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Substitution of *Hordeum marinum* ssp. *gussoneanum* chromosome 7HL into wheat homoeologous group-7

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Abstract Ditelosomic (Dt) 7HL^{mar}(7D) and monotelosomic (Mt) 7HL^{mar}(7A) and 7HL^{mar}(7B) wheat–barley substitution lines were developed by crossing monosomic 7A, 7B and 7D lines of common wheat cv. Saratovskaya 29 with disomic wheat–barley addition lines ($2n = 44$) that carry telocentric chromosomes 7HL^{mar} from *Hordeum marinum* ssp. *gussoneanum* 4×. Genomic in situ hybridisation confirmed the presence of barley chromosomes in the wheat genome. The compensating ability of the telosome in each combination was assessed by its transmission rate to progenies of plants with $2n = 41 + t$ chromosomes. Seed set and transmission rates of the telosome depended on the identity of the competing wheat homoeologue. Of the three chromosomes wheat, the telosome 7HL^{mar} compensated better for chromosome 7D and poorly for 7B. These and other data are discussed with respect to the phylogenetic relationships between the wheat chromosomes of group 7 and the chromosome of *H. marinum,* and the practical utility of these lines for wheat improvement is evaluated.

Keywords Chromosome transmission · Chromosome elimination · Compensating ability · Ditelosomic · Monotelosomic

Introduction

Genus *Hordeum* L. comprises more than 30 species (von Bothmer et al. 1991), many of which have valuable agronomic and adaptive traits and can be considered new sources of genes for wheat improvement. Cultivated barley, *Hordeum vulgare* L., is a particularly important crop because it exhibits gene-controlled resistance to biotic and abiotic stresses (Cattivelli et al. 2002; Molnár et al. 2007), earliness (Murai et al. 1997) and various nutritional traits (Zou et al. 2012) that would be useful in wheat.

The development of chromosome addition and substitution lines is an essential step in a transfer of useful genes among related species. Six of the seven possible wheat–barley (i.e., *Triticum aestivum* L.–*H. vulgare*) disomic addition lines and 13 of the 14 possible ditelosomic addition lines were produced by Islam (1983). Substitutions of barley 3H, 4H, 6H and 7H chromosomes into homoeologous groups 3, 4, 6 and 7 were reported by Islam and Shepherd (1992, 1993), while the substitution of 2H into group 2 by Yuan et al. (2003). Several winter wheat–winter barley additions a substitution were produced by Molnár-Láng et al. (2000), Molnár et al. (2007), Szakács and Molnár-Láng (2007, 2010).

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Wild barley species *H. spontaneum* C. Koch, *H. chilense* Roem et Schult and *H. marinum* Hudson have also been successfully hybridised with wheat. Sets of wheat lines with additions of *H. spontaneum* or *H. chilense* chromosomes were developed (Miller et al. 1982; Taketa and Takeda 2001), and a new cereal crop, Tritordeum, was produced by crossing *H. chilense* to hexaploid or tetraploid wheat (Alvarez et al. 1992). Resistance to root-knot nematode, common bunt and *Septoria*; tolerance to salt; and a high carotenoid content were introduced into wheat from *H. chilense* (Hernández et al. 2001; Said et al. 2012). Successful hybridisation of wheat to *H. marinum* and subsequent amphiploid production was achieved by Islam et al. using cv. Chinese Spring as the hexaploid wheat parent (Islam 2002; Islam et al. 2007).

In nature, *H. marinum* is confined to saline meadows, riverbeds and marshes along the seacoast and inland, and as a weed in pastures and waste grounds (von Bothmer et al. 1991). Thus, it frequently receives attention as a putative donor of salt stress tolerance (Colmer et al. 2006). It also shows better root aeration and higher water-logging tolerance than many other species in *Triticeae* (McDonald et al. 2001; Garthwaite et al. 2003). Combined tolerance to salinity and water logging were also observed (Malik et al. 2009). Amphiploids have been obtained by hybridisation of *H. marinum* subsp. *gussoneanum* 4× to common wheat (Pershina et al. 1988, 2004); backcrossing the F_1 hybrid to wheat restored fertility. Of these progeny, alloplasmic wheat–barley $7H^{mar}(7D)$ substitution lines, a ditelosomic $7HL^{mar}$ addition line and a line with three chromosome substitutions [$1H^{mar}(1B)$, $5H^{mar}(5D)$ and $7H^{mar}(7D)$] have been isolated (Numerova et al. 2004; Trubacheeva et al. 2008). These chromosome substitution and addition lines are valuable cytogenetic stocks for breeding programmes, gene mapping and studies of homoeologous relationships between barley and wheat genomes.

The aim of this work was to study the substitution abilities of the *H. marinum* ssp. *gussoneanum* 4× telosome $7HL^{mar}$ for wheat homoeologous group 7 chromosomes in hybrid progeny with $20'' + 1' + t'$ and monotelosomic lines during the development of wheat–barley substitution lines.

Materials and methods

Single-chromosome substitutions of the *H. marinum* telosome $7HL^{mar}$ for wheat homoeologues 7A, 7B and 7D were developed using standard procedures (Unrau 1959; Riley and Kimber 1966) of crossing monosomic 7A, 7B and 7D lines of *T. aestivum* cv. Saratovskaya 29 (S29) with the wheat–barley ditelosomic addition line $7HL^{mar}$ ($21'' + t''$). The donor of the barley chromosome was the cv. Pyrotrix 28-*H. marinum* subsp. *gussoneanum* 4× ditelosomic addition line. C-banding and genomic in situ hybridisation (GISH) confirmed the chromosomal composition of the donor line (Trubacheeva et al. 2008).

Of the F_1 hybrids obtained, plants with $20'' + 1' + t'$ were selected based on pairing at the first meiotic metaphase (MI) ($20'' + 7A' + 7H^{mar}L'$, $20'' + 7B' + 7H^{mar}L'$ or $20'' + 7D' + 7H^{mar}L'$, depending on the monosomic used in the cross). These were self-pollinated, and their progenies were screened to identify ditelosomic substitutions $20'' + t''$. To confirm each substitution, monotelosomic substitution lines were crossed to the ditelosomics 7AL, 7BL and 7DL of cv. S29.

The F_1–F_5 plants were grown in a greenhouse, and the MI chromosome configuration were examined in pollen mother cells (PMCs) using the 2 % aceto-carmine smear method. GISH was performed as described by Mukai and Gill (1991).

Results

Nearly all plants from the initial crosses had 20 bivalents, one two-armed univalent and one telosome (Fig. 1a). In the combination involving 7D, 1 plant was isolated that had with 21 bivalents 1 univalent telocentric. Screening of the $20'' + 1' + t'$ plants at MI established that the barley telosome did not pair with homoeologous wheat chromosomes.

Verified 42-chromosome plants with $20'' + 1' + t'$ at MI were self-pollinated. Among the F_2 six genotypes were present: $20''$ (7 %, nullisomic); $21''$ (15 %, wheat disomic); $20'' + 1'$ (45 %, wheat monosomic); monotelosomic, $20'' + t'$ (8 %, monosomics for the barley telocentric); $20'' + 1' + t'$ (15 %, double monotelosomic); and $21'' + t'$ (10 %, monotelosomic addition of barley chromosome) (Table 1). Altogether, 33 % of plants screened carried barley telocentric. Among plants lacking it, the wheat monosomics were the most common (50 %) for 7A, 43 % for 7B and 44 % for 7D).

Among the F_2 hybrids, monotelosomic alien-substitution plants ($20'' + t'$) were selected. These must

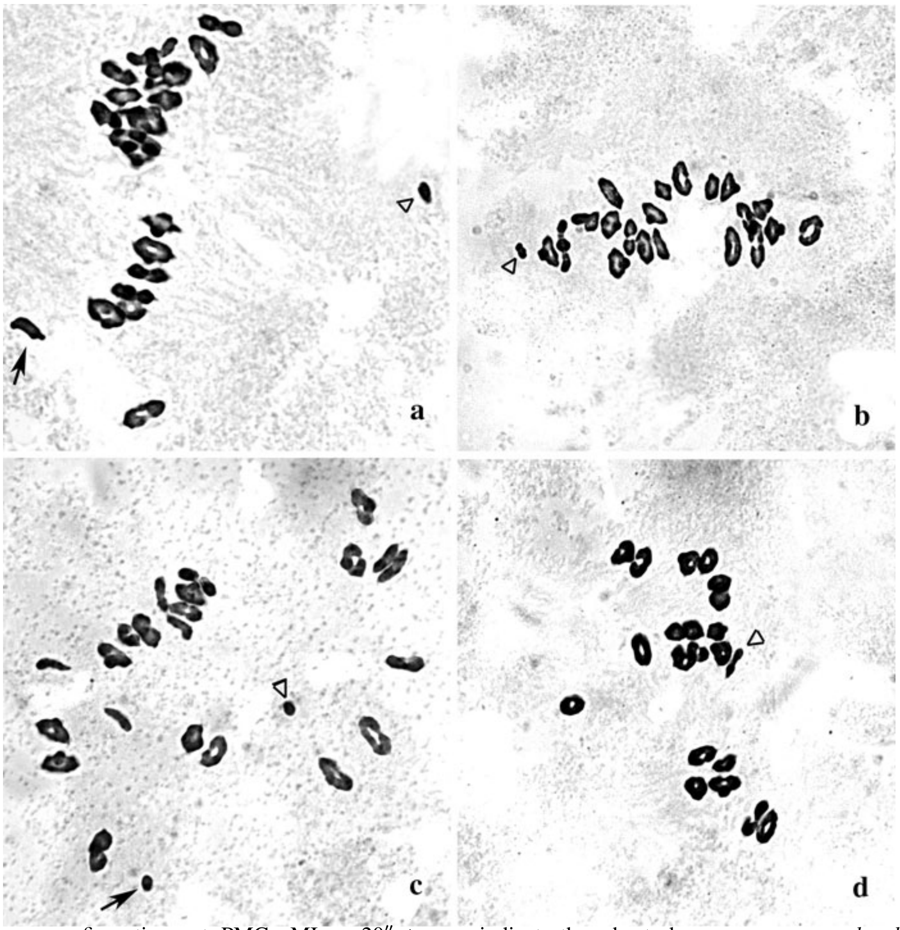

Fig. 1 Chromosome configurations at PMCs MI: **a** $20'' + 1'(7A) + t'$ ($7HL^{mar}$); **b** $20'' + t'$, $(Mt)7HL^{mar}(7D)$; **c** $20'' + t'(7HL^{mar}) + t'(7DL)$ and **d** $20'' + t''$, $(Dt)7HL^{mar}(7D)$. *Arrows* indicate the wheat chromosomes; *arrowheads* indicate barley telosomes

have been produced by fusion of $n = 20$ and $n = 20 + t$ gametes. At MI, these had 20 wheat bivalents and univalent barley telosome substituted for pairs of wheat chromosomes 7A, 7B and 7D (Fig. 1b), depending on the original cross. The frequencies such plants were 13, 2 and 19 % for $7HL^{mar}$-7A, $7HL^{mar}$-7B and $7HL^{mar}$-7D, respectively (Table 1). This suggests a good transmission rate, hence good compensation, of the barley telosome for two-armed wheat homoeologues.

Table 1 The transmission rate of barley telosome $7HL^{mar}$ and wheat chromosomes 7A, 7B and 7D in F_2 hybrids

Type of chromosome substitution	Number of plants and chromosome configuration at MI						Number of plants examined
	Without $7HL^{mar}$			With $7HL^{mar}$			
	$20''$	$21''$	$20'' + 1'$	$20'' + t'$	$20'' + 1' + t'$	$21'' + t'$	
$7HL^{mar}$-7A	2 (13 %)	3 (18 %)	8 (50 %)	2 (13 %)	1 (6 %)	–	16
$7HL^{mar}$-7B	3 (8 %)	6 (15 %)	17 (43 %)	1 (2 %)	8 (20 %)	5 (12 %)	40
$7HL^{mar}$-7D	–	2 (13 %)	7 (44 %)	3 (19 %)	2 (12 %)	2 (12 %)	16
Total	5 (7 %)	11 (15 %)	32 (45 %)	6 (8 %)	11 (15 %)	7 (10 %)	72

The substitution status of the selected $20'' + \mathrm{t}'$ lines was confirmed by a chromosome pairing analysis in testcrosses to appropriate ditelocentric stocks of wheat S29. Configurations of $20'' + \mathrm{t}'$ and $20'' + \mathrm{t}' + \mathrm{t}'$ (Fig. 1c) at MI confirmed that these lines were monotelosomic substitution lines. Two telosomes when present together, always remained unpaired, indicating an alien origin of one of them; $20'' + \mathrm{t}'$ configuration, on the other hand, indicated that the wheat homologue to the wheat telocentric used in a given combination was absent.

The monotelosomic lines were fertile and vigorous, but had fewer spikelets per spike and low seed set (Fig. 2). The Mt7HL$^{\mathrm{mar}}$(7D) line had a higher sees set than the other two (Table 2). Pairing configurations at MI in the F$_{3-5}$ progenies of self-pollinated Mt7HL$^{\mathrm{mar}}$(7A), Mt7HL$^{\mathrm{mar}}$(7B) and Mt7HL$^{\mathrm{mar}}$(7D) plants are given in Table 3. Ditelosomics (Dt) should be frequent following self-pollination of monotelosomics. However, only nine ditelosomic 7HL$^{\mathrm{mar}}$(7D) lines with ($20'' + \mathrm{t}''$) were isolated from the F$_3$ hybrids (Fig. 1d). In Mt7HL$^{\mathrm{mar}}$(7D), 96 % of the examined progeny carried the barley telosome, of which 48 % were ditelosomics ($20'' + \mathrm{t}''$ and $20'' + \mathrm{t}' + \mathrm{t}'$) and 48 % were monotelosomics ($20'' + \mathrm{t}'$). Of the plants that lacked the barley telosome, one plant with a $19'' + 1'$ configuration was isolated. Additionally, we failed to isolate ditelosomics through the self-pollination of Mt7HL$^{\mathrm{mar}}$(7A), and Mt7HL$^{\mathrm{mar}}$(7B) monotelosomics ($20'' + \mathrm{t}'$) were obtained in only the F$_3$–F$_5$ progeny (Table 3). Of the Mt7HL$^{\mathrm{mar}}$(7A) and Mt7HL$^{\mathrm{mar}}$(7B) progeny, 53 and 68 % of the plants, respectively, were nullisomic ($20''$) or had 19 bivalents and 1 univalent, i.e., a somatic chromosome number of $2n = 39$.

Fig. 2 The spike morphology of the Mt7HL$^{\mathrm{mar}}$(7A), Mt7HL$^{\mathrm{mar}}$ (7B) and Mt7HL$^{\mathrm{mar}}$(7D) wheat–barley substitution lines (*left* to *right*)

Table 2 Seed fertility and the number of grains on the each spike in ten plants of the Mt7HL$^{\mathrm{mar}}$ (7A), Mt7HL$^{\mathrm{mar}}$ (7B), Mt7HL$^{\mathrm{mar}}$ (7D) and Dt7HL$^{\mathrm{mar}}$ (7D) substitution lines

Line	Number of grains on spike	Seed fertility (grain/spikelet)
Mt7HL$^{\mathrm{mar}}$ (7A)	8.4 ± 0.6	1.18 ± 0.1
Mt7HL$^{\mathrm{mar}}$ (7B)	7.5 ± 0.7	0.45 ± 0.2
Mt7HL$^{\mathrm{mar}}$ (7D)	11 ± 1.0	1.30 ± 0.1
Dt7HL$^{\mathrm{mar}}$ (7D)	28 ± 0.9	1.87 ± 0.1

The substituted barley telosomes were readily detected in the wheat background by GISH (Fig. 3). Most of the Dt7HL$^{\mathrm{mar}}$(7D) plants (85 %) had 20 normal bivalents and a ditelosomic bivalent (Fig. 1d). Three plants (15 %) chromosome pairing indicative of the loss of one wheat chromosome, as frequent occurrence among progenies of aneuploids. Telocentric 7HL$^{\mathrm{mar}}$ appeared to compensate well for wheat chromosome 7D with good vigour and fertility, and the average of 28 seeds per spike (Table 2).

Discussion

In this study, we produced ditelosomic 7HL$^{\mathrm{mar}}$(7D) and monotelosomic 7HL$^{\mathrm{mar}}$(7A) and 7HL$^{\mathrm{mar}}$(7B) wheat—*H. marinum* substitution lines. The lines are fertile, demonstrating homoeology between barley 7HL$^{\mathrm{mar}}$ telosome and wheat group 7 homoeologues. Previously, it was established that chromosome 7H$^{\mathrm{ch}}$ of wild diploid barley *H. chilense* could substitute and compensate for chromosomes 7A, 7B and 7D in wheat (Miller et al. 1985). Here we show that *H. marinum* does it as well. This agrees with data on homoeology between *H. vulgare* (cultivated barley) the common wheat chromosomes of homoeologous group 7 (Islam and Shepherd 1992; Yang et al. 2000). Furthermore, the physical order and linkage of molecular markers along

Table 3 The transmission of barley telosome 7HL$^{\mathrm{mar}}$ in the F$_{3\text{–}5}$ progeny of the 7HL$^{\mathrm{mar}}$(7A), 7HL$^{\mathrm{mar}}$(7B) and 7HL$^{\mathrm{mar}}$(7D) monotelosomics

Line	Number of plants and chromosome configuration at MI					Number of plants examined
	Without 7H$^{\mathrm{mar}}$		With 7H$^{\mathrm{mar}}$			
	20″	19″ + 1′	20″ + t′	20″ + t″	20″ + t′ + t′	
Mt7HL$^{\mathrm{mar}}$(7A)	19 (40 %)	6 (13 %)	22 (47 %)	–	–	47
Mt7HL$^{\mathrm{mar}}$(7B)	22 (60 %)	3 (8 %)	12 (32 %)	–	–	37
Mt7H$^{\mathrm{mar}}$(7D)	–	1 (4 %)	11 (48 %)	9 (39 %)	2 (9 %)	23
Total	41 (38 %)	10 (9 %)	45 (42 %)	9 (9 %)	2 (2 %)	107

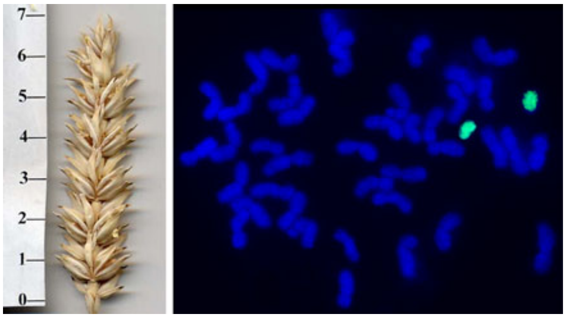

Fig. 3 Spike from a 7HL$^{\mathrm{mar}}$(7D) ditelosomic plant and a GISH image of a wheat–barley ditelosomic 7HL$^{\mathrm{mar}}$(7D) substitution. Barley telosomes are in *green*, wheat chromosomes are *blue*. (Color figure online)

the homoeologous group 7 chromosomes is almost identical in wheat and barley (Hohmann et al. 1995). Previous cytogenetic work has suggested that *H. chilense* chromosomes are more similar to the D genome than to the A or B genomes of wheat (Cabrera et al. 1995; Wang et al. 2005). Furthermore, the distribution patterns of the Afa-family repetitive sequences in the individual chromosomes of *H. vulgare* were similar to those of the homoeologous chromosome of *T. tauschii* (Tsujimoto et al. 1997). A comparative study of the molecular maps of the A, B and D genomes of wheat and the genome of *H. vulgare* indicated a very close colinearity between the molecular markers on the barley chromosomes and on the related wheat chromosomes, with the exception that the evolutionary translocations present in the A and B genomes of wheat are not present in barley or *T. tauschii*, the donor of the D genome (Linde-Laursen et al. 1997).

The transmission rate of the 7HL$^{\mathrm{mar}}$ telosome from plants with 20″ + 1′ + t′ was the highest for the 7D combination, and the lowest was for the combination with 7B.

Because of an uncoordinated behaviour of univalents, a double monosomic may create a range of gametes with different chromosome constitutions, some of them euploid and some aneuploid. Aneuploid gametes can participate in fertilisation (Sears 1953); however, their success rate is usually lower than that of euploid gametes with balanced chromosome constitutions. In a study, an assumption was made of the absence of gametic selection on the female and this assumption was apparently met. Any selection among female gametes would have rendered some of them non-functional, reducing seed set. No such effect was clearly apparent. On the other hand, gametic selection on the male would have eliminated some pollen grains without any noticeable reduction in seed set. On the male side, an assumption is made that an aneuploid pollen suffers in competition with euploid pollen, and that among euploid pollen, that with better genetic compensation of an alien chromosome for its missing wheat homoeologue has a better chance of effecting fertilization. The only truly euploid pollen in this study was the 21-chromosome combination with all group-7 wheat homoeologue present. Pollen grains with 20 + t were deficient for one chromosome arm. Yet, such grains quite successfully competed with all other classes, and so did some nullisomic pollen grains. Among pollen with alien substitutions, the most successful was that with chromosome 7HL replacing or 7D; the least successful was that with 7HL for 7B. Whether this reflects different genetic content of the three wheat homoeologues or perhaps different position of the centromere is not clear at this point.

The absence of ditelosomics substitutions for 7A and 7B may indicate incomplete compensation and no male transmission of 7HL. If this is the case, pollen nullisomic for 7A and 7B was more competitive than that carrying

7HL. Unfortunately, we did not make testcrosses on the $20'' + 1' + t'$ plants so we cannot ascertain that the absence of ditelosomics substitutions is the sole consequence of gametic selection on the male side. It needs to be pointed out that nullisomics of homoeologous group 7 in wheat are the only set of three that are sufficiently fertile to be maintained in collections (Sears 1953). Obviously, pollen nullisomic for group-7 chromosomes can be quite competitive. This might have affected the outcome of this study: strong selection for euploid (21) or almost-euploid (20 + t) pollen would have reduced the number of chromosome constitutions among progenies, and probably increased the recovery rates of disomic substitutions.

The $7HL^{mar}$ telosome served here as a cytological marker to identify the alien chromosome in the hybrid progeny and to isolate the substitution lines. The analysis of MI showed clearly that the $7HL^{mar}$ telosome did not pair with any of its wheat homoeologues. Of course, given that the *Ph1* locus was present, no such pairing was expected. Murai et al. (1997) showed that even in the *Ph1* absence, the level of homoeologous wheat–barley pairing was low. Shepherd and Islam (1992) reported that the telocentric barley chromosome did pair and recombine with wheat chromosomes in the absence of the *Ph1* gene in wheat. However, with low pairing, chromosome 2C of *Aegilops cylindrica* was used to induce chromosomal rearrangements in chromosome 7H of cultivated barley (Shi and Endo 2000), and structural changes were found in approximately 15 % of the progeny.

The development of new ditelosomic wheat–barley substitution lines will enable us to obtain additional information about the influence of *H. marinum* subsp. *gussoneanum* 4× $7HL^{mar}$ telosome on resistance to biotic and abiotic stresses.

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