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Gametocidal factor-induced structural rearrangements in rye chromosomes added to common wheat

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Abstract

The gametocidal factor on the *Aegilops cylindrica* chromosome $2C^c$ was used to induce and analyze the nature of chromosomal rearrangements in rye chromosomes added to wheat. For this purpose we isolated plants disomic for a given rye chromosome and monosomic for $2C^c$ and analyzed their progenies cytologically. Rearranged rye chromosomes were identified in 7% of the progenies and consisted of rye deficiencies (4.6%), wheat–rye dicentric and rye ring chromosomes (1.8%), and terminal translocations (0.6%). The dicentric and ring chromosomes initiated breakage–fusion–bridge cycles (BFB) that ceased within a few weeks after germination as the result of chromosome healing. Of 56 rye deficiencies identified, after backcrossing and selfing, only 33 were recovered in either homozygous or heterozygous condition covering all rye chromosomes except 7R. The low recovery rate is probably caused by the presence of multiple rearrangements induced in the wheat genome that resulted in poor plant vigor and seed set, low transmission, and an underestimation of the frequency of wheat–rye dicentric chromosomes. Genomic *in-situ* hybridization (GISH) analysis of the 33 recovered rye deficiencies revealed that 30 resulted from a single break in one chromosome arm followed by the loss of the segment distal to the breakpoint. Only three had a wheat segment attached distal to the breakpoint. Although some of the Gc-induced rye rearrangements were derived from BFB cycles, all of the recovered rye rearrangements were simple in structure. The healing of the broken chromosome ends was achieved either by the *de-novo* addition of telomeric repeats leading to deficiencies and telocentric chromosomes or by the fusion with other broken ends in the form of stable monocentric terminal translocation chromosomes.

Inroduction

Gametocidal (Gc) factors were discovered during the production of chromosome addition and alloplasmic lines from crosses of common wheat *Triticum aestivum* L. (2n=6x=42, AABBDD) with wild *Aegilops* species. Certain alien chromosomes containing gametocidal factors were preferentially or exclusively transmitted (for review, see Endo 1990). Gc factors are selfish genetic elements that

insure their preferential transmission by inducing chromosome breaks mainly in gametophytes lacking them (Finch *et al.* 1984, Nasuda *et al.* 1998). Endo & Gill (1996) used the Gc factors located on the chromosomes $2C^c$ of *Ae. cylindrica* Host (2n=4x=28, $D^cD^cC^cC^c$) and on chromosome $3C^t$ of *Ae. triuncialis* L. (2n=4x=28, $U^tU^tC^tC^t$) to produce a set of more than 400 deletion stocks in Chinese Spring wheat. The deletion lines are pivotal stocks for the physical mapping of the wheat genome (for review, see Gill & Gill 1994, Endo & Gill 1996).

Most wheat deletion stocks contained from one to four chromosome deficiencies, each arising from a single break in one chromosome arm (rarely both arms) and the loss of the distal fragment as revealed by C-banding and confirmed by extensive genetic mapping (Endo & Gill 1996). However, a small number of chromosome deficiencies appears to be more complex (Hohmann *et al.* 1994, Tsujimoto & Noda 1989). These data indicate that a certain proportion of the deficiencies may have a more complex origin. This problem, whether a chromosome deficiency is true (single break origin) or false (complex origin, perhaps involving multiple breaks) cannot be analyzed in wheat using existing cytological procedures. Instead, this problem can be tackled using marker rye (*Secale cereale* L., 2n=2x=14, RR) chromosomes introduced individually into wheat in a gametocidal genotype. The marker rye chromosomes can be distinguished from wheat by C-banding and genome painting. Thus, one can readily determine the nature of the origin of individual rye chromosome deficiencies. At the same time, the recovered rye deletion stocks can be isolated for physical mapping of the rye genome. The results on the nature of chromosome deficiencies induced by the Gc factor and the isolation of rye deletion stocks are reported here.

Material and methods

The material analyzed consisted of disomic wheat–alien addition (DA) lines where a pair of a given alien chromosome is added to the genome of wheat. The specific DA lines used were: Chinese Spring (CS) wheat–*Aegilops cylindrica* $DA2C^c$ (2n=44, $21W''+2C^{c''}$) (Endo 1988), and seven CS wheat-'Imperial' rye chromosome addition lines DA1R to DA7R (2n=44, $21W''+R''$) (Driscoll & Sears 1971, Mukai *et al.* 1992). Line $DA2C^c$ is in *Ae. kotschyi* Boiss. cytoplasm and was kindly provided by Dr. Y. Mukai, Laboratory of Plant Molecular Genetics, Osaka Kyoiku University, Osaka, Japan. All lines are maintained at the Wheat Genetics Resources Center, Manhattan, KS, USA.

DA1R to DA7R plants were crossed as females with plants of $DA2C^c$. The resulting double monosomic addition plants (2n=44, $21W''+R'+2C^{c'}$) produce four types of gametes: 21W, 21W+R, $21W+2C^c$, and $21W+R+2C^c$. Because univalents in wheat are known to be excluded in about three fourths of the gametes (Morris & Sears 1967), the expected frequencies are 9/16, 3/16, 3/16, and 1/16, respectively. Gametocidal (Gc) chromosomes are known to induce chromosome breaks in gametes lacking the Gc chromosome (Endo 1990, Finch *et al.* 1984, Nasuda *et al.* 1998). Thus, Gc-induced chromosome breaks in the rye target chromosomes is expected to occur in only 3/16 of the gametes, making screening ineffective. To improve the screening efficiency we backcrossed the double monosomic additions with the corresponding rye addition lines and screened the BC_1 progenies cytologically to identify plants disomic for a given rye chromosome and monosomic for the gametocidal chromosome $2C^c$ (2n=45, $21''+R''+2C^{c'}$). All gametes of these plants have the rye target chromosome and 75% are expected to lack chromosome $2C^c$ (21W+R) and, thus, are prone to chromosome breakage. These plants were either backcrossed with the corresponding rye addition line or selfed and the derived BC_2 and BC_1F_2 progenies screened by C-banding analysis to identify plants with chromosomal rearrangements in the rye chromosomes.

Cytogenetic analyses

The C-banding technique and the wheat–rye chromosome identification and nomenclature was according to Gill & Kimber (1974a, b), Gill *et al.* (1991), and Mukai *et al.* (1992). Microphotographs of chromosome preparations were taken with a Zeiss photomicroscope III using

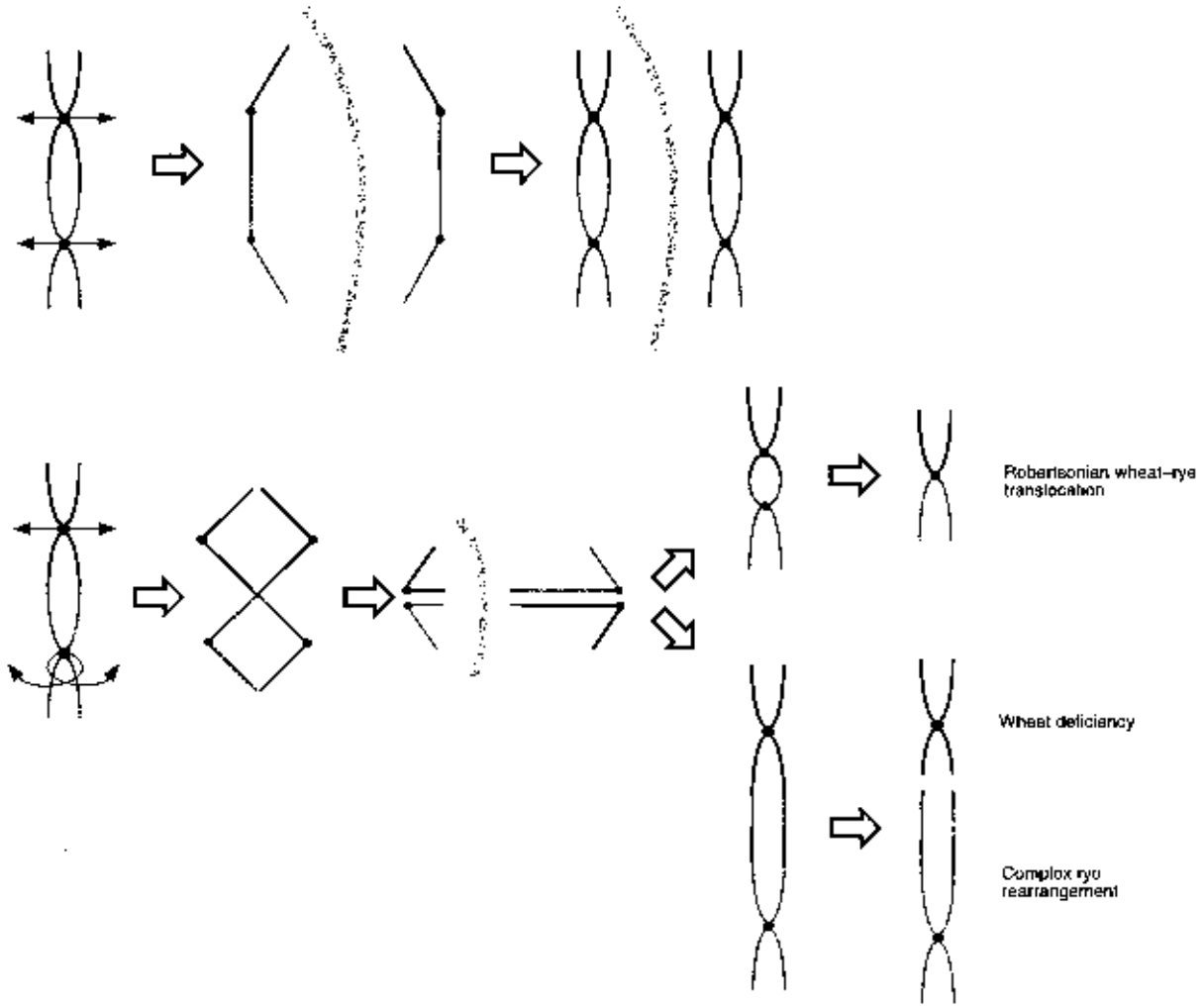

Figure 1. Chromosome-type BFB cycle induced by a wheat–rye dicentric chromosome. Depending on the orientation of the two centromeres the dicentric either segregates normally (upper row) or produces a double-chromatid bridge at mitotic ana-/telophase (lower row). The double-chromatid bridge is eventually ruptured by the formation of the new cell wall followed by the fusion of the broken ends and the cycle continues. Depending on the location where the double-chromatid bridge is ruptured and fusion of the sister chromatids has occurred, this process can produce pure wheat and rye deficiencies, Robertsonian wheat–rye translocations and deficiencies with complex rearrangements around the breakpoints. Black: wheat; gray; rye.

Kodak Imagelink HQ microfilm 1461. Genomic *in-situ* hybridization (GISH) was according to Pickering *et al.* (1997) using FITC-labeled genomic DNA of rye as probe and unlabeled genomic DNA of wheat as a blocker. The hybridization stringency was between 80 and 82%. Posthybridization washes were at 85–87% stringency. Signals were visualized using an Olympus BH-2 microscope equipped for phase contrast and epifluorescence. Images were either taken with Fujicolor Super G Plus 400 film or captured with a SPOT CCD camera using the appropriate SPOT 2.1 software (Diagnostics Instruments, Inc., Sterling Heights, Michigan, USA) and processed with PhotoShop 4.0 software (Adobe Systems Inc., San Jose, California, USA). Images were printed on a Kodak ds 8650 PS Color Printer.

Table 1. Structural rearrangements in the Imperial rye chromosomes added to Chinese Spring wheat recovered in progenies of plants disomic for a given rye chromosome and monosomic for the gametocidal chromosome $2C^c$.

Target chromosome	No. of plants analyzed	Rye deficiencies				Wheat–rye dicentrics	Wheat–rye and rye–rye translocations
		Identified	Recovered	Homozygous	Heterozygous		
1R	242	11	7	1RS-4, 1RS-6, 1RL-1, 1RL-2	1RS-5, 1RL-3, 1RL-5	6	1 (T6BS·6BL-1RL)
2R	69	4	2	2RS-1, 2RL-1		1	1 (T3BS·2RL)
3R	255	12	7	3RS-8	3RS-3, 3RS-7, 3RS-9 3RL-4, 3RL-5, 3RL-6	7[a] (1 ring)	2 (T2BS·3RS T4AL-3RL-3RS)
4R	347	16	8	4RL-2, 4RL-5, 4RL-10, 4RL-14	4RL-1, 4RL-7, 4RL-9, 4RL-11	4	1 (T?·4RS)
5R	226	12	8	5RL-1, 5RL-3, 5RL-6, 5RL-10	5RS-2, 5RL-5, 5RL-7, 5RL-8	4	2 (T5RS·5RL-5RS Tdef5RS·5RL-5RS)
6R	79	2	1	6RL-2			
Total	1218	56 (4.6%)	33 (2.7%)			22 (1.8%)	7 (0.6%)

[a] Including one wheat–rye tricentric and one rye–rye dicentric.

Results

Theoretical considerations

In the $2C^c$ gametocidal system, deficiencies most commonly result from a single break in a chromosome arm followed by the loss of the acentric fragment distal to the breakpoint (Endo 1988). If fusion occurs between two centric fragments then dicentric chromosomes are produced. Dicentric and ring chromosomes are known to initiate chromosome-type breakage–fusion–bridge (BFB) cycles (McClintock 1938, 1941, 1942, 1984). If the two centromeres in a dicentric chromosome orientate to opposite poles, a double chromatid bridge is formed at mitotic ana-/telophase, which is eventually ruptured by the formation of the new cell wall (Figure 1). Depending on the location where the double chromatid bridge has ruptured and fusion of the sister chromatids occurred, this can produce complex rearrangements around the breakpoints. GISH analysis on plants with chromosomal rearrangements derived from wheat–rye dicentric chromosomes allows us to detect complex rearrangements, which would result in zebra-type GISH patterns at the breakpoints (Figure 1).

Mutation frequencies and their nature

Plants with 2n=45 chromosomes that were disomic for a given rye chromosome and monosomic for chromosome $2C^c$ were obtained for all rye chromosomes except 7R because of its low transmission. A total of 1.218 BC_2 and BC_1F_2 plants were screened by C-banding for the presence of chromosomal rearrangements in the rye target chromosome. A large number of rearrangements in the A-, B-, and D-genome chromosomes of wheat were observed, but these were not tabulated. The frequency of rye chromosomal rearrangements in first-generation plants was 6.4% (Table 1). Two types of structural aberrations were observed. The majority of the rye rearrangements were identified as deficiencies (4.6%) that lacked a distal segment in one chromosome arm. The remaining were wheat–rye and rye–rye dicentrics (1.8%). GISH analysis using total genomic rye DNA as a probe was performed on 33 first-generation deficiencies recovered in

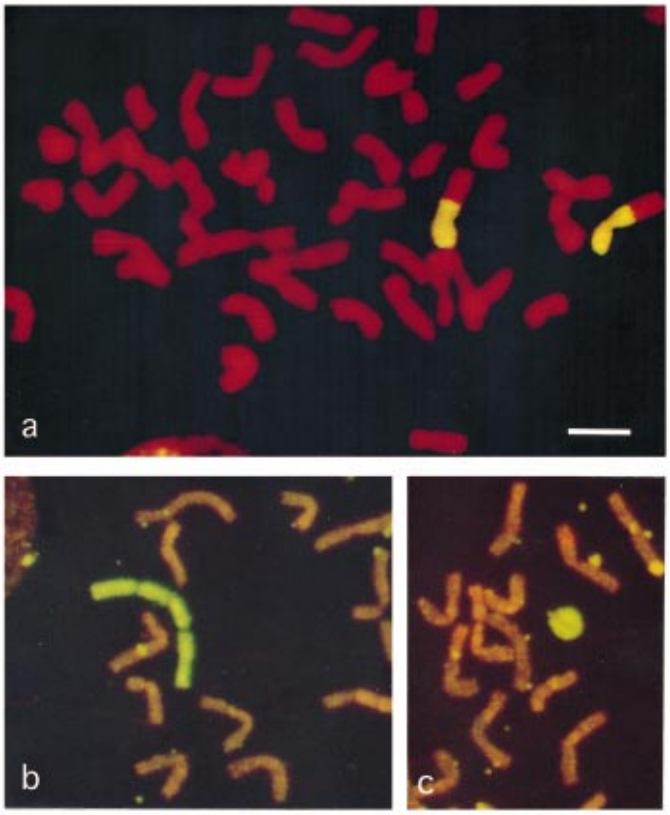

Figure 2. Genomic *in-situ* hybridization using total genomic rye DNA as a probe to mitotic metaphase chromosomes of plants with different rye rearrangements induced by the gametocidal chromosome $2C^c$; (**a**) the rearrangement recovered from the 1RL-2 deficiency identified as a terminal T1RS·1RL-? wheat-rye translocation; (**b**) a partial metaphase of a plant with a 3R dicentric; and (**c**) a partial metaphase of a plant with a 3R ring chromosome. Rye chromatin is visualized by its green–yellow FITC fluorescence, whereas wheat chromosomes are counterstained with propidium iodide and fluoresce red. Scale bar = 10 μm.

the next generation, for analyzing whether the deficient rye chromosomes had complex rearrangements at their breakpoints. Thirty resulted from a single break in one rye chromosome arm followed by the loss of the segment distal to the breakpoint and three (1RL-2, 4RL-2, 4RL-9) were identified as terminal wheat–rye translocation chromosomes (Figure 2a) with an unlabeled terminal wheat segment attached to the breakpoint. None of the analyzed rye deficiencies had a zebra-like GISH pattern at the breakpoints, which would indicate complex rearrangements derived from BFB cycles (Figure 1).

In addition to simple deficiencies, 21 wheat–rye dicentrics (including 1 wheat–rye tricentric) (Figure 3), 1 rye–rye dicentric (Figure 2b), and 1 rye ring chromosome (Figure 2c) (0.01%) were observed in first-generation plants (Table 1). The dicentric and ring chromosomes initiated chromosome-type BFB cycles. Different cells of the same root tip meristem had different permutations of the dicentric (Figure 4). Depending on the orientation of the two centromeres in a dicentric chromosome, the dicentric can either segregate normally at mitotic anaphase or form a double-chromatid bridge (Figure 5a). About half of the cells at mitotic anaphase (12 out of 21) in a plant with a 2DS·2DL-7DL·7DS dicentric chromosome had double chromatid bridges, which were eventually ruptured by the formation of the new cell wall (Figure 5b), and the BFB cycle continued. The BFB cycles ceased a few weeks after germination as a result of healing of the broken

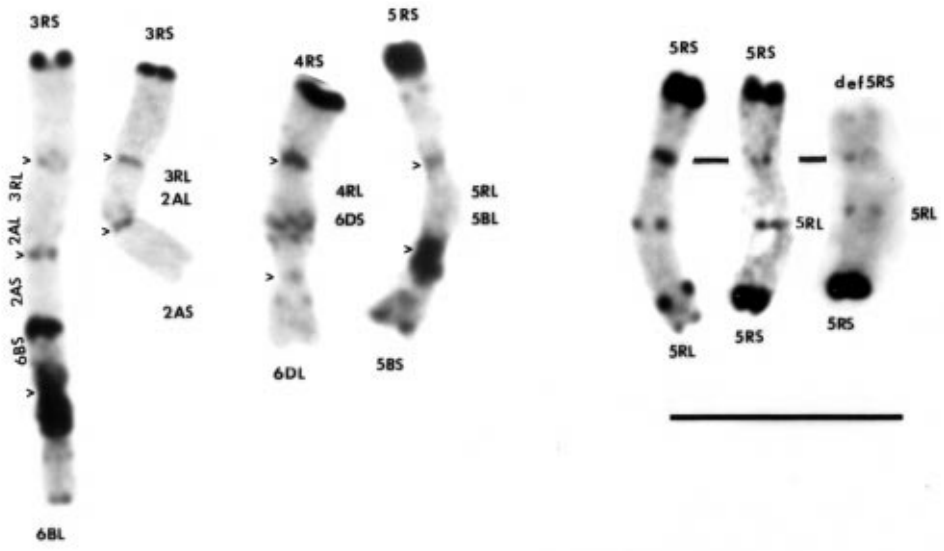

Figure 3. Multicentric wheat–rye and rye–rye translocation chromosomes induced by the gametocidal chromosome $2C^c$: (from left to right) 3RS·RL-2AL·2AS-6BS·6BL, 3RS·3RL-2AL·2AS, 4RS·4RL-6DS·6DL, 5RS·5RL-5BL·5BS, and 5R, T5RS·5RL-5RS, Tdef5RS·5RL-5RS. Scale bar = 10 μm.

chromosome ends. Chromosome healing was achieved by either the addition of telomeric repeats at the broken termini or fusion with other broken ends present in the same cell, which resulted in cytologically stable rye deficiencies and telocentric chromosomes or in wheat–rye Robertsonian whole-arm and terminal translocation chromosomes. Dicentric chromosomes never entered the meiotic divisions (Figure 4).

Seven wheat–rye translocation chromosomes (0.6%) were recovered in the second-generation plants (Table 1).Their origin was traced back to dicentric chromosomes undergoing BFB cycles in first-generation plants. Three of the seven wheat–rye translocations were identified as Robertsonian whole-arm translocations, two were terminal wheat–rye translocations, and two were intrachromosomal rye translocations (Figure 3).

Rye deletion stocks

Of the 56 rye deficiencies identified, 33 were recovered after backcrossing and selfing in either homozygous or heterozygous conditions (Figure 6). The majority of the rye deficiencies had breakpoints in their long arms. The short arms of all rye chromosomes are marked by large terminal C-bands, which makes the detection of long arm deficiencies easier than the identification of short arm deficiencies. Therefore, it is possible that some of the Gc-induced short arm deficiencies remained undetected.

Discussion

In the present study, 7% of the progenies derived from plants disomic for a given rye chromosome and monosomic for the gametocidal chromosome $2C^c$ had structurally rearranged rye chromosomes either in the form of rye deficiencies, wheat–rye dicentric, or wheat–rye translocation chromosomes. This frequency is similar to that of the $2C^c$-induced rearrangements in 'Betzes' barley (*Hordeum vulgare* L., 2n=2x=14, HH) chromosomes and telosomes added to CS wheat reported by Schubert *et al.* (1998) using the same gametocidal $2C^c$ *Ae. cylindrica* system. A slightly higher frequency of chromosomal rearrangements in rye chromosome 1R was reported by Endo *et al.* (1994) using the gametocidal chromosome $3C^t$ of *Ae. triuncialis*, which is known to have a more severe effect than $2C^c$.

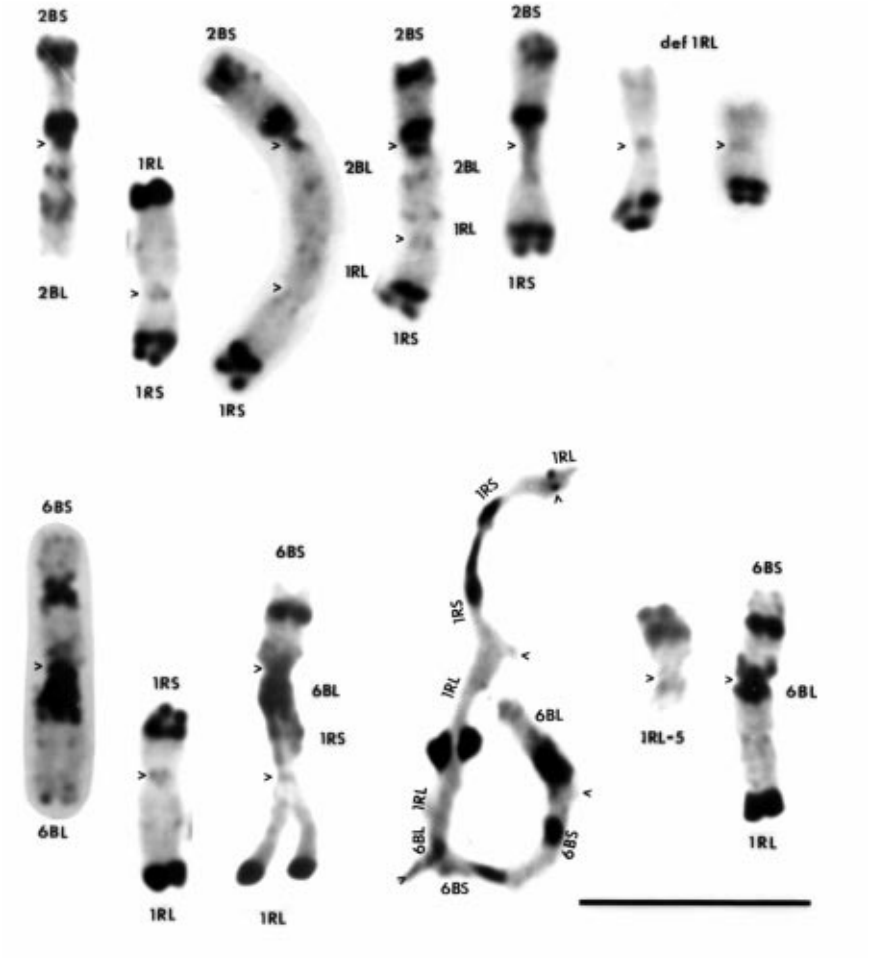

Figure 4. Wheat–rye dicentric chromosomes induced by the gametocidal chromosome $2C^c$. Upper row: permutations of a 2BS·2BL-1RL·1RS dicentric observed in different cells of the same root tip meristem with different sizes of the interstitial 2BL-1RL segment, a T2BS·1RS whole arm translocation, and two 1RL deficiencies with different sizes of the lost 1RL segments. Lower row: a 6BS·6BL-1RS·1RL dicentric observed in root tip meristems, meiotic metaphase I pairing of the same plant showing a quadrivalent consisting of 6BL·6BS//6BS·6BL-1RL//1RL·1RS//1RS·1RLdef., and the 1RL-5 deficiency and T6BS·6BL-1RL wheat–rye translocation recovered in the offspring of this plant. Note that in the case of the 6BS·6BL-1RS·1RL dicentric, not a deficiency in the 1RS arm as expected by the structure of the dicentric, but a 1RL deficiency together with a T6BS·6BL-1RL translocation chromosome was stabilized. Arrowheads point to the centromeres. Scale bar = 10 μm.

Of the 56 identified rye deficiencies only about half of them (33) resulted in cytologically stable rearrangements that were recovered in the derived backcross and selfed progenies. The low recovery rate may be due to several causes. Plants with rearranged rye chromosomes usually also had other rearrangements in the wheat chromosome complement. As a result many of them were weak and set few seeds. The reduced transmission frequencies of rearranged rye chromosomes may be another cause of low recovery. The number of plants classified as rye deficiencies may have been overestimated. Some of these plants might have had wheat–rye dicentrics that were still undergoing BFB cycles. However, because in some cases only a few metaphases were available for C-banding analysis the dicentrics remained undetected.

GISH analysis indicated that 30 of the 33 recovered rye deficiencies resulted from a single chromosome break followed by the loss of the segment distal to the breakpoint. Only three

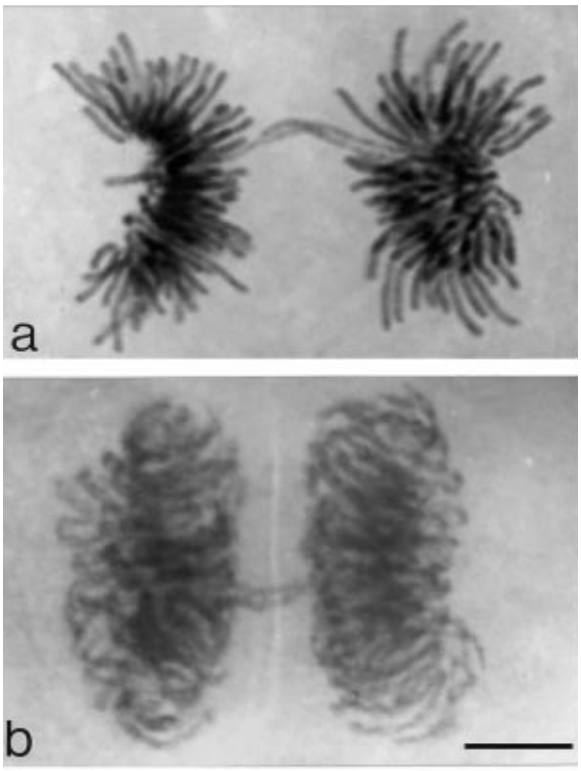

Figure 5. Mitotic ana-/telophases of a plant with a 2DS·2DL-7DL·7DS dicentric chromosome induced by the gametocidal chromosome $2C^c$; (**a**) anaphase with a double chromatid bridge and (**b**) telophase showing that the double chromatid bridge is ruptured by the formation of the new cell wall. Scale bar = 10 μm.

putative deficiencies had a wheat segment distally attached to the breakpoint. None of the recovered rye rearrangements had cytologically detectable complex rearrangements around the breakpoints, which is surprising because at least some of them were derived from wheat–rye dicentric chromosomes and the result of BFB cycles. Depending on the location where the double-chromatid bridges are ruptured and fusion of the sister chromatids has occurred, consecutive BFB cycles can produce complex rearrangements around the breakpoints. GISH analysis only allows detection of rearrangements involving both wheat and rye chromatin. Because of the lack of diagnostic proximal C-bands in most rye chromosomes, we do not know whether or not complex rearrangements involving only the deficient rye chromosome arm are present. However, the extensive use of the wheat deletion stocks produced using the $2C^c$ and $3C^t$ gametocidal systems (Endo & Gill 1996) in the physical mapping of the wheat genome usually failed to detect complex rearrangements. Only 7 out of 63 wheat deficiencies produced by the $2C^c$ and $3C^t$ systems (Endo & Gill 1996) were observed to have complex chromosomal rearrangements (Hohmann *et al.* 1994). On the other hand, Tsujimoto & Noda (1989) used the stronger Gc factors located on chromosome 2S of *Ae. speltoides* Tausch. (2N=2x=14, SS) to induce deficiencies in the long arm of wheat chromosome 5A. Restriction fragment length polymorphism (RFLP) analysis revealed that most of them (15 out of 19) had complex rearrangements (Ogihara *et al.* 1994). Our data suggest that as a result of consecutive BFB cycles, the segment between the two centromeres of a dicentric wheat–rye chromosome becomes shorter and shorter and will eventually be stabilized as either a pure wheat or rye deficiency or in an extreme case, in the form of wheat–rye whole arm translocation, which were also recovered.

Previous studies revealed that both meiotic divisions are normal in plants monosomic for a Gc factor but that chromosome breakage occurs prior to the DNA synthesis phase of the first postmeiotic interphase predominantly in gametophytes lacking the Gc factor (Finch *et al.* 1984, Nasuda *et al.* 1998). The amount of Gc-induced chromosome breakage depends on the Gc system and wheat genetic background (Tsujimoto & Tsunewaki 1985a, 1985b). The present data using marker rye chromosomes show that essentially all damaged chromosomes are healed in the gametophytic stage either by *de-novo* addition of telomeres (Friebe *et al*. 2000) or by fusion with other broken chromosomes. The majority of the rye rearrangements identified were first generation deficiencies that arose from *de-novo* addition of telomeres in the preceding gametophyte. A small minority were second generation deficiencies and translocations derived from BFB cycles that were initiated by dicentric and ring chromosomes. In these cases chromosome healing by *de-novo* addition of telomeres or fusion of broken ends occurred in meristematic sporophytic tissues. Thus, if one wishes to recover simple deficiencies for genome mapping projects, it would be desir-

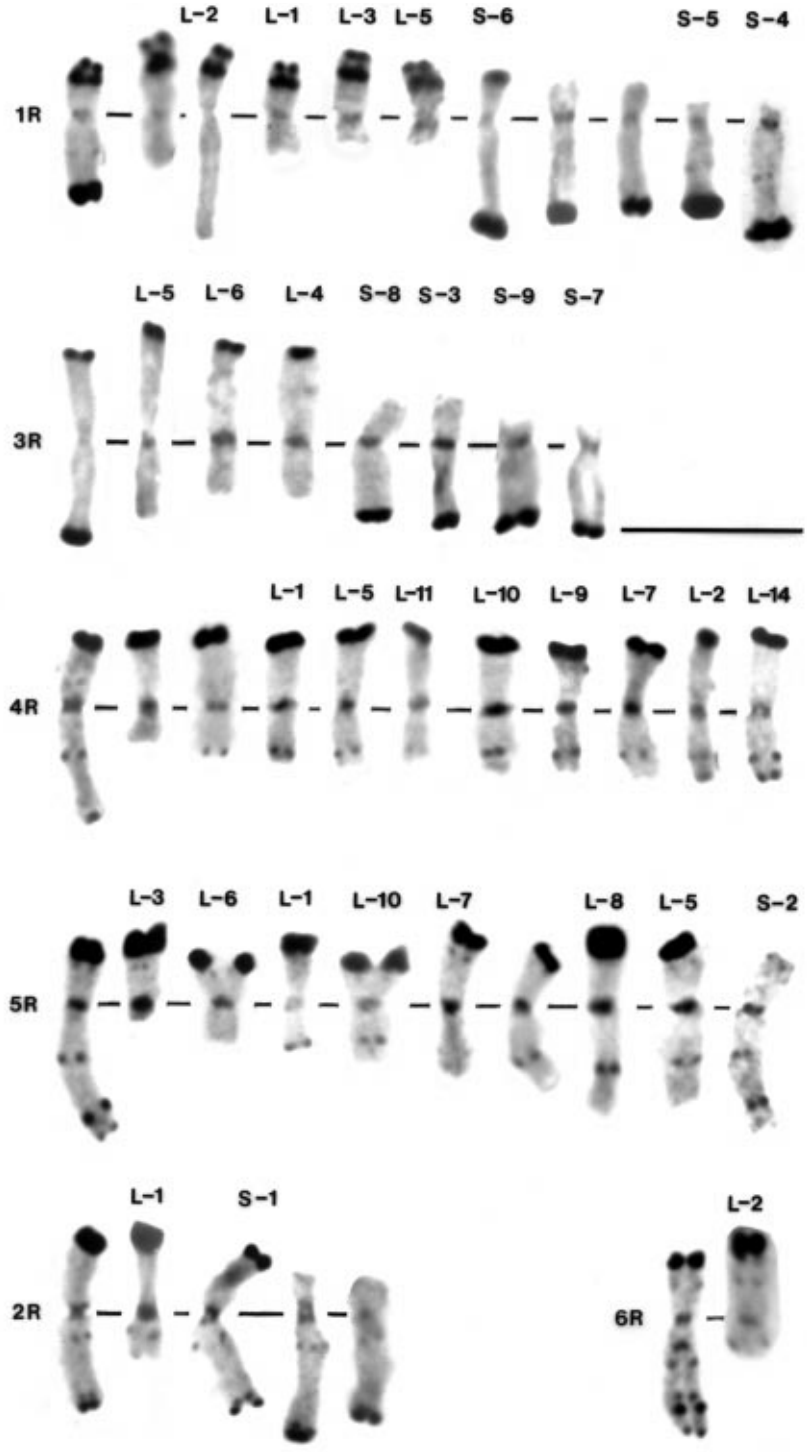

Figure 6. Rye chromosome deficiencies induced by the gametocidal chromosome $2C^c$. Identifiers above the chromosomes indicate that the deficiency was recovered in either disomic or monosomic condition. Note that the originally identified rye deficiency 1RL-2 is different from the rearrangement recovered in the offspring (shown right). This plant was also monosomic for chromosome $2C^c$, which induced a second rearrangement in the offspring of this plant. GISH analysis identified the stabilized 1R-2 deficiency as a terminal wheat–rye translocation with an unidentified distal wheat segment in the long arm (see also Figure 2a). Scale bar = 10 μm.

able to screen them in first generation plants and discard any new deficiencies recovered in subsequent generations, which are likely to be more complex. This was the strategy followed by Endo & Gill (1996) in the isolation of the majority of the deletion stocks of wheat.

Although the chromosome-damaging effect of the Gc factor on chromosome $2C^c$ is mainly restricted to the first postmeiotic interphase of gametophytes lacking the Gc factor, a low level of damage may occur at later stages in the presence of the Gc chromosome. The latter is suggested by the recovery of one rye–rye dicentric and one T5RS·5RL-5RS translocation chromosome in the progeny of a plant that was disomic for either 3R or 5R and monosomic for $2C^c$. The rearrangements involve two rye chromosomes and thus, are likely to have occurred in the zygote, because only one rye homologue is present in the gametophytes. Similarly, King & Laurie (1993), using the gametocidal chromosome $4S^{sh}$ of *Aegilops sharonensis* Eig ($2n=2x=S^{sh}S^{sh}$), reported that some of the Gc-induced chromosome breakage occurred in the zygotes.

Meiotic metaphase I pairing analysis (Naranjo & Fernández-Rueda 1991) and RFLP analysis (Devos *et al.* 1993) revealed that the rye genome is highly rearranged compared to that of wheat and 1R is the only rye chromosome that is not structurally rearranged. The rye deficiencies obtained in the present study will be useful for the physical mapping of the interchanged segments.

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