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A 1BL/1RS translocation contributing to kernel length increase in three wheat recombinant inbred line populations

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Abstract: The 1BL/1RS wheat-rye translocation has been widely utilized in wheat genetic improvement and breeding programs. Our understanding on the effects of the 1BL/1RS translocation on wheat kernel size (e.g. length and width) is limited despite of numerous studies reporting about the effects on kernel weight. Here, we identified a wheat 1BL/1RS translocation line 88-1643 with higher kernel length (KL) using fluorescence *in situ* hybridization (FISH), genomic *in situ* hybridization (GISH) and molecular markers. To detect the possible role of the 1BL/1RS translocation in KL, kernel width (KW), and thousand-kernel weight (TKW), three recombinant inbred line (RIL) populations were constructed by crossing 88-1643 and three other wheat lines. As expected, the results showed that the values of KL in lines carrying 1RS were significantly higher than those carrying 1BS in three RIL populations at multiple environments, indicating that a major and stably expressed allele or gene responsible for increasing KL is most likely located on 1RS from 88-1643. Additionally, in one RIL population, the increased KL contributed significantly to the increase in TKW. Collectively, the 1BL/1RS translocation reported here is of interest to reveal molecular mechanism of the gene controlling KL and will be useful for improving wheat yield.

Keywords: correlation; multiple environments; validation populations; wheat yield

Common wheat (*Triticum aestivum* L., 2*n* = 6*x* = 42, AABBDD) is one of the most important crops accounting for approximately 20% of human consumed food calories (Distelfeld & Fahima 2007). It has been estimated that the global demand for wheat will increase by a further 40% by 2020 (Rajaram 2014). Thus, breeding wheat cultivar with higher grain yield has been always the key goal for wheat scientists. Yield is a complex quantitative trait controlled by plentiful minor effect genes and easily affected by various environments (Slafer et al. 2014). One of the main factors affecting wheat yield is thousand-kernel weight (TKW) which is usually determined by kernel length (KL), kernel width (KW) and kernel thickness (KH) (Campbell et al. 1999).

Rye (*Secale cereal* L.) is one of the most important related species used for wheat genetic improvement and breeding programs. Its chromosome arm 1RS can replace 1BS, 1AS or 1DS of wheat to form different translocation lines (Rogowsky et al. 1991; Lukaszewski 1995, 2006; Rubio et al. 1999). The most commonly utilized in wheat breeding is the 1BL/1RS

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translocation (Baum & Appels 1991; Graybosch et al. 1999; Zhou et al. 2004; Ehdaie et al. 2014; Molnár-Láng et al. 2014). 1RS is a useful source of genes for multiple disease resistance including *Yr9* (Zeller 1973), *Pm8* (Singh et al. 1990), *Sr31* (Zeller 1973), and *Lr26* (Mago et al. 2002). Despite plentiful wheat cultivars possess 1BL/1RS translocations (Rabinovich 1998; Zhou et al. 2004; Hoffmann 2008; Landjeva et al. 2010; Bagherikia et al. 2014), the sources of wheat-rye translocations are likely limited when analyzing these cultivars' pedigrees (Villareal et al. 1998; Ren et al. 2006; Schlegel & Korzun 2010; Trubacheeva et al. 2011). Thus, increasing studies are focusing on identifying and introducing more novel 1BL/1RS translocations (Ren et al. 2009, 2018; Qi et al. 2016 to find more possibilities in wheat breeding.

Numerous studies also reported that the lines carrying 1RS can increase wheat yield mainly by improving TKW in various populations (Moreno-Sevilla et al. 1995; Kim et al. 2004; Waines & Ehdaie 2007; Xiao et al. 2011; Ren et al. 2012, 2017, 2018; Kaur et al. 2017). KL and KW are two factors determining KTW. However, few of previous studies have analysed effects of 1BL/1RS translocation on KL and KW.

In this study, we evaluated the effects of a 1BL/1RS translocation from wheat cultivar 88-1643 on KL, KW, and TKW in three RIL populations across multiple environments.

MATERIAL AND METHODS

Plant materials. Three wheat populations with 88-1643 as a common parent developed at Triticeae Research Institute of Sichuan Agricultural University were used in this study. They were derived from crosses 88-1643 × CNM16 (8CN, 146 F_7–F_9 lines), 88-1643 × Mianmai 37 (M37; 8M, 172 F_4–F_5 lines), and 88-1643 × Chuanmai 104 (CM104; 8CM, F_4–F_5 168 lines). Wheat line 88-1643 with longer kernel was bred and stored in Triticeae Research Institute (Figure 1). CNM16 showing shorter kernel is a mutant of the commercial wheat cultivar Chuannong 16 (Figure 1). M37 and CM104 with shorter kernels used for generating the validation populations are two commercial wheat cultivars (Figure S1 in Electronic Supplementary Material (ESM)).

The 8CN population was planted at Chongzhou (103°38'E, 30°32'N) in 2018 (2018CZ), Wenjiang (103°51'E, 30°43'N) in 2018 and 2019 (2018WJ and 2019WJ), and Ya'an (103°0'E, 29°58'N) in 2018 (2018YA). The 8M an 8CM populations were planted at Chongzhou in 2018 and 2019 (2018CZ and 2019CZ).

Each line was single-seed planted in one row of 2 m in length with 10 cm between plants within a row and 30 cm between rows (Liu et al. 2018; Ma et al. 2019). The lines in all the environments were all designed by random block. Nitrogen and superphosphate fertilizers were applied at a rate of 80 and 100 kg/ha, respectively, at sowing (Yu et al. 2018). Field management was performed according to the common practices and we have sprayed fungicides and pesticides for keeping the normal growth of plants for seed harvest. At least five spikes of different plants in each line were harvested when ripening. In addition, the 8CN population was also planted in greenhouse of Sichuan Agricultural University in 2017 (2017GH). Each line was single-seed planted in one pot (twenty centimeters in diameter). The glasshouse condition and management methods followed the study reported by Ma et al. (2014).

Phenotypic identification. Thirty full and uniform kernels of each line were scanned by Epson Expression

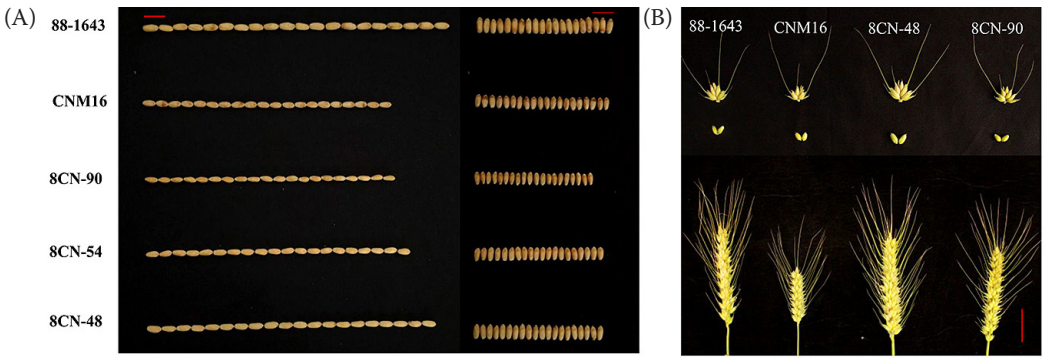

Figure 1. Phenotype of the parents 88-1643 and CNM16 (scale bar = 1cm) (A) and some randomly selected recombinant inbred lines derived from the parents (scale bar = 5cm) (B)

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10000 XL (Seiko Epson Corporation, Japan). KL and KW were evaluated by WinSEEDLE (Instruments Regent, Inc., Canada) based on the output images, and the average value of data was finally calculated for further analysis. TKW was calculated as 10 times of 100 kernel weight of each line.

GISH and FISH based identification of the 1BL/1RS translocation. Fluorescence *in situ* hybridization (FISH) and genomic *in situ* hybridization (GISH) were used to identify the 1BL/1RS translocation in 88-1643, CNM16, CM37, and CM104 according to the methods described by Qi et al. (2016).

Markers based identification of 1BL/1RS translocation lines. The DNA was extracted by using the cetyltrimethylammonium bromide method (Saghai-Maroof et al. 1984). Two 1RS-specific markers *x-sec-p1*/*x-sec-p2* (Chai et al. 2010) and *O-sec5'-A*/*O-sec3'-R* (Singh et al. 1990), and two 1BS-specific simple sequence repeat (SSR) markers *O11B3/O11B5* (Chai et al. 2010) and *Gwm11* (Röder et al. 1998) were used to characterise 1RS and 1BS chromosome arm in the 8CN, 8M, and 8CM populations. All primer sequences are shown in Table 1. 20 µL PCR reaction mixtures contained 10 µL mix, 8 µL ddH_2O, 1ul DNA (100 ng/ul), 0.5 µL forward primer (10 µM) and 0.5 µL reverse primer (10 µM), and this system is used for all the sample. The PCR reaction was carried out with the following amplification procedure: 5 min at 94 °C (initial denaturation), 35 cycles of 45 s at 94 °C, 45 s at proper temperature (51 °C for *O-sec5'-A/O-sec3'-R*; 55 °C for *Gwm11*; 60 °C for *O11B3/O11B5*; and 63 °C for *x-sec-p1/x-sec-p2*; annealing temperature), and 1 min at 72 °C (extension). An additional 10-min extension followed after the 35 cycles. The mix was 2× Taq Master Mix (Dye Plus), and was purchased from Vazyme Biological Technology Limited (Chengdu, P.R. China). Primers were synthesised by TsingKe Biological Technology Limited (Gaoxin Zone, Chengdu, P.R. China). Amplification products were detected by 2% concentration agarose gels.

Statistical analysis. SAS (Ver. 8.0; SAS Institute, Cary, North Carolina) was used for calculating the best linear unbiased predictors (BLUPs) value for the 8CN population's kernel traits from different environments. According to the method described by Smith et al. (1998), broad-sense heritability (H^2) across different environments was estimated. SPSS (Ver. 22; IBM SPSS, Armonk, USA) was used to detect difference for KL, KW, and TKW between lines carrying 1RS and 1BS using student's *t*-test ($P < 0.05$).

RESULTS

Phenotypic evaluation and correlation analysis. The phenotype for three kernel traits of 8CN population and their parents in different environments are listed in Table 2. 88-1643 had consistently and significantly higher values for KL than CNM16 in each of the investigated environments. For KW, CNM16 is significantly wider than 88-1643. For TKW, the value of 88-1643 is significantly higher than CNM16 (Table 2, Figure 1). For 8CN population, the frequency distribution for three kernel traits in all different environments and BLUP showed continuous distributions with ranges from 5.58 to 9.30 mm in KL, 2.33 to 4.35 mm in KW and 21.57 to 68.97 g in TKW (Figure 2). Transgressive segregation was observed in three kernel traits and the broad-sense heritability (H^2) of KL, KW and TKW were 0.74, 0.41 and 0.21 respectively (Table 2).

All three kernel traits showed significant positive correlations with each other in populations 8CN

Table 1. Sequences of 1RS- and 1BS-specific markers on 1BS in wheat

Marker	Primer sequence (5'-3')	Annealing temperature (°C)	Arm location	References
O-SEC5'-A/O-SEC3'-R	F: CTATTAGTTCGAAAAGCTTATGA R: GCATATGACTCAAATTATTTTTT	51	1RS	Singh et al. (1990)
*x-sec-p1/x-sec-p*2	F: ACCTTCCTCATCTTTGTCCT R: CCGATGCCTATACCACTACT	63	1RS	Chai et al. (2010)
Gwm11	F: GGATAGTCAGACAATTCTTGTG R: GTGAATTGTGTCTTGTATGCTTCC	55	1BS	Röder et al. (1998)
O11B3/O11B5	F: GTTGCTGCTGAGGTTGGTTC R: GGTACCAACAACAACAACCC	60	1BS	Chai et al. (2010)

F – forward primer; R – reverse primer

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and 8CM. For 8M population, significant positive correlation was observed between KW and TKW only (Table 3).

GISH and FISH based identification of 1BL/1RS translocation. FISH was carried out using probe pSc119.2 and pTa535 to determine wheat-rye translocated chromosomes. The pSc119.2 probe gives green fluorescent signals on the telomeres and faint fluorescent signals on sub-telomeres region of a pair of chromosomes in 88-1643 (Figure 3A), indicating that the rye chromosome 1RS was translocated to the short arm of wheat chromosome 1B (1BS). To further confirm the result, GISH was further carried out. The root tip somatic cells of 88-1643 had a compensating wheat-rye robertsonian translocation with red hybridization signals (Figuer 3B). Hence, FISH analysis combined with GISH revealed that 88-1643 is a translocation line containing 1BL/1RS translocation chromosome. Similarly, GISH and FISH analysis results indicated that other three wheat genotypes CNM16, M37 and CM104 did not contain 1BL/1RS translocation chromosome (Figure 3C–H).

Molecular-markers based identification of 1BL/1RS translocation lines. As expected, the amplifying products with the 1RS-specific markers

Table 2. Phenotype of parents and RIL in different environments

Environment	Parents		RIL			H^2 (%)
	88-1643	CNM16	min	max	mean	
KL (mm)						
2019WJ	8.72**	7.29	6.96	8.87	7.92	
2018CZ	9.26**	7.64	7.47	9.30	8.31	
2018WJ	8.76**	7.27	7.22	9.03	7.83	0.74
2018YA	8.28**	6.72	6.91	9.10	7.99	
2017GH	8.78**	6.91	5.58	8.75	7.22	
BULP	8.64	7.23	6.94	8.79	7.83	
KW (mm)						
2019WJ	3.79*	3.88	3.16	4.14	3.80	
2018CZ	3.90*	4.08	3.39	4.35	3.89	
2018WJ	3.69**	3.87	3.04	4.26	3.76	0.41
2018YA	3.22*	3.66	2.78	4.15	3.69	
2017GH	3.06*	3.53	2.33	3.76	3.18	
BULP	3.46	3.67	3.45	3.79	3.63	
TKW (g)						
2019WJ	62**	51.3	35.71	68.33	54.60	
2018CZ	65.54**	51.52	31.91	68.97	53.26	
2018WJ	62.40**	52.97	31.40	68.14	54.82	0.21
2018YA	nd	nd	21.57	68.69	49.43	
BULP	61.89	52.47	46.77	61.97	53.28	

H^2 – indicates the broad-sense heritability; BULP – the best linear unbiased predictors; *, **correlation significant at the 0.05, 0.01 level; nd – data not determined; KL – kernel length; KW – kernel width; TKW – thousand-kernel weight; RIL – recombinant inbred line; WJ – Wenjiang; CZ – Chongzhou; YA – Yaan; GH – greenhouse

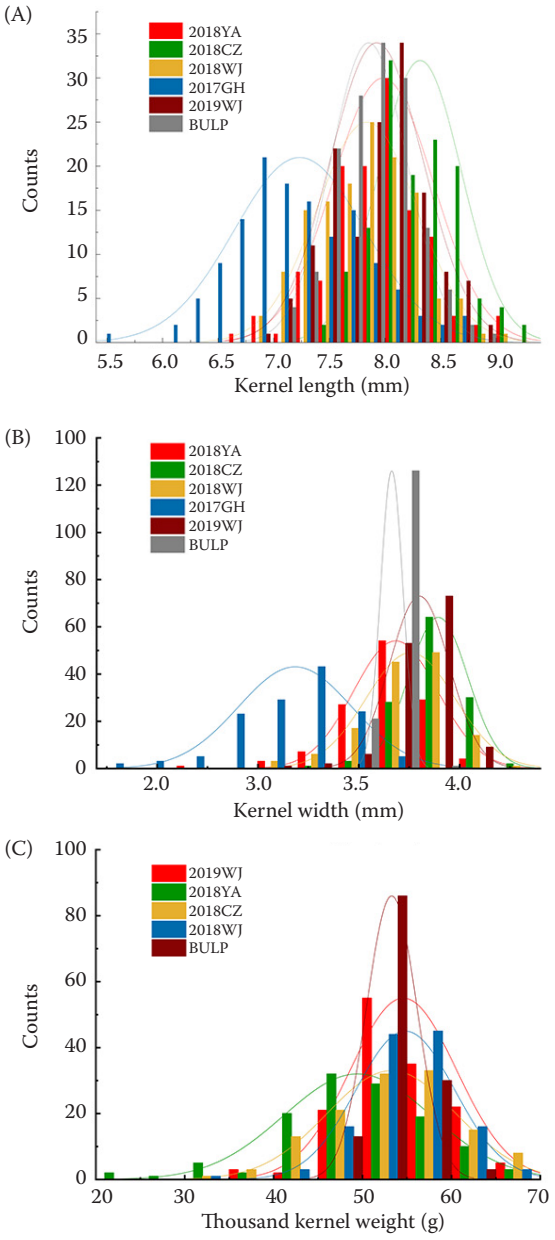

Figure 2. Frequency distribution of the kernel length (A), width (B) and thousand kernel weight (C) at different environments in the 8CN population
BLUP – the best linear unbiased predictor

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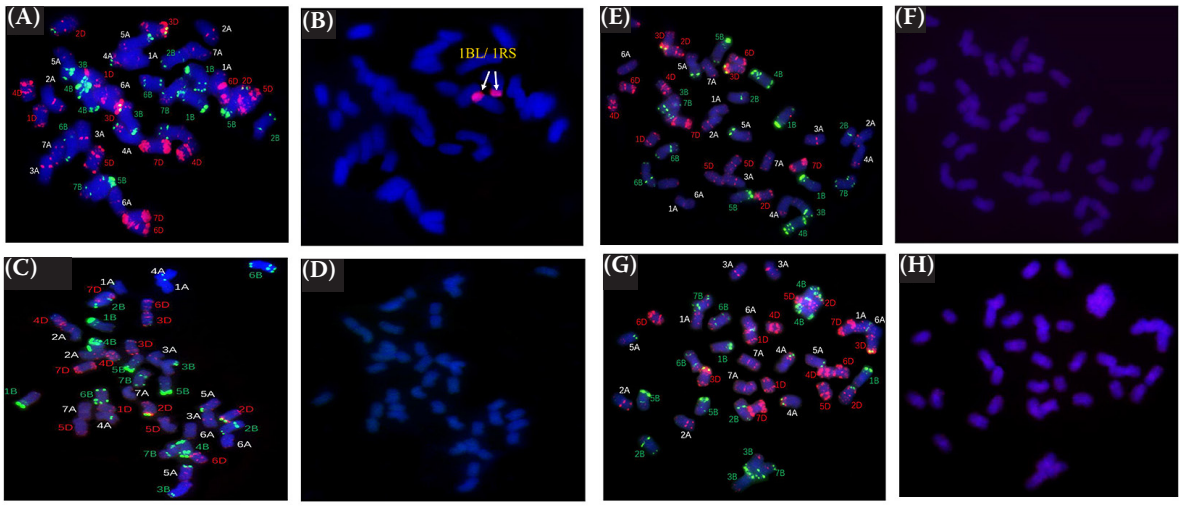

Figure 3. Fluorescence *in situ* hybridization (FISH) and Genomic *in situ* hybridization (GISH) based identification of four wheat accessions; images of (A), (C), (E), (G) showed FISH results and (B), (D), (F), (H) showed corresponding GISH patterns; the signals of pSc119.2 and pTa535 are marked in green and red, respectively; (A),(C), (E), (G) – FISH patterns of 88-1643, CNM16, CM104 and M37; (B), (D), (F), (H) – GISH patterns of 88-1643, CNM16, CM104 and M37 Arrows indicate wheat-rye 1BL/1RS translocation chromosomes

Table 3. Correlation for kernel traits in three populations

Population	Kernel traits	KL	KW	TKW
8CN	KL	1		
	KW	0.270**	1	
	TKW	0.599**	0.404**	1
8M	KL	1		
	KW	–0.218	1	
	TKW	0.151	0.359**	1
8CM	KL	1		
	KW	0.399**	1	
	TKW	0.546**	0.763**	1

**correlation significant at the 0.01 level; KL – kernel length; KW – kernel width; TKW – thousand-kernel weight

were detected in 88-1643 only. No PCR amplifying products was obtained in the three non-1RS wheat lines, including CNM16, M37, and CM104. The SSR analysis indicated that amplifying products with the 1BS-specific markers were detected in CNM16, M37, and CM104, and no products was obtained in 88-1643 (Figure 4). These results further verified that the 1BS arm of wheat had been substituted by the 1RS arm of rye in 88-1643.

The 1RS- and 1BS-specific markers were further used to identify lines carrying 1RS and 1BS chromosome arms in 8CN, 8M, and 8CM populations. Finally, 82 and 57 of the 146 lines in 8CN population were 1BS and 1RS lines, respectively. The remaining 7 lines could not be determined given the presence

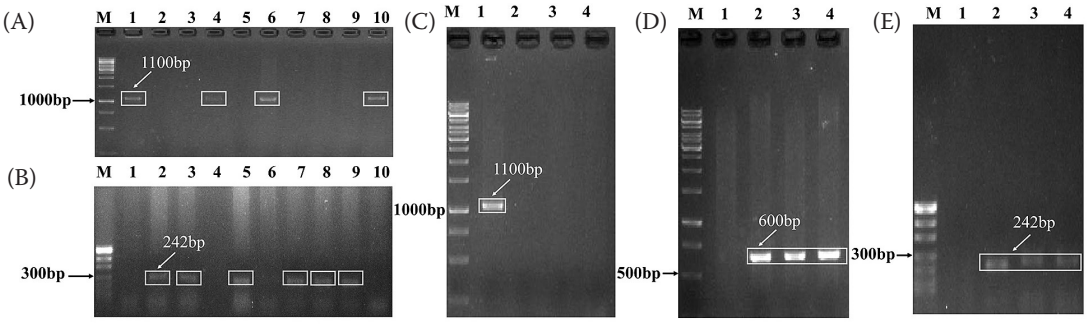

Figure 4. Amplification patterns of 1RS-specific markers *ω-sec-p1/ ω-sec-p2* (A, C) and 1BS-specific marker *Xgwm11* (B, E) and *O11B3/O11B5* (D)

For (A–B) lanes are: M – marker, 1 – 8CN-96, 2 – 8CN-97, 3 – 8CN-98, 4 – 8CN-99, 5 – 8CN-100, 6 – 8CN-101, 7 – 8CN-102, 8 – 8CN-103, 9 – 8CN-104, 10 – 8CN-105; for (C–E) lanes are: M – marker, 1 – 88-1643, 2 – CNM16, 3 – M37, 4 CM104

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Table 4. The differences for kernel traits between translocated and non-translocated lines in different populations and different environments

	KL		KW		TKW	
	1RS	1BS	1RS	1BS	1RS	1BS
2019-8CN-WJ	8.20**	7.72	3.78	3.83*	57.54**	52.61
2018-8CN-YA	8.20**	7.83	3.67	3.70	51.83	48.77
2018-8CN-CZ	8.52**	8.15	3.89	3.90	55.35**	50.97
2018-8CN-WJ	8.07**	7.64	3.74	3.77	55.53	55.05
2017-8CN-GH	7.49**	7.01	3.15	3.21	nd	nd
8CN-BLUP	8.06**	7.69	3.66	3.67	54.24**	52.46
2019-8M	8.10*	7.84	3.65	3.71	59.27	58.69
2018-8M	8.01**	7.76	3.85	3.94	59.12	58.58
2019-8CM	7.83*	7.63	3.53	3.57	47.82	46.56
2018-8CM	7.90*	7.72	3.90	3.94	60.27	56.69

*, **correlation significant at the 0.05, 0.01 level; nd –data not determined; KL – kernel length; KW – kernel width; TKW – thousand-kernel weight; WJ – represents the environment Wenjiang; CZ – represents the environment Chongzhou; YA – represents the environment Yaan; GH – represents the environment greenhouse

of unstable amplified bands and they were thus not included for further analysis. For the randomly selected 60 lines in 8M and 8CM populations. 34 and 29 lines, respectively, carried 1RS and 26, and 31 lines, respectively, carried 1BS. These lines were used for validating the effects of the 1BL/1RS translocation on kernel traits.

Differences between 1BS and 1RS lines for kernel-related traits. Significant analysis showed that the values of KL in 1RS lines were significantly

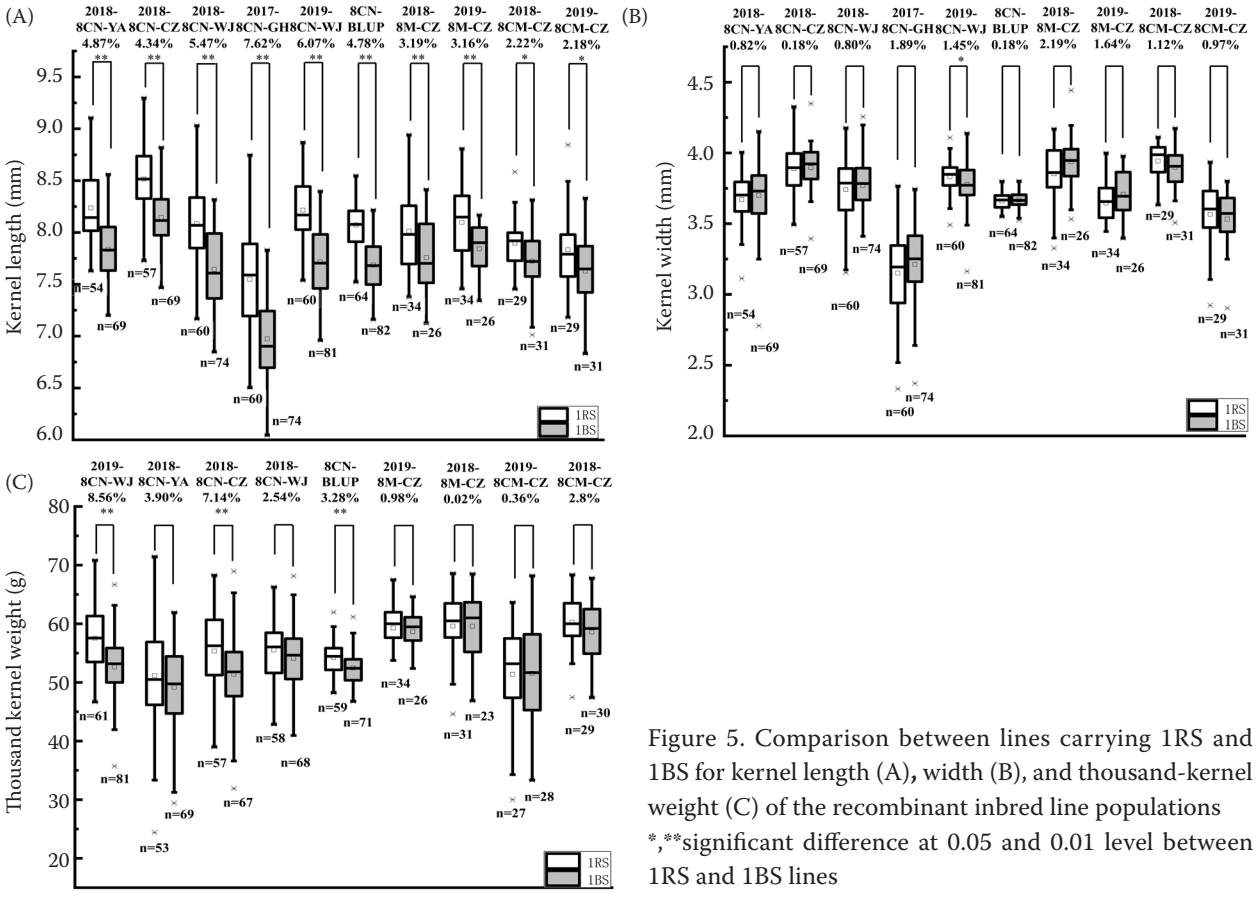

Figure 5. Comparison between lines carrying 1RS and 1BS for kernel length (A), width (B), and thousand-kernel weight (C) of the recombinant inbred line populations
*,**significant difference at 0.05 and 0.01 level between 1RS and 1BS lines

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higher than those in 1BS lines in the population of 8CN for all the five environments and BLUP dataset. The values of TKW in 1RS lines were significantly higher than those in 1BS lines for two environments and BLUP dataset. The value of KW in 1RS lines were significantly higher than those in 1BS lines in one environment only (Table 4, Figure 5).

In addition, two validation populations 8M and 8CM were further evaluated for the effects of 1BL/1RS translocation on KL, KW, and TKW. The results showed that the value of KL in 1RS lines was significantly higher than 1BS lines in all the environments for both 8M and 8CM populations. No significant differences were detected for KW and TKW (Table 4, Figure 5).

DISCUSSION

In this study, significant positive correlations between KL and both KW and TKW were detected in the 8CN and 8CM but not 8M populations. This suggests that KL may contribute to an increase in TKW. KW was positively correlated with TKW in three populations supported by previous studies (Ramya et al. 2010; Yu et al. 2014; Cui et al. 2016), further showing its potential in increasing TKW. These different correlations among kernel traits could be understandable given that there may be different loci controlling them.

The KL was significantly higher in 1RS lines than that in 1BS lines in all the three RIL populations at various environments, indicating that a major and stably expressed allele or gene responsible for increasing KL is most likely located on 1RS from 88-1643. Our present result was also supported by the study from Xiao et al. (2011) who reported that a 1BL/1RS translocation can increase KL and KW. Except for this study, to our knowledge, few of previous studies have analyzed effects of 1BL/1RS translocation on KL and KW. Thus, the 1BL/1RS translocation reported here could be of interest for further uncovering molecular mechanism of the gene controlling KL.

In this study, the TKW of the lines carrying 1RS were significantly higher than those carrying 1BS in two environments and BLUP dataset for 8CN population. But no significant differences were detected for 8M and 8CM populations. These results again suggest that the 1BL/1RS translocation has different roles in different backgrounds (Saghai-Maroof et al. 1984; Singh et al. 1990; Xiao et al. 2011; Zhao et al. 2012; Zhang et al. 2015; Kaur et al. 2017; Ren et al. 2018; Howell et al. 2019; Nie et al. 2019)

Given the stable and significant effect of 1RS on KL, we conclude that the increase of TKW in the 8CN population was mostly contributed by the increase in KL. The likely existence of other loci controlling TKW in the parent of 8M and 8CM, i.e. M37 and CM104, respectively, may interfere with the detection of the real contribution from 1RS. Thus no significant differences were detected between lines carrying 1RS and 1BS in the 8M and 8CM populations.

In conclusion, the present study combined with previous studies demonstrated that different wheat genetic backgrounds could cause diverse effects of 1BL/1RS translocations on agronomic traits (Peake et al. 2011; Zhao et al. 2012). The 1BL/1RS translocation from 88-1643 has significant positive effects on KL, thus contributing to an increase of TKW in given genotypes. In our ongoing breeding project, 88-1643 is being widely crossed with various target wheat parents to hopefully improve wheat yield.

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