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The gametocidal chromosome as a tool for chromosome manipulation in wheat

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Abstract

Many alien chromosomes have been introduced into common wheat (the genus *Triticum*) from related wild species (the genus *Aegilops*). Some alien chromosomes have unique genes that secure their existence in the host by causing chromosome breakage in the gametes lacking them. Such chromosomes or genes, called gametocidal (Gc) chromosomes or Gc genes, are derived from different genomes (C, S, S^l and M^g) and belong to three different homoeologous groups 2, 3 and 4. The Gc genes of the C and M^g genomes induce mild, or semi-lethal, chromosome mutations in euploid and alien addition lines of common wheat. Thus, induced chromosomal rearrangements have been identified and established in wheat stocks carrying deletions of wheat and alien (rye and barley) chromosomes or wheat–alien translocations. The gametocidal chromosomes isolated in wheat to date are reviewed here, focusing on their feature as a tool for chromosome manipulation.

Introduction

Genes use various strategies for their survival in host organisms. Genes beneficial to their hosts are maintained not only in the individuals but also in the population, simply by realizing 'the survival of the fittest'. Some genes, DNA sequences, or chromosomes, even though they are not beneficial to the hosts at all, are known to ensure their survival in 'selfish' manners. The most famous examples are transposable elements, which are present in all organisms from bacteria to human beings. Transposable elements increase their copies by migrating to different chromosomal locations or by making copies that can move to other chromosomal regions. In this way they ensure their existence in a selfish manner. B chromosomes are also a well-known example of selfish genetic elements. They are widely distributed both in the plant and animal kingdoms, although they are dispensable extra chromosomes. Most B chromosomes in plants ensure their existence by accumulating in their hosts through meiotic or mitotic drive (Jones 1995).

In wheat, a group of chromosomes called gametocidal (designated as Gc hereafter) chromosomes are known to remain in host plants in a selfish way. Gc chromosomes were first isolated during the production of alien cytoplasm substitution lines or alien chromosome addition lines in common wheat (*Triticum aestivum* L., $2n = 6\times = 42$). Certain alien chromosomes were not removed during backcrossing the hybrid between wild species (the genus *Aegilops*) as female and wheat to wheat ($6\times$ or $4\times$) (Maan 1975, Endo & Tsunewaki 1975). Miller *et al.* (1982) obtained alien additions of the same chromosome in an attempt to produce all seven alien chromosome

additions of *Ae. sharonensis* Eig in common wheat. Such exclusive retention of alien chromosomes in common wheat was attributed to their unique Gc action, causing sterility in gametes without the Gc chromosome. Finch *et al.* (1984) demonstrated that the Gc chromosome (designated as the 'cuckoo' chromosome) ensures its transmission by causing chromosome breaks in meiospores lacking it. The gametes with semi-lethal chromosomal breakage can be fertilized to produce offspring carrying chromosomal mutations, which are stabilized in the subsequent generations (Endo 1988). Endo (1990) reviewed the Gc chromosomes, describing their homoeology to wheat chromosomes and relationships between the Gc chromosomes derived from different *Aegilops* species. During the past 15 years, Gc chromosomes have been utilized for the production of deletion stocks in common wheat and for the rearrangement of alien chromosomes added to common wheat. In this article the Gc chromosomes isolated in wheat so far are summarized, and their uses as a tool for chromosome manipulation in wheat are described.

Gc chromosomes isolated in wheat

Twelve Gc chromosomes were listed by Endo (1990), and since then two more chromosomes were confirmed to have Gc action (Endo & Gill 1996, Kynast *et al.* 2000). These Gc chromosomes are listed in Table 1. They are derived from three basic genomes C, S, or M, and belong to homoeologous group 2, 3, or 4. Figure 1 shows the C-banding patterns of the Gc chromosomes, which are distinct from those of wheat chromosomes but somewhat similar among the Gc chromosomes belonging to the same homoeologous groups. Two Gc chromosomes T2B-2S$^{sp.au}$ and T2B-2S$^{sp.li}$ are wheat 2B chromosomes with translocated segments from *Ae. speltoides* Tausch.

The intensity of the Gc action is variable, from lethal to semi-lethal, and is affected by the genotypes of the common wheat lines where the Gc chromosomes are present (Endo 1990). Six Gc chromosomes, 2S^{lo}, 2S^{sh}, T2B-2S$^{sp.au}$, 4S^{lo}, 4S^{sh} and 4S^{sh}#2, cause complete sterility in gametes without themselves in 'Chinese Spring' wheat and therefore are exclusively transmitted to the offspring. Chromosome 3C exerts severe Gc action in Chinese Spring but has mild, semi-lethal action in some other cultivars, implying the presence of an inhibitor gene in those cultivars. Four Gc chromosomes, T2B-2S$^{sp.li}$, 2C, 3C^{SAT} and 4M^{g}, induce semi-lethal chromosome breaks in Chinese Spring, and structurally rearranged wheat chromosomes can be retained and isolated. Chromosome 3C and 3C^{SAT} were both derived from the same *Ae. triuncialis* L. plant, but their Gc action in Chinese Spring differs in intensity; that of 3C is lethal but that of 3C^{SAT} is semi-lethal (Endo & Gill 1996). The long arms of the two Gc chromosomes have identical C-banding patterns (Figure 1), and both successfully substitute for wheat homoeologous group 3 chromosomes (Endo 1978, unpublished data). This implies either that 3C is a derivative of 3C^{SAT} or that 3C^{SAT} is a rearranged 3C that acquired its satellite from one of the *Ae. triuncialis* SAT chromosomes. In either case this would suggest that the satellite has a Gc-inhibitor-like function.

As reviewed by Endo (1990) and Tsujimoto (2005), there are at least three different types of Gc chromosomes in terms of their action: 3C is totally different from the group-2 Gc chromosomes, and 4S^{lo} and 4S^{sh} are epistatic to T2B-2S$^{sp.au}$, T2B-2S$^{sp.li}$, and 2S^{sh}. For example, in a plant double monosomic for 3C and 2S^{sh} or 4S^{lo}, functional gametes need to have both Gc chromosomes. In a plant double monosomic for 2S^{sh} and 4S^{lo}, gametes carrying 4S^{lo} are functional regardless of the presence of 2S^{sh}. Chromosome 4S^{lo} seems to have two separate Gc genes, one of which has the same Gc action as that of 2S^{sh}. The types of Gc action of 2C, 3C^{SAT} and 4M^{g} have not yet been studied. It is noteworthy that T2B-2S$^{sp.au}$, 4S^{lo} and 4S^{sh} cause mutations in zygotes when these chromosomes are introduced into hybrids through male gametes. A cross between euploid common wheat and the T2B-2S$^{sp.au}$ disomic line as a male generated mutations in one of four loci for spike phenotypic characters in 7.1% (16/225) of the hybrids, but no such mutation (0/122) was found in the reciprocal cross (Tsujimoto 2005).

Structurally rearranged Gc chromosomes have been obtained (Figure 1). Endo (1996) isolated three rearranged 2C chromosomes: a long-arm telosome, t(2CL), a long-arm isochromosome, i(2CL), and a deletion in the long arm, and found that the first two retained the Gc action, and the last did not. This indicates that the 2C *Gc* gene is located in the distal half of the long arm. An isochromosome of the long arm of 3C, i(3CL), and a fragment chromosome of 3C, del(3CL), both have the Gc action, indicating that the 3C *Gc* gene is located on the proximal region

Table 1. Gametocidal chromosomes isolated in common wheat

Designation[1]	Derived species (genome formula)	Reference[2]	Proposed *Gc* gene symbol
2C	*Ae. cylindrica* (CCDD)	Endo 1990 (cylindrica), Endo 1996 (2C), Endo & Gill 1996 (*A. cylindrica*), Friebe *et al*. 2000 ($2C^c$)	
t(2CL)	*Ae. cylindrica* (CCDD)	Endo 1996, Nasuda *et al*. 1998 ($2C^cL$)	
i(2CL.)	*Ae. cylindrica* (CCDD)	Endo 1996	
$2S^{lo}$	*Ae. longissima* (S^lS^l)	Endo 1990 (longissima (2))	
$2S^{sh}$	*Ae. sharonensis* (S^lS^l)	Endo 1990 (sharonensis (1))	*Gc1-S^{l}1* (Tsujimoto 1995)
i($2S^{sh}$L)	*Ae. sharonensis* (S^lS^l)	This study	
T2B-$2S^{sp.au}$	*Ae. speltoides* ssp. *aucheri* (SS)	Endo 1990 (speltoides (1)), Nasuda *et al*. 1998 (T2B-2S)	*Gc1* (Tsujimoto & Tsunewaki 1984), *Gc1a* (Tsujimoto & Tsunewaki 1988), *Gc1-B1a* (Tsujimoto 1995)
T2B-$2S^{sp.li}$	*Ae. speltoides* ssp. *ligustgica* (SS)	Endo 1990 (speltoides (2)), Endo 1996 (T2BS.2BL-2SL)	*Gc1b* (Tsujimoto & Tsunewaki 1988), *Gc1-B1b* (Tsujimoto 1995)
3C	*Ae. triuncialis* (UUCC)	Endo & Tsunewaki 1975 (i), Endo 1990 (triuncialis)	*Gc3-C1* (Tsujimoto 1995)
del(3CL)	*Ae. triuncialis* (UUCC)	This study	
i(3CL)	*Ae. triuncialis* (UUCC)	This study	
$3C^{st}$	Synthetic *triuncialis* (UUCC)	Endo 1990 (syn-triuncialis)	
$3C^{SAT}$	*Ae. triuncialis* (UUCC)	Endo 1996 (*A. triuncialis*)	
$4S^{lo}$	*Ae. longissima* (S^lS^l)	Tsujimoto & Tsunewaki 1985b ($4S^l$), Endo 1990 (longissima (1))	*Gc2-S^{l}1a* (Tsujimoto 1995)
t($4S^{lo}$L)	*Ae. longissima* (S^lS^l)	This study	
$4S^{sh}$	*Ae. sharonensis* (S^lS^l)	Tsujimoto & Tsunewaki 1985b ($4S^{sh}$), Miller *et al*. 1982 ($4S^l$), Endo 1990 (sharonensis (2)); Friebe *et al*. 2003 ($4S^{sh}$#1)	*Gc2-S^{l}1b* (Tsujimoto 1995), *Gc2* (Friebe *et al*. 2003)
t($4S^{sh}$L)	*Ae. sharonensis* (S^lS^l)	This study	
T4B-$4S^{sh}$	*Ae. sharonensis* (S^lS^l)	Nasuda *et al*. 1998 (T4B-$4S^{sh}$), Friebe *et al*. 2003 (T4B-$4S^{sh}$#1)	*Gc2* (Friebe *et al*. 2003)
$4S^{sh}$#2	*Ae. sharonensis* (S^lS^l)	Endo 1990 (sharonensis (3))	
$4M^g$	*Ae. geniculata* ($U^gU^gM^gM^g$)	Friebe *et al*. 1999, Kynast *et al*. 2000	

[1]The numerals and capital letters represent the homoeologous groups and the genomes to which the Gc chromosomes belong, respectively. The superscript letters are short for the species names from which the Gc chromosomes were derived. Rearranged Gc chromosomes are designated according to Gill *et al*. (1991). T: translocation, del: terminal deletion, t: telosome, i: isochromosome.
[2]The designations in parentheses after the references are the synonyms of the Gc chromosomes. Original sources (before 1990) relevant to the Gc chromosomes can be found in the references in Endo (1990).

of the long arm (unpublished data). Gc telocentric chromosomes of the long arms of $4S^{lo}$, t($4S^{lo}$L), and of $4S^{sh}$, t($4S^{sh}$L), have been isolated, and a Gc wheat 4B chromosome with the $4S^{sh}$ long arm telomeric heterochromatin transposed to the tip of the long arm (T4B-$4S^{sh}$) spontaneously arose (Figure 1, unpublished data). This suggests that the Gc genes of $4S^{lo}$ and $4S^{sh}$ are located in the distal end of the long arm. T2B-$2S^{sp.au}$ and T2B-$2S^{sp.li}$ have a different C-banding pattern than that of normal 2B in the distal region of the long arm (Figure 1), where their *Gc* genes are probably located.

Tsujimoto (2005) proposed a 'restriction–modification' model to explain the dual function of the *Gc* gene; namely, chromosome breakage and protection against the breakage. This dual-function model is supported by the presence of a suppressor gene against 3C (Tsujimoto & Tsunewaki 1985a), and by the isolation of a knockout mutation of the *Gc* gene on $4S^{sh}$, which only has the protection function (Friebe *et al*. 2003).

Deletion stocks and deletion mapping of wheat chromosomes

Chromosome 2C induces semi-lethal chromosomal mutations in gametes lacking it, and telomeres are promptly formed at the broken ends (Tsujimoto *et al*.

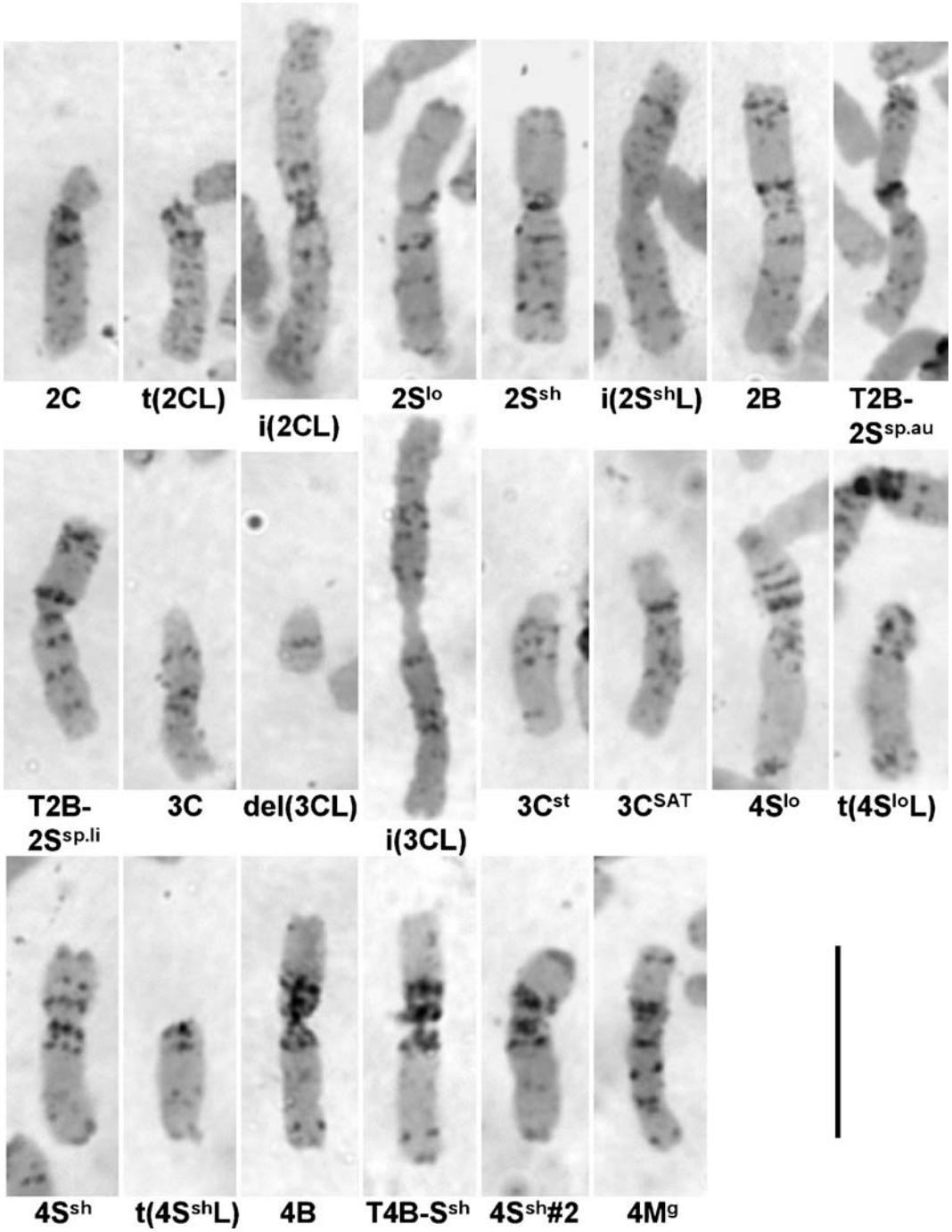

Figure 1. C-banding images of Gc chromosomes. See Table 1 for the chromosome designations. Bar = 10 μm.

1997). Therefore, most of the 2C-induced aberrations can be retrieved in the progeny, except for complicated structural changes such as dicentric chromosomes. Most of the 436 deletions of Chinese Spring were identified by C-banding in the progeny of the monosomic 2C addition line of Chinese Spring (Endo & Gill 1996). About 80% of the deletions were established as homozygous stocks. Extensive deletions in certain chromosome arms, such as the long arms of group-5 chromosomes, do not become

homozygous by self-pollination. Such deletions can be made hemizygous by crossing the deletion heterozygotes with appropriate nullisomic–tetrasomic stocks, for example, by crossing a 5A long-arm deletion heterozygote with nullisomic 5A-tetrasomic 5B, in which the four doses of 5B compensated for the deficiency of 5A.

Wheat stocks that are homozygous or hemizygous for deleted chromosomes are of great value in chromosome mapping, namely deletion mapping. The great advantage of deletion mapping over genetic mapping is that no allelic polymorphism is needed; therefore, it is not necessary to analyse many individuals of a mapping population as in genetic mapping experiments. Using a collection of deletion stocks, we can determine the approximate chromosomal region of the gene responsible for a certain trait and can also order DNA markers. Some of the traits and DNA markers mapped to wheat chromosomes by the use of Gc-induced deletions are listed in Table 2. The loss of the *Q* gene for speltoid suppression was often found in the deletion stocks, and the positional cloning of the gene was conducted based on the physical map and fine-genetic map constructed using the deletion stocks (Faris *et al*. 2005). Werner *et al*. (1992) mapped RFLP markers using the deletion stocks for the first time and compared the cytological maps with the genetic maps of the same RFLP. This study

Table 2. Traits and DNA markers mapped with Gc-induced rearranged chromosomes

Trait/DNA marker[1]	Chromosomal location[2]	Reference[3]
Trait (gene symbol)		
Speltoid suppression (*Q*)	5A	Endo & Mukai 1988, Tsujimoto & Noda 1990, Endo & Gill 1996, Faris & Gill 2001
β-Amylase (*β-Amy-A2*)	5A	Tsujimoto & Noda 1990
Male fertility	4B	Endo *et al*. 1991
Restorer for *Ae. kotschyi* cytoplasm (*Rfv1*)	1B	Mukai & Endo 1992
Meiotic chromosome pairing	2A	Endo & Gill 1996
Inhibitor of awnedness (*B2*)	6B	Endo & Gill 1996
Pairing homoeologous (*Ph1*)	5B	Gill *et al*. 1993a, Endo & Gill 1996
Biosynthesis of benzoxazinones (*TaBx1-TaBx5*)	4A, 4B, 4D, 5A, 5B, 5D	Nomura *et al*. 2003
Waxy proteins (*Wx*)	4A, 7A	Yamamori *et al*. 1994
Starch granule proteins (*Sgp*)	7A, 7B, 7D	Yamamori & Endo 1996
Putative ω-gliadin	1A	Masoudi-Nejad *et al*. 2002a
Rust resistance (*Sr31, Lr26, Yr9*)	1R	Masoudi-Nejad *et al*. 2002b
Secalins (*Sec-1*)	1R	Masoudi-Nejad *et al*. 2002b
DNA marker		
RFLP	1A, 1B, 1D	Kota *et al*. 1993, Gill *et al*. 1996b
RFLP	1B	Tsujimoto *et al*. 2001
RFLP	2A, 2B, 2D	Delaney *et al*. 1995a
RFLP	3A, 3B, 3D	Delaney *et al*. 1995b
RFLP	4A, 4B, 4D	Mickelson-Young *et al*. 1995
RFLP	5A	Ogihara *et al*. 1994
RFLP	5A, 5B, 5D	Gill *et al*. 1993a, 1996a
RFLP	6A, 6B, 6D	Gill *et al*. 1993b, Weng *et al*. 2000
RFLP	7A, 7B, 7D	Werner *et al*. 1992, Hohmann *et al*. 1994, 1995b
RFLP, SSR	3A, 3B, 3D	Dilbirligi *et al*. 2006
SSR	All 21 wheat chromosomes	Goyal *et al*. 2005
EST	All 21 wheat chromosomes	Qi *et al*. 2004
AFLP, STS	7H	Serizawa *et al*. 2001
SSR, AFLP	7H	Masoudi-Nejad *et al*. 2005
EST	7H	Nasuda *et al*. 2005a
SSAP	1R	Nagy & Lelley 2003

[1]AFLP: amplified fragment length polymorphism, EST: expressed sequence tag, RFLP: restriction fragment length polymorphism, SSAP: sequence-specific amplified polymorphism, SSR: simple sequence repeat, STS: sequence tagged site.
[2]A, B and D represent the wheat genomes, R represents the rye genome, and H represents the barley genome.
[3]References on the deletion mapping of EST for individual wheat homoeologous groups are cited in Qi *et al*. 2004.

and subsequent comparative studies of the genetic and physical maps of the RFLP in wheat revealed that crossing-over is generally more frequent in the distal region than in the proximal region of wheat chromosomes and that hotspots of chromosome breakage correspond to gene-rich regions (see the references in Table 2). The deletions stocks were also used to construct bin maps of 7104 expressed sequence tag (EST) unigenes for all 21 wheat chromosomes in seven homoeologous groups (Qi *et al.* 2004). The bin maps revealed that the EST density increases relative to the physical distance from the centromere. It should be noted that some deletion chromosomes may have submicroscopic interstitial deletions (Hohmann *et al.* 1995a).

Deletion stocks and physical mapping of barley chromosomes

Thanks to its hexaploid nature, common wheat can accommodate alien chromosomes of related species. The Gc system has been demonstrated to be effective in inducing breakage in alien chromosomes added to common wheat. A series of alien addition lines carrying individual chromosomes of barley (*Hordeum vulgare*) were developed by Islam *et al.* (1981). The 2C and $3C^{SAT}$ chromosome was introduced into alien addition lines of Chinese Spring carrying respective Betzes barley chromosomes except 1H (Shi & Endo 1997, unpublished data). Chromosomal rearrangements were induced in barley chromosomes, as well as in wheat chromosomes, at high frequencies by 2C (Shi & Endo 1999, 2000) and by $3C^{SAT}$ (Endo 2003). Rearranged 7H chromosomes were used in mapping ALFP (Serizawa *et al.* 2001), SSR and AFLP (Masoudi-Nejad *et al.* 2005), and EST (Nasuda *et al.* 2005a). Masoudi-Nejad *et al.* (2005) demonstrated that the methodology of radiation hybrid mapping is applicable to the construction of a 7H physical map using the rearranged 7H chromosomes. The centromeric regions of barley chromosomes seem to be vulnerable to breaks by the Gc system. Many barley telocentric chromosomes and Robertsonian wheat– barley translocations have been isolated. For two 7H telosomes with truncated centric ends, it was shown that centromeric repeats (gypsy retroelements and AGGGAG satellites) of barley are neither necessary nor sufficient for centromere function and de novo centromere formation may occur in barley (Nasuda *et al.* 2005b).

Deletion stocks and deletion mapping of rye chromosome 1R

Endo *et al.* (1994) first showed that 3C induces chromosome mutations in rye chromosome 1R in more than 10% of the progeny of a common wheat line that was disomic for 1R, substituted for wheat 1B in 'Burgas 2' wheat, and monosomic for 3C. Friebe *et al.* (2000) found rearranged rye chromosomes in 7% of the progenies of 45-chromosome plants that were disomic for a given 'Imperial' rye chromosome (1R to 6R, except 7R) and monosomic for chromosome 2C. Using a collection of wheat lines carrying rearranged 1R chromosomes derived from Burgas 2 (unpublished data), Masoudi-Nejad *et al.* (2002b) conducted deletion mapping for disease resistance genes on the satellite of 1R. It has been proved that the Gc system is also effective in inducing breakage in rye B chromosomes added to common wheat (unpublished data). They obtained deletions and isochromosomes of the B chromosomes and, moreover, translocations between the B and A (wheat) chromosomes.

Concluding remarks

Gc chromosomes are not rare in plants. In rice a group of hybrid sterility genes are known to eliminate gametes with opposite alleles (Morishima *et al.* 1992). Such chromosomes or genes most probably played an evolutionary role in reproductive isolation and genome rearrangement. Once introduced, the Gc chromosome must have spread, due to its selfish nature, first in a population and then into other populations, and intruded into other species through introgression, eradicating gametes without itself, like a Trojan horse. During this process, genome structures have diversified and species have differentiated. Now we know one of the secrets of genome rearrangements occurring in nature and have learned to exploit the Gc chromosomes to induce chromosome breakage rather freely in common wheat. The Gc system is an effective means to induce chromosomal mutations and, what is better, is safer and easier to handle than mutagens; however, we do not know how effective the Gc system is in inducing gene mutations. A good use of the Gc system is in the production of deletion lines in common wheat, not only for wheat chromosomes but

also alien chromosomes added to common wheat. Deletion mapping has been conducted extensively in wheat as described above. Another use of the Gc system might be to induce wheat–alien translocations with the view of introducing useful alien chromatin into the wheat genomes. Because Gc-induced wheat–alien translocations are random, and therefore mostly imbalanced, those with minute alien segments and with the minimum loss of wheat chromatin are preferable for breeding purposes. For genetic studies, wheat–alien translocations are as useful as plain deletions of the alien chromosomes. Unusual dissection of chromosomes by the Gc system will provide researchers with new tools, such as truncated barley telocentric chromosomes without the centromeric repeats (Nasuda *et al*. 2005b) and rye B chromosomes separated into the proximal segments including the centromere and distal segment including the rye-B-specific repeats (unpublished data). There is no doubt that a collection of deletions and translocations, whose breakpoints divide an alien chromosome into limited regions, are extremely useful for physical chromosome mapping. Work is in progress to produce a collection of common wheat lines that carry various rearrangements of individual chromosomes of rye and barley. Wheat lines carrying the Gc chromosomes, deletion stocks of Chinese Spring and wheat lines carrying rearranged rye and barley chromosomes are available from http://www.shigen.nig.ac.jp/wheat/komugi/strains/aboutNbrpLgku.jsp).

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