Chapter 5
Gametocidal Genes

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5.1 Introduction

Long before the practice of genetic manipulation, many chromosomes and genes have been introgressed into cultivated plants from related wild and crop plants. Generally alien chromosomes introduced into crops by interbreeding are stably maintained by substituting for homoeologous chromosomes in the hosts. Otherwise, alien chromosomes would be eventually eliminated from the descendants of initial hybrids by occasional nonsegregational events because they are surplus, namely dispensable chromatin to the hosts. Even in an exceptional case of successful alien introgression, namely the substitution of rye chromosome 1R or 1B/1R translocation in bread wheat (Schlegel and Korzun 1997), the introgressed rye chromosome would be lost in the descendants of the inter-varietal crosses without cytological check or phenotypic selection.

However, there are certain chromosomes and genes that stay in host plants in a selfish manner once they are introgressed through interspecific crossing. Such genes or chromosomes are called "pollen killer" (Cameron and Moav 1957; Loegering and Sears 1963) or "gamete eliminator" (Rick 1966; Sano 1990) or gametocidal chromosomes (Endo 1990, 2007); hereafter in this chapter, the author collectively call such genetic factors as gametocidal (Gc) chromosomes/genes and use the term "Gc system" to refer to the mode of action of the Gc gene. The term "gametocidal"

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was first adopted in a paper by Maan (1975), in which the behavior of an alien chromosome exclusively transmitted in common wheat was described with the following sentence: "There was thus an apparent gametocidal action of the sporophyte having an *Aegilops* chromosome on the gametes lacking this chromosome."

Gc chromosomes, which are dispensable to the host, ensure the predominance of gametes containing them over gametes lacking them, presumably by killing or damaging the latter gametes. This situation occurs when Gc chromosomes are in hetero- or hemizygous condition, causing preferential transmission and persistent existence of the Gc chromosomes in hosts (Fig. 5.1). Superficially similar cases of preferential transmission of introgressed chromosomes were reported in some cytoplasmic substitution lines of wheat, in which the abnormal behavior of the alien chromosome can be attributed to the interaction between nuclear and cytoplasmic genes (Tsuji and Murata 1976; Nakata et al. 1993). Specific chromosomes derived from the cytoplasm donors are indispensable to the viability of zygotes of the wheat lines carrying the alien cytoplasm; therefore, the alien chromosomes persist in the wheat lines. These chromosomes do not have Gc genes but so-called fertility-restorer genes. The Gc gene might occur by mutation, but it would easily be regarded as a normal allele of a mutated gametic lethal gene. In rice, hybrid sterility genes were identified as Gc genes in linkage analysis of the backcross progeny of intra- and interspecific hybrids. In this chapter two well-documented cases of the Gc system in wheat and rice are described.

5.2 Gametocidal Chromosomes in Wheat

5.2.1 *Preferential Transmission of Alien Chromosomes*

Many interspecific hybrids were made between wheat and its related wild species, and the hybrids were repeatedly backcrossed to wheat in order to produce alien chromosome addition and substitution lines (Jiang et al. 1994), and also to produce alien cytoplasm substitution lines (Tsunewaki et al. 1996). Even though hybrids are

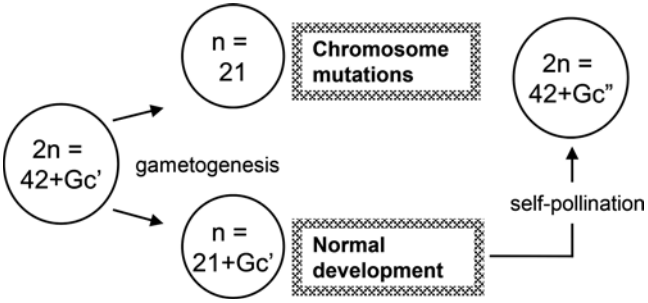

Fig. 5.1 Schematic diagram of Gc action in common wheat carrying a single Gc chromosome. 42 and 21 represent the wheat chromosome numbers in zygotes and in gametes, respectively. +Gc′ and +Gc″ stand for the addition of one dose and two doses of gametocidal chromosome, respectively

highly sterile, in backcross progeny normal fertility, especially female fertility, is restored, as the genome constitution of the progeny gets close to that of the recurrent parent. However, there are some cases where certain alien chromosomes tenaciously persist in a selfish way in the backcross progeny. Endo and Tsunewaki (1975) tried to substitute the nuclear genome of natural and synthetic strains of *Aegilops triuncialis* for that of common wheat by repeated backcrossing. After five backcrosses, however, the backcross progeny still carried an extra chromosome from the cytoplasm donors, without improving their male and female fertility. They did not know whether the sterility was caused by the interaction between the *Aegilops* chromosome and the cytoplasmic genome, or by the *Aegilops* chromosome by itself. Maan (1975) tried to substitute the nucleus of common wheat into the cytoplasm of *Ae. longissima* and *Ae. sharonensis*, and obtained partially sterile plants having one *Aegilops* chromosome. Crossing such plants as pollen parents to euploid common wheat, he again obtained partially sterile offspring carrying the *Aegilops* chromosome, and found the selfed progeny to be exclusively disomic for the *Aegilops* chromosome. Thus the sporophyte having the *Aegilops* chromosome apparently exerted a Gc action on gametes not containing it (Fig. 5.1). Miller et al. (1982) backcrossed the F_1 hybrid between common wheat and *Ae. sharonensis* in an attempt to produce a set of addition lines of *Ae. sharonensis* into common wheat. However, they found all addition lines to contain one and the same alien chromosome, typically corresponding to a Gc chromosome. Finch et al. (1984) showed that such a Gc chromosome (called "cuckoo" chromosome) ensures its transmission by causing chromosome breaks in meiospores lacking it. Similarly, a chromosome derived from decaploid *Thinopyrum ponticum* (formerly *Agropyron elongatum*), named $7el_2$ for its homoeology to wheat group 7 chromosomes, was found to carry a Gc gene(s), which, in the wheat background, induced its preferential transmission through female gametes and abortion of those lacking it (Scoles and Kibirge-Sebunya 1983).

5.2.2 *Diversity of Gc Chromosomes in the Genus* Aegilops

After the first findings of Gc chromosomes in wheat, many more Gc chromosomes were found in various species of the genus *Aegilops* possessing different genome (genomes C, S and M) and belonging to different homoeologous groups (groups 2, 3, 4, and 6) (for review see Endo 1990, 2007; Tsujimoto 2005). Their identity in terms of the Gc action was investigated in double monosomic plants for different Gc chromosomes (Endo 1982, 1985). When a plant carried both chromosome 3C and 2S or both 3C and 4S, only gametes with both Gc chromosomes were functional, and the plant had severely reduced fertility. On the other hand, from a plant carrying both 2S and 4S, gametes carrying 4S were functional, regardless of the presence or absence of 2S, with the plant having a similar fertility to that of the 4S monosomic addition plants (Fig. 5.2). The former case shows that the Gc action of 3C is

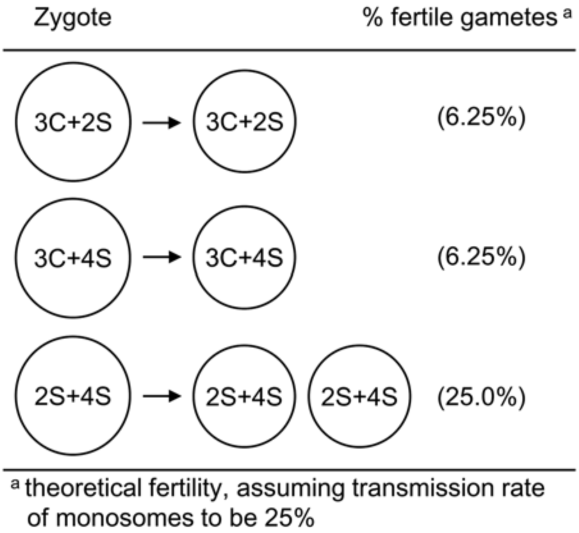

Fig. 5.2 Schematic diagram of Gc action in common wheat carrying two different types of Gc chromosomes 3C, 2S, and 4S. The diagram is based on the data published by Endo (1982). The actual seed set percentages from hand pollination with euploid wheat pollen are 6.5 % for 3C+2C, 5.4 % for 3C+4S, and 15.0 % for 2S+4S (see text for details)

independent from that of 2S and 4S, and therefore both Gc chromosomes should coexist in functional gametes. The latter case, instead, suggests either that 4S epistatically suppresses the Gc action of 2S or that 4S has two Gc genes, one of which is the same as that located on 2S.

5.2.3 Modification of Gc Action

Depending on the host cultivar into which a Gc chromosome is introduced, the Gc action varies. Chromosome 2C, for instance, has a complete Gc action and is therefore exclusively transmitted to the progeny in the common wheat cultivar Jones Fife, whereas its Gc action becomes incomplete in the common wheat cultivar Chinese Spring, in whose background chromosome 2C can be lost in part of the progeny (Endo 1988). Chromosome 3C has a severe Gc action in Chinese Spring and some other common wheat cultivars, but it displays almost no Gc action in Norin 26, which possesses the *Igc1* Gc-inhibitor gene on chromosome 3B (Tsujimoto and Tsunewaki 1985). In both cases of incomplete Gc action, semi-lethal chromosomal mutations occur in gametes lacking the Gc chromosome, and structurally rearranged chromosomes are transmitted to the progeny.

The Gc gene in sporophytes seems to have a dual function, i.e. to induce chromosomal mutations in gametes that lack it and to suppress such mutations in gametes that include it. This was demonstrated by a knockout mutation for the *Gc2* gene on *Ae. sharonensis* chromosome 4S, which renders the former function ineffective, while having no influence on the latter function (Friebe et al. 2003).

5.2.4 Use of Gc Gene in the Production of Deletion and Dissection Lines

Thanks to its hexaploid nature, common wheat can tolerate aneuploidy and chromosomal structural changes to a considerable extent. Using mostly chromosome 2C, Endo and Gill (1996) produced about 350 homozygous deletion lines of Chinese Spring wheat that contain deletions of various size in specific chromosomes. These lines are useful in cytologically mapping (deletion mapping) of genes and especially DNA markers to the missing chromosomal regions (Werner et al. 1992; Qi et al. 2004). Most of the Chinese Spring deletion lines, together with the Gc chromosomes, are available from NBRP-wheat website (http://www.shigen.nig.ac.jp/wheat/komugi/strains/aboutNbrpLgku.jsp).

The Gc system can be usefully applied to the induction of structural changes in alien chromosomes introduced into common wheat, particularly in the case of alien chromosomes from species distantly related to wheat, showing little tendency to undergo homoeologous recombination with wheat chromosomes even under genetically permissive conditions (see Chap. 6). As an example, the *Ae. cylindrica* Gc chromosome 2C was introduced into all barley disomic addition lines into Chinese Spring wheat, except for 1H (Shi and Endo 1997). Chromosomal rearrangements were induced by the 2C gametocidal system for each barley chromosome, including 2H (Joshi et al. 2011), 3H (Sakai et al. 2009), 4H (Sakata et al. 2010), 5H (Ashida et al. 2007), 6H (Ishihara et al. 2014), and 7H (Schubert et al. 1998; Serizawa et al. 2001; Masoudi-Nejad et al. 2005; Nasuda et al. 2005). The Gc system was similarly proved to be effective in inducing structural rearrangements in rye chromosome 1R introduced into common wheat (Endo et al. 1994; Masoudi-Nejad et al. 2002; Gyawali et al. 2009, 2010; Li et al. 2013). Genomic in situ hybridization (GISH) represents a useful tool to identify Gc-induced structural changes of alien chromo-

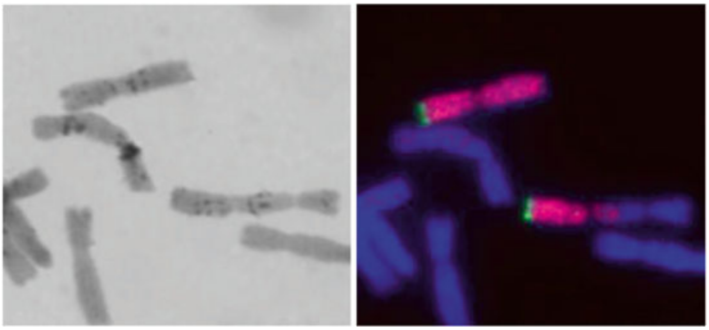

Fig. 5.3 C-banding (*left*) and fluorescence in situ hybridization (*right*) images showing normal barley chromosome 2H and a translocation between 2H and a wheat chromosome induced by the gametocidal system. Green fluorescence represents the barley subtelomeric sequences HvT01 and pink fluorescence shows barley chromatin. This translocation is seemingly part of a dicentric chromosome

somes in common wheat (Fig. 5.3). Since both terminal deletions and wheat-alien translocations enable cytological mapping of alien chromosomes, the present author have been developing many common wheat lines carrying deletions and translocations of alien chromosomes, collectively named "dissection lines." Comparative studies of cytological and genetic maps conducted in the above studies revealed that crossing-over is generally more frequent in the distal region than in the proximal region for all the wheat, barley, and rye chromosomes that were studied.

5.3 Gametocidal Genes in Rice

5.3.1 Hybrid Sterility by Allelic Interaction at a Single Locus and Selective Gamete Abortion

There are two species of cultivated rice, *Oryza sativa* L. ($2n=24$) and *O. glaberrima* Steud. ($2n=24$), which originated in Asia and West Africa, respectively. *O. sativa* has two subspecies ssp. *japonica* and ssp. *indica*. Hybrids between the two species or between the two subspecies normally form 12 bivalents at meiosis, but it is well known that sterility, on the male or both male and female side, is prevalent in these hybrids.

Among many gene loci responsible for female sterility in *indica-japonica* hybrids, S_5 is a major one (Ikehashi and Wan 1996). There are three alleles at the S_5 locus, an indica allele, S_5^i, in *indica* varieties, a japonica allele, S_5^j, in *japonica* varieties, and a neutral allele, S_5^n, in some varieties of a third, *javanica* subspecies or wide compatibility varieties. In the hybrid with genotype S_5^i/S_5^j, gametes carrying the S_5^j allele are aborted, while no gamete abortion occurs in the hybrid with genotypes S_5^i/S_5^n and S_5^j/S_5^n. Therefore, the S_5^n allele has been incorporated into various rice cultivars to obtain fertile hybrids in hybrid rice breeding (Ikehashi 2009). The S_5^i allele acts like a Gc gene (cf. Fig. 5.1) and the S_5^n allele is the equivalent of the abovementioned inhibitor gene *Igc1* which knocks out the Gc gene of 4S (see Sect. 5.2.3).

Sano et al. (1979) repeatedly (eight times) backcrossed the male sterile but partially female fertile hybrid between *O. sativa* and *O. glaberrima* to each of the parents to obtain semi-sterile isogenic lines having the genetic background of the *sativa* and *glaberrima* parents. Self-pollination of these lines produced fully fertile progeny plants, and backcrossing these lines to the parents produced semi-sterile progeny plants. They applied a model, described as "one locus sporo-gametophytic interaction," to the sterility in the interspecific hybrid, assuming that the *sativa* and *glaberrima* parents have two sterility genes $S_1^aS_1^a$ S_2S_2 and S_1S_1 $S_2^aS_2^a$, respectively, and that if an S_1 or S_2 gene is present in the maternal tissue, gametes with S_1^a or S_2^a deteriorate (Fig. 5.4). This explanation conforms to the gametocidal system in wheat involving two different Gc chromosomes, when S_1 and S_2 are assumed to correspond to, e.g., 2C and 3C, respectively (cf. Fig. 5.2).

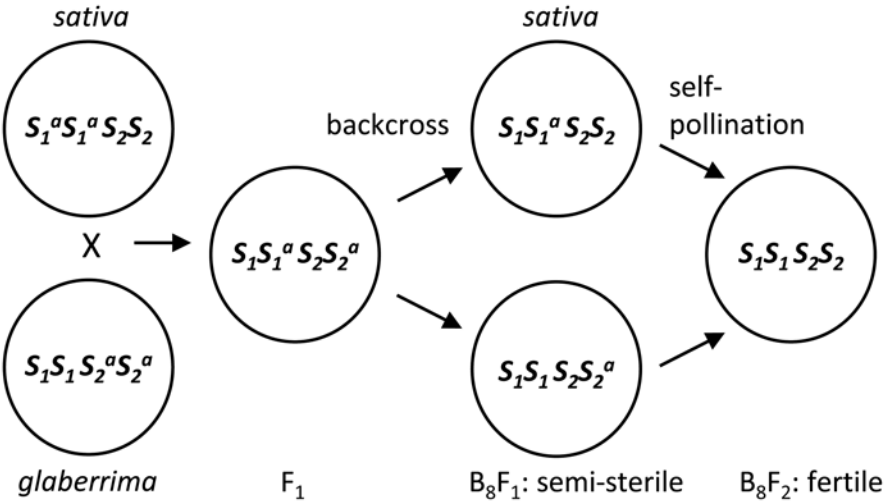

Fig. 5.4 Schematic diagram of hybrid sterility in rice, based on the description of hybrid sterility between *O. sativa* and *O. glaberrima* reported by Sano et al. (1979). See text for details

5.3.2 Epistatic Control of Hybrid Sterility Genes

Sano (1990) found that the intensity of hybrid sterility, namely Gc action, caused by the S_1 gene varied depending on *O. sativa* cultivars into which S_1 was introduced, and that the Gc action decreased as the S_1-containing chromosomal segment from *O. glaberrima* became smaller as a result of recombination during backcrossing. He inferred that S_1 and some modifiers linked to S_1 form a gene complex showing profound hybrid sterility.

Kubo et al. (2008) used rice near-isogenic lines carrying IR24 (ssp. *indica*) genomic segments in the genetic background of Asaminori (ssp. *japonica*) and found two new loci, *S24* and *S35*, causing male semi-sterility in this inter-subspecific combination. The *S24* locus has the IR24 allele (*S24*-ir) and the Asaminori allele (*S24*-as), and *S24*-ir acts as a pollen killer: the heterozygotes (*S24*-ir/*S24*-as) produce two types of microgametophytes after meiosis, with pollen carrying *S24*-as selectively aborted, and, as a consequence, exclusive transmission of pollen with the *S24*-ir allele to the offspring. On the other hand, the *S35* locus, also with two alleles, *S35*-ir and *S35*-as, shows the male semi-sterility phenotype only in the progeny carrying the *S24*-ir allele, i.e., the *S24*-ir/*S24*-ir *S35*-ir/*S35*-as and *S24*-ir/*S24*-as *S35-ir*/*S35*-as genotypes. This suggests an epistatic interaction occurring between the two hybrid sterility genes in rice, similar to what hypothesized in wheat between the Gc genes on *Aegilops* chromosomes 2S and 4S (cf. Fig. 5.2). Kubo et al. (2011) found that the hybrid male sterility caused by *S24* is also epistatically controlled by the *EFS* gene, which has two alleles, the dominant *indica* allele (*EFS*-*i*) and the recessive *japonica* allele (*efs*-*j*). The *EFS*-*i* allele in sporophytes counteracts the pollen sterility caused by *S24* heterozygosity, but the *efs*-*j* allele does not. Although *S24* and *EFS* are located on different chromosomes, *EFS* seems to act like the S_5^n allele against the S_5^i in *indica*-*japonica* hybrids.

The mutational origin of hybrid sterility genes in rice was demonstrated in irradiation experiments (Wan and Ikehashi 1996a). Variety Miyukimochi, which is an irradiated mutant from Toyonishiki, has two hybrid sterility genes, $S5^j$ and $S7^j$, while Toyonishiki carries a neutral allele, $S7^n$; therefore $S7^n$ must have been mutated into $S7^j$ by irradiation. A second case is that of the experimental line 02428 that has the wide compatibility allele $S5^n$. This line is derived from a progeny population of a hybrid whose parents both have $S5^j$; therefore, $S5^j$ must have mutated into $S5^n$ in both parents as a result of irradiation. The second case is similar to the knocked-out Gc gene of chromosome 4S in wheat (Sect. 5.2.2), but the first case, i.e., the creation of a Gc gene, is not known in wheat.

5.3.3 Evolutionary Implication of the Gametocidal System

Hybrid sterility prevents the movement of genes from one population to the other within a species, which keeps both populations distinct and eventually leads to speciation. Suppose two Gc genes of different type, which do not compensate for each other, are in different populations; hybrids between the two populations will suffer from sterility due to the gametocidal action. In case the two different Gc genes are on nonhomologous chromosomes, one-fourth of the gametes produced by the hybrid become fertile because the nonhomologous chromosomes segregate at random in meiosis (cf. Fig. 5.2). On the other hand, if the Gc genes are on homologous chromosomes, all gametes of the hybrid become sterile, because the homologous chromosomes pair and segregate from each other in meiosis I, and therefore no gametes will possess both Gc genes. Thus, sexual isolation would be established in a species between two populations that easily cross-fertilized.

The formation of new Gc genes or the alteration of existing Gc genes by mutation is most probable as reported in rice (Wan and Ikehashi 1996a) and wheat (Friebe et al. 2003). There are various hybrid sterility gene loci in *O. glaberrima* (Sano 1990) and *O. sativa* (Wan and Ikehashi 1996b). Gc chromosomes of various homoeologous groups have been introduced into wheat from different *Aegilops* species, including those from the S genome of *Ae. sharonensis*, which involve homoeologous groups 2 and 4, and those from the C genome of *Ae. cylindrica* and *Ae. triuncialis*, which are in homoeologous groups 2 and 3, respectively (Endo 1990, 2007). All the mentioned Gc chromosomes/genes have presumably been involved in the sexual isolation and speciation of wheat and rice. A suggestive example of sexual isolation within a species is seen in hybrids between allopatric accessions of *Ae. caudata*, which have normal meiotic chromosome pairing, but produce completely sterile pollen (Ohta 1992). This sterility might be explained as the result of the occurrence of two different alleles at the Gc loci on homologous chromosomes of the allopatric accessions. If so, since the Gc alleles segregate during meiosis I into separate daughter cells, none of the microgametophytes produced by the hybrids will receive both Gc alleles and will be thus able to develop into fertile pollen.

The presence of incomplete Gc action suggests that the Gc system is involved in the karyotype evolution of the genus *Aegilops*. Incomplete Gc action induces chromosomal rearrangements in hybrids heterozygous for a Gc gene, and gametes with rearranged chromosomes will survive and take part in self-fertilization. The karyotype of the selfed progeny will stabilize when the Gc gene will become homozygous, and some well-balanced karyotypes might be established in separate populations. Although not well investigated yet, chromosomal mutations also occur in the zygotes of hybrids between 4S addition line and euploid common wheat, only when chromosome 4S is transmitted through pollen (Tsujimoto 2005). Thus, the Gc system might have induced karyotype changes in gametes and zygotes of interspecific hybrids that were formed during polyploid evolution of wheat and *Aegilops* species.

The abovementioned Gc genes or chromosomes are only those showing pronounced Gc action. Considering the omnipresence of such highly penetrant Gc genes in plants, there must be more Gc genes with low penetrance throughout almost all plant species, and, altogether, they must have played a major role in the evolution of plants, in terms of karyotype diversification and speciation by sexual isolation. Probably the same is true for animals. This sort of selfishness of Gc genes might be the nature of living organisms as is more prevalent in human society.

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