



## Heterotic effects of wheat-rye chromosomal translocations on agronomic traits of hybrid wheat (*Triticum aestivum* L.) under an adequate moisture regime

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### Summary

Translocated chromosomes T1BL·1RS and T1AL·1RS have been widely used in many wheat (*Triticum aestivum* L.) breeding programs to develop high yielding cultivars. The objective of this study was to evaluate the heterotic effects of T1BL·1RS + T1AL·1RS, T1BL·1RS, and T1AL·1RS on yield and yield components of hybrid wheat grown under adequate moisture regimes. Thirteen hybrid wheats and seven parents with different chromosome constitutions relative to T1AL·1RS and T1BL·1RS were evaluated in a randomized complete block design. Variable performance was observed among the hybrids tested. Two of the three hybrids with T1BL·1RS + T1AL·1RS, produced 25.26% and 44.64% more grain than the hybrids with only T1BL·1RS. This was due to increased biomass, harvest index (HI) and spike density. However, the combination of these two translocations resulted in reduced kernels/spike, spikelets/spike and spike length compared to the T1BL·1RS translocation alone. When comparing closely related parents, the parent with T1AL·1RS produced 23.51% more grain yield than the non-translocated parent. The presence of T1AL·1RS resulted in 10.37% heterotic advantage for yield due to increased biomass, KW, and spike density. When the two wheat-rye translocated chromosomes are present in the same hybrid, T1AL·1RS seems to have a positive effect on yield through spike density and HI, but masks the effects of T1BL·1RS for some agronomic traits.

**Abbreviations:** NT – non-translocated; HI – harvest index; KW – kernel weight

### Introduction

Bread wheat (*Triticum aestivum* L.) – rye (*Secale cereale* L.) translocated chromosomes have been widely used in wheat breeding programs to develop high yielding, disease resistant cultivars (Rajaram et al., 1983; Lukaszewski, 1990). T1BL·1RS and T1AL·1RS have been the most widely utilized of the wheat-rye translocated chromosomes. The T1BL·1RS translocation has a direct influence on yield components (Villareal et al., 1991, 1995) and also protects yield

potential by conferring resistance to diseases, such as leaf rust (*Lr26*), stripe rust (*Yr9*), stem rust (*Sr31*) and powdery mildew (*Pm8*) (McIntosh, 1983). However, the T1BL·1RS-derived resistances to leaf rust, stripe rust and powdery mildew have been overcome in many areas of the world (Zeller & Hsam, 1984; Bennett, 1984). The 1RS chromosome segment on T1AL·1RS, also known as ‘Amigo’ translocation, carries genes for resistance to greenbug (*Gb2*) and powdery mildew (*Pm17*) (Heun et al., 1990).

One goal of tapping desirable genes from the 1RS segment is to improve yield potential in wheat through increased heterosis. However, yield heterosis is a variable trait that depends on parental combinations and environmental conditions. In wheat, agronomic traits such as spike density, kernels/spike, kernels/spikelet, kernel weight, and number of spikelets/spike are important for heterotic assessment because they directly influence yield potential. Studies on wheat under different environmental conditions have shown that heterosis for yield ranges from -10 to 127% (Livers & Heyne, 1968; Borghi et al., 1988). Martin et al. (1995) reported mid-parent heterosis ranging from -14 to 27.8% for grain yield, -2.9 to 7.9% for kernel weight and -7.5 to 2.8% for protein concentration in spring wheat. These studies were based on parents that did not carry any wheat-rye translocations. The T1BL·1RS translocation has been found to increase grain yield, biomass and KW of pure lines by 9–10%, 11–12%, 4–6%, respectively (Carver & Rayburn, 1994). This observation is in agreement with the findings of Villareal et al. (1995; 1998) showing that T1BL·1RS significantly increases grain yield, harvest index, grains/m<sup>2</sup>, grains/spike, 1000-kernel weight and test weight. However, the effects of wheat-rye translocation chromosomes on yield and yield components have not been quantified in hybrid wheat. The objectives of this research were to determine relative and heterotic effects of T1BL·1RS + T1AL·1RS, T1BL·1RS and T1AL·1RS on yield and yield components of hybrid winter wheat grown under adequate moisture supply.

## Materials and methods

### *Genotypes*

Two winter wheat cultivars (Jagger and Karl 92), and five experimental wheat lines (X86036-AX-11, KS84063-2W, KS84063-4W, KS90175-1-1, and KS89180B-2-1-1) were used to develop hybrids in the greenhouse in the autumn of 1997 and 1998 (Table 1). The selection of parental genotypes was based on yield potential and wheat-rye translocation chromosome constitution. Jagger, which is non-translocated (NT), is high yielding and well adapted to the Central Plains of the United States. Karl 92 (NT) and X86036-AX-11 (T1AL·1RS) are closely related hard red winter wheats that differ for the T1AL·1RS translocated chromosome (Table 1). Jagger (NT),

KS84063-2W (NT), and KS84063-4W (T1BL·1RS) are closely related sister lines that differ for the T1BL·1RS chromosome, grain quality and phenological traits (Table 1). KS89180B-2-1-1 (T1BL·1RS) and KS90175-1-1 (T1BL·1RS) were used to develop hybrids, but had no closely related lines with different chromosome constitutions. Jagger, X86036-AX-11 and Karl 92 are early in maturity while the rest of the parents are medium in maturity.

From the seven parents, 13 hybrids were produced and categorized into five groups (Table 1). Group 1 hybrids with T1BL·1RS + T1AL·1RS, T1BL·1RS and T1AL·1RS were produced from two pairs of closely related lines. Groups 2 and 3 involved KS89180B-2-1-1 and KS90175-1-1 as female parents, respectively. In each case, the female was used to make hybrids with Karl 92, its T1AL·1RS related line and Jagger. In group 4, Jagger was crossed to KS84063-4W (T1BL·1RS) and X86036-AX-11 (T1AL·1RS) with the aim of comparing the performance of hybrids with the T1BL·1RS and T1AL·1RS chromosomes. Group 5 consisted of hybrids produced from the two pairs of closely related parents. In this group, the first hybrid was produced by crossing X86036-AX-11 (T1AL·1RS) to Karl 92 (NT) to produce a hybrid with only one copy of T1AL·1RS, while the second hybrid was produced by crossing KS84063-4W (T1BL·1RS) with KS84063-2W (NT). From these two hybrids, heterotic effects of T1AL·1RS and T1BL·1RS wheat-rye translocated chromosomes were estimated.

### *Hybrid seed production in the greenhouse*

The seven parents were planted in plastic flats (50 cm × 30 cm × 7 cm) in a greenhouse at 20–21 °C. Seven days after germination (Feekes stage 1), the flats were transferred to a cold chamber set at 8 °C with a photoperiod of 8 hours/day for 8 weeks. At the end of the vernalization period, four vigorous seedlings were transplanted into 20-cm diameter plastic pots filled with soil (1 perlite:1 loam: 1 peat moss). A total of 80 seedlings for each parent were transplanted into 20 pots. Pots were placed in the greenhouse maintained at 20/18 °C day and night cycle, respectively. The light in the greenhouse was supplemented with halogen lamps placed 1.5 m above the base of the pot to maintain a 16-hour photoperiod. Plants were watered by an automated system until they attained physiological maturity. At heading stage (Feekes stage 10.1), female parents were emasculated and then pollinated 3–5 days later with the appropriate male parent

Table 1. Seven winter wheat (*Triticum aestivum* L.) and 13 hybrids and with different chromosomal translocations produced in the greenhouse during autumn of 1997 and 1998

Parent/hybrid	Chromosome constitution/pedigree
<i>Parent</i>	
Jagger	Non-translocated; KS75216/PV/3/Stephens
KS84063-2W	Non-translocated; KS75216/PV/3/Stephens
KS84063-4W	T1BL·1RS; KS75216/PV/3/Stephens
Karl 92	Non-translocated; PlainsmanV/3/KAW/Atlas50//Parker* 5/Agent
X86036-AX-11	T1AL·1RS; T200/PV/OD51/4/PlainsmanV/3/KAW/Atlas50//Parker* 5/Agent
KS89180B-2-1-1	T1BL·1RS; XGH8010*73-23/XGH8010-1-4-2-26/3/107349/ X811252//1374
KS90175-1-1	T1BL·1RS; Sut/Art//Sxld/4/Nwt/3/Syn 19/Egl//T101
<i>Hybrid</i>	
<i>Group 1</i>	
KS84063-4W × X86036-AX-11	T1BL·1RS + T1AL·1RS
KS84063-4W × Karl 92	T1BL·1RS+1B
KS84063-2W × X86036-AX-11	T1AL·1RS+1A
<i>Group 2</i>	
KS89180B-2-1-1 × X86036-AX-11	T1BL·1RS + T1AL·1RS
KS89180B-2-1-1 × Karl 92	T1BL·1RS +1B
KS89180B-2-1-1 × Jagger	T1BL·1RS +1B
<i>Group 3</i>	
KS90175-1-1 × X86036-AX-11	T1BL·1RS + T1AL·1RS
KS90175-1-1 × Karl 92	T1BL·1RS+1B
KS90175-1-1 × Jagger	T1BL·1RS+1B
<i>Group 4</i>	
Jagger × X86036-AX-11	T1AL·1RS+1A
Jagger × KS84063-4W	T1BL·1RS+1B
<i>Group 5</i>	
X86036-AX-11 × Karl 92	T1AL·1RS+1A
KS84063-2W × KS84063-4W	T1BL·1RS+1B

to produce test hybrids (Table 1). All emasculated heads were covered with glassine bags to prevent stray pollen from fertilizing florets.

#### Field experiment

A two-year field study was conducted at Berthoud, Colorado (40° 45'N; 105° 30'W). The field was disc ploughed, harrowed to fine tilth, and leveled. Ridges 0.75 m in width were constructed and separated by 0.5 m wide irrigation channels. The trials were planted on 5 March 1998 and 25 February 1999 in a field previously planted to beans (*Phaseolus vulgaris*).

A Randomized Complete Block Design (RCBD) was adopted for this study. Four replicates were planted in 1998 and three replicates were planted in 1999. In the second year, three replicates were used due to insufficient quantities of hybrid seed. Each plot was planted on a 0.75 m wide ridge and consisted of

two rows 1.5 m in length and 30 cm apart, with seed spaced at 4cm within the rows. Plots were seeded with a single row, hand-operated seed drill (Hege Model 91) at a seeding rate of 60 kg/ha. Unplanted alleys (0.5 m wide) were used to separate blocks. Nitrogen (N) and phosphorus (P) were applied at the rate of 56 kg N/ha and 67 kg P/ha, during the autumn of 1997 and 1998. Additional N was applied at the rate of 56 kg/ha during the spring of 1998 and 1999. During the growing season, approximately 400 mm of water was supplied through surface irrigation in four splits of 100 mm each.

#### Data collected

At physiological maturity, spike density from each plot was estimated by counting the number of spikes from a 0.6 m × 0.3 m area. Plant height was measured as the distance from the ground level to the

spike tip excluding the awns and was recorded as an average of four samples. From a sample of 10 spikes/plot, spike length was measured from the base of the spike to the tip of the terminal spikelet excluding the awns. The number of spikelets/spike, kernels/spike and kernels/spikelet were determined from the same sample.

Plots were harvested during the first week of August in both 1998 and 1999. An area of 1.2 m × 0.6 m was hand-harvested by cutting at the base of the plant. The bundles were weighed to determine the biomass and then threshed with a 9-horsepower stationary Vogel thresher to determine the grain yield. Harvest index (HI) was computed by determining the ratio of grain yield to above-ground biomass. Kernel weight (KW) was estimated from a random sample of 500 kernels on a plot basis. Thirteen grams of grain were drawn from each sample and ground in a Cyclone Sample Mill (UDY). The resultant flour was analyzed for protein content using near infrared reflectance (NIR, Model Percon Inframatic 8620).

#### *Statistical analysis*

Combined analyses of variance were conducted for yield, height, spike length, protein and yield components using SAS Proc GLM (SAS Inst., 1990). In this analysis, the genotype was considered as a fixed effect, while year and replications within year were considered as random effects. The genotype mean squares for all traits were partitioned into variation between hybrid and parents, within hybrids and within parents. These factors were also considered as fixed effects. The year × genotype interaction mean squares were also subdivided into year × (hybrid vs. parent), year × hybrid and year × parent and were categorized as random effects. High parent heterosis (HPH) for all traits measured was computed using the formula:

$$HPH = \left[ \frac{(H - P_1)}{P_1} \right] \times 100,$$

where H is the mean performance of the hybrid for the character of interest and  $p_1$  is the mean performance of the best parent. For all traits measured, *F*-tests were used to detect the difference between hybrids with T1BL·1RS + T1AL·1RS vs. T1BL·1RS and T1AL·1RS vs. T1BL·1RS. The effects of T1AL·1RS on yield and yield components of pure line parents were determined by detecting the difference between the closely related parents. The effects of the T1BL·1RS translocation could not be determined because KS84063-4W, a line with this translocation, has

a long vernalization requirement and did not flower normally.

## **Results**

### *Combined analysis of variance for yield and yield components*

Significant ( $p < 0.01$ ) effects due to year for yield, kernels/spike, kernels/spikelet, KW, biomass, spike density, height and protein content were observed (Table 2), implying that the two seasons were different. No year effect for spike length was detected. Genotypic effects were significant ( $p < 0.01$ ) for all traits measured. The combined analyses also indicated that the contrasts between hybrids vs. parents were significant ( $p < 0.05$ ) for kernels/spike, kernels/spikelet, biomass and HI. Effects due to hybrids and parents were also significant ( $p < 0.05$ ) for all traits. The results also revealed significant ( $p < 0.01$ ) genotype × year interaction for yield, kernels/spikelet, KW, biomass, HI, spike density, spikelets/spike, spike length and protein content. However, no significant genotype × year interaction for kernels/spike was observed. Year × (hybrid vs. parent) interaction mean squares were significant ( $p < 0.01$ ) for biomass and height. Effects due to year × hybrid interaction were significant ( $p < 0.05$ ) for all traits except height and protein content. Mean squares for year × parent interaction were significant ( $p < 0.01$ ) for yield, KW, biomass, HI, spike density, number of spikelets/spike and protein content (Table 2).

### *Relative effects of T1BL·1RS + T1AL·1RS, T1BL·1RS and T1AL·1RS wheat-rye translocated chromosomes on yield and some yield components of hybrid wheat*

Research has produced inconsistent results regarding the T1BL·1RS translocation effects on agronomic traits of recombinant inbred wheat (Carver & Rayburn, 1994; Moreno-Sevilla et al., 1995), partly due to the effects of the background in which the translocation is placed (Moreno-Sevilla et al., 1995). In this study, the effects of T1BL·1RS + T1AL·1RS and T1AL·1RS translocations relative to T1BL·1RS, for yield and yield components varied between hybrids (Figure 1). No significant relative effects on yield, KW, HI and spike density were observed in the KS84063-4W × X86036-AX-11 (T1BL·1RS + T1AL·1RS) hybrid. In comparison, NT × T1AL·1RS

Table 2. Mean squares for yield, yield components, height, spike length and protein content of 13 hybrids and seven inbred wheat (*Triticum aestivum* L.) parents tested at Berthoud, Colorado in 1998 and 1999

Source of variation	df	Yield (ton ha <sup>-1</sup> )	Kernels/ spike	Kernels/ spikelet	Kernel weight (mg)	Biomass (ton ha <sup>-1</sup> )	HI
Year	1	63.01**	1068.94**	0.51**	212.29**	447.44*	0.023**
Rep. within Year	5	0.78	21.22	0.27	11.42	8.84	0.001
Genotype	19	7.14**	227.99**	8.60**	46.94**	25.97**	0.023**
Hybrid vs. Parent	1	18.93**	253.298*	0.84**	332.75**	124.62**	0.027*
Hybrid	12	6.39**	145.95**	0.38**	25.93**	15.04**	0.014**
Parent	6	12.37**	451.21**	0.54**	41.33**	30.23**	0.041**
Genotype × Year	19	1.58**	18.59	1.32**	12.45**	11.97**	0.002**
Year × (Hybrid vs. Parent)	1	1.20	18.86	0.11	2.68	42.93**	0.000
Year × Hybrid	12	0.66**	26.39*	0.09**	7.98**	8.29*	0.001*
Year × Parent	6	3.40**	2.93	0.03	23.02**	13.74**	0.004**
Error	95	0.31	14.10	0.03	2.71	3.48	0.001
CV		13.70	7.55	6.32	6.06	12.56	13.11

\*, \*\* Significant at  $p < 0.05$  and  $p < 0.01$ , respectively.

Table 2. Continued

Source of	df	Spike/m <sup>2</sup>	Spikelets/ spike	Height (cm)	Spike length (cm)	Protein (g kg <sup>-1</sup> )
Year	1	1767710.75**	45.28**	405.58**	0.01	4719.11**
Rep. within Year	5	16034.78	1.62	45.41*	0.25	55.02
Genotype	19	94989.25**	10.28**	125.98**	1.79**	311.92**
Hybrid vs. Parent	1	111713.84*	0.02	124.39	1.50	1.39
Hybrid	12	58154.34**	6.19**	129.155**	1.69**	290.51**
Parent	6	165871.64**	20.16**	119.91**	2.05**	406.39**
Genotype × Year	19	33383.55**	1.59**	34.59*	0.41**	116.85**
Year × (Hybrid vs. Parent)	1	83085.80	0.04	142.20*	0.11	88.52
Year × Hybrid	12	23390.54**	1.69**	32.97	0.48**	29.92
Year × Parent	6	41085.89**	1.64**	19.89	0.31	295.06**
Error	95	7315.51	0.51	19.22	0.16	30.59
CV		13.41	3.79	5.08	3.96	2.87

\*, \*\* Significant at  $p < 0.05$  and  $p < 0.01$ , respectively.

(KS84063-2W × X86036-AX-11) produced significantly ( $p < 0.01$ ) more yield (27.54%), HI (34.78%), and spike density (50.57%) than the hybrid with a single copy of T1BL·1RS translocation. However, kernels/spike, spikelets/spike, biomass and spike length were significantly ( $p < 0.05$ ) reduced for hybrids with T1AL·1RS + T1BL·1RS relative to the T1BL·1RS hybrid.

Positive effects for yield (25.26–44.64%), biomass (19.62%), HI (23.07–26.31%) and spike density (6.66–15.59%) were observed in T1BL·1RS

+ T1AL·1RS (KS89180B2-1-1 × X86036-AX-11 and KS90175-1-1 × X86036-AX-11) relative to NT × T1BL·1RS hybrids (Figure 2). Compared to T1BL·1RS × NT, the relative effects on spikelets/spike (–5.52 to –12.04%), and spike length (–5.36 to –8.73%) were negative for all hybrids with T1BL·1RS + T1AL·1RS (Figure 2). These results showed that placing the two wheat-rye translocated chromosomes in the same genetic background can have negative effects on certain yield components. In this case, the T1BL·1RS + T1AL·1RS hybrids more closely re-

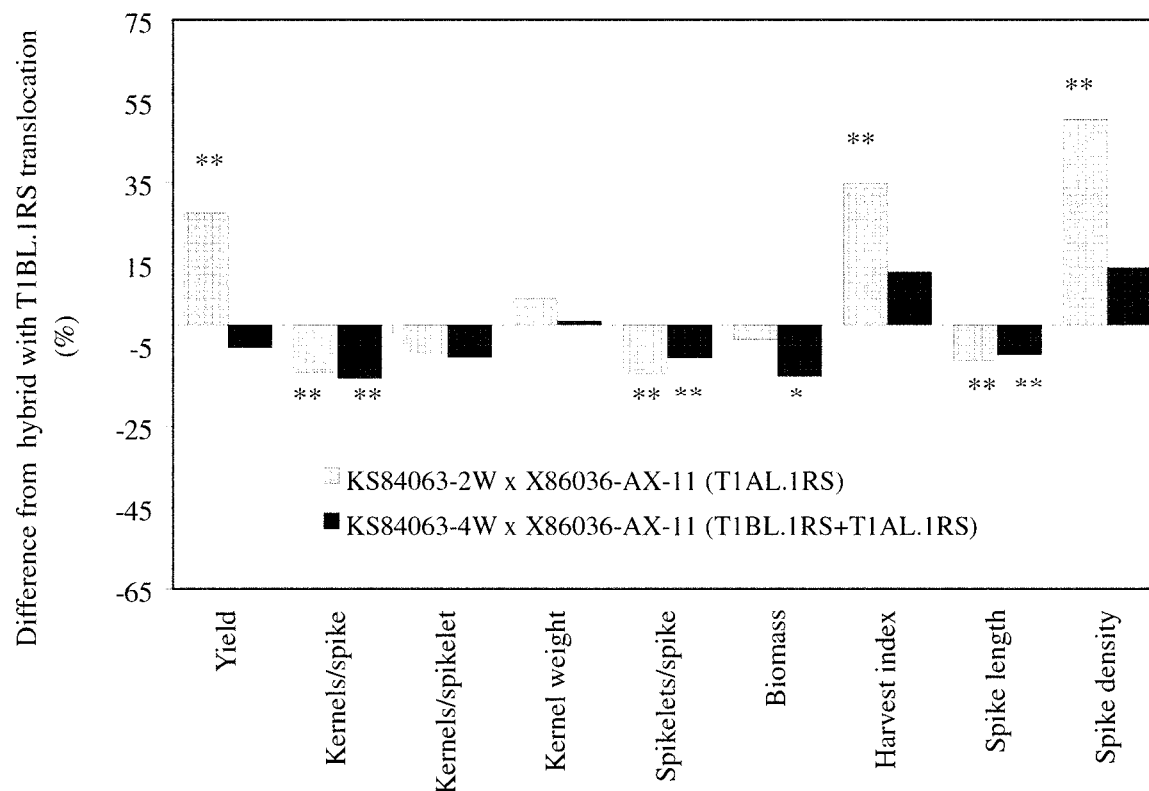


Figure 1. Relative effects of T1BL·1RS + T1AL·1RS and T1AL·1RS translocations on yield and yield components compared to T1BL·1RS in hybrid wheat (*Triticum aestivum* L.) evaluated at Berthoud, Colorado under adequate moisture. Hybrid with T1BL·1RS translocation was KS84063-4W × Karl 92. (\*\*\*) Significant at  $p < 0.05$  and  $p < 0.01$ , respectively.)

sembled T1AL·1RS × NT hybrids than T1BL·1RS × NT hybrids. This suggests that when the two translocations are combined, T1AL·1RS is dominant to T1BL·1RS for spikelets/spike, kernels/spike and spike length.

The NT and T1AL·1RS related pure line parents were also compared to determine the relative effects of homozygous T1AL·1RS translocation on yield and yield components. The result indicated that T1AL·1RS significantly increased yield (23.51%), biomass (14.36%), HI (10.71%) and spike density (10.59%) compared to the closely related NT pure line (Figure 3). However, this chromosome reduced spikelets/spike and spike length compared to the parent with normal chromosome 1A. This phenomenon was also detected in some of the test hybrids in the trial. The reduction in number of spikelets/spike and spike length may have contributed to the significant decrease in number of kernels/spike of the T1AL·1RS line compared to the NT line.

#### Heterosis

In the first group, the hybrid with both T1BL·1RS + T1AL·1RS translocations showed negative high parent heterosis for all the traits except KW. In contrast, the hybrid with a single copy of T1BL·1RS showed significant ( $p < 0.05$ ) high parent heterosis for biomass (30.95%), and height (4.16%) (Table 3). The NT × T1AL·1RS (KS84063-2W × X86036-AX-11) hybrid had a 5.17% heterotic advantage for KW but heterosis for spike length and height was negative due to the effects of the T1AL·1RS translocation (Table 3). All hybrids in the first group exhibited negative heterosis for protein content.

In contrast to the first group of hybrids, the T1BL·1RS + T1AL·1RS in the second group had 23.45% and 12.80% high parent heterosis for yield and biomass, respectively. Heterosis for kernels/spike and spikelets/spike for this hybrid was negative (Table 3). The NT × T1BL·1RS hybrid did not show positive heterosis for any trait; however, the NT × T1BL·1RS

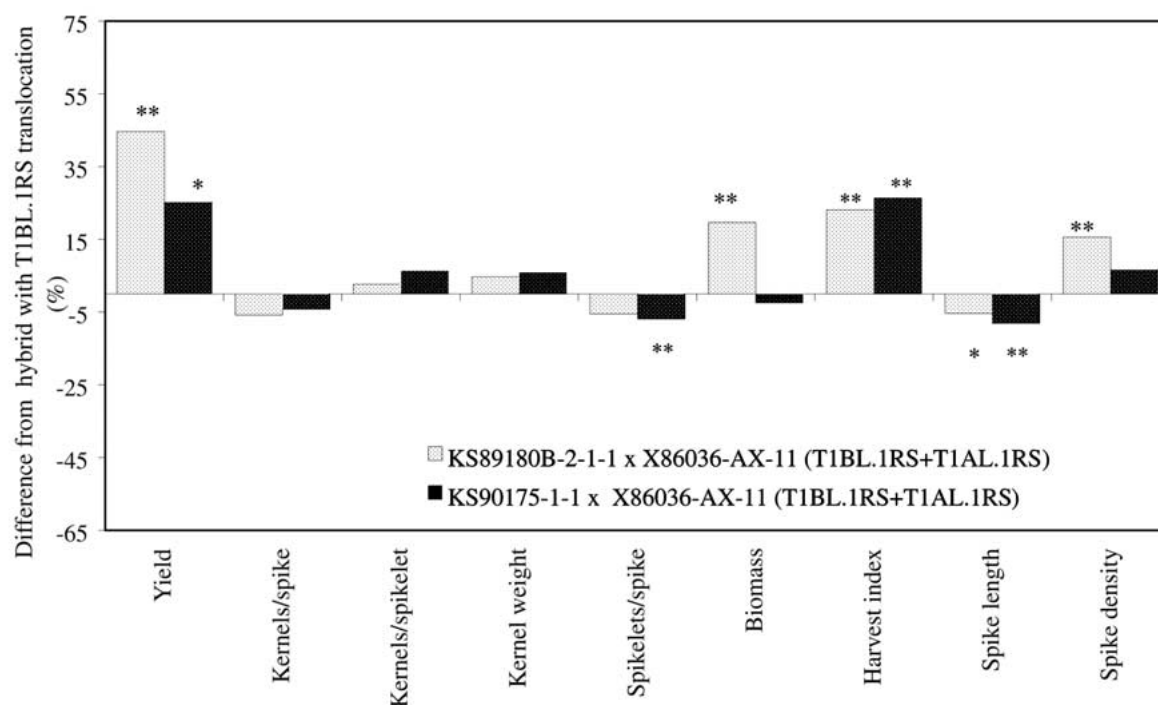


Figure 2. Relative effects of T1BL.1RS + T1AL.1RS translocations on yield and yield components of hybrid wheat (*Triticum aestivum* L.) evaluated at Berthoud, Colorado under adequate moisture. (\*, \*\* Significant at  $p < 0.05$  and  $p < 0.01$ , respectively.)

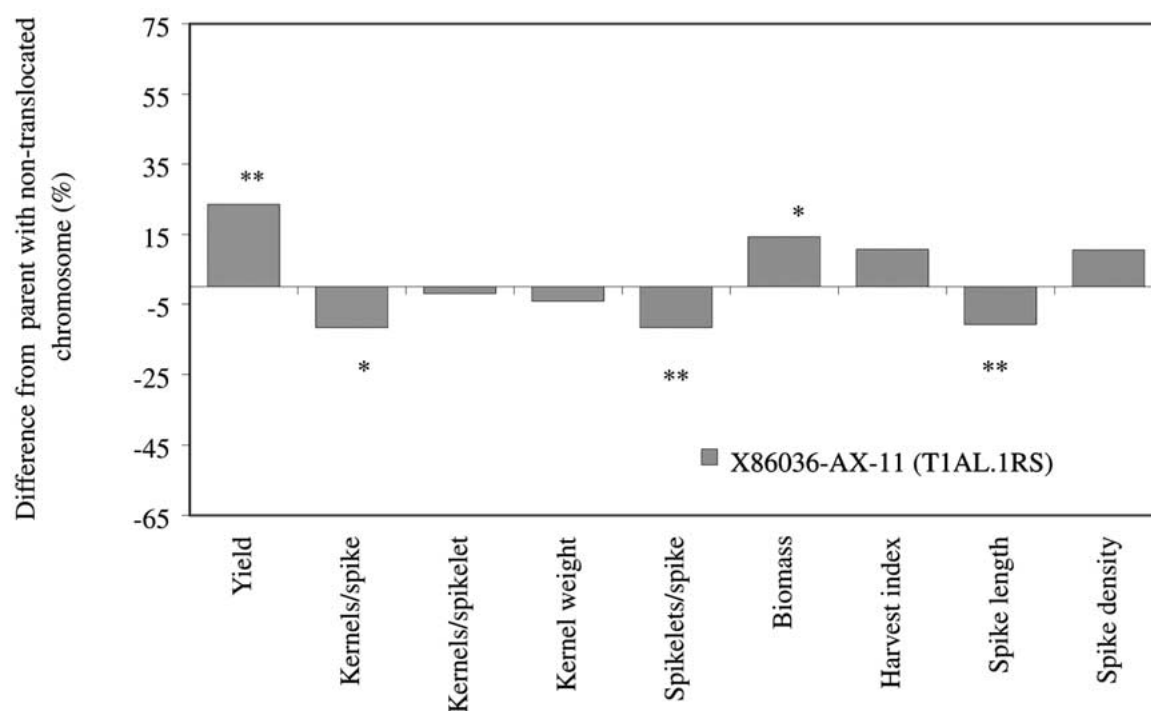


Figure 3. Relative effects of T1AL.1RS translocations on yield and yield components as compared to non-translocated related wheat (*Triticum aestivum* L.) cv. Karl 92. evaluated at Berthoud, Colorado. (\*, \*\* Significant at  $p < 0.05$  and  $p < 0.01$ , respectively.)

Table 3. High parent heterosis for yield, yield components, spike length, height and protein content of 13 hybrid wheat (*T. aestivum* L.) with T1BL·IRS + T1AL·IRS, T1BL·IRS and T1AL·IRS wheat-rye translocated chromosomes evaluated under irrigation in Berthoud, Colorado (2-year data)

Hybrid	Yield (%)	Kernel weight (%)	Kernels spike (%)	Spikelets/ spike (%)	Biomass (%)	HI (%)	Spike/m <sup>2</sup> length (%)	Spike content (%)	Protein (%)		
Group 1											
KS84063-4W × X86036-AX-11	(T1BL·IRS + T1AL·IRS)	-21.14**	+1.68	-12.89**	-6.41**	-0.95	-20.52**	-19.58**	-3.67*	-3.97	-7.81**
KS84063-4W × Karl 92	(T1BL·IRS)	+1.76	-2.92	-0.01	+2.08	+30.95**	-16.94*	-12.37**	-0.30	+4.16*	-6.46**
KS84063-2W × X86036-AX-11	(T1AL·IRS)	+6.69	+5.17*	+4.13	-3.19	+6.20	+2.22	+6.62	-3.73*	-7.51**	-3.08
Group 2											
KS89180B-2-1-1 × X86036-AX-11	(T1BL·IRS + T1AL·IRS)	+23.45**	+4.03	-19.38**	-8.35**	+12.80*	+5.02	-0.52	+1.67	+2.77	-2.56
KS89180B-2-1-1 × Karl 92	(T1BL·IRS)	-5.31	-5.51	-15.79**	-3.64*	-3.50	-4.34	-5.07	+1.10	-3.63	-1.17
KS89180B-2-1-1 × Jagger	(T1BL·IRS)	+11.05	+2.03	-15.20**	-10.09**	-9.65	-0.92	-23.92**	+3.46*	+3.20	-4.31
Group 3											
KS90175-1-1 × X86036-AX-11	(T1BL·IRS + T1AL·IRS)	-18.55**	+15.45**	-29.18**	-7.98**	+6.10	-3.94*	-18.09**	-3.52**	+3.39	+11.16**
KS90175-1-1 × Karl 92	(T1BL·IRS)	-20.83**	+4.79	-25.57**	-1.80	+14.15*	-32.15**	-14.45**	-0.06	-1.91	+4.48**
KS90175-1-1 × Jagger	(T1BL·IRS)	-7.76	+8.65**	-14.83**	-12.24**	+0.30	-10.16**	-18.17**	-0.05	+5.69*	+1.89
Group 4											
Jagger × X86036-AX-11	(T1AL·IRS)	+13.22**	+10.48**	-18.15**	+0.13	+7.50	+3.60**	+6.20	-0.57	-1.37	-3.17
Jagger × KS84063-4W	(T1BL·IRS)	+2.19	+13.86**	-0.69	-4.13*	+11.45*	-8.55*	-5.40	+7.63*	+11.99**	-6.24**
Group 5											
X86036-AX-11 × Karl 92	(T1AL·IRS) <sup>†</sup>	+10.37*	+3.02	+2.36	-2.07	+7.16**	-10.91	+3.56	-5.99**	-2.61	-3.13
KS84063-2W × KS84063-4W	(T1BL·IRS) <sup>‡</sup>	-23.41*	-9.69	-0.48	+0.95	-10.95	-12.17*	-8.11	+2.93	+0.66	-5.17**

\* \*\* Significant at  $p < 0.05$  and  $p < 0.01$ , respectively.

† Hybrid developed from closely related parents that differ for T1AL·IRS wheat-rye translocated chromosome.

‡ Hybrid developed from closely related parents that differ for T1BL·IRS wheat-rye translocated chromosome.



hybrid from KS89180B-2-1-1  $\times$  Jagger had a heterotic advantage for spike length.

In the third group, the T1BL·1RS + T1AL·1RS hybrid showed heterosis of 15.45% for KW and 11.16% for protein content (Table 3). In comparison, the closely related hybrid with a single copy of T1BL·1RS showed positive high parent heterosis for biomass (14.15%) and protein content (4.48%). The other T1BL·1RS  $\times$  NT (KS90175-1-1  $\times$  Jagger) hybrid in group 3 had 8.65% HPH for KW and 5.69% for height. Heterosis for kernels/spike, spikelets/spike, HI and spike density were negative for all the hybrids (Table 3).

In the fourth group, the NT  $\times$  T1AL·1RS hybrid produced higher yield (13.22%), HI (3.60%) and KW (10.48%) than the best parent (Table 3). On the other hand, the NT  $\times$  T1BL·1RS hybrid showed greatest heterosis for KW, biomass and height (Table 3).

In the fifth group, T1AL·1RS  $\times$  NT hybrid produced 10.37% and 7.16% more yield and biomass, respectively, than the best parent while spike length was 5.99% shorter than the best parent (Table 3). No positive significant heterosis was noted for any trait measured for the NT  $\times$  T1BL·1RS hybrid.

## Discussion

In this study, the relative effects of T1BL·1RS + T1AL·1RS and T1AL·1RS translocations on yield and yield components were determined by comparing performance of seven hybrids to hybrids with a single copy of the T1BL·1RS translocation. Of the three hybrids with both wheat-rye translocated chromosomes, KS84063-4W  $\times$  X86036-AX-11 produced lower yield, kernels/spike, kernels/spikelet, spikelets/spike, biomass, protein content, and spike length than the hybrid with a single copy of T1BL·1RS translocation (Figures 1 and 2). The other two T1BL·1RS + T1AL·1RS hybrids increased yield compared to the hybrid with a single copy of T1BL·1RS due to increased HI and spike density. These hybrids did have reduced spike length. The third T1BL·1RS + T1AL·1RS hybrid (KS90175-1-1  $\times$  X86036-AX-11) showed a significant decrease in spikelets/spike. The T1BL·1RS translocation tends to improve spike length, kernels/spike, spikelets/spike, biomass, HI and protein in pure line wheat (Mackendry et al., 1996; Villareal et al., 1998). However, it is evident that this translocation cannot improve kernels/spike, spike-

lets/spike or spike length in the presence of T1AL·1RS under adequate moisture.

When the two wheat-rye translocated chromosomes are placed in the same genetic background, increased yield is derived from the positive effects of the T1AL·1RS translocation on tillering ability, rather than the typical effects of T1BL·1RS. Because a recessive gene, *tin*, responsible for restriction of tillering is located on chromosome 1AS (McIntosh et al., 1998) in the T1AL·1RS translocation lines, the 1RS segment replaces this gene and may explain why hybrids with T1AL·1RS tiller more than hybrids with T1BL·1RS (Figure 1). The high number of tillers is a key component of increased HI for T1AL·1RS hybrids. This phenomenon was also reflected in the parent, X86036-AX-11, which is homozygous for the T1AL·1RS translocation, compared to its relative with no chromosomal translocation. The T1AL·1RS line yielded 23.51% more grain than NT (Karl 92) due to enhanced spike density, biomass and HI (Figure 3).

When placed in the same background, the effects of the T1AL·1RS tended to be dominant to those of the T1BL·1RS for key yield components. This could be due to replacement of chromosome 1AS by 1RS. In this study, kernels/spike, spikelets/spike and spike length were reduced when 1AS was present in a hemizygous state, and T1AL·1RS was present in both homozygous and hemizygous states.

Because the two 1RS segments used in this study are translocated on to different homoeologous chromosomes (1B and 1A), the presence of T1AL·1RS translocation can epigenetically control genes for spikelets/spike, grains/spike and spike length. This complex interaction between 1AS and 1RS could have influenced the negative effects observed in these traits in the hybrids with the two translocations in the same background (Viera et al., 1990). It appears that the presence of 1AS in homozygous condition is necessary for expression of heterotic effects of T1BL·1RS on various agronomic traits.

Often, heterotic effects for yield and yield components in wheat vary with the genetic background and distance between the parents (Shamsuddin, 1985; Cox & Murphy, 1990). In this study, variability was expected to come from the translocated rye segment and genetic background. In a review, Briggles (1963) indicated that heterosis for yield and other agronomic traits vary with genetic background. Heterotic effects for T1BL·1RS + T1AL·1RS, T1BL·1RS and T1AL·1RS translocations on agronomic traits in different genetic backgrounds were clearly manifested. Under ad-

equate moisture supply, contributions of T1BL·1RS + T1AL·1RS, T1AL·1RS and T1BL·1RS translocations towards improvement of yield and yield components varied with the environment and female parents used. In this study, two of the three hybrids with T1BL·1RS + T1AL·1RS showed a relatively stable and positive effect on yield compared to T1BL·1RS. This implies that the genetic background or hybrid combination has an influence on the expression of genes on the 1RS segment.

In the first group (Table 3), T1BL·1RS × NT (KS84063-4W × Karl 92) exhibited positive heterotic advantage for biomass (Table 3). Increased KW, kernels/spike, biomass and spike density may have contributed to the heterotic advantage for yield observed in NT × T1AL·1RS (KS84063-2W × X86036-AX-11). Apparently, the T1BL·1RS translocation seems to improve KW, kernels/spikelet and biomass in hybrids as compared to their best parents.

In the second group, the hybrid with T1BL·1RS + T1AL·1RS translocations showed heterotic advantage for yield primarily because of an increase in KW, biomass and HI (Table 3). Although hybrids responded well to moisture supply for these traits, heterotic advantage for yield in this hybrid could be attributed to the effect of the T1AL·1RS translocation on spike density, which subsequently increased biomass and HI.

In the third group, hybrids involving KS90175-1-1 (T1BL·1RS) as a female parent showed significant heterotic advantage for KW and protein content (Table 3). The negative heterosis for kernels/spike was mostly due to background effects and confirms that the T1BL·1RS translocation increases and stabilizes grain yield and some yield components in certain genetic backgrounds (Lukaszewski, 1990; Villareal et al., 1991; Moreno-Sevilla et al., 1995). The T1BL·1RS × NT (KS90175-1-1 × Jagger) hybrid only showed heterosis for KW and height, despite the fact that the parents are not closely related.

In the fourth group, it was not possible to partition the effects of wheat-rye translocated chromosomes because the male parents were not closely related. However, heterosis observed on NT × T1AL·1RS could be partly attributed to the positive effects of T1AL·1RS on KW, biomass, HI and spike density (Table 3). In this group, NT × T1AL·1RS produced the highest yield because of increased spike density and HI. Inbred wheat cultivars with T1BL·1RS have been shown to be superior for grain yield, biomass, KW and spike fertility (Schlegel & Meinel, 1994; Moreno-Sevilla et

al., 1995). Because the parents were closely related, heterosis for KW, biomass and spike length detected on the NT × T1BL·1RS hybrid are likely due to the 1RS segment.

Hybrids in the fifth group were derived from closely related parents and quantified the effect of hemizygous T1AL·1RS and T1BL·1RS translocations on various agronomic traits. The T1AL·1RS showed heterotic effects for yield under ample moisture supply because of increased biomass. However, NT × T1BL·1RS hybrid in this group did not show significant positive heterosis for any agronomic traits.

## Conclusion

The T1BL·1RS translocation generally increased kernels/spike, spikelets/spike and spike length in hybrids. These are important traits that enhance yield potential of wheat. However, the magnitude of improvement depends on the genetic background because not all hybrids with the T1BL·1RS showed improvement in these traits. The T1AL·1RS translocation increased yield by enhancing tillering ability and ultimately increasing HI. This phenomenon was observed in hybrids, and also in the parent that had the homozygous T1AL·1RS translocation. When the T1BL·1RS and T1AL·1RS wheat-rye translocations were put in the same genetic background, the hybrids showed improved spike density and HI while spike length, and the number of spikelets/spike were reduced compared to the hybrid with only T1BL·1RS. This indicates that gene(s) for spikelets/spike and spike length on T1BL·1RS translocation were not expressed in the presence of T1AL·1RS translocation, resulting in fewer kernels/spike. Therefore, heterotic effects were mainly due to the T1AL·1RS translocation. Although the combination of the two translocations can boost yield in hybrids grown under ample moisture supply, it is not advisable to combine the two translocations in the same genetic background in pure line wheat because of the formation of an unstable quadrivalent between 1B, T1BL·1RS, T1AL·1RS and 1A chromosomes at metaphase stage. As a result, the use of T1BL·1RS + T1AL·1RS translocations should be restricted to production of hybrid wheat rather than recombinant inbred wheat.

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