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A set of new 1RS translocations from wheat cv. Amigo in a uniform genetic background

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Abstract Wheat-rye translocation 1RS.1AL from cv. Amigo is still popular in wheat breeding and commercial cultivars. It introduces several disease and pest resistance genes from rye into wheat, and appears to enhance root system development. To create a set of uniform stocks for precise tests, the rye arm 1RS was separated from the wheat arm in the translocation by misdivision of centromeres in univalents, fused into a complete chromosome 1R, and then re-translocated to all group-1 wheat chromosomes 1A, 1B and 1D, creating a set of three translocation and three substitution lines in a uniform background of cv. Pavon 76. Misdivision frequencies of the chromosomes mirrored those observed earlier in that shorter chromosomes broke less frequently than the long ones, and chromosomes from previous misdivision-fusion events misdivided more frequently than normal intact chromosomes. This set of chromosome lines with 1RS from cv. Amigo increases to three the number of such translocations stocks in wheat.

Keywords Wheat-rye translocation · Centric misdivision · Centric fusion · Genetic stocks

Introduction

Wheat-rye translocation chromosome 1RS.1BL demonstrates the value of introgressions from related species into crops. Originally, this translocation is said to have been selected for “triticale-like” resistance to wheat pest and diseases (Zeller and Hsam 1983). It appeared, apparently as a spontaneous event, among progenies of triticale × wheat hybrids. The resistance was due to the presence of resistance genes *Lr26*, *Sr31*, *Yr 9* and *Pm8* on the introgressed rye arm, offering resistance to leaf rust, stem rust, yellow rust and powdery mildew, respectively. The translocation spread throughout Europe but its world-wide impact begun to be felt only when the International Center for the Improvement of Maize and Wheat (CIMMYT) introduced it to its wheats (Rajaram et al. 1983) and distributed it to cooperators around the world. By now, it is present in at least 800 released cultivars all over the world; its frequency in some groups of cultivars exceeds 50% (Mujeeb-Kazi et al. 2013; Rabinovich 1998).

The dramatic spread of the translocation was not slowed down by the breakdown of resistance. As resistances kept breaking down it became obvious that the translocation had a positive effect on grain yield, especially in water stressed environments (Villareal et al. 1998). Eventually, Waines and collaborators (Ehdaie et al. 2003; Waines and Ehdaie 2007; Sharma et al. 2009) have shown that the translocation

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increases root biomass, more so under water stress than under normal water availability.

To facilitate studies of the effects of the 1RS rye arm in wheat, chromosome arms in the original translocation, as it was present in one of the Veery lines from CIMMYT and originating from cv. Kavkaz, were separated by centric misdivision in double monosomics $20'' + 1RS.1BL + 1BS.1RL$ to create reconstructed chromosomes 1R and 1B. In the next step, the two arms from the original translocation (1RS and 1BL) were re-translocated: 1RS to each of the three group-1 homoeologues in cv. Pavon 76, creating translocations $1RS_k.1AL_p$, $1RS_k.1BL_p$ and $1RS_k.1DL_p$, while the 1BL arm was translocated to 1BS of Pavon 76 creating 1B chromosome properly listed as $1BS_p.1BL_v$. Reconstructed chromosome 1R is properly listed as $1RS_k.1RL_e$. Subscript “p” indicates the Pavon 76 origin of an arm; subscripts “k” and “v” Kavkaz and Veery origins of chromosome arms, respectively; “e” denotes the long arm of rye chromosome 1R from CIMMYT line E12165 (Lukaszewski 1993, 1997). Reconstructed chromosome 1R was substituted for each of the group-1 homoeologues of wheat. This created a set of essentially isogenic lines, quite suitable for tests of the position effect of the 1RS arm ($1RS_k.1RL_e$ and $1BS_p.1BL_k$ have never been used in any tests).

Another introgression of rye 1RS arm in wheat with some popularity among wheat breeders is translocation 1RS.1AL first released in cv. Amigo (Sebesta and Wood 1978). This translocation was created to introduce greenbug (*Schizaphis graminum* Rondani) resistance from rye cv. Insave. The translocation was relatively frequent in the US wheats, especially soft wheats of the South-Eastern US (Lukaszewski 1990). Its popularity appears to be dropping as shown through genotyping of entries in several soft wheat nurseries (<https://www.ars.usda.gov/southeast-area/raleigh-nc/plant-science-research/docs/small-grains-genotyping-laboratory/regional-nursery-marker-reports/page-2/>) and hard red wheat nurseries (<https://www.ars.usda.gov/southeast-area/raleigh-nc/plant-science-research/docs/small-grains-genotyping-laboratory/regional-nursery-marker-reports/page-2/>). Apart from *Gb5*, the rye arm of the Amigo translocation also introduces *Lr24* and *Pm17* (Hsam and Zeller 1997; Hsam et al. 2000). The original translocation 1RS.1AL from Amigo increased root biomass in Pavon 76 by 9% (Waines and Ehdaie 2007); of the three 1RS_v

translocation in Pavon, 1RS_v.1AL_p increased root biomass by ca. 30%. This implies that 1RS from the Kavkaz source may be more effective in increasing root biomass than that from Amigo, but the position effect may also play a role. No direct comparisons of the translocations is possible: 1RS_v.1AL_p and 1RS.1AL from cv. Amigo differ not only by the rye arm but also by the non-recombining portion of 1AL originating from Amigo. With distal concentration of crossing over in wheat (Lukaszewski and Curtis 1993), linkage drag assures that a substantial portion of that 1AL remains unchanged through cycles of hybridization and breeding. This chromosome manipulation exercise was undertaken in part to remedy this problem. Following the path taken with the Kavkaz translocation, the 1RS arm in the Amigo source was untranslocated from its 1AL arm, reconstructed into a complete 1R chromosome, and then re-translocated to each of the three group-1 homologues in cv. Pavon 76.

Materials and methods

The 1RS.1AL translocation originating from cv. Amigo was obtained from Dr. B. Friebe, Kansas State University, Manhattan KS, USA. It was transferred into cv. Pavon 76 by backcrosses. BC₇/F₂ translocation homozygotes were crossed to a line of cv. Pavon 76 with the $1AS_p.1RL_e$ translocation where 1RL originated from a CIMMYT line E12165 and 1AS was of Pavon 76 (see Lukaszewski 1993). The F₁ hybrids, double monosomic $20'' + 1RS_a.1AL_a' + 1AS_p.1RL_e'$ (where '' and ' indicate disomic and monosomics state, respectively), were self-pollinated and their progenies screened for the presence of complete chromosome 1R (centric translocation $1RS_a.1RL_e$). Plants with such chromosomes 1R were crossed to nullisomics 1B and 1D of Pavon 76, triple monosomics $19'' + 1A' + 1B' + 1R'$ and $20'' + 1B' + 1D' + 1R'$ were selected, grown and self-pollinated. Among their progenies plants with translocations $1RS_a.1AL_p$, $1RS_a.1BL_p$, $1RS_a.1DL_p$ and substitutions of chromosome $1RS_a.1RL_e$ for 1A, 1B or 1D were isolated. Among their progenies translocation homozygotes and disomic substitutions were isolated. Subscripts a, p, e, indicate the origin of chromosome arms, from Amigo, Pavon 76, E12165, respectively.

Misdivision frequencies were expressed as the numbers of misdivision products of individual chromosomes (such as telocentrics, isochromosomes and fusion products) recovered in the number of plants screened. Screening was focused on isolation of the desired translocations and not precise karyotyping of each plant. Consequently, misdivision frequencies of 1A and 1D are probably underestimated. All screening was done by C-banding using the high-throughput method (Lukaszewski and Xu 1995).

Results and discussion

To reconstruct complete chromosome 1R from the 1RS.1AL Amigo translocation 119 progeny from a double monosomics $20'' + 1RS_a.1AL_a' + 1AS_p.1RL_e'$ were screened; eleven misdivision products of 1RS.1AL and eight of 1AS.1RL were recovered, for the misdivision frequency of 9.2 and 6.7%, respectively. Among recovered chromosomes was one reconstructed chromosome 1R, designated $1RS_a.1AL_e$. Progenies from a backcross of this plant as male to monosomics 1B and 1D of Pavon were screened and triple monosomics $19'' + 1A' + 1B' + 1RS_a.1RL_e'$ and $19'' + 1A' + 1D' + 1RS_a.1RL_e'$ were selected. In each cross combination several such triple monosomics were recovered. Their progenies were screened for the presence of centric translocations $1RS_a.1AL_p$, $1RS_a.1BL_p$ and $1RS_a.1DL_p$. Along the way, disomic substitutions of $1RS_a.1RL_e$ for chromosomes 1A, 1B and 1D were also recovered. Among progeny of triple monosomics $19'' + 1A' + 1B' + 1RS_a.1RL_e'$ 184 plants were screened and 55 misdivision products were recovered, among them two translocations $1RS_a.1BL_p$ and one translocation $1RS_a.1AL_p$. Reconstructed chromosome $1RS_a.1AL_e$ misdivided with 14.1% frequency; chromosomes 1A and 1B of Pavon with 7.6 and 8.1% frequencies, respectively. Among 220 progeny of triple monosomics $19'' + 1A' + 1D' + 1RS_a.1RL_e'$ 57 misdivision products were observed, among them four translocations $1RS_a.1AL_p$ and three $1RS_a.1DL_p$. Reconstructed chromosome $1RS_a.1RL_e$ misdivided with 16.8% frequency; chromosomes 1A and 1D of Pavon with 5.5 and 3.6% frequencies, respectively. Along the way disomic substitutions of $1RS_a.1RL_e$ for chromosomes 1A and 1D were also recovered.

Misdivision frequencies of the chromosomes tested here do not deviate from the general pattern observed before (Lukaszewski 1993, 1997, 2010): there appears to be a general relationship between chromosome length and susceptibility to misdivision, with 1D, the shortest, misdividing with the lowest frequency and 1B, the longest, with the highest. Also, chromosomes that have undergone a previous round of misdivision and fusion, such as the original translocation $1RS.1AL$ of Amigo and $1AS_p.1RL_e$, as well as the reconstructed chromosome $1RS_a.1RL_e$, misdivided more frequently than original chromosomes. The Amigo translocation was recovered following irradiation (Sebesta and Wood 1978), but it is a typical centric translocation with the breakpoint located in the centromere region. The actual mechanism by which it was generated is unclear. It might have been a fortuitous event of two chromosomes fragmented across the centromeres by irradiation, or misdivision of two univalents in meiosis failing to pair because of some other consequences of irradiation, but it is still a centric breakage-fusion chromosome. Higher tendency of reconstructed chromosomes and centric translocation to misdivide may be a consequence of asymmetrical breakage across the centromere which, following fusion, creates chromosomes with higher numbers of active centromeric units. It may also indicate increased fragility of such centromeres. On the other hand, the relationship between chromosome length and susceptibility to misdivision may be misleading and probably does not hold across the entire genome. The author did experience situations when long chromosomes (such as 3R of rye and 3B of wheat) misdivided infrequently, or when the same chromosome from two different backgrounds misdivided with different frequencies. Such allelic-like differences had been noted before (Sears 1973).

The C-banding patterns of 1RS arms in the 1RS.1AL translocation of Amigo and the 1RS.1BL translocation of Kavkaz are identical. A complete set of figures illustrating all misdivision and misdivision-fusion products of 1RS.1BL from Kavkaz has been published (Lukaszewski 1993, 1997); those sets include the same recipient group-1 chromosomes of Pavon 76 as used here. Therefore, no illustrations are provided here as they would be a clear duplication.

This exercise produces a set of substitutions $1RS_a.1R_e(1A)$, $1RS_a.1RL_e(1B)$ and $1RS_a.1RL_e(1D)$ and a set of translocations $1RS_a.1AL_p$, $1RS_a.1BL_p$ and

IRS_a-1DL_p in the background of Pavon 76. This background is relatively uniform; all stocks before the exercise had at least seven backcrosses to standard Pavon 76; a cross to nullisomics raises it to at least eight. This material may be suitable for fairly precise experiments on the effects of the 1RS arm from different sources, and three such sets are now available: with 1RS from Kavkaz, from Amigo and E12165. In addition, position effects can be studied, also in the context of allelic variation that is likely present on these three arms. Since the three arms are translocated to original long arms of Pavon 76, any possible drag effect of the non-recombining portions of the long arms is also eliminated.

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