1972; CLEMENT, 1975). The well-known case of cytoplasmic male sterility in the allogamous onion, first to be utilized in hybrid seed production, also originated spontaneously and repeatedly within the species (JONES and CLARKE, 1943; PETERSON and FOSKETT, 1953); later, two different plasmatypes (*S* and *T*) could be differentiated (SCHWEISGUTH, 1973). Autoplasmy

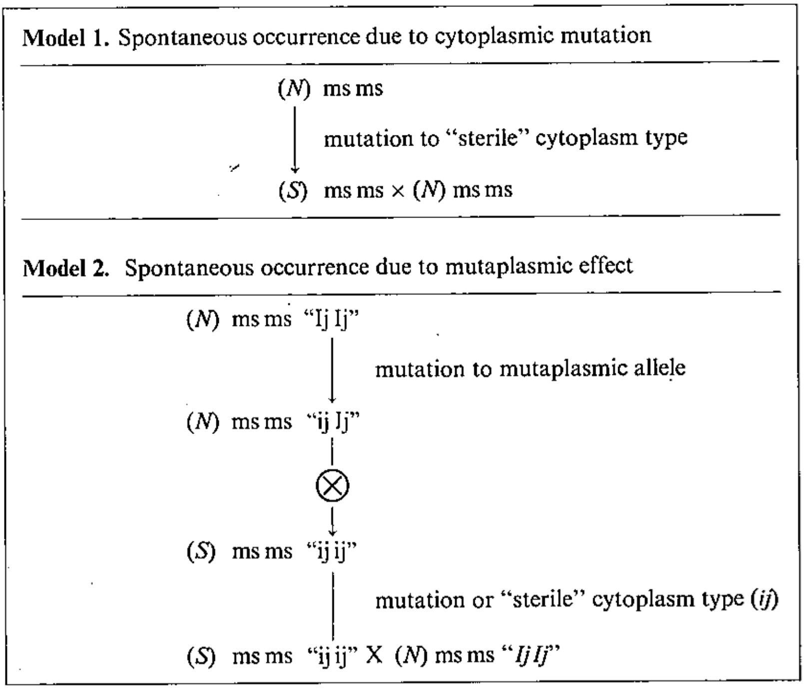


Fig. 3.42. Models for the spontaneous origin and maintenance of male sterility inducing cytoplasm ("autoplasmy")

has also been indicated for the outbreeding rye *(Secale cereale)*. GEIGER and MORGENSTERN (1975) could trace 15 cytoplasmic male sterile sources to at least two different male sterile plasmatypes ("Pampa" and "Primitive Persion" cytoplasms).

Intraspecific diversity of male sterile plasmatypes must be the result of plasmatype mutation. In allogamous species the maintenance of a mutated plasmatype by slow rejection of plasmon-sensitive alleles is feasible, whereas such mutation would be lost in the presence of exposed plasmon-sensitive alleles under extreme autogamy. Thus, autoplasmy can be expected to crop up upon crossing isolated cultivars of cross-pollinated plants. In contrast, male sterile plasmatypes in the inbreeding wheat are all of hybrid (intergeneric or interspecific) ancestry ("Alloplasmy"). Substitution of wheat nuclei differentiated male sterile cytoplasma from *Aegilops* species—caudata, ovata and speltoides plasmatypes, and from male sterile cytoplasms of *Triticum* species—araraticum, boeoticum, dicoccoides, timopheevi and Zhukovskyi plasmatypes (see KIHARA and TSUNEWAKI, 1967; MAAN and LUCKEN, 1972).

Alloplasmic "male sterile" plasmatypes are differentiated quite commonly by substitution of nuclei of autogamous plants: in *Nicotiana* the induction of male sterility by the combination of cytoplasm of one species with the partial or complete genome of another species appears to be a widespread phenomenon. Genetic restorers to pollen fertility can usually be found in these cases in certain chromosomes of the species contributing the cytoplasms (SMITH, 1968). Thus, substitution of nuclei of cultivated tobacco *(N. tabacum)* differentiated male sterile cytoplasms from *N. bigelovii, N. debnyi, N. megalosiphon, N. plumbaginifolia, N. rustica, N. suaveolens* and *N. undulata* (see EDWARDSON, 1970). Similarly, the substitution lines of the autogamous upland cotton *(Gossypium hirsutum)* differentiated male sterile cytoplasms from *G. arboreum, G. anomalum* and *G. harknessii* (MEYER, 1969, 1975). Interspecific hybrid ancestry of male sterile plasmatypes is also indicated in peppers, *Capsicum frutescens, C. peruvianum* and *C. pendulum* cytoplasms interacting with plasmon-sensitive alleles derived from *C. annuum* (OHTA, 1973; RUSINOVA-KONDAREVA, 1965; FRANKEL, unpubl.); and in flax, *Linum floccosum* cytoplasm interacting with plasmon-sensitive alleles from *L. usitatissimum* (GAJEWSKI, 1937). The well-known case of cytoplasmic male sterility which originated from intraspecific crosses between "procumbent" and "tall" races of flax (see EDWARDSON, 1970) and cytoplasmic male sterility originating from crosses between *indica* and *japonica* rice (SHINJYO, 1972a, b), involved distant geographical races or subspecies. In flax the "procumbent" cytoplasm interacts with plasmon-sensitive alleles from the "tall" races, and in rice the *indica* cytoplasm interacts with plasmon-sensitive alleles from the *japonica* subspecies. In view of the mentioned examples as well as the theoretical consideration of the fate of male sterile cytoplasms, alloplasmic origin of male sterile plasmatypes—as pictured in Fig. 3.43—should be expected to be the rule in extreme autogamous plants. Hence, the wider the taxonomic differences between two organisms, the greater the expected plasmatype difference of autogams.

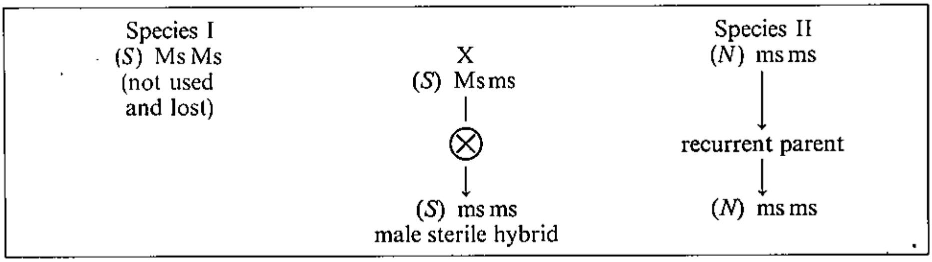


Fig. 3.43. Origin of male sterility inducing cytoplasm after crosses between genetic isolated species or populations ("alloplasmy")

3.4.1.4 Utilization of Gynodioecy in Plant Breeding

The association of numerous genetic factors into a single genome requires crosses between many parents differing at the loci concerned. Breaking and recombination in close linkage groups amplify further the extent of crossing requirements. Because of the impractically large numbers of parents needed, plant breeding is faced with the dilemma of working in a very restricted range of elite material relative to the total variability available in the crop. Large, random mating populations of parents are often the only feasible means of achieving the desired combination of quantitative factors.

SUNESON (1951, 1956) first demonstrated that nuclear male sterility genes make the development of random mating populations possible also in mainly self-pollinating crops. Substantial amounts of heterozygosity may be retained by genic male sterility (Jain, 1961; Lloyd, 1975) and composite crosses can be established in self-pollinated plants. Thus, male sterility in artificial populations of inbreeding crops can be a useful tool in plant breeding. The application of nuclear male sterility to recurrent selection schemes, as in soybeans (Brim and Stuber, 1973) or sorghum (Doggett, 1972), capitalizes on the fact that resulting lines need not carry restorer genes, as they would have to if cytoplasmic male sterility were to be used (Gilmore, 1964).

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		Cytoplasmic male sterility		Gene-cytoplasmic male sterility	
	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

3.4.2.1 Genic Male Sterility (Mendelian Male Sterility)

Expression of genic male sterility may take a variety of forms ranging from abortion of anthers, malformation of anthers, abortion of pollen at various stages during microsporogenesis and indehiscense of anthers ("functional male sterility"), to highly extruded stigmata ("positional male sterility"); these expressions will be discussed later on. Generally, genic male sterile mutants appear to have a much more stable expression than cytoplasmic or gene-cytoplasmic male sterile types.

Sporophytic control of the trait is a general feature of recessive genic male sterility. Consequently, all gametes of the heterozygote are functional and only the female gametes of the homozygote recessive are functional. This, of course, permits survival of the male sterility alleles in natural populations. Selective abortion of microspores, sporophytically controlled by an alien locus, has been reported in the progeny of an interspecific tobacco cross (CAMERON and MOAV, 1957).

The overwhelming majority of analyzed cases of Mendelian male sterility show control by single recessive factors (see Section 3.4.1.2 above). Large numbers of non-allelic recessive male sterility alleles have been found within the same species. In all these cases, the presence of a single recessive gene in homozygote condition leads to the expression of male sterility. A few cases of double recessive male sterility have been reported (e.g. in cotton: WEAVER, 1968). Double recessive male sterility in monoecious plants is exemplified by the babats$_2$ts$_2$ and skskts$_2$ts$_2$ genotypes of maize (see Section 3.2.1.2).

A few cases of monogenic dominant male sterility have been reported, such as in *Solanum* (SALAMAN, 1910), *Coleus* (FORD, 1950) and *Streptocarpus* (ZEVEN, 1972). Although a few cases of dominant abortion of pollen during microsporogenesis have been reported (e.g. Ms$_4$ and Ms$_7$ in cotton: MURTHI and WEAVER, 1974), most dominant male sterile phenotypes appear to be "functional male sterile", leaving the option of forced pollen release open. Epistatic gene action between a dominant and recessive gene leads to male sterility in *Lactuca* (RYDER, 1963) and in *Origanum* (LEWIS and CROWE, 1956); in these cases male steriles are FFhh or Ffhh genotypes, the double recessives may or may not be lethal, and FFHH, FFHh, FfHH and FfHh are bisexual. The literature on genic male sterility has been reviewed by JAIN (1959) and GOTTSCHALK and KAUL (1974).

Genic male sterility has repeatedly been reported to occur spontaneously (see ALLARD, 1953; RICK, 1945; REIMAN-PHILLIP and FUCHS, 1971). Genic male sterility has also been induced artificially: two X-ray-induced recessive male sterile mutants of *Petunia* were studied by WELZEL (1954). An apetalous and antherless recessive mutant of *Tagetes erecta*, induced by X-rays (BOLZ, 1961), is presently used in hybrid seed production (HORN, 1974). Genic male sterility has also been induced by gamma rays in watermelon and tomato (WATTS, 1962; KWASNIKOW et al., 1970), and by chemical mutagen in peppers and pea (BREUILS and POCHARD, 1975; KWASNIKOW et al., 1970).

Pleiotropic effects of male sterility alleles (or close linkages with these alleles) have been reported in a number of cases. Reduced female fertility in the homozygous recessive (e.g. in an apetalous and antherless *Antirrhinum:* SINK, 1966), or reduced pollen fertility in the heterozygote (e.g. in hybrid tomato produced with ms$_{41}$: ANDRASFALVY, 1974), may cause problems in the production of hybrid cultivars. On the other hand, certain marker phenotypes associated with male sterility genes can lead to a more efficient hybrid seed production procedure (see Section 3.4.4.2.1 below).

3.4.2.2 Cytoplasmic and Gene-Cytoplasmic Male Sterility

Rare events, such as loss of restorer genes in the breeding population after initial wide crosses, or recent mutations toward a male sterile plasmatype, may serve as plausible explanations for the few cases reported of male sterility controlled solely by the maternal cytoplasm (see JAIN, 1959; BERNINGER et al., 1970). Furthermore, many cases of cytoplasmic male sterility proved, upon additional study, to be actually affected also by Mendelian genes, e.g. in corn (see RHOADES, 1933; DUVICK, 1965; GRACEN and GROGEN, 1974), sugarbeet (see OWEN, 1945), and *Petunia* (EDWARDSON and WARMKE, 1967; VAN MARREWIJK, 1969). The absence of a plasmon-genome interaction in cytoplasmic male steriles tends to make phenotypic expression of the trait more stable than in gene-cytoplasmic or genic male steriles. Lack of plasmon–genome interaction produces male steriles only in the progeny of male sterile plants.

In view of the dependence of various metabolic systems in the cytoplasm on nuclear attributes, the constancy of the genetic property of the plasmatype must be established. A change of the cytoplasm derived from the maternal parent may consequently be brought about by the action of nuclear genes. We know that nuclear genes may or may not inhibit or modify the action of the cytoplasm in a fertility-restored or non-restored genotype. In the former case the genetic property of the cytoplasm must remain latent in the restored genotype and show up again as a result of gene segregation to indicate genetic permanence of the maternal plasmatype. Furthermore, a contribution of the paternal cytoplasm to the zygote, as indicated in some cases could possibly cause a gradual change in the plasmatype upon successive backcrosses (see e.g. FLEMING, 1975, for paternal cytoplasmic influences on agronomic traits in maize; HAGEMANN, 1964, for status "paralbomaculatus" in *Pelargonium*, *Hypericum* and *Oenothera*). Such a possibility is considered graphically in Fig. 3.44. To date no change in the genetic properties of the maternal plasmatype by introgressive paternal cytoplasm has been reported for the male sterility trait (see e.g. MICHAELIS and MICHAELIS, 1948; BURK, 1960). Independence from Mendelian genes and constancy of the maternal transmission of the male sterile plasmatype have been repeatedly demonstrated by successive nuclear substitution experiments (e.g. JONES, 1956; DUVICK, 1965; FUKASAWA, 1967; SCHWEPPENHAUSER and MANN, 1968; see Fig. 3.45) or even by androgenesis (see e.g. GOODSELL, 1961). In contrast with all cases of genic male sterility, where expression of male sterility is controlled entirely sporophytically, gametophytic control on pollen function in heterozygous fertility-restored plants carrying male sterile cytoplasm has been reported in a number of cases. Data from maize populations expected to segregate indicate the occurrence of some type of selective fertilization in plants bearing the (*S*) cytoplasm and heterozygous for the fertility-restoring genes, resulting in a higher frequency of fertile plants than expected (BRIGGLE, 1957). BUCHERT (1961) showed that in the (*S*) plasmatype, only microspores which contain a dominant allele for fertility restoration, Rf_3, produce functional gametes, whereas male gametes containing the recessive allele, rf_3, abort. The female gametes of the (*S*) plasmatype all remain functional. In contrast to this, all microspores are functional in heterozygous plants, Rf_3rf_3, with the (*T*) plasma-

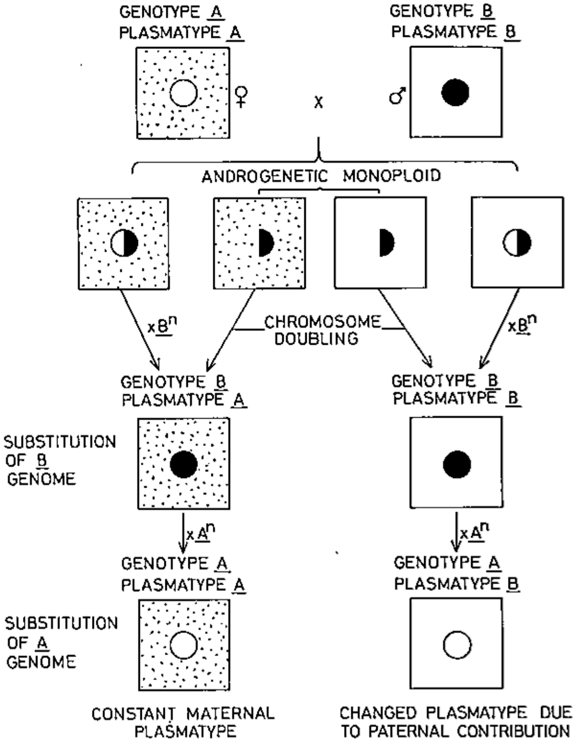


Fig. 3.44. Proof for the constancy of maternal plasmatype by substitution and restoration crosses. Dots in cytoplasm *(rectangle)* indicate male sterility inducing factors, dark nucleus *(circle)* indicates plasmon sensitive nuclear factors. *Left side:* constancy of maternal *right side:* constancy of paternal plasmatypes

type irrespective of the allele. The rf gametes may not function due to abortion or due to elimination when in competition with Rf gametes, as a result of differential pollen germination or growth (JOSEPHSON, 1964). In the case of a recessive restorer gene to the (*S*) cytoplasm, a suppressor of this gene, S^{Ga}, also operates gametophytically (SCHWARTZ, 1951).

Variation of pollen production in heterozygous fertility-restored plants and shifts of expected segregation ratios toward fertility have been reported in a number of plants. Studies by BARHAM and MUNGER (1950) showed reduced pollen production in heterozygous restored onion. Male sterile (*S*) ms ms plants did not produce any pollen; fertile homozygous plants—irrespective of the plasmatype—(*S*) Ms Ms or (*N*) Ms Ms produced about 82% viable pollen; and pollen production in the heterozygote (*S*) Ms ms was only 64%. These results have been interpreted as due to incomplete dominance. Deviating segregation ratios in onion crosses between male steriles and (relatively undefined) genotypes of pollen donors with a shift toward fertility have been interpreted as due to the action of modifier genes (NIEUWHOF, 1970). However, the malfunction of the plasmon-sensitive gamete in the (*S*) cytoplasm cannot as yet be ruled out in these cases.

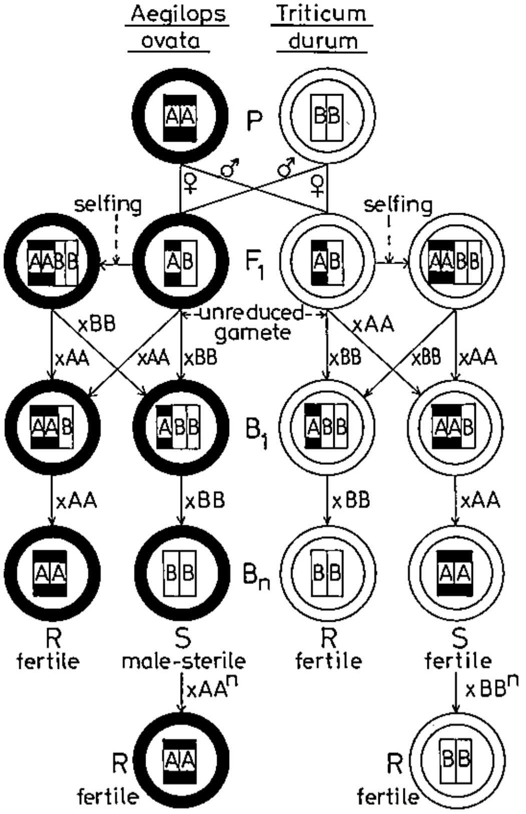


Fig. 3.45. Diagrammatic representation of the substitution and restoration of genome complements between *Aegilops ovata* and *Triticum durum*. *Inner circle:* nucleus and *outer zone:* cytoplasm. *Rectangle with A or B in inner circle:* haploid set of ovata and durum genome. S: substitution, R: restoration (after FUKASAWA, 1967)

The interacting mechanisms of the nuclear and cytoplasmic hereditary systems, causing gene-cytoplasmic male sterility, provide for a finer balance of fertility in the different genotypes than is possible with the purely nuclear system. Basic differential fertility levels, as found in natural and artificial gynodioecious populations, are further varied by environmental influences causing cyclic or seasonal fluctuations in the degree of male sterility (see e.g. DUVICK, 1965; PETERSON, 1958) usually not encountered with genic male sterility. Thus, the plasmon–genome–environment interaction produces a delicate balance in the expression of the trait.

The genetics of gene-cytoplasmic male sterility is abundantly documented in the literature for about 150 species and will not be detailed here (see reviews by EDWARDSON, 1956, 1970; CHOWDHURY and DUVICK, 1966; VARGHESE, 1968). "Restorer genetics", dealing with the interaction between plasmon-sensitive alleles and male-sterility-inducing plasmatypes, has become an important field of applied genetics due to its application in commercial hybrid seed production.

To be useful in hybrid seed production, genes restoring fertility of "male sterile" plasmatypes should be dominant. From an evolutionary point of view dominance of restorer genes is expected and, as a matter of fact, dominance of restorer genes is found with most "male sterile" plasmatypes [e.g. *C*, *S*, and *T* plasmatypes in maize (GRACEN and GROGAN, 1974); *S* and *T* plasmatypes in onion (VAN DER MEER, 1970; SCHWEISGUTH, 1973); timopheevi plasmatype in wheat (MILLER et al., 1974; BAHL and SAGE, 1972; MAAN, 1973)]. The presence of fertility restoring genes in populations carrying the "male sterile" plasmatype should be expected, whereas the recessive plasmon sensitive allele may occur in high frequency in populations carrying the normal plasmatype. Genetic studies, e.g. with onions (LITTLE et al., 1944; DAVIS, 1957; PIENAAR, 1958; KOBABE, 1958; BERNINGER, 1965; VAN DER MEER, 1970), crucifers (THOMPSON, 1972; BONNET, 1975), peppers (OHTA, 1972, 1973; FRANKEL and SHIFRISS, unpublished), and rice (SHINJYO, 1972a, 1972b), confirm correspondence of (*S*) plasmatypes with restorer genotypes in some populations while (*N*) plasmatypes can be found with plasmon-sensitive and/or restorer genotypes, the plasmon-sensitive allele often occurring with a very high frequency in (*N*) plasmatypes populations. We may then reach the conclusion that a non-sensitive cytoplasm may be combined with both sensitive and non-sensitive alleles in certain plant populations, and non-sensitive alleles may be combined with both sensitive and non-sensitive cytoplasm in other plant populations.

3.4.3 Structural, Developmental, and Biochemical Characterization of Male Sterility

We have so far categorized male sterility according to the inheritance pattern of the net effect, i.e., absence of viable pollen for fertilization. Characterization of male sterility by its final result makes possible generalization of a large number of cases of common hereditary, evolutionary and practical consequences. The male sterile phenotype may be described in any developmental stage and at different levels of details and compared with microgametogenesis in the normal phenotype. Structural, developmental and biochemical characterization of the androecium may help in understanding the sequence of events leading to male sterility and their control by hereditary elements. Absence of viable pollen for fertilization is often accompanied by additional phenotypical expressions of morphological or physiological nature, indicating pleiotropic effects of the male sterility genes or their close linkage with other genes controlling these expressions. We will try to integrate the present knowledge on genetically controlled events in microgametogenesis responsible for male sterility.

3.4.3.1 Developmental Modifications Leading to Breakdown in Microgametogenesis

Normal developmental organization of the androecium and of microgametogenesis has been described in Chapter 3.1.1 above. Comparative developmental studies of normal vs male sterile anthers reveal definite stages and modes of disturbances resulting in the absence of functional pollen. Figure 3.46 gives a schematic outline of probable events in microgametogenesis responsible for male sterility. The ontogenetic sequence of developmental stages at which the male sterile phenotype can first be identified, consists of the differentiation of androecium and microsporangium, microsporogenesis, microgametogenesis and anther dehiscence and will be discussed in that order. For a detailed review of the literature on stages and modes of disturbances leading to breakdown in microgametogenesis, the reader is referred to the paper of LASER and LERSTEN (1972) for cases of cytoplasmic male sterility and to the paper of GOTTSCHALK and KAUL (1974) for cases of genic male sterility.

3.4.3.1.1 Modifications in the Structural Differentiation of the Stamen

As we have seen in Chapter 3.2, in most cases the potentiality of sex suppression appears to be under hereditary control, whereas the degree of the expression depends largely on environmental conditions. Consequently, cases of male sex suppression in normally hermaphroditic flowers of monoecious plants vary in degree and are often vaguely defined as stamenless, antherless or simply as producing rudimentary, vestigial, warty, minute staminoida instead of normal stamens.

Failure of orderly stamen differentiation has been reported in a number of mutant genotypes of cultivated plants, e. g. in sorghum (KARPER and STEPHENS, 1936), maize (BEADLE, 1932), rice (CHANDRARATHNA, 1964), tobacco (RAEBER and BOLTON, 1955), snapdragon (SINK, 1966), pea (KLEIN and MILUTINOVIC, 1971); *Origanum vulgare* (LEWIS and CROWE, 1952), cucumber (BARNES, 1961), tomato (RICK, 1945b; LARSON and PAUR, 1948; BISHOP, 1954; HAFEN and STEVENSON, 1955, 1958), squash (SHIFRISS, 1945), and cotton (ALLISON and FISHER, 1964). All cases of faulty differentiation of the stamens, except cotton, appear to be controlled by single recessive genes, but their norm of reaction seems to be widely influenced by the environment. A good illustration of environmental influence is provided, on the one hand, by cases of artificial stamen suppression or sex reversion e. g. by morphactin in *Capsicum annuum* (JAYAKARAN, 1972) and in *Cannabis sativa* (MOHAN RAM and JAISWAL, 1971), respectively and, on the other hand, by artificial restoration of normal stamen differentiation e. g. by gibberellin in stamenless tomato (PHATAK et al., 1966). The relationship between level of gibberellin and the mutant genotype has recently been further clarified by SAWHNEY (1974). Male sex suppression often takes the form of differentiation into earlier sterile lateral members of the floral bud. Petals or petalloid structures are usually produced instead of stamens; this phenomenon is utilized in the production of "double flowered" cultivars of ornamentals such as stock *(Matthiola incana)* or begonia *(Begonia semperflorens)*. An example of petalloidy is presented in Fig. 3.47 (E), where male suppression is the result of interaction between the *Nicotiana undulata* plasmatype and plasmon-sensitive alleles. Male sex suppression is sometimes associated also with the suppression of the petals. Antherless and apetalous phenotypes have been reported, e. g.

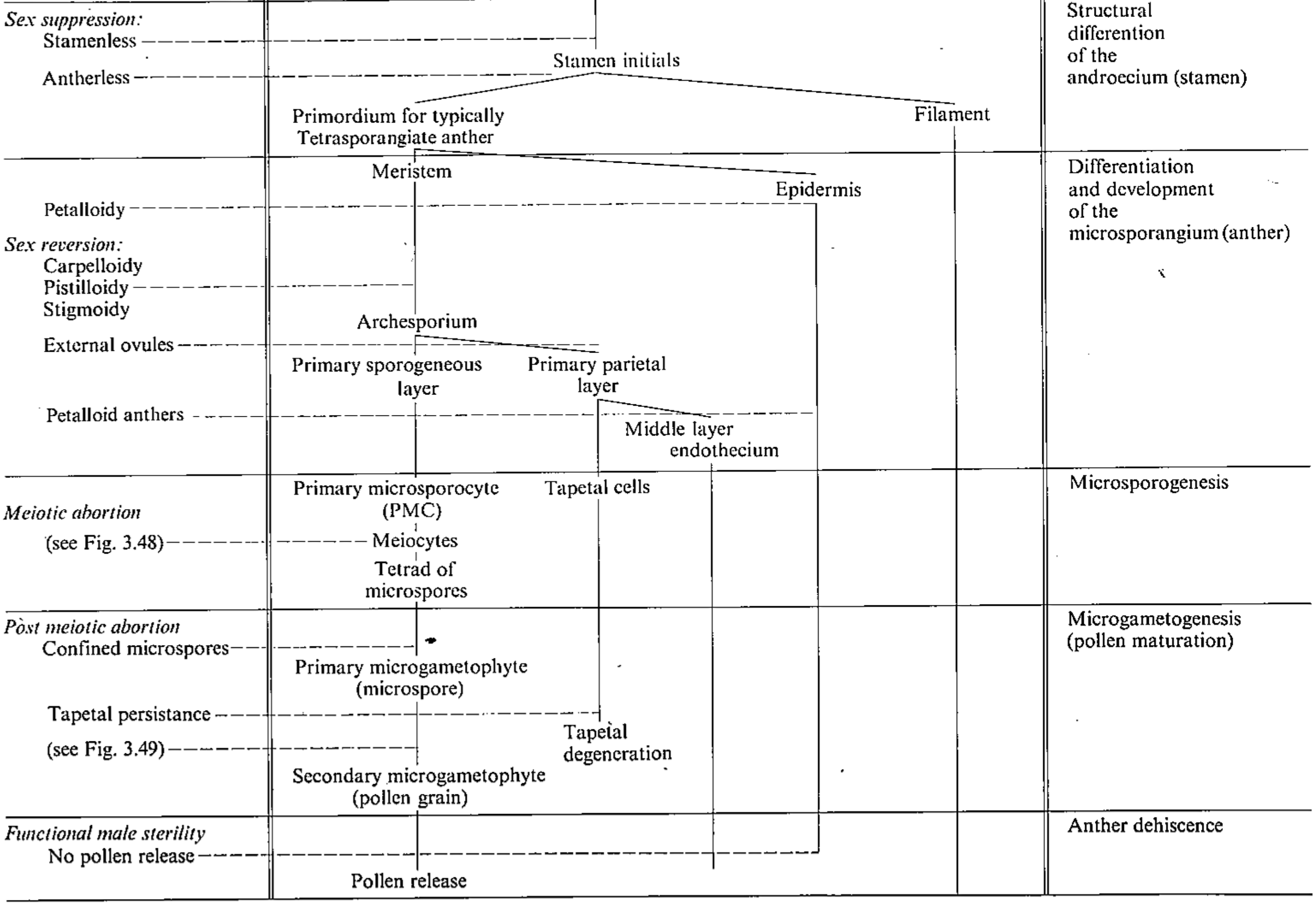


Fig. 3.46. Schematical outline of probable events in microgametogenesis responsible for male sterility

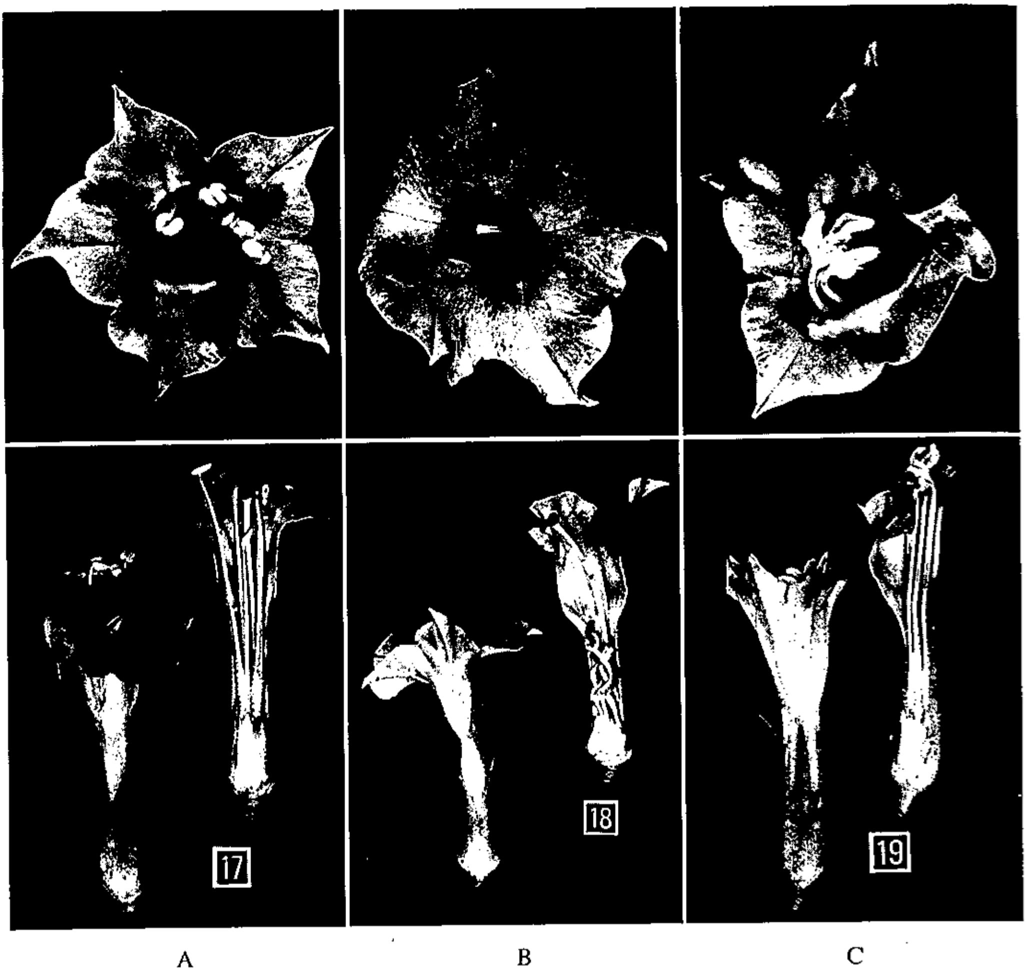
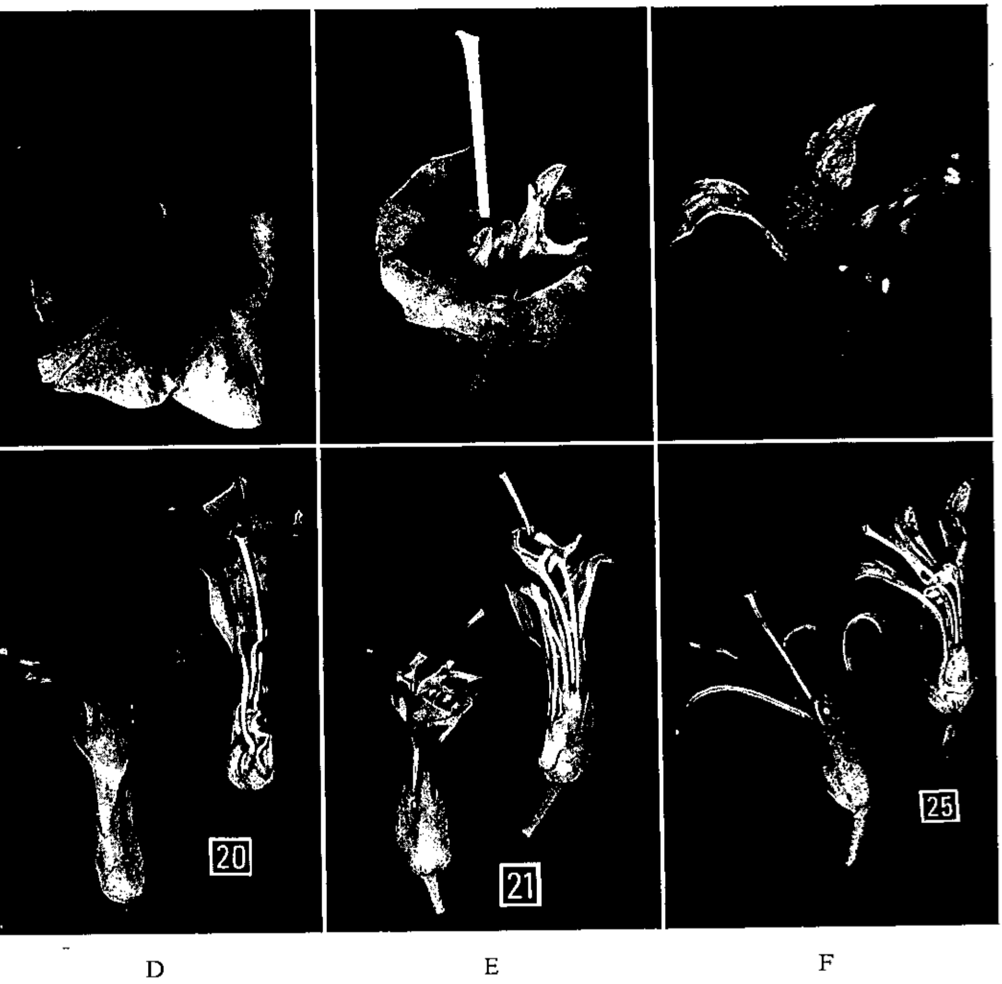


Fig. 3.47. Modifications in the structural differentiations of stamen or anthers as a result of interaction between *Nicotiana* plasmatypes and plasmon sensitive alleles in a *N. tabacum* × *N. glutinosa* hybrid: (A): *N. tabacum* plasmatype, cv "Hicks": phenotype normal, (B): *N. suaveolens* plasmatype, cv "Hicks": phenotype pistilloid, (C): *N. bigelovii* plasmatype, cv "Hicks": phenotype petalloid anthers, (D): *N. megalosiphon* plasmatype, cv "Hicks": phenotype carpelloid functional, (E): *N. undulata* plasmatype, cv "Hicks": phenotype petalloid, (F): *N. debnyi* plasmatype, cv Red Russian: phenotype stigmoid and split corrola

in zinnia (GOLDSMITH, 1968), snapdragon (SINK, 1966), thyme (APPL, 1933) and petunia (SINK, 1973).

3.4.3.1.2 Faulty Differentiation of the Anther

Aberrant anther differentiation most often indicates sex reversion which ranges from stigma-like extensions of the connective tissue in otherwise normal anthers to *stigmoid* male sterile anthers, *pistilloid* male sterile anthers to the development



of carpels instead of anthers with typical stigma and style, bearing ovules capable of development into normal seed *("Carpellody")*. A large number of cases of sex reversion can be related to plasmon–genome interaction (see Porter et al., 1965; Meyer, 1966; Fisher and Symko, 1973). Figure 3.47 (F) shows stigmoid, pistilloid [Fig. 3.47 (B)], and carpelloid [Fig. 3.47 (D)] phenotypes based on *Nicotiana debnyi*, *N. suaveolens* and *N. megalosiphon* plasmatypes respectively interacting with plasmon-sensitive alleles in a *N. tabacum* × *N. glutinosa* hybrid.

Sex reversion may also be expressed by the formation of external ovules on abnormally thickened staminal tubes [e. g. in interspecific hybrids of cotton (Meyer and Buffett, 1962) and tobacco (Burk, 1960) or in genic "stamenless" tomato (Sawhney and Greyson, 1973) and castor bean (Stein, 1965)].

Aberrant differentiation of the epidermal and primary parietal layers, and sometimes even of the primary sporogeneous layer often lead to petaloid anthers. If the primary sporogenous layer is also altered, such anthers are usually male sterile as, e. g., in a *Nicotiana bigelovii* plasmatype interacting with plasmon-sensitive alleles in a *N. tabacum* × *N. glutinosa* hybrid [Fig. 3.47 (C)], or in *Brassica nigra* plasmatype interacting with plasmon-sensitive alleles from *Brassica oleracea* (Pearson, 1972).

3.4.3.1.3 Breakdown in Microsporogenesis

Breakdown during microsporogenesis may involve a number of aberrations (see Fig. 3.48). The onset of irregularities seems to be related to faulty timing

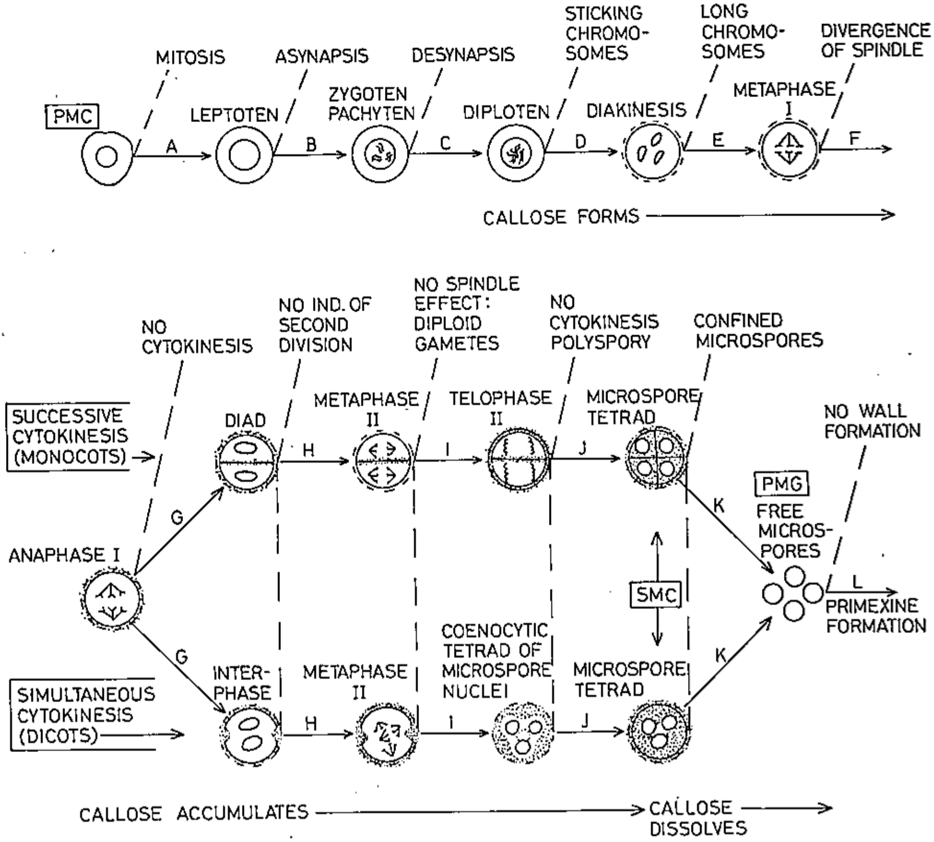


Fig. 3.48. Breakdown stages during microsporogenesis. A: Induction of meiosis, B: Pairing 1, C: Pairing 2, D: Terminalisation of chiasmata, E: Spiraling, F: Spindle effect, G: Cytokinesis (successive type), H: Induction of second division, I: Spindle effect, J: Cytokinesis, K: Microspore release, L: Primexine formation, PMC: Primary microsporocyte ($2n$), SMC: Secondary microsporocyte (n), PMG: Primary microgametophyte

and coordination of developmental sequences between sporocytes and tapetal cells since most cases show no definite stage but a range of abnormal behavior extending over part or all of the meiotic stages or even cover pollen maturation. The relative speed with which sporocytes undergo meiosis, the gradients in the degree of deviation, moving from the upper to the lower microsporangium and from the periphery of the PMCs to the middle of the locule, make critical evaluation of the exact stage of arrest in microsporogenesis difficult. Cells located in the upper anther lobes or near the tapetum appear usually less abnormal than cells in the lower anther lobes or farther away from the tapetum. Such observation, as well as the common occurrence of desynchronized groups of sporocytes, imply nutritional difficulties connected with tapetal development and unsynchronized activity.

The abortive process, though ordinarily not confined to definite stages, is recognized usually as an arrest centered on the early or final stages of meiosis [e.g. in tomato (see RICK and BUTLER, 1956) and in maize (see BEADLE, 1932)]. This may be so because of the relative duration of the meiotic stages or the relative genetic and metabolic autonomy of the meiocytes between late prophase and microspore tetrad stage as compared with the early and final stages of meiosis (see above).

In some male sterile genotypes, the primary (diploid) microsporocytes may not enter meiosis (Fig. 3.48 A); they may simply develop vacuoles and disintegrate [e.g. in winter squash (SINGH and RHODES, 1961) or tomato ms_3 (RICK, 1948)] or undergo synchronous mitosis instead of meiosis [e.g. in maize (PALMER, 1971) or raspberry (CRANE and THOMAS, 1949)].

Absence of pairing of homologous chromosomes during the first meiotic division (Fig. 3.48 B) has been reported in asynaptic male sterile mutants of maize (BEADLE, 1930) and tomato (ms_{10} RICK and BUTLER, 1956). Precocious separation of homologous chromosomes between pachytene and diplotene (i.e., desynapsis, Fig. 3.48 C), as found in male sterile alfalfa (CHILDERS, 1952) and pea (see GOTTSCHALK and KAUL, 1974), may be correlated with an observed chiasmata failure. Lack of terminalization of chiasmata (Fig. 3.48 D), resulting in sticky chromosomes, has been observed in male sterile violet (CLAUSEN, 1930), cowpea (SEN and BHOWAL, 1962) and tomato, ms_{18} (RICK and BUTLER, 1956). A few cases of faulty contraction of chromosomes (Fig. 3.48 E) have been reported for mutants of sweet pea (FABERGÉ, 1937), pea (see GOTTSCHALK and KAUL, 1974) and maize (BEADLE, 1932), arresting meiosis between diakinesis and metaphase I, exhibiting a "long chromosome phenotype".

In reviewing cases of male sterility showing irregularities during the first meiotic prophase, we may note that these are frequently associated with various degrees of impairment to the fertility of the female gamete. On the other hand, cases of male sterility showing irregularities in later stages only, never reveal impairment of female fertility. This may indicate that early in the sequence chromosomal pairing and gene recombination in both male and female sporocytes are controlled by the sterility genes, whereas a separate hereditary mechanism involves only microsporogenesis through metabolic upsets and nutritional deficiencies following the first metaphase. It may be of significance that meiotic irregularities after prophase I are always associated with deviant tapetal behavior (CHILDERS, 1952) and it may not be incidental that genic male steriles involving more than one locus and the majority of gene-cytoplasmic male steriles show abortion after the first meiotic division and characteristically do not affect female fertility.

Few cases of male sterility can be placed as being due to a breakdown between metaphase I and telophase II. Deficient callose formation has been found to be associated with abortion of meiocytes of cytoplasmic male sterile petunia (Frankel et al., 1969; Izhar and Frankel, 1971) and sorghum (Erichsen and Ross, 1963; Warmke and Overman, 1972). Divergent spindle orientation or action (Fig. 3.48 F) may lead to the formation restitution nuclei after the first meiotic division, [e. g. in potato (Ellison, 1936)]. Irregular spindle orientation after metaphase II (Fig. 3.48 I) is evident in genic male sterility of muskmelon (Bohn and Principe, 1964) and peppers (Novak et al., 1971). Cytokinesis may fail after telophase I in monocots (Fig. 3.48 G) featuring the successive type of cell plate formation, [e. g. in maize mutants ms$_8$ and ms$_9$ (Beadle, 1932)]. Quadripartition in the successive or simultaneous type of cytokinesis (Fig. 3.48 J) may not be completed and proper tetrads are not formed [e. g. in maize mutants ms$_4$ and ms$_{10}$ (Beadle, 1932) and pea mutants 395 (see Gottschalk and Kaul, 1974)].

Release of microspores from the tetrad bindings (Fig. 3.48 K) appears to be one of the most critical stages for the breakdown of microsporogenesis in male sterile mutants. Lack of enzymatic digestion of the callose envelope surrounding the young microspores in the tetrad seemingly starves the microspores and inhibits proper pollen production (Frankel et al., 1969; Izhar and Frankel, 1971). The sequel to progressive confinement of microspores within the callose envelope is arrest or disorganization of wall formation and mitosis of the microgametophyte and degenerated, sticky pollen grains [e. g. in *Aegilotricum* (Fukasawa, 1953), *Hordeum* (Mian et al., 1974; Chauhan and Singh, 1966), *Dactylis* (Filion and Christie, 1966), *Zea* (Modjolelo et al., 1966), *Solanum* (Abdalla and Hermsen, 1972), *Capsicum* (Horner and Rogers, 1974; Hirose and Fujime, 1975), *Petunia* (Edwardson and Warmke, 1972; Izhar and Frankel, 1971), *Cucumis* (Chauhan and Singh, 1968), *Lupinus* (Pakendorf, 1970), *Brassica* (Cole, 1959), and *Citrullus* (Kihara, pers. comm.)]. Release of microspores without subsequent primexine formation upon the primary microgametophyte (Fig. 3.48 L) has been mentioned as the first significant deviation from normal pollen maturation in male sterile mutants [e. g. in barley (Mian et al., 1974) and tomato (Rick, 1948)].

3.4.3.1.4 Abortion of the Microgametophyte

After release from the quartet callose capsule, the primary microgametophyte normally enters into a rapid stage of growth and develops vacuolation and exine (Fig. 3.49 M). Degeneration centered at this stage in microgametogenesis is very common in gene-cytoplasmic male steriles, e. g. in onion, beet, carrot and some crucifers (Laser and Lersten, 1972), and is frequently associated with delayed degeneration of the tapetum or other abnormal development of the tapetum or endothecium. Development of the microgametophyte may reach the stage of normal appearing vacuolate microspore but remain mononucleate, i.e. amitotic, and degenerate (Fig. 3.49 N). Such degeneration is known in particular in monocots (see Laser and Lersten, 1972; Gott-

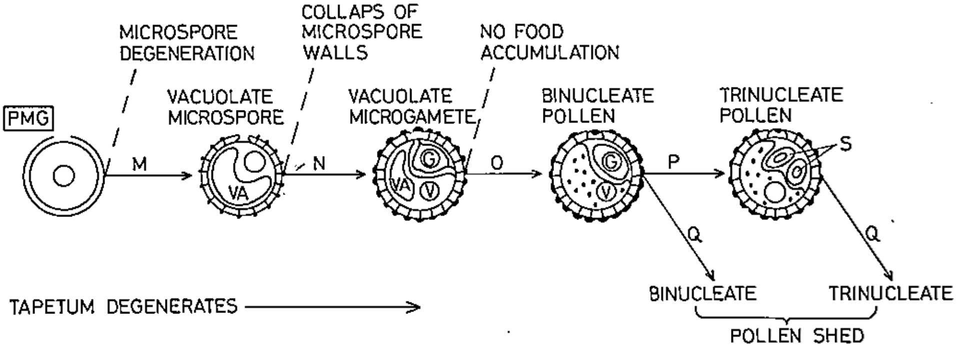


Fig. 3.49. Pollen abortion stages during microgametogenesis and functional male sterility. M: Exine and vacuole form, N: Microspore mitosis, O: Food reserve accumulation, P: Gamete mitosis, Q: Anther dehiscence, VA: vacuole, G: generative nucleus, V: vegetative nucleus, S: sperm cells

SCHALK and KAUL, 1974) and also is found correlated with abnormal tapetal activity and development (OVERMAN and WARMKE, 1972; PRITCHARD and HUTTON, 1972; HERVÁS, 1974; RAMANNA and HERMSEN, 1974). Amitosis is followed usually by collapse of the mononucleate microspore walls. Following microspore mitosis the vacuolate microgamete accumulates starch and other food reserves (Fig. 3.49 N). Cessation of further development associated with lack of food accumulation has been reported for gene-cytoplasmic male sterile grasses (e.g. for wheat—DE VRIES and IE, 1970; barley—SCHOOLER, 1967; sorghum—BROOKS et al., 1966; maize—KHOO and STINSON, 1957), and for genic male sterile tomato, ms_{13} (RICK, 1948), pea, mutant 195 B (GOTTSCHALK and KAUL, 1974), cucumber (WHELAN, 1972) and squash (FRANCIS and BERMIS, 1970). Non-degenerate tapetum appears to be correlated physiologically with the lack of build up of food reserves of the microgamete.

A review of the multitude of male sterile phenotypes reveals the most critical stages of the breakdown in microsporogenesis: clusters are evident at the early meiotic stages (stages A–E in Fig. 3.48), at the tetrad stage (stages J–K in Fig. 3.48), and at microspore maturation (stages M–N in Fig. 3.49). Sensitive phases in microgametogenesis appear to be related to concurrent events in the normal cataclysmic development of the tissue surrounding the sporocytes, through which nutritive material must either pass through or be metabolized: the tapetum (ECHLIN, 1971). Meiocytes and microspore tetrads are surrounded and isolated by a relatively impenetrable layer of callose which also undergoes normal cataclysmic build up and breakdown (WATERKEYN, 1964). Faulty timing of metabolic events during the short duration of many of the developmental stages in microgametogenesis (see e.g. FINCH and BENNETT, 1972; BENNETT and KALTSIKES, 1973; IZHAR and FRANKEL, 1973) must seriously affect the three mentioned phases in the development of the microgametophyte. The intimate metabolic relationship of an active tapetum with the early meiocytes obviously regulates nutrition and build up of the callose layers. The apparent enzymatic degradation of the callose envelope by glucanase activity of the declining and senescent tapetum is required to release the young microspore to the nutritive environment provided in part by degradation products of tapetal cells (see VASIL, 1967; MEPHAM and LANE, 1969; FRANKEL et al., 1969; ECHLIN, 1971; IZHAR and FRANKEL, 1971; STIEGLITZ and STERN, 1973). Thus, disturbance in the required physiological correlation between tapetal cells and developing microgametes must cause male sterility.

A number of generalizations can be made for male sterile phenotypes at the three critical phases of breakdown:

Early meiotic phase:	tapetum-deficient or disorganized callose—lack of formation or precocious digestion.
Tetrad phase:	tapetum—precocious or delayed degeneration callose—delayed digestion or persistence
Microspore maturation phase:	tapetum—persistent

The distribution of male sterile mutants studied (LASER and LERSTEN, 1972; GOTTSCHALK and KAUL, 1974) among phenotypes of the three phases appears to be different for plants of the successive versus the simultaneous type of cytokinesis and for gene-cytoplasmic versus genic male steriles (Table 3.28).

Table 3.28. Percentage distribution of male sterile phenotypes among three broad classes of abortion (based on LASER and LERSTEN, 1972; GOTTSCHALK and KAUL, 1974; and additional cases not covered by the two reviews)

Genetic type	Taxa	Breakdown phase		
		Early meiotic	Tetrad	Microspore maturation
Gene-cytoplasmic	all taxa	15	57	28
	dicots	27	58	15
	monocots	4	57	39
genic	all taxa	30	52	18
	dicots	32	56	12
	monocots	7	14	79

Due to gaps in the information available and to ranges of abnormal behavior often extending over several stages, assignment of phenotypes to a specific developmental phase is often quite imprecise. Nevertheless, the substantial comparison of the count of 62 cases of gene-cytoplasmic male sterilities (LASER and LERSTEN, 1972) and of 93 genic male sterilities (GOTTSCHALK and KAUL, 1974) seems to be indicative for quite significant differences: early meiotic breakdown is more frequently found among dicotyledonous plants (about 30%) than among monocotyledonous plants (about 6%). Very few tetrad breakdown types are found among monocotyledonous genic male steriles (14%) as compared with dicotyledonous genic male steriles, monocotyledonous and dicotyledonous gene-cytoplasmic male steriles (all about 57 % of the cases). The very high concentration of cases of genic male sterile monocots at the microspore maturation phase (79 %) is of particular interest.

In quite a number of important cultivated plants, belonging to the Amaranthaceae, Chenopodiaceae, Compositae, Gramineae, and Umbelliferae, pollen is shed trinucleate, i.e., its generative cell undergoes the additional mitosis before the pollen is shed (Fig. 3.49 P; KREMP, 1965; BREWBAKER, 1967). Trinucleate, as compared with binucleate pollen is regarded as more sensitive to dehydration, radiation and long storage, possibly because of its less pronounced exine and deprivation of the autonomous pollen grain of its reserves by the second mitotic division. The difficulties involved in observation of pollen mitosis may be responsible for the lack of exact information on the breakdown of what appears to be mature pollen grains (e.g. in some male sterile mutants of maize and wheat).

3.4.3.1.5 *Functional Male Sterility*

A number of male sterility genes prevent pollen release by modifying normal differentiation or functioning of the stomium and thus prevent release of otherwise fertile pollen through failure of anther dehiscence (Fig. 3.49 Q). Functional male sterile mutants leave the option of forced pollen release open and thus are found not only as recessive traits (as in tomato—see CLAYBERG et al., 1966) but also as dominant traits (see Chapter 3.1.2.1). Non-dehiscent anthers may be due to the absence of stomium (e.g. in eggplant—JASMIN, 1954; barley—ROATH and HOCKETT, 1971; rice—HOFF and CHANDRAPANYA, 1973); stomal cells may be tenacious and pressed by hooked petals which do not allow unfurling of corrolla (e.g. in ps mutant of tomato—LARSON and PAUR, 1948); and anthers may be reflexed or hard and filaments not elongating (e.g. in maize—SPRAGUE, 1939; clover—ATWOOD, 1944; tomato—CLAYBERG et al., 1966; grape—OLMO, 1943; and rubber—RAMAER, 1935).

3.4.3.2 Biochemistry of Male Sterility

The biochemistry of angiosperm pollen development was recently reviewed in detail by MASCARENHAS (1975). Therefore, we will restrict ourselves here to a few remarks on comparative biochemistry of the developmental phases in the male sterile and fertile microsporophylls. Differences in the level of a number of substances, their accumulation or disappearance during development, characterize normal versus disturbed biochemical communication between microsporocytes and the surrounding tissue (tapetum) in normal versus male sterile anthers. Such information describes effects, not causes. The hereditary elements responsible for male sterility may act autonomously in certain tissues or through a distant trigger, and regulation of their timing further conceals the source of the disturbed metabolism in male sterile anthers.

Several comparative studies of the free amino acid pool during microsporogenesis indicated differences between fertile and male sterile anthers. Many studies showed a characteristic deficiency of proline or cystine and accumulation of asparagine in sterile anthers, compared with fertile anthers (e. g. in wheat—FUKASAWA, 1954; RAI and STOSKOPF, 1974; maize—KHOO and STINSON, 1957; FUKASAWA, 1954; sorghum—SILVOLAP, 1968; KERN and ATKINS, 1972; petunia—IZHAR and FRANKEL, 1973). Other studies of sterile anthers indicate different alterations from the normal free amino acid pool, and phase-specific changes in the amount of some of the free amino acids are indicated in many studies. Since the balance of free amino acids in anthers may be subject to the action of several factors (e. g. protein and amino acid breakdown and synthesis, translocation into and out of the anther), alteration of the amino acid profile in sterile anthers may reflect either anabolic or catabolic processes. Thus, abnormally high asparagine accumulation may be associated with breakdown of the tissue (MCKEE, 1962; IZHAR and FRANKEL, 1973) or with some block in the metabolic pathway between asparagine and ornithine in the TCA cycle (FUKUSAWA, 1962).

Changes in the amino acid pool within the anther locule may in part account also for normal or abnormal changes of the pH in the anther locule. Such changes, associated with asparagine or glutamine accumulation in male sterile anthers of petunia, have been correlated with a drop in pH altering the timing of the phase-specific callase activity, causing breakdown in microsporogenesis by delayed or precocious action of the enzyme in genic male sterile or cytoplasmic male sterile mutants of petunia, respectively (IZHAR and FRANKEL, 1971, 1973). The dependence of callase activity on pH, lack of glucanase activity in the microsporocytes at all stages of meiosis, and its presence in the tapetum and anther locules at the time of the normal degradation of the callose matrix of the microspore quartet (ESCHERICH, 1961; STIEGLITZ and STERN, 1973), lead to the belief that faulty activation of the enzyme in the anther locule may be a primary factor in microspore abortion.

The rationale of exact timing of the callase activity, external to the microsporocytes, becomes even more evident in the view of the normal dynamics of callose and primexine synthesis which is at least in part internal to the microsporocytes. Studies of plastids during microsporogenesis suggest that polysaccharide reserves of starchy plastids disappear in microspores during callose and cellulosic primexine synthesis (DUPUIS, 1974). Recurrent, transitory formation of callose walls around the normal generative cell of the microgametophyte (GORSKA-BRYLASS, 1967; HESLOP-HARRISON, 1968; MEPHAM and LANE, 1970) after the orderly dissolution of the callose matrix of the tetrad capsule, accentuates the significance of the exact dynamics of synthesizing and degrading enzymes during microgametogenesis. The role of the callose wall, as providing a molecular filter and thereby establishing a certain degree of transitory autonomy for meiocytes, quartets of microspores, and perhaps also to the generative cells of the microgametophyte, has been proposed (HESLOP-HARRISON, 1964) and questioned (MASCARENHAS, 1975). Regardless of the true role of the callose walls, unquestionably any abnormal and untimely formation or dissolution has been shown to cause male sterility (FRANKEL et al., 1969; IZHAR and FRANKEL, 1971; HAYWARD and MANTHRI-

RATNA, 1972; NOVAK, 1972; OVERMAN and WARMKE, 1972; PRITCHARD and HUTTON, 1972; HORNER and ROGERS, 1974).

We have seen that genetic elements control breakdown in microsporogenesis and microgametogenesis locally within the anther through upsets in the biochemical communication between microsporocytes or microgametophytes and surrounding tissue. Genetic elements causing modification of the normal structural differentiation of the microsporophyll appear to act through hormonal metabolism at the stamen primordia level, causing sex suppression or reversion. Although we are not aware of direct comparative studies on hormone production or receptors during differentiation of male sterile and fertile flowers, responses to exogenous growth regulators, such as auxins, gibberellins and kinins (see Section 3.2.1.5 above), leave no doubt about the hormonal control system of sex suppression or reversion.

3.4.3.3 Male Sterility Genes and Their Action

3.4.3.3.1 Site of Male Sterility Factors

Male sterility genes are transmitted biparentally, uniparentally or both. Reversible suppression of uniparentally–maternally inherited male sterility by the action of chromosomal fertility restoration testifies not only to the constancy of the genetic determinants, but also to the independent production of RNAs and proteins by the nuclear and extranuclear genome of the plant. BOGORAD (1975) asserts that "compartmentalization of functions in membrane-limited nuclei, mitochondria and plastids is the hallmark of eukaryotic life, and understanding the genetic and metabolic interactions of organelles and the nuclear-cytoplasmic system (is) a central problem of cell biology". In this sense, male sterility and fertility restoration resulting from intergenomic cooperation may be conceived as a result of *one* gene product composed of two or more complementary subunits or of *two or more* structural and regulatory gene products coded by each of the two hereditary systems.

Uniparental transmission of the extrachromosomal factor can be understood if we assume that the sterility factor is located in a DNA-containing cytoplasmic fraction which is contributed to the progeny exclusively by the maternal parent. Mitochondria and plastids are considered the most likely candidates to carry the genetic information for cytoplasmic male sterility for they are membrane-limited organelles accommodating independent DNA, transfer RNA, ribosomes, and suitable synthetizing enzymes (see BORST, 1972; KIRK and TIENEY-BASSETT, 1967 respectively for mitochondria and plastids). Absence of mitochondria or plastids from the male germ cells, or some mechanism preventing male organelles from entering the egg cells, must be responsible for the exclusive maternal transmission of mitochondrial or plastid male sterility genes.

Studies indicate that most plastids and mitochondria of the angiosperm male gametophyte become incorporated into the vegetative cell, and the generative cell and resulting sperm cells receive very few if any plastids, although they contain mitochondria in most plants (for references, see MASCARENHAS, 1975). It is of interest to note that in those cases in which plastids were not found in the male generative cells (e.g. in maize—LARSON, 1963, 1965; petunia—SASSEN, 1964; *Impatiens*—VAN WENT, 1974; *Mirabilis jalapa*—LOMBARDO and GEROLA, 1968), chlorophyll variegation is transmitted only maternally ("status albomaculatus"), whereas in cases in which chlorophyll variegation can be transmitted biparentally ("status paralbomaculatus"), numerous proplastids have been identified in the generative cell (e.g. in *Pelargonium zonale*—LOMBARDO and GEROLA, 1968; *Oenothera hookeri*—WALLES, 1971; *Hypericum perforatum*—see HAGEMANN, 1964). In the absence of detailed information concerning the fate of paternal mitochondria of angiosperms during syngamy, the absence of plastids in the male generative cells may not be the only mechanism whereby paternal transmission is inhibited. Paternal mitochondria and plastids may or may not be excluded during syngamy; they may even prevail and exclude maternal mitochondria and plastids as indicated by the exclusive paternal origin of these organelles in some gymnosperms (GIARNORDOLI, 1974).

Our ignorance about the fate of cytoplasmic organelles before, during and after syngamy in the sexual offspring restricts assumptions regarding the site of the cytoplasmic male sterility gene to extrapolations based on pleiotropic or linked genetic markers. A number of alterations of the normal structure or function of mitochondria of plastids in cytoplasmic male sterile plants are considered indications of associated effects of action of the male sterile mitochondrial or plastidal genome. However, even such definition of the plasmon is complicated by the possibility of the presence and differential reproduction rate of more than one type of mitochondrion or plastid (see e.g. SCHÖTZ, 1958). Different plastid or mitochondrial types can be present in the same cell ("mixed cells") and somatic "sorting out" produces various chimeral arrangements of cells. As a result there may occur variable male sterile phenotypes or mosaic male sterile phenotypes in which the border of different organelle types coincides with the border between fertile and male sterile regions, such as in variegated *Oenothera* (STUBBE, 1959, 1960).

In the "iojap" genotype of maize, the plasmatype mutates not only to code for male sterility (see Fig. 3.42) but also for chlorophyll variegation. Nevertheless, the apparent independence of the two phenotypes led RHOADES (1950) to suspect that the mitochondrial genome is the site at which the male sterility factor is located. The southern corn leaf blight epidemics of 1970–1971 in the USA (TATUM, 1971; ULLSTRUP, 1972), associated with the *T* male sterile plasmatype, were followed by many comparative studies of specific effects of the responsible pathogen (*Helminthosporium maydis* race *T*) and its pathotoxin on mitochondria of normal versus male sterile and restored *T* plasmatypes. Sensitivity of the *T* plasmatype (MILLER and KOEPPE, 1971) appears to be related to the binding of the pathotoxin on the inner membrane of its sensitive mitochondrion (PETERSON et al., 1975). Pollen bioassay shows that the pathotoxin inhibits germination and growth of pollen of restored *T* plasmatypes, whereas pollen of normal or other restored male sterile plasmatypes is unaffected (LAUGHNAN and GABAY, 1973). The extent of the functional aberrations of the mitochondria introduced by the *T* male sterile cytoplasm can be modified by restorer genes (BARRATT and FLAVELL, 1975; WASTRUD et al., 1975), but susceptibility could not be overcome completely by nuclear gene resistance (SCOTT and FUTRELL, 1975). A similar situation is found with susceptibility of *T* male sterile maize inbreds and their hybrids to yellow leaf blight (*Phyllostica* sp.: see e.g. ARNY et al., 1970; LUNSFORD et al., 1955), and with susceptibility of male sterile plasmatypes of wheat to races of leaf rust (WASHINGTON and MAAN, 1974) and pepper to potato virus *X* (NAGAICH et al., 1968), although in these cases no direct studies of possible functional aberrations of their mitochondria have been made. Recent electrophoretic comparison of restriction endonuclease fragmented mitochondrial DNA of normal and *T* male sterile maize also revealed distinctions between the two cytoplasmic types (LEVINGS and PRING, 1976); these are thought to constitute additional evidence that the mitochondrion is the organelle involved in the inheritance of the trait.

The fact that the majority of cases of extrachromosomal inheritance in higher plants are male sterilities and chlorophyll variegations (see HAGEMANN, 1964; RHOADES, 1955) naturally led investigators to consider the plastid genome as the site of the mutant plasmagene (e.g. STINSON, 1960; STUBBE, 1964). Recent investigation on the genetic responsibility of the chloroplast genome for the large subunits of ribulose—1,5 diphosphate (RuDP) carboxylase-oxygenase may provide clues as to the plasmon-genome interaction causing gene-cytoplasmic male sterility (see KUNG, 1976). The enzyme (fraction 1 protein), comprising more than 50% of the total soluble leaf protein in plants, is responsible for the crucial reactions in both photosynthesis and photorespiration, and the code of a mutant plastid genome may thus alter qualitatively or quantitatively the generation of carbohydrates. Since the small subunits and the overall rate of synthesis of fraction 1 protein appear to be controlled by the nuclear genome, plasmon-genome interaction is easily conceived. A study with cytoplasmic male sterile tobacco confirmed that the three polypeptides of the large subunits of the enzyme are identical to those found in *Nicotiana suaveolens*, which served as the original female parent: and that the two polypeptides of the small subunits are identical to those found in *N. tabacum*, which served as the recurrent parent (CHEN et al., 1975).

Evidence from some graft experiments suggested asexual transformation to male sterility in the progeny of cytofertile symbionts of heteroplastic grafts (petunia—FRANKEL, 1956, 1962; EDWARDSON and CORBETT, 1961; BIANCHI, 1963; CORBETT and EDWARDSON, 1964; beet—CURTIS, 1967; maize—BOROWSKY, 1960; pepper—OHTA and CHUONG, 1975; tobacco—FRANKEL, unpubl.; alfalfa—THOMPSON and AXTELL, 1973). Other graft experiments did not confirm graft transmission of the sterility factor or its effects (petunia—VAN MARREWIJK, 1970; beet—CLEIJ, 1967; THEURER et al., 1968; maize—RHOADES, 1933; SHUMWAY and BAUMAN, 1966; pepper—OHTA, 1961; tobacco—SAND, 1960; BURK, 1960; wheat—ZEVEN, 1967; LACADENA, 1968; onion—VAN DER MEER and BENNEKOM, 1970; *Crotolaria*—EDWARDSON, 1967; *Epilobium*—MICHAELIS, 1940). Despite the conflicting results, such asexual transformation to male sterility has been attributed to the presence of and genetic information of latent viruses or other infectious agents in cytoplasmic male sterile plants (EDWARDSON and CORBETT, 1961; ATANASOFF, 1964, 1971). The idea of "infectious heredity" is supported by the fact of graft and seed transmission of some plant viruses causing various degrees of reduced male fertility (e.g. barley stripe mosaic virus—McKinney and Greeley, 1965; tobacco ring spot virus—Valleau, 1932; Desjardins et al., 1954; broad bean wilt virus—Crowley, 1957; Ohta, 1970; tobacco mosaic virus—McKinney, 1952; Ohta, 1970). The relation between virus infection and gene-cytoplasmic male sterility has been corroborated in experiments with peppers indicating that the action of the nuclear fertility-restoring alleles is actually reduced by virus infection (Ohta, 1975).

Graft-transmitted cytoplasmic male sterility behaved generally as a cytoplasmically inherited trait in successive generations but in one case the transmission resulted in Mendelian inheritance of male sterility (Frankel, 1962). This case has been explained as being due possibly to chromosomal association or integration of the extrachromosomal factor transmitted through the graft union. As such, male sterility would be due to alternative genetic factors analogous to the behavior of episomes in bacteria (Frankel, 1971). In other words, bits of genetic information for male sterility could be distributed and only transitorily compartmentalized among genomes of a variety of cell entitites (e.g. nuclei, mitochondria, plastids, symbionts, pathogens) and "gene distribution mutants" (Bogorad, 1975) may occur. A model of intergenomic and metabolic cooperation responsible for the mutant structure and function of cell organelles, the breakdown in microgametogenesis and associated phenotypic effects is indeed consistent with present knowledge of the genetics of male sterility and fertility restoration as well as of genetic continuity, distribution and exchange of male sterility factors among genomes of cell entities.

3.4.3.3.2 Pleiotropic Effects

Developmental modifications leading to the breakdown in microgametogenesis may be related developmentally to pollen abortion, but modifications of physiological traits leading to divergent agronomic performance among normal, male sterile and restored versions of otherwise isogenic material must be due to pleiotropic or linked effects of nuclear and extranuclear male sterility loci. Pollen sterility per se in non-restored genotypes may have a secondary effect and in maize shows yields about 2% higher than those of restored genotypes (Duvick, 1965). Reduced intraplant competition for assimilates by tassels during early development of the plant may explain such higher yields of non-restored hybrids (Criswell et al., 1974). However, such yield increases can be considered only a partial compensation for yield reductions of 2–4% among restored hybrids carrying *T* cytoplasm (Noble and Russell, 1963). Plant stature and leaf number are generally higher in hybrids with normal cytoplasm than with *T* cytoplasm (Duvick, 1965). Hybrids having restored *T* cytoplasm show earlier silk emergence and delayed pollen shedding when compared with normal versions (Grogan and Sarvella, 1964; Sarvella and Grogan, 1965). The disastrous southern corn leaf blight epidemics in the USA (see above) can be accounted for by comparative grain yield studies of corn hybrids in normal and *T* male sterile cytoplasm infected with *Helminthosporium maydis* (e.g. Lim et al., 1974).

ATKINS and KERN (1972) evaluated normal, cytoplasmic male sterile and restored versions of sorghum lines and hybrids, but did not find differences of practical importance. Studies of the effect of two tobacco male sterile plasmatypes (*Nicotiana megalosiphon* and *N. suaveolens)* on agronomic performance and chemical characteristics indicated adverse effects which could not be overcome by fertility restorer genes (MANN et al., 1962; POVILAITIS, 1972; HOSFIELD and VERNSMAN, 1974; respectively). Male sterile (A) lines of wheat carrying *Triticum timopheevi* cytoplasm show high preharvest seed sprouting whereas their fertile (B) counterparts do not sprout at all (DOIG et al., 1975). Five *Aegilops* plasmatypes induce parthenogenesis at high frequencies in common wheat (TSUNEWAKI, 1974). Suppression of the development of the flower beyond the stage in which the corolla emerges (blindness), bud blasting, and extreme delay of flowering are usually associated with male sterile plasmatypes of petunia; this makes such plasmatypes useless for hybrid seed production, although the adverse effects may be partly overcome by gibberellin treatment (IZHAR, 1972).

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 cytoplasmic male sterility 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.

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

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

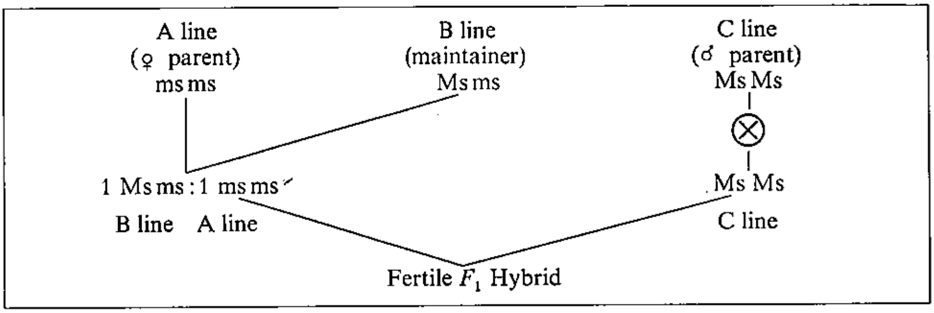


Fig. 3.50. A scheme for maintenance of parent lines and hybrid seed production using genetic male sterility

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.

3.4.4.1.2 Cytoplasmic Male Sterility

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.

3.4.4.1.3 Gene-Cytoplasmic Male Sterility

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.

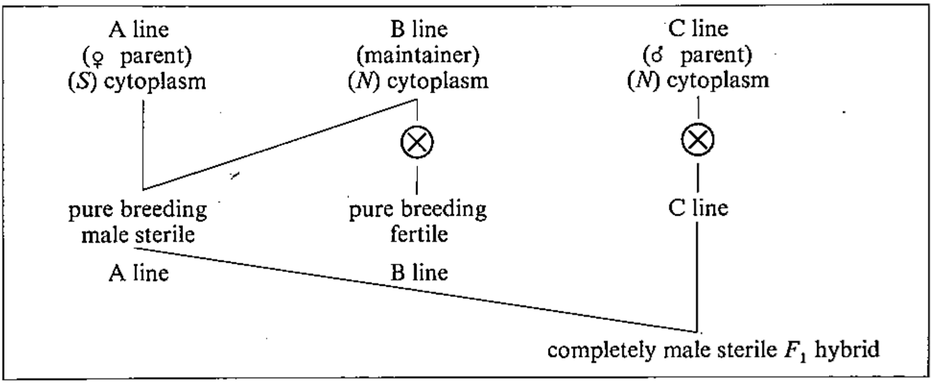


Fig. 3.51. A scheme for maintenance of parent lines and hybrid seed production using cytoplasmic male sterility

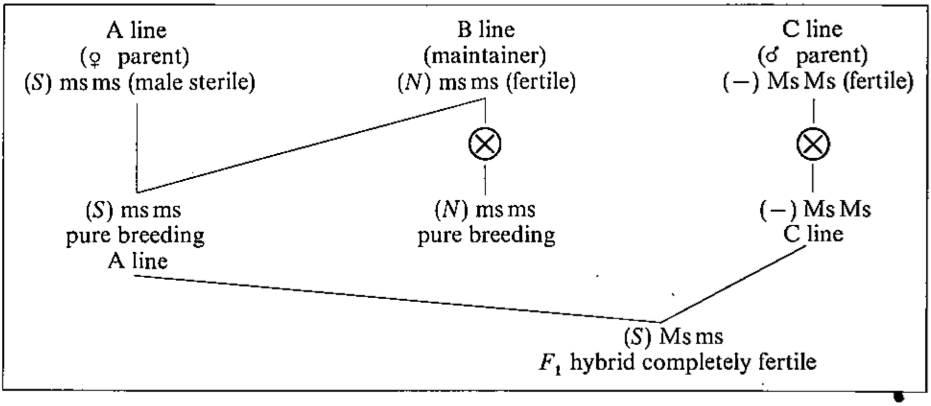


Fig. 3.52. A scheme for maintenance of parent lines and hybrid seed production using gene cytoplasmic male sterility

3.4.4.2 Application of Genic Male Sterility

Most efficient use of clever genetic manipulation of male sterility may be required to overcome a basic shortcoming in the use of genic male sterility, namely, the difficulty in obtaining economically a 100% genic male sterile stand. Consequently, the application of genic male sterility is still restricted to hybrid seed production of those cultivated plants in which cytoplasmic male sterility has not been found (e.g. in autogamous crops such as tomatoes and barley) or those in which the male sterile plasmatype shows inferior agronomic performance.

3.4.4.2.1 Genetic and Field Management Programs to Provide a Homogeneous Stand of the Genic Male Sterile Seed Parent

The customary maintenance scheme for the female parent of the hybrid (A line) will produce 50% heterozygous fertile plants (see Fig. 3.50), but a number of field management and genetic programs can be devised to provide an homogenous stand of the male sterile seed parent:

Selfing of Recessive Male Sterile Mutants. Many male sterile mutants will restore male fertility under certain natural or artificial environmental conditions (see e.g. JUSTUS and LEINWEBER, 1960; HANSCHE and GABELMAN, 1963; RICK and BOYNTON, 1965). Such conditions could be defined accurately and applied for the increase of pure A line seed. Functional male sterile mutants [see Chapter 3.4.3.1.5] produce, but do not release, pollen and can be selfed. However, due to the variable phenotype and unpredictable environmental conditions, reliable sterility of such mutants can often not be kept in the hybrid seed production field. To overcome this difficulty it may be useful to have in the A line recessive marker genes not present in the C line (♂ parent line). This way, the degree of contamination of the hybrid seed lot can be monitored and, in some instances, the selfed progeny of the A line can be removed in the nursery before transplanting.

Clonal Propagation of Male Sterile Mutants. A solid stand of male sterile plants can be established by vegetative propagation. Such a method may be economical in plants easily propagated vegetatively, such as brassicas (GABELMAN, 1975), cotton (SANTHANAM et al., 1972) and ornamentals (GOLDSMITH, 1968).

Physical Removal of Fertile Heterozygotes. In mutants which can be forced to self, stability of male sterility is usually not dependable under field conditions. Consequently we must use stable mutants and resort to removal of the heterozygous fertiles from the seed production field. Double density planting should be practised to insure a full stand in the field (see HORN, 1974; LAPUSHNER and FRANKEL, 1967). Normally, fertile plants must be removed before anthesis, since pollen shedding obviously endangers the production of pure hybrid seed. In many cases reliable identification of fertile plants also requires microscopical examination. However, in plants that are essentially self-pollinating, where no natural vectors for pollen transfer exist, and where hand pollination is practised (e.g. in tomatoes), we can wait for the first fruit to set upon selfing and then remove all plants bearing fruits.

The removal of heterozygous fertile plants may be facilitated by pleiotropic effects of the recessive male sterility gene, such as deviant structural differentiation of the corrolla, the stamens or the anthers [see Chapter 3.4.3.1.1 and 3.4.3.1.2]. In the absence of pleiotropic effects, marker genes closely linked to the male sterility locus with a clear phenotype expression may be used. Seedling markers are of special value since roguing at the seedling stage in the nursery is cheaper than removal of adult plants in the field. Some successful attempts have been made in this direction (in tomato CLAYBERG, 1966; SORRESSI, 1968; PHILOUZE, 1974; cabbage—SAMPSON, 1970; cucurbits—WHELAN, 1974; WATTS, 1962). Physiological markers, such as resistance to phytocides, can be used to leave only the homozygous male steriles in the hybrid seed production field (e.g. in barley—HAYES, 1959; WIEBE, 1960). Height differentials, resulting from linkage of stature with male sterility genes, can be used for roguing by way of pre-anthesis cutting of the taller heterozygous phenotypes, thus leaving a pure stand of the shorter homozygous male sterile (A line) phenotypes (WIEBE, 1968).

SINGLETON and JONES (1930) proposed to use close linkages between endosperm color and male sterility genes in maize to insure a pure stand of the male sterile parent in the hybrid seed production field. Since no close linkages were available the scheme was not found useful. However, the recent proposal of GALIANT (1975) for hybrid seed production of bicolor sweet corn, appears to resolve the problems of recombinants when linkage is fairly close; the scheme may potentially be exploited as well for other crops having a conspicuous endosperm coloration. The program makes use of a homozygous seed parent and a heterozygous maintainer (in the coupling phase) for white endosperm and male sterility (A line y–ms/y–ms; B line Y–Ms/y–ms). The male parent of the hybrid must be homozygous for fertility and yellow endosperm (C line Y–Ms/Y–Ms). The white seed from the maintenance field is separated by an electronic eye seed sorter to furnish A line seed mixed with a small proportion of recombinants. Separation of yellow seed from the hybrid seed production field removes all selfed seed of the recombinants (which will be white).

Use of Extra Chromosomes. A number of possibilities to obtain an 100% genic male sterile stand are made available by the breeding behavior of balanced tertiary trisomics or plants carrying an extra homoeologous chromosome derived from related species. Since chromosome segments on both sides of the breakpoint of the extra chromosome or the extra homoeologous chromosome are not transmitted through the pollen, fertility and marker genes located on them can aid in the identification of the male sterile genotypes. Schemes for utilizing balanced tertiary trisomics for hybrid seed production of diploid crops were outlined by RAMAGE (1965) and are presently used for the production of hybrid barley seed. These schemes use height, phytocide susceptibility, and seed size or shape differentials to selectively combine harvest or separate diploids, trisomics and F_1 hybrids. DRISCOLL (1972) proposed the use of genic male sterility of the crop plant and a corresponding fertility factor on an homoeologous alien chromosome. The principles of such an efficient scheme for hybrid wheat seed production are outlined in Fig. 3.53.

3.4.4.2.2 *Pollination Control*

Sufficient natural cross pollination in combination with male sterility would be desirable for economic hybrid seed production, but utilization of natural cross pollination in the production of hybrid seed on genic male sterile seed parents faces two types of problems: The highly self-fertilizing nature of many of those species where genic male sterility for hybrid seed production is of potential importance, and the very nature of male sterile flowers to be unattractive to pollen-gathering insects. Consequently, we may often find that pollen transfer from the C line to the A line by wind or insects does not result in sufficient seed set and that the activity of discriminating insect vectors may be limited to C line flowers. Even in flowers in which nectar is the main attractant, natural cross pollination of male sterile flowers often yields much less seed than hand pollination (see e.g. BREUILS and POCHARD, 1975).

Sometimes natural cross pollination may be improved by various means, such as: manipulating the ratio of pollen donors to seed parents, manipulating the spacing and location of pollen donors in relation to seed parents (planting

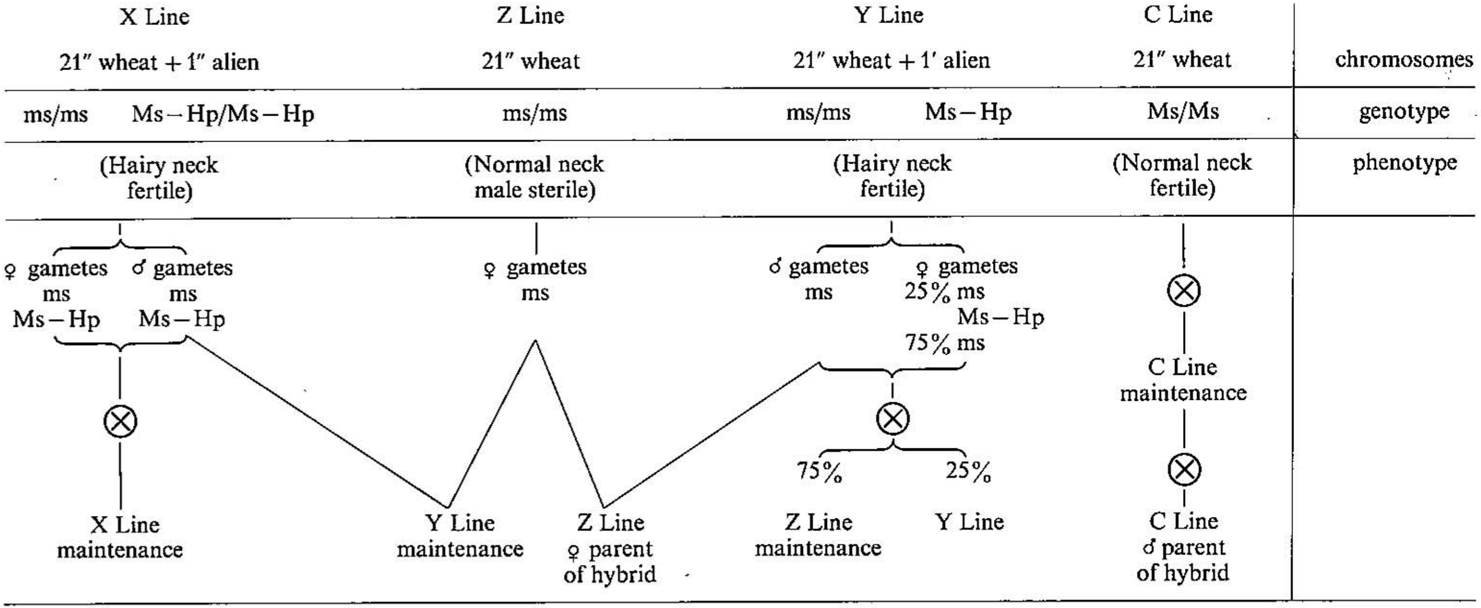


Fig. 3.53. The XYZ system of producing hybrid wheat (adapted from DRISCOLL, 1972)

design), choice of pollen donor (extent of pollen shedding, attraction to vectors, flower morphology), choice of male sterile seed parent (flower morphology, ovule and egg number per flower), choice of appropriate season and regions, and proper nicking of A and C lines. Some of these subjects have been discussed in Sections 1.3 and 2.3.2.3.

If natural cross pollination cannot be improved sufficiently, it can only be replaced by hand or otherwise artificially forced pollination, which may still be economical with high-value or widely spaced crops. The details of the production procedures depend on the flower biology of the species. As an example, Table 3.29 compares tomato hybrid seed production detailing the production steps required when hand-emasculated and -pollinated male fertile seed parents, hand-pollinated male sterile seed parents, or naturally cross-pollinated male sterile seed parents are used. Breakdown of time expenditures for efficient production methods with fertile seed parents (about 40% for emasculation, 15% for pollen collection and storage, 30% for hand pollination, 5% each for marking flowers, removal of fruits from uncontrolled pollination and selective harvesting of fruit), and a higher fruit set and seed count when using male sterile seed parents, attest that expenditures in maintenance of the male sterile line and the removal of heterozygotes in the hybrid seed production field are much more than offset by savings in time. Thus, when hand pollination is necessary in high-value autogamous plants (e.g. tomato, pepper, eggplant and flower crops), genic male sterile parents become a definite asset in hybrid seed production and sometimes may be decisive in its economics.

Table 3.29. Steps in the production of tomato hybrid seed (LAPUSHNER and FRANKEL, 1967)

	Production procedures		
	Use of male fertile female parents	Use of male sterile female parents and artificial pollination	Use of male sterile female parents and natural cross-pollination
Maintenance of male sterile line	–	+	+
Identification and removal of heterozygotes	–	+	+
Emasculation	+	–	–
Pollen collection and storage	+	+	–
Hand pollination	+	+	–
Marking of flowers	+	–	–
Removal of fruits from uncontrolled pollination	+	–	–
Selective harvesting of fruit	+	–	–

3.4.4.3 Use of Gene-Cytoplasmic Male Sterility

Gene cytoplasmic male sterility has already found large-scale application in the production of hybrid seed. In the USA, production based on gene-cytoplasmic male sterility reached about 90% of the cultivated area for hybrid sorghum, about 60% for hybrid sugar beet, and up to 85% for hybrid field corn (DUVICK, 1966). Hybrid cultivars of vegetable crops, produced by means of gene-cytoplasmic male sterility, comprise 94% of the sweet corn, 27% of the onion, and 7% of the carrot acreage in the United States (GABELMAN, 1974). In other highly developed countries the statistics are similar. The reason for such large-scale use of gene-cytoplasmic male sterility lies in the straightforwardness of the procedures providing for pure breeding male sterile A lines and fertility restoration in the hybrid. Male-sterility-inducing plasmatypes of "Autoplasmic" origin in allogamous plants (Fig. 3.42) and of "Alloplasmic" origin in autogamous plants (Fig. 3.43) have been found almost universally. Past experience showed that detection of a male-sterility-inducing plasmatype in a crop plant was always followed by the discovery of additional, distinct cytosteriles. Thus, it appears probable that cytoplasms causing male sterility and fertility restorer genes could very likely be found for any crop plant by combining various plasmatypes and genotypes. However, successful application of gene-cytoplasmic male sterility to F_1 hybrid seed production cannot be achieved by male sterile plasmatypes and restorer genes alone, but a number of obstacles have to be overcome.

Insufficient cross pollination to produce the hybrid seed is a problem mainly with autogamous plants. Flowers may stay closed (as in flax) or not expose their stigmata sufficiently to receive pollen (as in wheat). Obviously cleistogamous flowers cannot serve as pollen donors, and genetic control of anther extrusion may become important (see e.g. DE VRIES, 1973; SAGE and ISTURIZ, 1974). In entomophilous plants, effective transfer of pollen from the C line to A line may be hampered by preference of insects for the pollen fertile C line (see WILLIAMS and FREE, 1974). To overcome limitations in cross pollination, phenotypes with appropriate flower morphology, planting design, choice of season and region for growth, manipulation of pollen vectors, etc., could be of help (see above and DE VRIES, 1971; STOSKOPF and RAI, 1972; MILLER et al., 1974; MOFFETT and STITH, 1972). Concurrent receptivity of styles of the female parent and pollen shedding by the male parent ("nicking") are of utmost importance and must be manipulated genetically or by cultivation techniques, as outlined in Chapter 3.3.1.

Inbreeding depression is a problem with allogamous plants and results in low seed production of inbred parent lines. This may be due also to partial female sterility as a result of a pleiotropic effect of the male sterile plasmatype. A solution to the problem may be sought in the production of double-cross hybrids, as is general practice with field corn (RICHEY, 1950; DUVICK, 1965). Various combinations of male sterile cytoplasm and fertility restoration genes can be used in double-cross hybrid production schemes (see Fig. 3.54). Alternatively, when fertility of the hybrid is required, non-restored double-cross hybrid seed may be mixed (in cross-pollinated crops) with seeds of the same cross combination, using emasculation procedures.

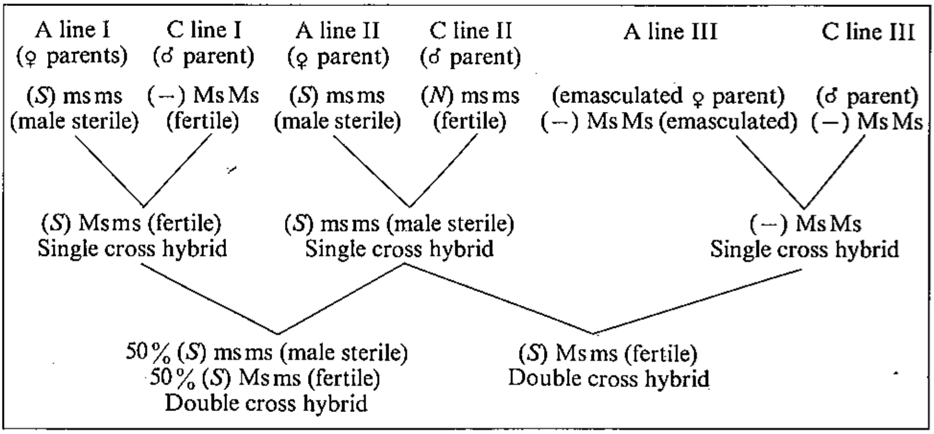


Fig. 3.54. Examples of alternative schemes for double-cross hybrid seed production using gene-cytoplasmic male sterility and fertility restoration

Unreliable stability of male sterility may make the desired genotype useless as seed parent or necessitate additional breeding work (e.g. in cotton—MEYER and MEYER, 1965; and alfalfa—BARNES and GARBOUCHEVA, 1973). The polyploid nature of species (e.g. wheat) and undesirable linkages may cause *complications in fertility restoration* and, as discussed in Chapter 3.4.3.3.2 above, *undesirable pleiotropic effects of the plasmatype* may cause inferior agronomic performance of the hybrid. In maize, yield advantage of hybrids produced with cytoplasmic male sterility is in some instances partly due to the absence of pollen (DUVICK, 1965), but restoration of pollen production removes this advantage. Mixing seed of an identical hybrid combination made with detasselling and with male sterility may improve yields of hybrids.

Where male fertility of the hybrid is of no importance ploidy combinations can be utilized. Triploid hybrids of root crops (e.g. sugar beets—KINOSHITA and NAGAO, 1968) or ornamental plants (e.g. begonia—HORN, 1971) can be conveniently produced by a tetraploid male sterile A line and a diploid C line. Female fertility in tetraploids is generally better than male fertility and haploid pollen is far more functional than diploid pollen.

We observe gynodioecy in natural populations, recognize multitudes of male-sterility-inducing plasmatypes, nuclear male sterility and fertility-restorer genes, and see large-scale application of male sterility for hybrid seed production. Therefore we may expect that the cross pollination mechanism based on male sterility will indeed increasingly serve plant breeding and mankind.

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