**GAMETOCIDAL GENES OF AEGILOPS:
SEGREGATION DISTORTERS IN WHEAT – AEGILOPS WIDE
HYBRIDIZATION**

Journal:	<i>Genome</i>
Manuscript ID	gen-2017-0023.R1
Manuscript Type:	Review
Date Submitted by the Author:	25-Mar-2017
Complete List of Authors:	M, Niranjana; Indian Agricultural Research Institute, Genetics;
Is the invited manuscript for consideration in a Special Issue? :	This submission is not invited
Keyword:	gametocidal genes, wheat, Aegilops, segregation distortion, deletion

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GAMETOCIDAL GENES OF *AEGILOPS*:

SEGREGATION DISTORTERS IN WHEAT – *AEGILOPS* WIDE HYBRIDIZATION

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Draft

ABSTRACT

Aegilops is a genus belonging to the Poaceae family which have played indispensable role in the evolution of bread wheat and continues to do so by transferring genes by wide hybridization. Being the secondary gene pool of wheat, gene transfer from *Aegilops* poses difficulties and segregation distortion is common. Gametocidal genes are the most well characterized class of segregation distorters reported in interspecific crosses of wheat with *Aegilops*. These are selfish genetic elements which ensure their preferential transmission to progeny at the cost of gametes lacking them without providing any phenotypic benefits to the plant causing a proportional reduction in fertility. Gametocidal genes (*Gc*) are reported in different species of *Aegilops* belonging to the sections *Aegilops* (*Ae. geniculata* and *Ae. triuncialis*), *Cylindropyrum* (*Ae. caudata* and *Ae. cylindrica*) and *Sitopsis* (*Ae. longissima*, *Ae. sharonensis* and *Ae. speltoides*). Gametocidal activity is mostly confined to 2, 3 and 4 homeologous groups of C, S, S¹, S^{sh}, M^g genomes. Removal of such genes is necessary for successful alien gene introgression and can be achieved by mutagenesis or allosyndetic pairing. However there are some instances where *Gc* genes are constructively utilized for development of deletion stocks in wheat, improving genetic variability and chromosome engineering.

Keywords: gametocidal genes, wheat, *Aegilops*, segregation distortion, deletion

INTRODUCTION

'Gametocidal' is a term derived by the combination of two words 'gamete' (egg or sperm) and 'cidal' (capable of killing) which imparts the meaning 'gamete killer'. This term was used by Endo (1990) to describe selfish genetic elements which ensure their preferential transmission to progeny at the cost of gametes lacking them, without providing any phenotypic benefits to the plant causing a proportional reduction in fertility. The gene(s) responsible for gametocidal action are designated as 'gametocidal' (*Gc*) genes (Mc Intosh 1988) and the alien chromosomes carrying *Gc* gene(s) are termed 'gametocidal' (Endo 1979) or 'cuckoo' chromosomes (Miller 1983), owing to its selfish behaviour. Gametocidal genes are the most well characterized class of segregation distorters reported in interspecific crosses of wheat with wild relatives belonging to *Aegilops* genus (Endo and Tsunewaki 1975; Maan 1975; Endo 1990). Segregation distortion is a regular phenomenon in wide hybridization where the allele(s) of a heterozygous locus segregates at a frequency different from that predicted as per Mendelian ratios (Sandler and Novitski 1957; Sandler *et al.* 1959). This deviation from Mendelian ratio results due to the preferential retention of chromosomal blocks carrying genes beneficial to its reproductive viability (Deven 2007). Whenever the transmission rate of a chromosome or gene is more than 0.5, the resulting transmission advantage or segregation distortion is collectively referred to as 'drive' (Houben 2017). Segregation distortion observed in interspecific and intraspecific crosses mainly arise from either pre-fertilization barriers like certation, abortion of male or female gametes or post-fertilization barriers like abortion of zygote/embryo (Lyttle 1991; Manabe *et al.* 1999). Segregation distortion of particular loci could cause serious problems in introgression breeding if they are closely linked to agronomically important genes. Likewise gene transfer from *Aegilops* sp. carrying gametocidal gene(s) will be problematic since the accidental transfer of these with the gene of interest will make the plant partially sterile. Gametocidal genes differ from other segregation distorters in the fact that their effect is evident in both male and female gametophytes and neither does it offer any reproductive advantage. In wheat a pollen killer gene (*Ki*) with dominant gene action has also been designated on long arm of 6B chromosome with similar gametocidal action (Sears and Loegering 1961; Loegering and Sears 1963) but its effect is limited only to male gametophyte. Another instance of genes with gametocidal action was reported in *Thinopyrum ponticum* (Syn.: *Agropyron elongatum*, *Lophopyrum ponticum*) in which the chromosome carrying *Sd1* and/or *Sd2* gene(s) (McIntosh *et al.* 1995) exhibited preferential transmission through the female gametes, but not through the male gametes (Kibirige-Sebunya and Knott 1983). Seed set was normal in homozygous plants and was greatly reduced in heterozygous plants. Zhang and

Dvorak (1990) mapped the *Sd1* locus proximal to leaf rust resistance gene *Lr19*. Even though *Gc*, *Ki* and *Sd* genes cause segregation distortion, *Gc* genes are unique in their mode of action. Plants carrying *Gc* genes in the hemi- (*Gc/-*) or heterozygous (*Gc/gc*) form are semi-sterile whereas homozygous (*Gc/Gc*) plants are fully fertile. Once a *Gc* gene is introduced into a population, it will rapidly increase its frequency by preferential transmission and will soon be fixed in the population since they are highly selfish and parasitic (Tsujimoto 2005).

Selfish genes that cause abortion of gametes which lack them by allelic interactions have been reported in other higher plants like tobacco, maize, tomato and rice also. When hybrids were derived by crossing *Nicotiana tabacum* and *N. plumbaginifolia*, an alien addition line (24tt + lp) with designated *Kl* (Pollen killer) locus causes abortion of pollen having only the complete complement of *Nicotiana tabacum* chromosomes while pollen having *Kl* locus are viable (Cameron and Moav 1957; Moav *et al.* 1968). In maize-*Tripsacum* hybrids an egg eliminator was reported in which an extra chromosome from *Tripsacum* was transmitted at a very high frequency to the progenies through the eggs (Maguire 1963). In case of tomato, a gene designated as *Ge* (gamete aborter) caused abortion of gametes only in certain hybrid combinations and its effect was equally evident in male as well as female gametes (Rick 1966). In rice a sterility factor tentatively designated as *S(t)* induced gametic abortion due to allelic interaction (Sano 1990). In the backcross derivatives between *Oryza sativa* and *Oryza glaberrima*, gamete abortion was reported in the male heterozygotes but the elimination of female gametes was incomplete. So the *S(t)* gene was proposed to be intermediate between a gamete eliminator and pollen killer. Similar DNA elements are found in the animal kingdom also, as for instance the P element (Crow 1983; Bregliano and Kidwell 1983) and Segregation Distorter (SD) system in *Drosophila melanogaster* (Lyttle 1991, 1993) and t haplotypes in mouse (Silver 1985, 1993). When males with autonomous P elements (P Strain/P cytotype) are crossed with females that lack P elements (M Strain/M cytotype), it results in high rate of mutation in the germ line cells which is referred to as 'hybrid dysgenesis' (Rubin *et al.* 1982; Kidwell *et al.* 1983; Engels *et al.* 1996; Castro *et al.* 2004; Hill *et al.* 2016). When an SD/SD+ heterozygous male fly is crossed to wild type SD+/SD+ female fly, the SD chromosome is recovered in more than 90% of the progenies (Hiraizumi *et al.* 1994; Larracuente and Presgraves 2012; Brand *et al.* 2015). The *t* haplotype (group of linked genes in the proximal half of chromosome 17 spanning ~20 cM) in mice is one of the best-studied examples of a selfish genetic element. The heterozygous males having only one copy of the *t* haplotype transfer the genetic element to over 95% of their progeny and offspring that inherit two copies of the haplotype die during development by an elaborate sperm-poisoning (gametocidal) system (Morita *et al.* 1992;

Sugimoto *et al.* 2014). Supernumerary (B) chromosomes are another group of selfish DNA with no apparent selective advantage still reported in all eukaryotic phyla, but are absent from some individuals of a population (Jones 1991; Houben 2017). B chromosomes are assumed to be derived from standard (A) chromosomes even though they fail to pair with them (Jones *et al.* 2008). They were first discovered leaf-footed plant bug insect *Metapodius* and later on reported in rye and in maize (Gotoh 1924; Kuwada 1925; Longley 1927; Randolph 1928).

***AEGILOPS* – A VALUABLE SOURCE OF DESIRABLE TRAITS**

Gametocidal chromosomes have been well documented in different species of *Aegilops* genus. *Aegilops* comprises of different annual grass species commonly known as ‘Goat grasses’. These wild species are found mainly in the Mediterranean Basin, southern Asia, the mountains of the Caucasus and Kashmir, and the Near East, growing at altitudes ranging from 0 to 2,000 m (Kilian *et al.* 2011). The genus *Aegilops* has been classified into five sections viz., *Aegilops*, *Cylindropyrum*, *Comopyrum*, *Sitopsis* and *Vertebrata* and a subgenus *Ambylopyrum* (genome not determined) (van Slageren 1994) (Table:1). The sections *Aegilops* (U genome and U with C, S, M, N genomes), *Cylindropyrum* (C- and CD- genomes) and *Vertebrata* (D-genome and D with M, N, S, U genomes) consist of diploid as well as polyploid species whereas the other two sections *Comopyrum* (M- or N-genomes) and *Sitopsis* (S-genome and its variants) comprise only diploid members (Kimber and Tsunewaki 1988; Kilian *et al.* 2011) (Table.1). Member species of *Aegilops* genus are a good source of valuable traits for wheat. Wheat rusts have been effectively controlled by genetic resistance and *Aegilops* species are good source of such resistance genes (Dvorak 1977; Tomar and Kochumadhavan 1996; Tomar and Menon 2001; 1956; Riley *et al.* 1968; Aghaee-Sarbarzeh *et al.* 2002; Prazak *et al.* 1997; Ozgen *et al.* 2004; Si n g h *et al.* 2004; Chhuneja *et al.* 2008; Bossolini *et al.* 2006; Marais *et al.* 2008; Marais *et al.* 2010a, c). For instance stem rust resistance genes *Sr32* (McIntosh *et al.* 1995), *Sr33* (Kerber 1979), *Sr34* (McIntosh 1982), *Sr38* (Bariana and McIntosh 1993), *Sr39* (Kerber and Dyck 1990); leaf rust resistance genes *Lr9* (Sears 1956), *Lr21* (Rowland 1974), *Lr22a* (Rowland 1974), *Lr28* (McIntosh 1982), *Lr32* (Kerber 1987), *Lr35* (Kerber and Dyck 1990), *Lr36* (Dvorak and Knott 1990), *Lr37* (Dvorak and Knott 1990), *Lr42* (Cox *et al.* 1994), *Lr47* (Dubcovsky *et al.* 1998), *Lr51* (Helguera 2005), *Lr54* (Marais *et al.* 2005), *Lr56* (Marais *et al.* 2006), *Lr57* (Kuraparthi *et al.* 2007a), *Lr58* (Marais *et al.* 2007; Kuraparthi *et al.* 2007b), *Lr59* (Marais *et al.* 2007), *Lr62* (Marais *et al.* 2009); yellow rust resistance genes *Yr8* (Riley *et al.*), *Yr17* (Bariana and McIntosh 1993), *Yr37* (Marais *et al.* 2005), *Yr38* (Marais *et al.* 2006), *Yr40* (Kuraparthi *et al.* 2007a), *Yr42* (Marais

et al. 2009) have been transferred so far from different species of *Aegilops*. Similarly genes imparting resistance to other diseases like powdery mildew (*Blumeria graminis* f. sp. *tritici* or *Erysiphe graminis*) (Spetsov *et al.* 1997; Stoilova *et al.* 2006; Miranda *et al.* 2007), eyespot (*Pseudocercospora herpotrichoides*) (Doussinault *et al.* 1983; Thiele *et al.* 2002) and tan spot (*Pyrenophora tritici-repentis*) (Tadesse *et al.* 2006) have been identified from *Aegilops* species. They are reported to be good source for tolerance to biotic stresses like nematodes (Martín-Sánchez *et al.* 2003; Montes *et al.* 2008; Coriton *et al.* 2009) and insects (Dubcovsky *et al.* 1998; Azhaguvel *et al.* 2010). In addition they also possess tolerance for soil salinity, drought (Shimshi *et al.* 1982; Farooq *et al.* 1992) as well as soil acidification (Berzonsky *et al.* 1989). Quality traits such as high total protein content, amino acid lysine, and the macronutrients iron and zinc in the kernels (Bluthner *et al.* 1988; Pestsova *et al.* 2001; Prazak *et al.* 2004; Rawat *et al.* 2009) have also been reported. In hybrid wheat development, *Aegilops* species played notable role both as source of cytoplasmic male sterility as well as fertility restoration thus playing a major role in developing hybrid wheat (Mukai and Tsunewaki 1980; Panayotov 1980; Mukai 1983; Tomar *et al.* 2001). Other genes resulting in good agronomic performance like long ears (Millet *et al.* 1988) and to pre-harvest sprouting (Gatford *et al.* 2002) have also been associated with *Aegilops*. In addition to this wide range of beneficial genes, *Aegilops* sp. is known to carry some interesting genes such as suppressor/inhibitor of *Ph1* locus (*Ph¹* gene) which disrupts the diploidizing system leading to pairing between homologous as well as homeologous chromosomes (Okamoto 1957; Sears & Okamoto 1958; Riley & Chapman 1958; Sears 1977) and gametocidal genes (*Gc*) (Endo 1979, 1990; Endo and Tsunewaki 1975; Maan 1975; Miller 1983). Hence the transfer of alien genes from *Aegilops* species may become problematic if the gene(s) of interest is tied to gametocidal gene(s) (Marais *et al.* 2003; Marais and Pretorius 1996).

DISCOVERY OF GAMETOCIDAL ACTIVITY

Alien chromosomes carrying gametocidal genes were unintentionally introduced into common wheat (*Triticum aestivum* L.) and durum wheat (*Triticum durum* L.) during the production of alloplasmic (Tsunewaki 1980, 1993; Endo 1990) or alien chromosomal addition lines (Endo and Katayama 1978; Miller *et al.* 1982; Kota and Dvorak 1988; Friebe *et al.* 1993, 1999) by crossing with *Aegilops* species (Endo and Tsunewaki 1975; Maan 1975; Endo 1979, 1982, 1985; Tsujimoto and Tsunewaki 1983). Even after several rounds of backcrossing with wheat, these selfish chromosomes were not eliminated (Endo and Tsunewaki 1975). Gametocidal genes (*Gc*) are reported in different species of *Aegilops* belonging to the sections *Aegilops* (*Ae. geniculata* and *Ae. triuncialis*),

Cylindropyrum (*Ae. caudata* and *Ae. cylindrica*) and ***Sitopsis*** (*Ae. longissima*, *Ae. sharonensis* and *Ae. speltoides*) (Table:1). All of the diploid progenitor species possessing *Gc* genes are reported to be outbreeding in nature (Tsujimoto 2005).

Gc* genes reported in species of Section *Aegilops

Under the section *Aegilops*, eight species are classified out of which two tetraploid species viz., *Aegilops triuncialis* (CCUU) and *Aegilops geniculata* (U⁵U⁵M⁵M⁵) have been reported to show gametocidal activity. During the efforts to transfer cytoplasm by successive substitutive backcrossing from various *Aegilops* species, Endo and Tsunewaki (1975) noticed extreme female sterility in cytoplasmic substitution lines of common wheat with *Ae. triuncialis*. Cytological investigation revealed that these sterile lines carried an extra chromosome from their cytoplasmic donor without exception and the sterility derived from the inviability of extra chromosome free gametes in a plant carrying the chromosome. In *Aegilops geniculata*, a new gametocidal (*Gc*) factor was identified (Kynast *et al.* 2000). When transferred to Chinese Spring wheat, monosomic *Triticum aestivum*–*Ae. geniculata* addition plants undergo chromosome breakage and anaphase bridges were observed at ana/telophase of the first (29%) and second (11%) pollen mitosis. In case of *Aegilops triuncialis* gametocidal activity was attributed by the C genome whereas in *Aegilops geniculata* by M⁵ genome.

Gc* genes reported in species of Section *Cylindropyrum

Cylindropyrum section is comprised of a diploid species, *Ae. caudata* (CC; Syn: *Ae. margrafi*) and a tetraploid species *Ae. cylindrica* (CCDD). In both the species gametocidal activity has been reported in the C genome. In case of *Ae. caudata*, a chromosome was found to be selectively retained in common wheat (Endo and Katayama 1978). Monosomic addition plants for a gametocidal C chromosome to common wheat showed semi-sterility because only gametophytes with a gametocidal chromosome are functional while those without this chromosome are aborted. As a result, gametocidal chromosomes were preferentially transmitted to the next generation. Gametocidal activity in *Ae. cylindrica* was identified during development of alloplasmic lines (Endo 1979). An F₁ hybrid of *Ae. cylindrica* (as female) and a common wheat variety was repeatedly backcrossed to various kinds of common wheat in order to produce various cytoplasm substitution lines with different nuclei of common wheat. One of them with Jones Fife background was noticed to produce plants aberrant in appearance. This particular line had a chromosome with a subterminal centromere possibly derived from *Ae. cylindrica* and showed

poor seed-set in every backcross generation. This indicated association between partial fertility and selective retention of this *cylindrica* chromosome.

Gc genes reported in species of Section *Sitopsis*

In *Sitopsis* section three species were reported to exhibit gametocidal activity viz., *Ae. speltoides*, *Ae. sharonensis* and *Ae. longissima*. Evidence for the presence of gametocidal genes in *Ae. speltoides* came into light during the efforts to develop cms lines from *Ae. speltoides*. The alloplasmic lines of bread wheat carrying G-type cytoplasm derived from *Aegilops speltoides* subsp. *aucheri* showed around 50% reduction of female fertility compared with the alloplasmic lines of the same bread wheat lines carrying G-type cytoplasms from other sources. This reduction of female fertility is owed to a gametocidal gene derived from *Ae. speltoides*. This gene has been preferentially transmitted through 16 successive backcrosses in which common wheat was the recurrent pollen parent, and has been present in the heterozygous state in every backcross generation. The karyotype and meiotic chromosome pairing of hybrid from reciprocal crosses between (*Ae. speltoides*) – cv. Chinese Spring and (*Triticum aestivum*) – cv. Chinese Spring are normal, indicating that the gametocidal gene derived from an *Ae. speltoides* chromosome subsequently was translocated to a wheat chromosome. This is the first case reported of the integration of a gametocidal gene into a wheat genome and the symbol given to it was *Gcl*. (Tsujimoto and Tsunewaki 1984). Another gametocidal gene unique from *Gcl* was found in a common wheat cultivar Chinese Spring carrying the cytoplasm of *Aegilops speltoides* strain KU 5725 (Plant Germplasm Institute, Kyoto University). Monosomic analysis revealed that both this gene and *Gcl* are located on chromosome 2B. The two genes appear to be allelic and so have been designated as *Gcl1a* (Instead of *Gcl*) and *Gcl1b*. Nonetheless the two genes differ in their ability to induce hybrid dysgenesis in wheat: *Gcl1a* causes endosperm degeneration and chromosome aberrations, whereas *Gcl1b* results in abnormal seed lacking the shoot primodium (Tsujimoto and Tsunewaki 1988). The near isogenic line of Chinese Spring with *Gcl1a*, being homozygous for *Gcl1a* was morphologically the same as Chinese Spring without *Gcl1a*, except for a slight reduction of fertility from 99.3 to 96.5 per cent (Tsujimoto and Tsunewaki 1983). When it was crossed to Chinese Spring, shriveled seeds that germinate at low frequency were obtained (Tsujimoto and Tsunewaki 1988a, b). Two novel sources of gametocidal genes were reported in *Ae. longissima* and *Ae. sharonensis* which is distinct from *Ae. speltoides* (Endo 1985; Tsujimoto 1994).

Gc GENES: CHROMOSOMAL LOCATION AND CLASSIFICATION

Gametocidal activity is mostly confined to 2, 3 and 4 homeologous groups of C, S, S¹, S^{sh}, M^g genomes. The chromosomal location of *Gc* genes have been reported in most of the species: chr 3C of *Aegilops triuncialis* L. (CCUU) (Endo and Tsunewaki 1975) and *Ae. caudata* L.(CC) (Endo and Katayama 1978); chr 2C of *Ae. cylindrica* (CCDD) (Endo 1979, 1988, 1996); chr 4S¹ or 2S¹ of *Ae. longissima* Schweinf. & Muschl. (S¹S¹) (Endo 1985; Friebe *et al.* 1993; Tsujimoto 1994, 1995) and *Ae. sharonensis* (S¹S¹) Eig (Maan 1975; Endo 1982, 1985; Miller *et al.* 1982); chr 2S or 6S of *Ae. speltoides* Tausch (SS) (Tsujimoto and Tsunewaki 1983, 1984, 1985a, 1988; Kota and Dvorak 1988); and chromosome 4M^g of *Ae. geniculata* (UUMM) (Friebe *et al.* 1999; Kynast *et al.* 2000). In the catalogue of gene symbols for wheat, six gametocidal genes have been designated viz., *Gc1-B1a* and *Gc1-B1b* from *Ae. speltoides* subsp. *aucheri* and *Ae. speltoides* subsp. *ligustica* respectively; *Gc1-S11* and *Gc2-S11b* from *Ae. sharonensis*; *Gc2-S11a* from *Ae. longissima*; *Gc3-C1* from *Ae. triuncialis* (Mc Intosh). Also a suppressor gene namely *IGc* have been reported in the cultivar Norin 26 (Mc Intosh), which represses the gametocidal action of 3C chromosome of *Ae. triuncialis* (Tsujimoto and Tsunewaki 1985). No other genes limiting the gametocidal action have been reported elsewhere.

Tsujimoto (1995) had studied the functional relationship between these six gametocidal genes and classified them into three functional groups. Interactions were investigated by analysis of wheat hybrids among lines carrying different gametocidal genes. The first group comprises of two *Gc* genes (*Gc1a* and *Gc1b*) on 2S of *Ae. speltoides* and one gene (*Gc-S¹3*) on chromosome 2S¹ of *Ae. sharonensis*. The second group consists of two genes (*Gc-S¹1* and *Gc-S¹2*) on chromosome 4S¹ of *Ae. longissima* and *Ae. sharonensis*. Plants carrying *Gc* genes of both the first and the second group produced progeny with higher frequencies of chromosome breakage than those found in the progeny of single gene carriers. The third group comprises of *Gc* gene (*Gc-C*) on chromosome 3C of *Ae. triuncialis* which did not have any interaction with *Gc* genes belonging to the other two groups. The nomenclature of *Gc* genes described here is slightly different from that used in the catalogue of gene symbols for wheat. Endo (2011) studied the relationship among gametocidal chromosomes from *Aegilops triuncialis*, *Ae. sharonensis* and *Ae. longissima*. Double monosomic addition lines having two gametocidal chromosomes from any two of the abovementioned species were developed and pairing behavior of these two chromosomes were studied. The *Aegilops* chromosomes did not pair with one another in the double monosomic addition lines. Both gametocidal chromosomes were almost always transmitted through both male and female gametes in the progeny of the double monosomic addition lines having *triuncialis* and *sharonensis* chromosomes as well as

the *triuncialis* and *longissima* chromosomes. While in the progeny of the double monosomic addition line with the *sharonensis* and *longissima* chromosomes, only the *longissima* chromosome was preferentially transmitted through male and female gametes.

MODE OF ACTION

The mode of *Gc* action is different from other segregation distorter systems because of two reasons: (i) selfish nature leading to destruction of gametes lacking *Gc* genes and (ii) effect on both male and female gametogenesis. Previous studies have indicated that *Gc* genes ensure their preferential transmission by causing chromosomal breaks in gametophytes lacking *Gc* genes resulting in deletions and translocations (Finch *et al.* 1984; King and Laurie 1993; Nasuda *et al.* 1998). Meiotic analysis had revealed that gametocidal activity resulted in occurrence of univalent chromosomes, multivalent configurations, chromosome fragments, chromosome bridges and laggards at different stages (Fig.1). For instance in PMCs of F₁ between the Chinese Spring-gametocidal chromosome 2C disomic addition line (CS-2C) and Chinese Spring-*Lophopyrum elongatum* 6E disomic addition line (CS-6E), a high frequency of univalent chromosomes and a moderate frequency of multivalent chromosomes during metaphase I were observed along with a large number of chromosome fragments, chromosome bridges and laggards at anaphase I and II (Hai-Bin Zhao *et al.* 2014). Such aberrations are mainly caused by chromosome splitting and translocation induced by the *Gc* chromosome 2C. Similarly in the cross progenies between Chinese Spring-*Aegilops* 2C disomic addition and Chinese Spring-*Elytriga* disomic addition the number of univalents exceeded the expected limit and showed trivalents and tetravalents. In these F₁ progenies, the highest seed set was 62.09 per cent and the lowest was 30.92 per cent (Liu Feng-Qi *et al.* 2007). Gametocidal chromosome 2S derived from *Ae. speltoides* was also reported to be inducing chromosome breaks in *Triticum aestivum* cultivar *Ningnong* and 5R/5A wheat-rye substitution lines. Meiotic study in the hybrid F₁ at metaphase I and II stages revealed high frequency of univalents and multivalent; and at anaphase I and chromosomal abnormalities such as a large number of lagging chromosomes, chromosomal fragments and chromosomal bridges were observed (Chen Xia *et al.* 2008). In plants monosomic for chromosome 4S^{sh} from *Aegilops sharonensis*, approximately 50 per cent of meiocytes at the first post-meiotic mitosis contained chromosome fragments and these fragments (termed as SSS-separated segments) comprised of a pair of equal length parts of two sister chromatids (Finch *et al.* 1984). The frequency of transmission of chromosome 4S^{sh} through both the male and female gametes, when in the monosomic condition in a range of genetic backgrounds, has been shown to be at least 97.8 per cent. The ability of 4S^{sh} chromosome for

chromosome fragmentation is reported not only in meiospores but also in developing embryos and endosperms. The types of aberration were similar to those seen at first pollen grain mitosis in plants monosomic for chromosome 4S^{sh}. So it was assumed that a single mechanism may be responsible for aberrations in meiocytes, embryos and endosperms (King *et al.* 1991b).

When gametocidal genes (*Gc*) segregate, the gametes lacking *Gc* gene become abortive and only the gametes carrying the *Gc* gene are fertile (Tsujiimoto 2005). The selectively retained chromosomes cause sterility of both male and female gametes that are lacking the alien chromosome and thereby ensure their preferential transmission (Endo 1978). The mode of action of *Gc* genes is 'sporopytic' in nature because the genetic makeup of the sporophyte controls the sterility of the gametophyte not carrying the *Gc* gene (Maan 1975). Gametocidal chromosomes act in both directions as male and female gametes without the *Gc* gene become abortive. As a result only gametes with the *Gc* gene are transmitted to the next generation. The phenotype of *Gc* action in the female germline is manifested as sporadic seed set on spikes and in the male germline it is evident as a mixture of normal and abortive pollen grains (Tsujiimoto 2005). Homozygotes for the *Gc* gene do not show gametic abortion so they can be maintained indefinitely by selfing like a normal plant showing good pollen fertility and seed set. However when such plants are crossed to non carriers of *Gc* genes, the F₁ (hetero-/hemi-zygous for *Gc* gene) will show gametic abortion and result in severe reduction in pollen fertility and seed setting. In majority of the cases elimination of non-carrier gametes appears to be complete (Marais and Pretorius 1996). Nevertheless the extent and severity of chromosomal breakage and gamete elimination varies for different *Gc* genes. For instance, the action of the *Gc* gene located on the *Ae. sharonensis* 'cuckoo' chromosome 4S^{sh} (Miller *et al.* 1982; King *et al.* 1991; Nasuda *et al.* 1998) is very strong and results in extensive chromosomal breakage prior to the S-phase of the first postmeiotic interphase in gametophytes lacking *Gc* genes. As a result, only gametes with the *Gc* gene are functional, which causes semisterility and leads to 100% transmission of the *Gc2* carrier chromosome to the offspring (Friebe *et al.* 2003). In addition, chromosome fragments (in the form of single chromatid segments-SCSs) have been observed during early embryo and endosperm development of plants carrying cuckoo chromosomes (King and Laurie 1993; de las Heras 1999). Broken chromosome ends exhibit a tendency to fuse and form dicentric chromosomes (McClintock 1941; Werner *et al.* 1992) and break-fusion-bridge (BFB) cycle is evident. While weaker *Gc* genes like the one located on *Ae. cylindrica* chromosome 2C only induce moderate breakage, and the *Gc* chromosome is not selectively retained. In the offspring of such plants the recovery of chromosomal rearrangements is possible and

allows for the production of deletion stocks in many plant species. Endo (1988a) suggested that when the gametocidal action is intense, gametophytes without the alien chromosome may suffer severe chromosome breakage and become sterile ensuring exclusive transmission of the alien chromosome. On the contrary when the gametocidal action is mild, gametophytes without the alien chromosome are fertilized, suffering slight chromosome damage, and develop into plants with chromosomal aberrations (Tsujimoto 2005).

Attempts for unraveling the molecular mechanisms underlying gametocidal action using *Gc* knock-out mutants have been carried out. One knockout mutation at the *Gc2* locus on *Ae. sharonensis* chromosome 4S^{sh} was identified and characterized cytologically. This study is the first step toward an understanding of *Gc* function at the molecular level (Friebe *et al.* 2003). According to the literature, there are two phenotypes connected with the mechanism responsible for the preferential transmission of the *Gc* chromosomes (Endo 1990; Tsujimoto 2005). The first phenotype induces chromosome breakages, while the second prevents chromosome breakages. Breaker element may be responsible for double strand breaks in DNA resulting in deletions and translocations. Double strand breaks are naturally happening in cell at a base level as a result of normal cellular processes and metabolic by-products like reactive oxygen species. Their frequency is increased by environmental exposure to irradiation, other chemical agents, or ultraviolet (UV) light. When the breaker element alone is present it is possible that it induces higher frequency of double strand breaks. Cells have evolved several mechanisms to repair these double strand breaks. But when the breaker element alone is present these repair mechanisms may fail to function. When both elements are present, the chromosome aberrations do not occur in gametes, because the gametocidal action is neutralised by the inhibitor. Action of the Inhibitor element may be to suppress the formation of double strand breaks by efficient repair mechanisms. Friebe *et al.* (2003) reported the development of a knock-out wheat mutant carrying the *Gc2* locus on *Ae. sharonensis* chromosome 4S^{sh}, which has lost the chromosome fragmentation function, but has retained the inhibitor element. Nonetheless, the molecular marker mapping enabled to localise *Gc* loci on a region proximal to a block of sub-telomeric heterochromatin on chromosome 4S^{sh}L of *Ae. sharonensis* (Knight *et al.* 2015).

PRACTICAL APPLICATIONS

Although gametocidal genes prove to be a menace while alien gene introgression, they were found useful in other contexts. Utilization of gametocidal chromosomes in cytogenetics and plant breeding is based on two peculiar properties, one is the ability to induce mutations via chromosomal rearrangements and second is the ability for

preferential transmission. The practical implications of gametocidal system in plant breeding have been reviewed. The *Gc* system have been hypothesized to be an effective way to induce mutations via chromosomal rearrangements generating new variation in the germplasm (Endo 1990, 2007). It is conceived as safer and easier alternative to handling dangerous mutagens. The gametocidal chromosome 3C of *Ae. triuncialis* is known to induce chromosomal aberrations in wheat. The efficiency of 3C in inducing mutations in 1R of rye (*Secale cereale* L.) was studied by Endo *et al.* (1994) and reported more than 10% deletions and wheat-rye translocations in 1R. This peculiar property of 3C was utilized for transfer of alien genes from rye to common (Masoudi-Nejad *et al.* 2002). Chromosome 3C along with 1R of rye was brought together in a common wheat line to know efficiency of 3C in inducing transfer of small 1R segments to wheat. Progenies having chromosomes translocated with segments of the 1R satellite were identified (2A, 2D, 3D, 5D and 7D). Such plants positive for 1R translocations were tested for the presence of a storage protein locus *Sec-1* and a cluster of resistance genes for wheat rust diseases, *Sr31*, *Lr26* and *Yr9*. The 2A and 2D translocations had the *Sec-1* and three rust resistance loci. The 3D and 5D translocations had *Sr31*, *Lr26* and *Yr9* but not *Sec-1*. The 7D translocation lacked *Sec-1*, *Lr26* and *Yr9*, but the presence of *Sr31* in this translocation was not determined. Hence the 3C gametocidal system was demonstrated to be effective in transferring small rye chromosome segments. In a recent study the gametocidal property of 4M^g chromosome derived from *Ae. geniculata* (Syn.: *Ae. ovata*) was utilized for improving genetic variability in triticale by inducing chromosomal rearrangements between *Ae. ovata* (UUMM) and hexaploid triticale (AABBRR) genomes. The *Ae. geniculata* × *Secale cereale* (UUMMR) amphiploids and triticale cultivar Moreno were used to produce hybrids by reciprocal crosses to develop triticale-rye translocations (Kwiatek *et al.* 2016).

King *et al.* (1991a) have exploited the property of preferential transmission of 4S^{sh} of *Ae. sharonensis* for the imparting complete transmission of dwarfing gene *Rht2* located on 4D chromosome in certain semidwarf European varieties which tend to lose 4D chromosome leading to tall offtypes. Translocations involving *Ae. sharonensis* chromosome 4S^{sh} and *Rht2* carrying *Triticum aestivum* chromosome 4D arms were created. Plants carrying such translocations showed complete transmission of *Rht2* gene in both pollen and egg. Similar approach was undertaken for the production of stable 44-chromosome wheat lines (King *et al.* 1992). Wild relatives of wheat carry many genes of potentially high agronomic value. As the transmission frequency of alien chromosomes added to the euploid wheat complement is low, commercial exploitation of such lines is limited. If the additional chromosome is preferentially transmitted like the gametocidal chromosomes this problem could be overcome.

Hence translocations involving the long arm of the *Ae. sharonensis* chromosome 4S^{sh} and the long and short arms of chromosome 1U from *Ae. umbellulata* were isolated. The 1U chromosome contains *Glu-U1* gene on the long arm which encodes high-molecular-weight (HMW) subunits of glutenin and *Gli-U1* gene on the short arm which encodes gliadins both playing a major role in improving bread making quality. Majority of progeny derived from self-fertilization of the 42W+ 4S^{sh}/1U individuals possessed 44 chromosomes and they possessed good quality traits also. Thus they proved that these translocations are stable and preferentially transmitted. Nevertheless, the applicability of this scheme to breeding programmes will depend on their effect on agronomic characters as lines carrying translocations are normally inferior to euploid wheat.

One remarkable practical utilization of *Gc* genes was for the development of deletion stocks. Endo and Gill (1996) successfully utilized gametocidal system in developing deletion stocks in wheat using two alien monosomic addition lines one with an *Ae. cylindrica* chromosome and other an *Ae. triuncialis* chromosome and one alien translocation line having a small chromosomal segment from *Ae. speltoides* translocated to the the long arm of 2B (T2BS.2BL-2SL). Most of the deletions were isolated from *Ae. cylindrica* addition line as gametocidal activity is weak and is capable of inducing only moderate chromosomal breakage. Hence gametes lacking *Gc* genes may be viable but possessing few deletions. In such manner, 436 deletions were identified and deletion homozygotes were established for about 80% of the deletions. Similarly deletion stocks were developed in barley (Shi and Endo 1999, 2000) and rye (Friebe *et al.* 2000a). The deletion stocks developed using gametocidal genes have been effectively used for physical mapping of genes, ESTs and SSR markers to deletion bins (Serizawa *et al.* 2001; Qi *et al.* 2004; Sourdille *et al.* 2004).

REMOVAL OF GAMETOCIDAL PROPERTY

Gametocidal genes can cause trouble while transfer of desirable alien genes from *Aegilops*. If linked to the gene of interest they can create segregation distortion (Marais and Pretorius 1996). In addition, semi sterility of lines carrying these genes in heterozygous state is unsolicited in plant breeding. Mutation is one of the candidate approaches for getting rid of gametocidal genes. Ethyl methane sulfonate (EMS) is a chemical mutagen which induces point mutations in the form of G/C to A/T transitions (Krieg 1963). EMS induced mutagenesis had been successful in knocking out the *Gc2* gene transferred to wheat as a wheat-*Ae. sharonensis* T4B-4Ssh#1 translocation chromosome. As a result one putative *Gc2* mutant was identified which restores spike fertility and shows Mendelian

segregation (Friebe *et al.* 2003). Hypothetically other types of mutagens will also equally be useful for knocking out the action of gametocidal genes. Another possibility is by inducing homeologous pairing to create recombinants lacking gametocidal genes but positive for the beneficial genes. This technique has been implemented by Marais *et al.* (2010b) in breaking association between rust resistance genes and gametocidal genes derived from *Ae. speltoides*. Introgressions S24 and S13 located on chr#3A harbouring leaf rust and stem rust resistance genes could not be commercially exploited due to associated gametocidal (*Gc*) genes. Allosyndetic pairing induction was used in an attempt to remove the *Gc* gene(s) and putative primary recombinants with improved fertility and plant type were obtained.

CONCLUSION

Aegilops belongs to the secondary gene pool which possesses at least one genome homologous to wheat. It is proven to be a good source of genes conferring good agronomic traits, resistance to biotic and abiotic stresses, quality traits, male sterility, fertility restoration and much more. Hence it can play a major role in widening the genetic base of cultivated wheat. Gene transfer from wild species is not an easy task. *Aegilops* species have some genes which will be undesirable if co-transferred with the gene of interest to the wheat genome, like the gametocidal genes. This impedes the transfer of gene of interest and its utilization in plant breeding. In such cases removal of loci responsible for gametocidal activity becomes necessary. Some instances of successful elimination have been reported utilizing mutagenesis or homeologous pairing induction. Nevertheless the gametocidal genes have been utilized constructively in other contexts. Most remarkable one is the development of deletion stocks in wheat, barley and rye. These deletion stocks proved to be valuable tools in physical mapping of genes to deletion bins. The ability of gametocidal genes to induce mutations via chromosomal rearrangements has been utilized to create variability. Gametocidal chromosomes can be translocated with the gene of interest and the complete transmission of the concerned gene can be achieved.

Acknowledgement: Dr. Tomar SMS, Dr. Vinod and my colleagues in Division of Genetics, Indian Agricultural Research Institute, New Delhi, India

REFERENCES

- Aghaee – Sarbarzeh, M., Ferrahi, M., Singh, S., Singh, H., Friebe, B. and Gill, B.S. 2002. *Ph-I*-induced transfer of leaf and stripe rust-resistance genes from *Aegilops triuncialis* and *Ae. geniculata* to bread wheat. *Euphytica* 127: 377–382.
- Azhaguvel, P., Rudd, J.C., Ma, Y.Q., Luo, M.C. and Weng, Y.Q. 2012. Fine genetic mapping of greenbug aphid-resistance gene *Gb3* in *Aegilops tauschii*. *Theor Appl Genet* 124(3): 555-564. doi: 10.1007/s00122-011-1728-z.
- Bariana, H.S. and McIntosh, R.A. 1994. Characterization and origin of rust and powdery mildew resistance genes in VPM1 wheat. *Euphytica* 76: 53–61.
- Bariana, H.S. and McIntosh, R.A. 1993. Cytogenetic studies in wheat XV- Location of rust resistance genes in VPM1 and their genetic linkage with other disease resistance genes in chromosome 2A. *Genome* 36: 476-482.
- Berzonsky, W.A. and Kimber, G. 1989. Tolerance to aluminium of *Triticum* N-genome amphiploides. *Plant Breed* 103: 37–42.
- Bluthner, W.D. and Schumann, E. 1988. Use of *Aegilops* and tetraploid wheat for wheat protein improvement. *Hod Roślin Aklim Nasien* 32 (1/2): 203–206.
- Bossolini, E., Krattinger, S.G. and Keller, B. 2006. Development of simple sequence repeat markers specific for the *Lr34* resistance region of wheat using sequence information from rice and *Aegilops tauschii*. *Theor Appl Genet* 113: 1049–1062. doi:10.1007/s00122-006-0364-5.
- Brand, C.L., Larracuente, A.M. and Presgraves, D.C. 2015. Origin, evolution, and population genetics of the selfish *Segregation Distorter* gene duplication in European and African populations of *Drosophila melanogaster*. *Evolution* 69(5): 1271–1283.
- Bregliano, J.C. and Kidwell, M.G. 1983. Hybrid dysgenesis determinants. In: Shapiro JA (ed.) *Mobile Genetic Elements*. Academic Press, New York, pp. 363-410.

- Cameron, D.R. and Moav, R. 1957. Inheritance in *Nicotiana tabacum*. XXVII. Pollen killer, an alien genetic locus inducing abortion of microspores not carrying it. *Genetics* 42: 326-335.
- Castro, J.P. and Carareto, C.M.A. 2004. *Drosophila melanogaster* P transposable elements: mechanisms of transposition and regulation. *Genetica* 121: 107–118.
- Chhuneja, P., Kaur, S., Goel, R.K., Aghaee – Sarbarzeh, M., Prashar, M. and Dhaliwal, H.S. 2008. Transfer of leaf rust and strip rust resistance from *Aegilops umbellulata* Zhuk. to bread wheat (*Triticum aestivum* L.). *Genet Resour Crop Evol* 55: 849–859. doi:10.1007/s10722-007-9289-3
- Coriton, O., Barloy, D., Huteau, V., Lemoine, J., Tanguy, A.M. and Jahier, J. 2009. Assignment of *Aegilops variabilis* Eig chromosomes and translocations carrying resistance to nematodes in wheat. *Genome* 52: 338-346.
- Cox, T.S., Raupp, W.J. and Gill, B.S. 1994. Leaf rust resistance genes *Lr41*, *Lr42* and *Lr43* transferred from *Triticum tauschii* to common wheat. *Crop Science* 34(2): 339-343.
- Crow, J.F. 1983. Hybrid dysgenesis and P factor in *Drosophila*. *Jpn J Genet* 58: 621-625.
- de las Haras, J.I., King, I.P. and Parker, J.S. 2001. 5-azacytidine induces chromosomal breakage in root tips of wheat carrying the cuckoo chromosome 4SL from *Aegilops sharonensis*. *Heredity* 87:474-479.
- de las Heras, J.I. 1999. Preferentially Transmitted Alien "Cuckoo" Chromosomes from *Aegilops* Spp. in Wheat. PhD Thesis, University of Reading, U.K.
- Deven, R.S. 2007. Genomic targeting and mapping of a gametocidal gene in wheat. Ph. D dissertation. Kansas State University.
- Doussinault, G., Delibes, A., Sanchez-Monge, R. and Garcia –Olmedo, F. 1983. Transfer of a dominant gene for resistance to eyespot disease from a wild grass to hexaploid wheat. *Nature* 303: 698–700.

- Dubcovsky, J., Lukaszewski, A.J., Echaide, M., Antonelli, E.F. and Porter, D.R. 1998. Molecular characterization of two *Triticum speltoides* interstitial translocations carrying leaf rust and greenbug resistance genes. *Crop Sci.* 38: 1655-1660.
- Dvorak, J. 1977. Transfer of leaf rust resistance from *Aegilops speltoides* to *Triticum aestivum*. *Canadian J of Genet And Cytol* 19: 133-141.
- Dvorak, J. and Knott, D.R. 1990. Location of a *Triticum speltoides* chromosome segment conferring resistance to leaf rust in *Triticum aestivum*. *Genome* 33: 892-897.
- Dyck, P.L. and Kerber, E.R. 1970. Inheritance in hexaploid wheat of adult plant leaf rust resistance derived from *Aegilops squarrosa*. *Canadian J Genet & Cytology* 12: 175-180.
- Endo, T.R. 1978. On the *Aegilops* chromosomes having gametocidal action on common wheat. *Proc V Int Wheat Genet Symp, New Delhi* 1: 306-314.
- Endo, T.R. 1979. Selective gametocidal action of a chromosome of *Aegilops cylindrica* in a cultivar of common wheat. *Wheat Inf Serv* 50: 24-28.
- Endo, T.R. 1982. Gametocidal chromosomes of three *Aegilops* species in common wheat. *Canadian J of Genet and Cytol* 24 (2): 201-206.
- Endo, T.R. 1985. Two types of gametocidal chromosome of *Ae. sharonensis* and *Ae. longissima*. *Jpn J Genet* 60: 125-135.
- Endo, T.R. 1988a. Induction of chromosome structural changes by a chromosome of *Aegilops cylindrica* L. in common wheat. *J Hered* 79: 366-370.
- Endo, T.R. 1988b. Chromosome mutations induced by gametocidal chromosomes in common wheat. *Proc VII Int Wheat Genet Symp, Cambridge* 1: 259-263.
- Endo, T.R. 1990. Gametocidal chromosomes and their induction of chromosome mutation in wheat. *Jpn J Genet* 65: 135-152.

- Endo, T.R. 1996. Allocation of a gametocidal chromosome of *Aegilops cylindrica* to wheat homoeologous group 2. *Genes Genet Syst* 71: 243–246.
- Endo, T.R. 2007. The gametocidal chromosome as a tool for chromosome manipulation in wheat. *Chromosome Res* 15(1): 67-75.
- Endo, T.R. 2011. Gametocidal chromosomes of three *Aegilops* species in common wheat. *Genome* 24(2):201-206. DOI: 10.1139/g82-020
- Endo, T.R. and Gill, B.S. 1996. The deletion stocks of common wheat. *J Hered* 87: 295-307.
- Endo, T.R. and Katayama, Y. 1978. Finding of a selectively retained chromosome of *Aegilops caudata* L. in common wheat. *Wheat Inf Serv* 47/48: 32-35.
- Endo, T.R. and Tsunewaki, K. 1975. Sterility of common wheat with *Aegilops triuncialis* cytoplasm. *J Hered* 66: 13-18.
- Endo, T.R., Yamamoto, M. and Mukai, Y. 1994. Structural changes of rye chromosome 1R induced by a gametocidal chromosome. *Jpn J Genet* 69: 13-19.
- Engels, W.R. 1996. P elements in Drosophila. In: Saedley H, Gierl A, editors. *Transposable Elements*. Berlin: Springer-Verlag pp. 103–123.
- Farooq, S., Iqbal, N., Asghar, M. and Shah, T.M. 1992. Intergeneric hybridization for wheat improvement – IV. Expression of salt tolerance gene (s) of *Aegilops cylindrical* in hybrids with hexaploid wheat. *Cer Res Comm* 20(1–2): 111–118.
- Finch, R.A., Miller, T.E. and Bennett, M.D. 1984. "Cuckoo" *Aegilops* addition chromosome in wheat ensures its transmission by causing chromosome breaks in meiospores lacking it. *Chromosoma* 90: 84-88.
- Friebe, B., Kynast, R.G. and Gill, B.S. 2000. Gametocidal factor induced structural rearrangement in rye chromosomes added to common wheat. *Chromosome Res* 8: 101-511.

- Friebe, B., Tuleen, N., Jiang, J. and Gill, B.S. 1993. Standard karyotype of *Triticum longissimum* and its cytogenetic relationship with *T. aestivum*. *Genome* 36: 731-742.
- Friebe, B., Zhang, P., Nasuda, S. and Gill, B.S. 2003. Characterization of a knock-out mutation at the *Gc2* locus in wheat. *Chromosoma* 111: 509-517.
- Gatford, K.T., Hearnden, P., Ogbonnaya, F., Eastwood, R.F. and Halloran, G.M. 2002. Novel resistance to pre-harvest sprouting in Australian wheat from the wild relative *Triticum tauschii*. *Euphytica* 126: 67–76.
- Gotoh, K. 1924. U“ber die Chromosomenzahl von *Secale cereale* L. *Botanical Magazine Tokyo* 38: 135–152.
- Hai-Bin Zhao, Li-Juan Zhao, Li-Wei Zhao, Hong-Mei Yuan, Yan-Ming Zhang, Wen-Li Xin, Lian-Fa Sun, Chang-Hong Guo and Ji-Lin Li. 2013. Chromosome Deletion and Translocation in Chinese Spring-*Lophopyrum Elongatum* 6E Disomic Addition Lines Induced by the Gametocidal Chromosome 2C from *Aegilops Cylindrica*. *Biotechnology & Biotechnological Equipment*, 27(2): 3638-3643, doi: 10.5504/BBEQ.2012.0146
- Helguera, M., Vanzettia, L., Soriab, M., Khan, I.A., Kolmer, J. and Dubcovsky. 2005. PCR Markers for *Triticum speltoides* Leaf Rust Resistance Gene *Lr51* and Their Use to Develop Isogenic Hard Red Spring Wheat Lines. *Crop Sci.* 45 (2): 728-734.
- Hill, T., Schlotterer, C. and Betancourt, A.J. 2016. Hybrid Dysgenesis in *Drosophila simulans* Associated with a Rapid Invasion of the P-Element. *PLoS Genet* 12(3). doi: 10.1371/journal. pgen.1005920.
- Hiraizumi, Y., Albracht, J.M. and Albracht, B.C. 1994. X-linked elements associated with negative segregation distortion in the SD system of *Drosophila melanogaster*. *Genetics* 138: 145–152.
- Houben, A. 2017. B Chromosomes – A Matter of Chromosome Drive. *Front. Plant Sci.* 8:210. doi: 10.3389/fpls.2017.00210
- Huang, L., Zhang, L.Q., Liu, B.L., Yan, Z.H., Zhang, B., Zhang, Y.L. and Liu, D.C. 2011. Molecular tagging of a stripe rust resistance gene in *Aegilops tauschii*. *Euphytica* 179: 313-318.

- Jones, R.N. 1991. B-chromosome drive. *American Naturalist* 137: 430-442. Jones, R.N., Viegas, W., Houben, A. 2008. A Century of B Chromosomes in Plants: So What? *Annals of Botany* 101: 767–775. doi:10.1093/aob/mcm167
- Kerber, E.R. 1987. Resistance to leaf rust in wheat: *Lr32*, a third gene derived from *Triticum tauschii*. *Crop Science* 27: 204-206.
- Kerber, E.R. and Dyck, P.L. 1979. Resistance to stem and leaf rust of wheat in *Aegilops squarrosa* and transfer of a gene for stem rust resistance to hexaploid wheat. pp. 358–364. In S. Ramanujam (ed.) *Proc. Int. Wheat Genet. Symp.*, 5th, New Delhi, India.
- Kerber, E.R. and Dyck, P.L. 1990. Transfer to hexaploid wheat of linked genes for adult-plant leaf rust and seedling stem rust resistance from an amphiploid of *Aegilops speltoides* x *Triticum monococcum*. *Genome*. 33: 530-537.
- Kibirige-Sebunya, I. and Knott, D.R. 1983. Transfer of stem rust resistance to wheat from an *Agropyron* chromosome having a gametocidal effect. *Can J Genet Cytol* 25: 215–221.
- Kidwell, M.G. 1983. Evolution of hybrid dysgenesis determinants in *Drosophila melanogaster*. *Proc Natl Acad Sci* 80: 1655–9.
- Kilian, B., Mammen, K., Millet, E., Sharma, R., Graner, A., Salamini, F., Hammer, K. and Ozkan, H. 2011. *Aegilops*. [In:] *Wild crop relatives: genomic and breeding resources cereals*. Chittaranjan Kole (ed.), Springer-Verlag Berlin, Heidelberg, pp 1–76.
- Kimber, G. and Tsunewaki, K. 1988. Genome symbols and plasma types in the wheat group. In: Miller TE, Koebner RMD (eds) *Proceedings of the 7th international wheat symposium, 1987*, Cambridge, pp 1209–1211.
- King, I.P. and Laurie, D.A. 1993. Chromosome damage in early embryo and endosperm development in crosses involving the preferentially transmitted 4SL1 chromosome of *Aegilops sharonensis*. *Heredity* 70:5259.

- King, I.P., Koebner, R.M.D., Schlegel, R., Reader, S.M., Miller, T.E. and Law, C.N. 1991a. Exploitation of a preferentially transmitted chromosome from *Aegilops sharonensis* for the elimination of segregation for height in semi-dwarf bread wheat varieties. *Genome* 34, 944-949.
- King, I.P., Miller, T.E. and Koebner, R.M.D. 1991b. Determination of the transmission frequency of chromosome 4S of *Aegilops sharonensis* in a range of genetic backgrounds. *Theor Appl Genet* 81: 519-23.
- King, I.P., Purdie, K.A., Miller, T.E., Law, C.N. and Rogers, W.J. 1992. Exploitation of chromosome 4S, from *Aegilops sharonensis* for the production of stable 44 chromosome wheat. *Heredity* 69: 160-165.
- Knight, E., Binnie, A., Draeger, Moscou, Rey, M.D., Sucher, J., Mehra, S., King, I. and Moore, G. 2015. Mapping the 'breaker' element of the gametocidal locus proximal to a block of sub-telomeric heterochromatin on the long arm of chromosome 4S^{sh} of *Aegilops sharonensis*. *Theor Appl Genet* 128:1049–1059. doi 10.1007/s00122-015-2489-x.
- Kota, R.S. and Dvorak, J. 1988. Genomic instability in wheat induced by chromosome 6Bs of *Triticum speltoides*. *Genetics* 120:1085-1094.
- Kuraparthi, V., Chhuneja, P., Dhaliwal, H.S., Kaur, S., Bowden, R.L. and Gill, B.S. 2007a. Characterization and mapping of cryptic alien introgression from *Aegilops geniculata* with new leaf rust and stripe rust resistance genes *Lr57* and *Yr40* in wheat. *Theor Appl Genet* 114(8): 1379-1389.
- Kuraparthi, V., Sood, S., Chhuneja, P., Dhaliwal, H.S., Kaur, S., Bowden, R.L. and Gill, B.S. 2007b. A cryptic wheat–*Aegilops triuncialis* translocation with leaf rust resistance gene *Lr58*. *Crop Sci.* 47(5): 1995-2003.
- Kuwada, Y. 1925. On the number of chromosomes in maize. *Botanical Magazine Tokyo* 39: 227–234.
- Kwiatk, M., Majka, M., Slusarkiewicz-Jarzina, A., Ponitka, A., Pudelska, H., Belter, J. and Wiśniewska, H. 2016. Transmission of the *Aegilops ovata* chromosomes carrying gametocidal factors in hexaploid triticale (*×Triticosecale* Wittm.) hybrids. *J Appl Genetics* 57: 305–315. doi 10.1007/s13353-015-0332-3.

- Kynast, R.G., Friebe, B. and Gill, B.S. 2000. Fate of Multicentric and Ring Chromosomes Induced by a New Gametocidal Factor Located on Chromosome 4M^g of *Aegilops geniculata*. *Chr Res* 8 (2): 133–139.
- Larracuente, A.M. and Presgraves, D.C. 2012. The selfish Segregation Distorter gene complex of *Drosophila melanogaster*. *Genetics*. 192(1): 33-53. doi: 10.1534/genetics.112.141390.
- Liu Feng-Qi, Min, Q.U., Yan-Ming, Z., Xue-Ting, Z., Ji-Lin, L.I. 2007. Cytogenetic Studies on the Cross progenies Between Chinese Spring *Aegilops* 2C Disomic Addition and Chinese Spring *Elytriga* Disomic Addition. *Bulletin of Botanical Research* 27(1): 89-93.
- Liu, W.X., Jin, Y., Rouse, M., Friebe, B., Gill, B. and Pumphrey, M.O. 2011. Development and characterization of wheat-*Ae. searsii* Robertsonian translocations and a recombinant chromosome conferring resistance to stem rust. *Theor and Appl Genet*. Accepted.
- Loegering, W.Q. and Sears, E.R. 1963. Distorted inheritance of stem rust resistance of Timstein wheat caused by a pollen-killing gene. *Canadian J of Genet and Cytol*. 5: 65-72.
- Longley, A.E.. 1927. Supernumerary chromosomes in *Zea mays*. *Journal of Agricultural Research* 35: 769 – 784.
- Lyttle, T.W. 1991. Segregation distorter. *Annu Rev Genet* 25: 511– 557
- Lyttle, T.W. 1993. Cheaters sometimes prosper: distortion of Mendelian segregation by meiotic drive. *Trends Genet* 9: 205–210.
- Maan, S.S. 1975. Exclusive preferential transmission of an alien chromosome in Common wheat. *Crop Science* 15 (3). doi: 10.2135/cropsci1975.0011183X001500030002x
- Maguire, M.P. 1963. High transmission frequency of a *Tripsacum* chromosome in corn. *Genetics* 48: 1185-1194.
- Manabe, M., Ino, T., Kasaya, M., Takumi, S., Mori, N., Ohtsuka, I. and Nakamura, C. 1999. Segregation distortion through female gametophytes in interspecific hybrids of tetraploid wheat as revealed by RAPD analysis. *Hereditas* 131: 47–53. doi: 10.1111/j.1601-5223.1999.00047.x.

- Marais, F., Marais, A., McCallum, B. and Pretorius, Z. 2009. Transfer of leaf rust and stripe rust resistance genes *Lr62* and *Yr42* from *Aegilops neglecta* Req. ex Bertol. to common wheat. *Crop Science* 49(3): 871-879. doi:10.2135/cropsci2008.06.0317.
- Marais, G.F., Badenhorst, P.E., Eksteen, A. and Pretorius, Z.A. 2010a. Reduction of *Aegilops sharonensis* chromatin associated with resistance genes *Lr56* and *Yr38* in wheat. *Euphytica* 171 (1): 15–22. doi:10.1007/s10681-009-9973-9.
- Marais, G.F., Bekker, T.A., Eksteen, A., McCallum, B., Fetch, T. and Marais, A.S. 2010b. Attempts to remove gametocidal genes co-transferred to common wheat with rust resistance from *Aegilops speltoides*. *Euphytica* 171(1): 71-85.
- Marais, G.F., Kotze, L. and Ekstein, A. 2010c. Allosyndetic recombinants of the *Aegilops peregrina*- derived *Lr59* translocation in common wheat. *Plant Breeding* 129: 356-361.
- Marais, G.F., McCallum, B. and Marais, A.S. 2006. Leaf rust and stripe rust resistance genes derived from *Aegilops sharonensis*. *Euphytica* 149: 373–380. doi:10.1007/s10681-006-9092-9.
- Marais, G.F., McCallum, B. and Marais, A.S. 2008. Wheat leaf rust resistance gene *Lr59* derived from *Aegilops peregrina*. *Plant Breed.* 127 (4): 340–345. doi:10.1111/j.1439-0523.2008.01513.x.
- Marais, G.F., McCallum, B., Snyman, J.E., Pretorius, Z.A. and Marais, A.S. 2005. Leaf rust and stripe rust resistance genes *Lr54* and *Yr37* transferred to wheat from *Aegilops kotschyi*. *Plant Breed.* 143: 115–123. doi:10.1007/s10681-006-9092-9.
- Marais, G.F. and Pretorius, Z.A. 1996. Gametocidal effects and resistance to wheat leaf rust and stem rust in derivatives of a *Triticum turgidum* ssp. *durum*/*Aegilops speltoides* hybrid. *Euphytica* 88(2): 117–124. doi:10.1007/BF00032442
- Marais, G.F., Pretorius, Z.A., Marais, A.S. and Wellings, C.R. 2003. Transfer of rust resistance genes from *Triticum* species to common wheat. *South African Journal of Plant and Soil* 20(4): 193-198. doi: 10.1080/02571862.2003.10634934.

- Martin-Sanchez, J.A., Gomez –Colmenarejo, M., Del Mora, J., Sin, E., Montes, M.J., Gonzalez-Belinchon, C., Lopez-Brana, I. and Delibes, A. 2003. A new Hessian fly resistance gene (H30) transferred from the wild grass *Aegilops triuncialis* to hexaploid wheat. *Theor Appl Genet* 106: 1248–1255.
- Masoudi-Nejad, A., Nasuda, S., McIntosh, R.A. and Endo, T.R. 2002. Transfer of rye chromosome segments to wheat by a gametocidal system. *Chromosome Res* 10: 349–357
- McClintock, B. 1941. The stability of broken ends of chromosomes in *Zea mays*. *Genetics* 26: 234-282.
- McIntosh, R.A. 1988. Catalogue of gene symbols for wheat. *Proc VII Int Wheat Genet Symp, Cambridge* 2:1225-1323.
- McIntosh, R.A. et al. 1995. Catalogue of gene symbols for wheat. *Proceedings of the 8th International Wheat Genetics Symposium* 1333-1500.
- McIntosh, R.A., Miller, T.E. and Chapman, V. 1982. Cytogenetical studies in wheat XII. *Lr28* for resistance to *Puccinia recondita* and *Sr34* for resistance to *P. graminis tritici*. *Zeitschrift für Pflanzenzüchtung* 89, 295–306.
- McIntosh, R.A., Yamazaki, Y., Devos, K.M., Dubcovsky, J., Rogers, W.J. and Appels, R. 2003. Catalogue of Gene Symbols for Wheat (Supplement).
- McIntosh, R.A., Yamazaki, Y., Dubcovsky, J., Morris, C., Somers, D.J., Appels, R. and Devos, K.M. 2008. Catalogue of gene symbols of wheat. *Proc. 11th Intern. Wheat Genetics Symp., Brisbane Qld, Australia*.
- Miller, T.E. 1983. Preferential transmission of alien chromosomes in wheat. In *Proceedings of the 2nd Kew Chromosome Conference*, eds Brandham P. E., Bennett M. D., editors. (London: George Allen & Unwin;) pp 173–182.
- Miller, T.E., Hutchinson, J. and Chapman, V. 1982. Investigation of a preferentially transmitted *Aegilops sharonensis* chromosome in wheat. *Theor Appl Genet* 61: 27-33

- Millet, E., Avivi, Y., Zaccani, M. and Feldman, M. 1988. The effect of substitution of chromosome 5S of *Aegilops longissima* for its wheat homoeologous on spike morphology and on several quantitative traits. *Genome*. 30: 473–478.
- Miranda, L.M., Bland, D.E., Cambron, S.E., Lyster, J.H., Johnson, J., Buntin, G.D. and Murphy, J.P. 2010. Genetic mapping of an *Aegilops tauschii*-derived Hessian fly resistance gene in common wheat. *Crop Science* 50: 612-616.
- Miranda, L.M., Murphy, J.P., Marshal, D., Cowger, C. and Leath, S. 2007. Chromosomal location of *Pm35*, a novel *Aegilops tauschii* derived powdery mildew resistance gene introgressed into common wheat (*Triticum aestivum* L.). *Theor Appl Genet* 114 (8): 1451–1456. doi:10.1007/s00122-007-0530-4.
- Moav, J., Moav, R. and Zohary, D. 1968. Spontaneous morphological alterations of chromosomes in *Nicotiana* hybrids. *Genetics* 59: 57-63.
- Montes, M.J., Andres, M.F., Sin, E., Lopez- Brana, I., Martin-Sanchez, J.A., Romero, M.D. and Delibes, A. 2008. Cereal cyst nematode resistance conferred by the *Cre7* gene from *Aegilops triuncialis* and its relationship with *Cre* genes from Australian wheat cultivars. *Genome* 51(5): 315–319. doi:10.1139/G08-015.
- Mukai, Y. 1983. Determination of the chromosome arm carrying a male fertility restoring gene against the cytoplasm of *Ae. uniariata* in wheat. *Mem Osaka Kyoiku Univ III* 32: 42-53.
- Mukai, Y. and Tsunewaki, K. (Ed.) (1980) Genetic diversity of the cytoplasm in *Triticum* and *Aegilops*. Japan society for the promotion of science, Tokyo.
- Nasuda, S., Friebe, B. and Gill, B.S. 1998. Gametocidal genes induce chromosome breakage in the interphase prior to the first mitotic cell division of the male gametophyte in wheat. *Genetics* 49: 1115-1124.
- Okamoto, M. 1957. Asynaptic effect of chromosome V, *Wheat Inf. Serv.*, 5:6.

- Ozgen, M., Yildiz, M., Ulukan, H. and Koyuncu, N. 2004. Association of gliadin protein pattern and rust resistance derived from *Aegilops umbellulata* Zhuk. in winter *Triticum durum* Desf. Breed Sci. 54: 287–290.
- Panayotov, I. 1980. New cytoplasmic male sterility sources in common wheat: Their genetical and breeding considerations. Theor Appl Genet 56(4): 153–160.
- Pestsova, E.G., Borner, A. and Roder, M.S. 2001. Development of a set of *Triticum aestivum* - *Aegilops tauschii* introgression lines. Hereditas 135 (2–3): 139–143. doi:10.1111/j.1601-5223.2001.00139.x
- Prazak, R. 1997. Evaluation of brown rust (*Puccinia recondita* f. sp. tritici) infection in *Aegilops* species and *Triticum aestivum* L. cv. Gama. J Appl Genet 38B: 123–127.
- Prazak, R. 2004. Porównanie zawartości białka w ziarnie gatunków *Aegilops* i *Triticum*. / Comparision of protein content in the grain of *Aegilops* and *Triticum*. Zesz Probl Post Nauk Rol. 497: 509–516. (in Polish)
- Qi, L.L., Echaliier, B., Chao, S., Lazo, G.R., Butler, G.E., Anderson, O.D., Akhunov, E.D., Dvorak, J., Linkiewicz, A.M., Ratnasiri, A., Dubcovsky, J., Bermudez Kandianis, C.E., Greene, R.A., Kantety, R., La Rota, C.M., Munkvold, J.D., Sorrells, S.F., Sorrells, M.E., Dilbirligi, M., Sidhu, D., Erayman, M., Randhawa, H.S., Sandhu, D., Bondareva, S.N., Gill, K.S., Mabmoud, A.A., Ma, X.F., Miftahudin, Gustafson, J.P., Conley, E.J., Nduati, V., GonzalezHernandez, J.L., Anderson, J.A., Peng, J.H., Lapitan, N.L., Hossain, K.G., Kalavacharla, V., Kianian, S.F., Pathan, M.S., Zhang, D.S., Nguyen, H.T., Choi, D.W., Fenton, R.D., Close, T.J., McGuire, P.E., Qualset, C.O. and Gill, B.S. 2004. A chromosome bin map of 16,000 expressed sequence tag loci and distribution of genes among the three genomes of polyploid wheat. Genetics 168:70-112.
- Randolph, L.F.. 1928. Types of supernumerary chromosomes in maize. Anatomical Record 41: 102.
- Rawat, N., Tiwari, V.K., Singh, N., Randhawa, G.S., Singh, K., Chhuneja, P. and Dhaliwal, H.S. 2009. Evaluation and utilization of *Aegilops* and wild *Triticum* species for enhancing iron and zinc content in wheat. Genet Resour Crop Evol. 56: 53–64. doi:10.1007/s10722-008-9344-8

- Rick, C.M. 1966. Abortion of male and female gametes in the tomato determined by allelic interaction. *Genetics* 53: 85-96.
- Riley, R. and Chapman, V. 1958. Genetic control of the cytologically diploid behavior of hexaploid wheat. *Nature* 182: 713-715.
- Riley, R., Chapman, V. and Johnson, R. 1968. Introduction of yellow rust resistance of *Aegilops comosa* in wheat by genetically induced homoeologous recombination. *Nature* 217: 383-384.
- Rowland, G.G. and Kerber, E.R. 1974. Telocentric mapping in hexaploid wheat of genes for leaf rust resistance and other characters derived from *Aegilops squarrosa*. *Can J Genet and Cytol* 16: 137-144.
- Rubin, G.M., Kidwell, M.G. and Bingham, P.M. 1982. The molecular basis of P-M hybrid dysgenesis: the nature of induced mutations. *Cell* 29: 987-994.
- Sandler, L., Hiraizumi, Y. and Sandler, I. 1959. Meiotic drive in natural populations of *Drosophila melanogaster*. I. The cytogenetic basis of segregation-distortion. *Genetics*, 44: 233-250.
- Sandler, L. and Novitski, E. 1957. Meiotic Drive as an Evolutionary Force. *The American Naturalist* 91: 105-110. doi: 10.1086/281969.
- Sano, Y. 1990. The genic nature of gamete eliminator in rice. *Genetics* 125(1): 183-191.
- Sears, E.R. 1956. The transfer of leaf rust resistance from *Aegilops umbellulata* to wheat. *Brookhaven Symp Biol.* 9: 1-22.
- Sears, E.R. 1977. An induced mutant with homoeologous pairing in common wheat. *Can J Genet Cytol* 19: 585-593.
- Sears, E.R. and Okamoto, M. 1958. Intergenomic chromosome relationships in hexaploid wheat, *Proc. X Int. Congr. Genet., Montreal*, 2: 258-259.
- Sears, E.R. and Loegering, W.Q. 1961. A pollen-killing gene in wheat. *Genetics* 46:897.

- Serizawa, N., Nasuda, S., Shi, F., Endo, T.R., Prodanovic, S., Schubert, I. and Kunzel, G. 2001. Deletion-based physical mapping of barley chromosome. *Theor Appl Genet* 103: 827–834
- Shi, F. and Endo, T.R. 2000. Genetic induction of chromosome rearrangements in barley chromosome 7H added to common wheat. *Chromosoma* 109: 358-363.
- Shimshi, D., Mayora, M.L. and Atsmon, D. 1982. Response to water stress in wheat and related wild species. *Crop Sci.* 22: 123–128.
- Silver, L.M. 1985. Mouse *t* haplotypes. *Annu. Rev. Genet.* 19: 179–208.
- Silver, L.M. 1993. The peculiar journey of a selfish chromosome: mouse *t*-haplotypes and meiotic drive. *Trends Genet.* 9: 250–254.
- Singh, S., Franks, C.D., Huang, L., Brown-Guedira, G.L., Marshall, D.S., Gill, B.S. and Fritz, A. 2004. *Lr41*, *Lr39*, and a leaf rust resistance gene from *Aegilops cylindrica* may be allelic and are located on wheat chromosome 2DS. *Theor Appl Genet.* 108: 586–591. doi:10.1007/s00122-003-1477-8
- Soliman, A.S., Heyne, E.G. and Johnston, C.O. 1963. Resistance to leaf rust in wheat derived from *Aegilops umbellulata* translocation lines. *Crop Sci.* 3: 254-256.
- Sourdille, P., Singh, S., Cadalen, T., Brown-Guedira, G.L., Gay, G., Qi, L., Gill, B.S., Dufour, P., Murigneux, A. and Bernard, M. 2004. Microsatellite-based deletion bin system for the establishment of genetic-physical map relationships in wheat (*Triticum aestivum* L.). *Funct Integr Genomics* 4(1): 12-25.
- Spetsov, P., Mingeot, D., Jacquemin, J.M., Samardijeva, K. and Marinova, E. 1997. Transfer of powdery mildew resistance from *Aegilops variabilis* into bread wheat. *Euphytica* 93: 49–54.
- Stoilova, T. and Spetsov, P. 2006. Chromosome 6U from *Aegilops geniculata* Roth carrying powdery mildew resistance in bread wheat. *Breed Sci.* 56: 351–357.
- Sugimoto, M. 2014. Developmental genetics of the mouse *t*-complex. *Genes Genet. Syst.* 89: 109–120

- Tadesse, W., Hsam, S.L.K., Wenzel, G. and Zeller, F.J. 2006. Identification and monosomic analysis of tan spot resistance genes in synthetic wheat lines (*Triticum turgidum* L. × *Aegilops tauschii* Coss.). *Crop Sci.* 46: 1212–1217.
- Takashi Morita, T., Hiroshi Kubota, Keiko Murata, Masami Nozaki, Christiane Delarbrei, Keith Willison, Yoko Satta, Mitsuru Sakaizumiii, Naoyuki Takahata, Gabriel Gachelin and Aizo Matsushiro. 1992. Evolution of the mouse t haplotype: Recent and worldwide introgression to *Mus musculus*. *Proc. Natl. Acad. Sci.* 89: 6851-6855,
- Thiele, A., Schumann, E., Peil, A. and Weber, W.E. 2002. Eyespot resistance in wheat x *Aegilops kotschy* backcross lines. *Plant Breed.* 121: 29–35. doi:10.1046/j.1439-0523.2002.00669.x
- Tomar, S.M.S., Anbalagan, S. and Singh, R. 2001. Three line approach for development of hybrid wheat. *Diamond Jubilee symp. Hundred years of Post Mendelian Genetics and Plant Breeding Retrospect-Prospects*, New Delhi Abst pp 67-68.
- Tomar, S.M.S. and Kochumadhavan, M. 1996. Genetic resources for disease resistance in wild diploid *Triticum* and *Aegilops* species. *Indian J. Pl. Genet. Resour.* 9: 53-61.
- Tomar, S.M.S. and Menon, M.K. 2001. Genes for resistance to rusts and powdery mildew in wheat. *Indian agricultural research Institute, New Delhi* pp. 152.
- Tsujimoto, H. 1994. Two new sources of gametocidal genes from *Aegilops longissima* and *Ae. sharonensis*. *Wheat Inf Serv* 79: 42-46.
- Tsujimoto, H. 1995. Gametocidal genes in wheat and its relatives. IV. Functional relationships between six gametocidal genes. *Genome* 38(2): 283-289. doi:10.1139/g95-035.
- Tsujimoto, H. 2005. Gametocidal genes in wheat as the inducer of chromosome breakage. *Memorial Issue, Wheat Information Service No.100. Frontiers of Wheat Bioscience:* 33-48.
- Tsujimoto, H. and Tsunewaki, K. 1983. Genetic analyses on a gametocidal gene originated from *Aegilops aucheri*. *Proc VI Int Wheat Genet Symp, Kyoto:* 1077-1081.

- Tsujimoto, H. and Tsunewaki, K. 1984. Gametocidal genes in wheat and its relatives. I. Genetic analyses in common wheat of a gametocidal gene derived from *Aegilops speltoides*. Canadian J. Genet and Cytol 26(1): 78-84. doi: 10.1139/g84-013
- Tsujimoto, H. and Tsunewaki, K. 1985. Gametocidal genes in wheat and its relatives. II. Suppressor of the chromosome 3C gametocidal gene of *Aegilops triuncialis*. Can J Genet. Cytol 27: 178- 185.
- Tsujimoto, H. and Tsunewaki, K. 1988. Gametocidal genes in wheat and its relatives. III. Chromosome location and effects of two *Aegilops speltoides*-derived gametocidal genes in common wheat. Genome. 30(2): 239-244. doi:10.1139/g88-041
- Tsunewaki, K. 1980. Genetic Diversity of the Cytoplasm in *Triticum* and *Aegilops*. Jpn Soc Prom Sci, Tokyo.
- Tsunewaki, K. 1993. Genome-plasmon interactions in wheat. Jpn J Genet 68: 1-34.
- van Slageren, M.W. 1994. Wild wheats: a monograph of *Aegilops* L. and *Amblyopyrum* (Jaub. & Spach) Eig (Poaceae). Wageningen: Wageningen Agricultural University Papers 94-7.
- Werner, J.E., Kota, R.S., Gill, B.S. and Endo, T.R. 1992. Distribution of telomeric repeats and their role on the healing of broken chromosome ends in wheat. Genome 35: 844-848.
- Williamson, V. and Dubcovsky, J. 2010. The new resistance gene to root-knot nematodes *Rkn3* is present in the 2NS introgression from *Ae. ventricosa* into common wheat. In preparation.
- Xia, C., Lu-Lu, X., Ding Hai-Yan, Ying-Bo, X.U. and Ji-Lin, L.I. 2008. Study on Meiosis Comparison of Pollen Grain of F₁ Hybridized by Gametocidal Substitution Lines and Wheat. Bulletin of Botanical Research 4: 392-395.
- Zhang, H.B. and Dvorak, J. 1990. Characterization and distribution of an interspersed repeated nucleotide sequence from *Lophopyrum elongatum* and identification of a segregation distortion with it. Genome 33: 927–936.

Table 1: Classification of *Aegilops* genus as per Van Slageren (1994) and genomic formulas of different *Aegilops* sp. (Kimber and Tsunewaki, 1988; Kilian *et al.*, 2011)

<i>Aegilops</i> species	Ploidy level	Genomic formula	<i>Aegilops</i> species	Ploidy level	Genomic formula
Section <i>Aegilops</i>			Section <i>Sitopsis</i>		
<i>Aegilops umbellulata</i> (Syn. <i>Ae. lorentii</i>)	2x	U	<i>Aegilops bicornis</i>	2x	S ^b
<i>Aegilops biuncialis</i>	4x	UM	<i>Aegilops searsii</i>	2x	S ^s
<i>Aegilops columnaris</i>	4x	UM	<i>Aegilops longissima</i> *	2x	S ^l
<i>Aegilops geniculata</i> * (Syn. <i>Ae. ovata</i>)	4x	UM	<i>Aegilops sharonensis</i> *	2x	S ^{sh}
<i>Aegilops peregrina</i> (Syn. <i>Ae. variabilis</i>)	4x	SU	<i>Aegilops speltoides</i> *	2x	S
<i>Aegilops triuncialis</i> *	4x	CU	Section <i>Vertebrata</i>		
<i>Aegilops kotschyi</i>	4x	SU	<i>Aegilops tauschii</i> (Syn. <i>Ae. squarrosa</i>)	2x	D
<i>Aegilops neglecta</i> (Syn. <i>Ae. triaristata</i>)	6x	UMN	<i>Aegilops ventricosa</i>	4x	DN
Section <i>Cylindropyrum</i>			<i>Aegilops crassa</i>	4x	DM
<i>Aegilops caudata</i> * (Syn. <i>Ae. markgrafii</i>)	2x	C	<i>Aegilops crassa</i>	6x	DDM
<i>Aegilops cylindrica</i> *	4x	CD	<i>Aegilops vavilovii</i>	6x	DMS
Section <i>Comopyrum</i>			<i>Aegilops juvenalis</i>	6x	DMU
<i>Aegilops comosa</i>	2x	M	Subgenus <i>Ambylopyrum</i>		
<i>Aegilops uniaristata</i>	2x	N	<i>Ambylopyrum muticum</i>	nd	nd

[Note: * Indicate species in which gametocidal activity is reported]

Fig.1 Meiotic metaphase I in PMCs of *Aegilops speltoides*-wheat introgression lines heterozygous for gametocidal genes [Note: Arrows denote configurations like univalents (U), trivalent (T) and Isochromosome (I)]

333x85mm (150 x 150 DPI)

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