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ORIGINAL PAPER

Wheat *Ms2* confers complete male sterility without penalizing other traits

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Abstract
Male sterility is a useful trait in traditional and hybrid wheat breeding. A dwarf male-sterile wheat line that harbors two tightly linked dominant traits, one, the dwarf gene *Rht-D1c* (originally called *Rht10*), and the other, the male-sterility gene *Ms2* (the two genes linkage group is collectively called *RMs2*), has been widely used in wheat breeding programs in China. The dominant *Ms2* (or *RMs2*) locus confers complete male sterility in wheat. In this study, we compared the plant height and spike traits in the *Ms2* (or *RMs2*)-isogenic BC_2F_1 lines that were derived from four soft white winter (SWW) wheat of the US Pacific Northwest (PNW), and the SWW line 'Brundage' that harbored an *Ms2* transgene. The dominant *Ms2* gene had no essential effects on agronomic traits, including plant height, spikelet length and spikelet numbers per spike, in the BC_2F_1 plants of SWW wheats and the T_2 transgenic 'Brundage'. In an open pollination environment in field, the *Ms2*-positive BC_2F_1 plants had a 79% natural seed-setting rate, but the *RMs2*-positive BC_2F_1 plants had only a 60% natural seed-setting rate, suggesting that the *Ms2* system is more practical for cross-pollination than the *RMs2* one. This difference is probably due to the extreme plant height-reducing effect (45% reduction on average) and the late anthesis effect (3–5 days in general) of the *Rht-D1c* locus. Collectively, these investigations showed that the dominant *Ms2* gene has no detrimental effects on plant and spike growth in five PNW wheat varieties/lines, therefore can become a valuable gene tool for traditional and hybrid breeding in wheat.

Keywords Plant height · *Rht-D1c* and *Ms2* linkage (=*RMs2*) · Seed-setting rate · Spike trait · *Triticum aestivum*

Introduction

Wheat male sterility has been widely used in traditional and hybrid breeding. Male sterility is common in angiosperms (Kaul et al. 1988), it refers to a condition in which flower anthers display partial or complete abortion without any diminution of pistil development. Two types of male sterility, sporophytic and gametophytic, have been documented (Yamagata et al. 2007). Sporophytic male sterility is caused by developmental defects in sporophytic tissues (Wilson et al. 2001), while gametophytic male sterility is caused by developmental defects in pollen grains (Durbarry et al. 2005). In wheat, eight genic male sterility (GMS) loci have been reported (McIntosh et al. 2013) and the genes associated with three of them have been cloned, i.e., *ms1* (Tucker et al. 2017; Wang et al. 2017), *Ms2* (Ni et al. 2017; Xia et al. 2017), and *ms5* (Pallotta et al. 2019).

Ms2 is a dominant gene conferring a 'non-pollen type' and complete male sterility (Deng and Gao 1982; Ni et al. 2017). F_1 seeds obtained from crossing will segregate in a 1:1 ratio between male-sterile and male-fertile progeny (Deng and Gao 1982) guaranteeing that *Ms2* plants will always be heterozygous. In 1980s, Liu et al. developed a dwarf male-sterile wheat by linking the dominant dwarf gene *Rht-D1c* (*Rht10*) and *Ms2* (collectively called *RMs2*) (Liu and Yang 1991). Both *Ms2* and *RMs2* have been widely used in wheat breeding programs in China (Yang et al. 2009). Until 2009, more than 30 wheat cultivars and 66 lines have been released by the *Ms2* and *RMs2* breeding systems in China (Zhai et al. 2009). In 2017, Ni et al. cloned the *Ms2* gene using map-based cloning and this work was soon

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confirmed by an independent study (Xia et al. 2017). *Ms2* is a gain-of-function allele due to a retrotransposon insertion in the promoter of the recessive *ms2* gene (Ni et al. 2017). *Ms2* represents a novel protein that interacts with eukaryotic initiation/elongation factors, GTP-binding proteins, and seven ribosomal proteins in yeast-two-hybrid assays (Ni et al. 2017). These interactions with the cellular translation machinery may be the cause of *Ms2* male sterility.

In China, the *Ms2*-derived male-sterile and fertile plants were comparable in appearance and in anthesis (Deng and Gao 1980, 1982). Other than its exclusive use in China, there is no report of the *Ms2* gene effect in non-Chinese wheat germplasm. To extend the utilization of *Ms2* gene, its effect on agronomic traits of PNW wheat varieties/lines was investigated in this study.

Materials and methods

Plant materials and growth conditions

Two male-sterile wheat lines, 'Xiaoyan 6 + *Ms2*' ('XY6$_{Ms2}$') and 'LM15$_{RMs2}$' (Ni et al. 2017), were used as donors for the *Ms2* gene introgressions. Four PNW wheat varieties/lines, including '01-10704A', '08-00802B', 'LCS Artdeco', and 'Puma', were used as recurrent parents to generate respective BC_2F_1 hybrids. Winter wheat 'Brundage' was used as explant for the genetic transformation of *Ms2*. The BC_2F_1 plants were grown on the Parker Farm (Moscow, Idaho, USA) in the 2019–2020 growing season. For each genetic background, the recurrent parent, *Ms2* hybrids and *RMs2* hybrids were each planted in neighboring rows that were 25 cm apart and 1.5 m long. Materials were planted in October 2019 and data were collected in July 2020. The transgenic plants and wild-type (WT) 'Brundage' were grown in greenhouse of the University of Idaho (UI) under a 16-h photoperiod with a day temperature of 22–25 ℃ and a night temperature of 15–20 ℃.

Genetic transformation with the *Ms2* gene

The wheat *Ms2* gene was excised from the plasmid PC976 (Ni et al. 2017) and ligated into a high copy plasmid, PC414C, using the restriction enzymes *Asc*I and *Not*I. The resulting plasmid, PC414C-*Ms2*, was amplified in *E. coli*, and the *Ms2* fragment was gel purified after cutting with *Asc*I and *Not*I. The *Ms2* fragment and the *BAR* (bialaphos resistance) gene on PC174 (Zhang et al. 2019) were co-transformed into the 'Brundage' using biolistic bombardment (Lv et al. 2014). The treated immature embryos were selected in media supplemented with 3 mg·L^{-1} bialaphos (Gold Biotechnology, St Louis, MO, USA). Putative transgenic plants were tested for their resistance to 340 ppm glufosinate-ammonium (Finale Herbicide; Bayer, Leverkusen, Germany).

Genotyping of transgenic plants

Plant DNA was extracted from leaf tissue (Yuan et al. 2012), quantified on an ND-1000 spectrophotometer (ThermoFisher Scientific, Waltham, MA, USA), and diluted to 100 ng ul^{-1}. PCR markers, *HT5* and *X26* (Ni et al. 2017), were used to genotype the *Ms2* gene in transgenic plants. PCR primers were 5'-GGCTCTGATACCAAATGTTGTTG-3' plus 5'-CGTAGATGCGGACCCAGGGGAT-3' for *HT5*, and 5'-CAAATTCCATCTCACCGATCTCTT-3' plus 5'- ATG GTGGTGTGCCCCTAAAAAG-3' for *X26*. PCR conditions were 95 ℃ for 5 min, 38 cycles of 95 ℃ for 30 s, 65 ℃ for *HT5* (or 60 ℃ for *X26*) for 30 s, and 72℃ for 60 s for *HT5* (or 30 s for *X26*), and a final extension at 72 ℃ for 7 min. PCR products were separated on a 1% agarose gel and visualized by ethidium bromide staining.

Collection and analysis of agronomic traits

For the BC_2F_1 and transgenic T_2 plants, we recorded plant height, spike length, spikelets per spike and fertility status at the late-anthesis stage. For spikelets, we only counted the well-developed ones, and excluded the basal and terminal spikelets that were poorly developed. The seed-setting rates per spike measured the fertility of the first two primary florets in the well-developed spikelets in an open pollination environment. Only the primary tiller, normally the tallest and strongest shoot of each plant, was used for measuring plant height and seed-setting rates. We used SAS 9.4 (SAS Institute Inc., Cary, NC, USA) to process the collected data, which involved the use of GLM and UNIVARIATE procedures. Analysis of Variance (ANOVA) was performed for significance test.

Results

Conventionally transferred *Ms2*/*RMs2*

In the BC_2F_1 generation, plants segregated into the male-sterile and male-fertile groups, as the *Ms2* (or *RMs2*) and *ms2* genetic groups. Plant height was compared among different groups. Under all four genetic backgrounds, the *Ms2* (*Ms2ms2*) and *ms2* (*ms2ms2*) genetic groups were not significantly different from the WT *ms2* group (*ms2ms2*, recurrent parent) ($P > 0.05$) (Table 1)—apart from *Ms2* of 'Puma' (4.2 cm difference). Except for the 8.1 cm difference of '08-00802B' ($P < 0.05$), the *Ms2* and *ms2* genetic groups in BC_2F_1 were comparable to each other ($P > 0.05$) (Table 1). Therefore, *Ms2* had no essential effect on plant

Table 1 Plant height and the spike traits in BC_2F_1

Recurrent parent	Genetic group & plant number	Plant height (cm)	Spike length (cm)	Spikelets per spike	Seed-setting rate (%)
01-10704A	WT (*ms2*) ($n=10$)	88.8 ± 4.3^a	10.2 ± 0.6^a	19.4 ± 0.5^a	97.2 ± 1.8^a
	Ms2 ($n=10$)	88.2 ± 6.0^a	8.8 ± 0.5^b	16.4 ± 1.8^b	82.2 ± 10.7^b
	ms2 ($n=10$)	88.8 ± 6.7^a	9.4 ± 0.7^{ab}	17.8 ± 1.5^{ab}	95.8 ± 3.7^a
	RMs2 ($n=6$)	44.3 ± 3.8^b	8.8 ± 0.8^b	16.8 ± 1.5^b	66.0 ± 12.2^c
08-00802B	WT (*ms2*) ($n=11$)	76.8 ± 4.7^{ab}	11.1 ± 0.5^a	18.6 ± 1.0^a	97.6 ± 2.7^a
	Ms2 ($n=9$)	74.7 ± 8.7^b	9.7 ± 1.2^b	17.2 ± 2.0^a	77.2 ± 9.7^b
	ms2 ($n=10$)	82.8 ± 5.6^a	10.5 ± 0.6^{ab}	18.5 ± 1.7^a	92.4 ± 7.8^a
	RMs2 ($n=5$)	44.2 ± 7.1^c	10.4 ± 1.0^{ab}	18.8 ± 1.6^a	39.7 ± 13.3^c
LCS artdeco	WT (*ms2*) ($n=10$)	79.5 ± 4.0^{ab}	9.9 ± 0.5^a	18.5 ± 1.0^a	96.8 ± 1.7^a
	Ms2 ($n=7$)	77.1 ± 4.1^a	9.6 ± 1.1^a	19.3 ± 1.4^a	70.7 ± 11.8^b
	ms2 ($n=4$)	74.6 ± 1.8^a	8.9 ± 0.8^a	18.0 ± 1.4^a	94.3 ± 6.4^a
	RMs2 ($n=5$)	46.1 ± 7.0^b	9.2 ± 0.6^a	18.2 ± 2.1^a	59.9 ± 13.3^c
Puma	WT (*ms2*) ($n=10$)	91.4 ± 4.5^a	10.6 ± 0.7^a	18.0 ± 1.2^a	97.0 ± 3.6^a
	Ms2 ($n=10$)	87.2 ± 4.6^b	9.7 ± 0.7^b	19.1 ± 1.4^a	84.5 ± 7.6^b
	ms2 ($n=5$)	88.6 ± 6.1^{ab}	10.2 ± 0.7^{ab}	18.8 ± 1.5^a	98.6 ± 3.2^a
	RMs2 ($n=5$)	44.0 ± 4.1^{ab}	9.3 ± 0.6^b	17.6 ± 0.9^a	74.1 ± 13.2^c

Mean ± SD (stand error) are recorded for the four traits. Means followed by the same letter (a, b, or c) are not significantly different at $p < 0.05$ in Tukey-Kramer analysis. The sample size is indicated by '$n=$' positioned in the brackets

height in the tested wheat. In contrast, due to the *Rht-D1c* gene, the *RMs2* groups in BC_2F_1 were always dwarf, extremely shorter than any other genetic groups ($P < 0.01$) (Table 1). This is well characterized by the fact that while the average plant height of all four *Ms2* genetic backgrounds was 82.4 cm that of the *RMs2* was only 44.6 cm. So, the *Rht-D1c* gene itself caused a 45.9% reduction in plant height averagely.

Other agronomic traits including spike length, spikelets per spike and seed-setting rate were further analyzed. For spike length, the *Ms2* and *ms2* as well as *RMs2* genetic groups were not significantly different in each of the four wheat genetic backgrounds ($P > 0.05$) (Table 1). However, the spike length of the *Ms2* and/or *RMs2* groups in BC_2F_1 was somewhat more reduced than those in the WT *ms2* groups of '01-10704A', '08-00802B', and 'Puma' lines ($P < 0.05$)—these differences ranged from 0.9 to 1.4 cm. It may require a few more backcrosses to compensate this spike length difference.

Spikelets per spike are an important yield component. In the BC_2F_1 plants, the *Ms2* and *ms2* genetic groups were not significantly different in each of the four wheat genetic backgrounds ($P > 0.05$); and the *RMs2* linkage did not impact the spikelet numbers compared to the *ms2* group ($P > 0.05$) (Table 1). In comparison to the WT *ms2* group of the recurrent parent, the spikelet numbers per spike of the *Ms2* and *RMs2* groups in BC_2F_1 were only reduced in '01-10704A' ($P < 0.05$)—15.5 and 13.4% differences, respectively. From this, it is concluded that the *Ms2* gene does not essentially affect spikelet numbers per spike in common wheat.

To utilize *Ms2* GMS system in a large-scale hybrid seed production, it is important to know how it affects the seed-setting rate in an open pollination environment. In this study, the seed-setting rate was only based on the first two florets of the well-developed spikelets in a spike. All spike heads of the BC_2F_1 and the recurrent parents were left open for possible cross-pollination in the field. In BC_2F_1, the *Ms2* gene caused male-sterility, but when the *Ms2*-containing plants were allowed to cross pollinate, they displayed an average seed-setting rate of 79.4% in the *Ms2* group and 60.2% in the *RMs2* group as compared to the average (95.0%) of the *ms2* group (Table 1). Apparently, *Ms2*-based male-sterile plants are able to produce seeds in an open-cross environment on a relatively high percentage. However, the seed-setting rates of the *Ms2* and *RMs2* groups were significantly reduced when compared to the *ms2* group in BC_2F_1 and in the recurrent parents ($P < 0.05$) (Table 1). Due to the *Rht-D1c* gene a further significant reduction was also observed (19.2% difference between the averages of the *Ms2* and *RMs2* groups).

Genetically transformed *Ms2*

To validate the effect of *Ms2*, we transformed the dominant *Ms2* gene into the PNW winter wheat 'Brundage'. In total, 2190 immature embryos of 'Brundage' were treated, and 32 embryos survived in the selection media supplemented with bialaphos. From 11 immature embryos, we obtained 11 putative T_0 plants, of which four plants, PT1 to PT4 each from an independent embryo, exhibited the classic male sterility of the *Ms2* genotype and were positive for the dominant *Ms2*

gene (Fig. 1). Three transgenic T_0 plants, PT2–PT4, were also resistant to the Finale herbicide (Fig. 1).

Pollen grains of the WT 'Brundage' were used to pollinate the male-sterile transgenic lines (PT2–PT4). As expected, nearly half male-fertile and half male-sterile plants were obtained in both T_1 and T_2 generations, and the male-sterility trait was inherited from T_0 to T_2 generations. The transgenic plants and the WT 'Brundage' were genotyped using the *Ms2*-specific markers: *X26* and *HT5* (Fig. 1). This clearly distinguished the dominant *Ms2* group in the male-sterile T_2 segregants from the recessive *ms2* group. At the T_2 generation, we compared the two genetic groups of each transgenic line. For plant height, spike length, and spikelets per spike, although there were slight differences between the *Ms2* and *ms2* groups in each line, these differences were insignificant ($P > 0.05$) (Table 2).

To compare with the WT 'Brundage' (the WT *ms2* group), we pooled the *Ms2* group data and the *ms2* group data of PT2, PT3, and PT4. All data sets for plant height, spike length, and spikelets per spike data met the *ANOVA* assumptions ($P > 0.05$). Again, no significant differences were present for plant height, spike length, and spikelets per spike among the three genetic groups: WT *ms2*, T_2 *Ms2*, and T_2 *ms2* ($P > 0.05$) (Fig. 2a–c). When developing heads in greenhouse-grown plants were bagged, the T_2 *Ms2* group had zero seed set (Fig. 2d). In contrast, the WT *ms2* group had a 96% seed set, and the T_2 *ms2* group had an 81% seed set (Fig. 2d, Supplemental Fig. 1), very similar to that of *Ms2* group in BC_2F_1. Taken together, the dominant *Ms2* gene conferred complete male sterility in transgenic wheat, while having insignificant effects on traits of height, spike length, and spikelet numbers per spike.

Discussion

The male sterility gene *Ms2* is a valuable tool in wheat breeding. Although the *Ms2* gene has been extensively studied in China, how well this gene might function in non-Chinese wheat germplasm remained unknown. In this study, the *Ms2* gene and/or *RMs2* linkage were backcrossed into four PNW SWW wheat lines and transferred into an

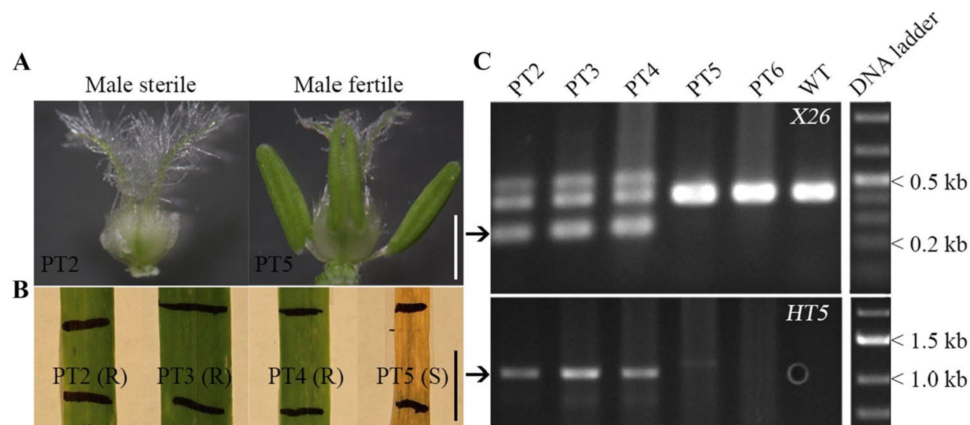

Fig. 1 Characteristics of the T_0 transgenic 'Brundage'. **a** Florets from putative transgenic T_0 plants displayed male-sterile (left) and male-fertile (right) phenotypes. Scale bar = 1 mm. **b** Putative transgenic T_0 plants were resistant (R) or susceptible (S) to Finale herbicide as it shown in leaf segments. Scale bar = 1 cm. **c** PCR test of three putative transgenic T_0 plants. PT2, PT3, and PT4 were positive for the dominant *Ms2* gene. Black arrows mark specific band of a dominant *Ms2* gene. WT represents the wild-type 'Brundage'

Table 2 Plant height and spike traits of the T_2 transgenic 'Brundage'

Lines	Genetic group & plant number	Plant height (cm)	Spike length (cm)	Spikelets per spike
PT2	*Ms2* ($n = 13$)	69.3 ± 13.1	10.0 ± 1.5	21.1 ± 4.3
	ms2 ($n = 27$)	64.4 ± 10.0	10.4 ± 1.7	20.9 ± 4.6
PT3	*Ms2* ($n = 14$)	73.8 ± 11.4	10.6 ± 2.0	19.5 ± 4.6
	ms2 ($n = 22$)	71.2 ± 13.7	9.9 ± 1.6	18.1 ± 3.6
PT4	*Ms2* ($n = 19$)	69.0 ± 14.8	9.8 ± 2.0	19.8 ± 2.9
	ms2 ($n = 14$)	72.8 ± 12.5	10.0 ± 1.2	20.9 ± 4.0

Mean ± SD (stand error) are recorded for the three traits. The sample size is indicated by '$n =$' positioned in the brackets. In each line the *Ms2* and *ms2* groups are insignificantly different ($P > 0.05$) in ANOVA analysis

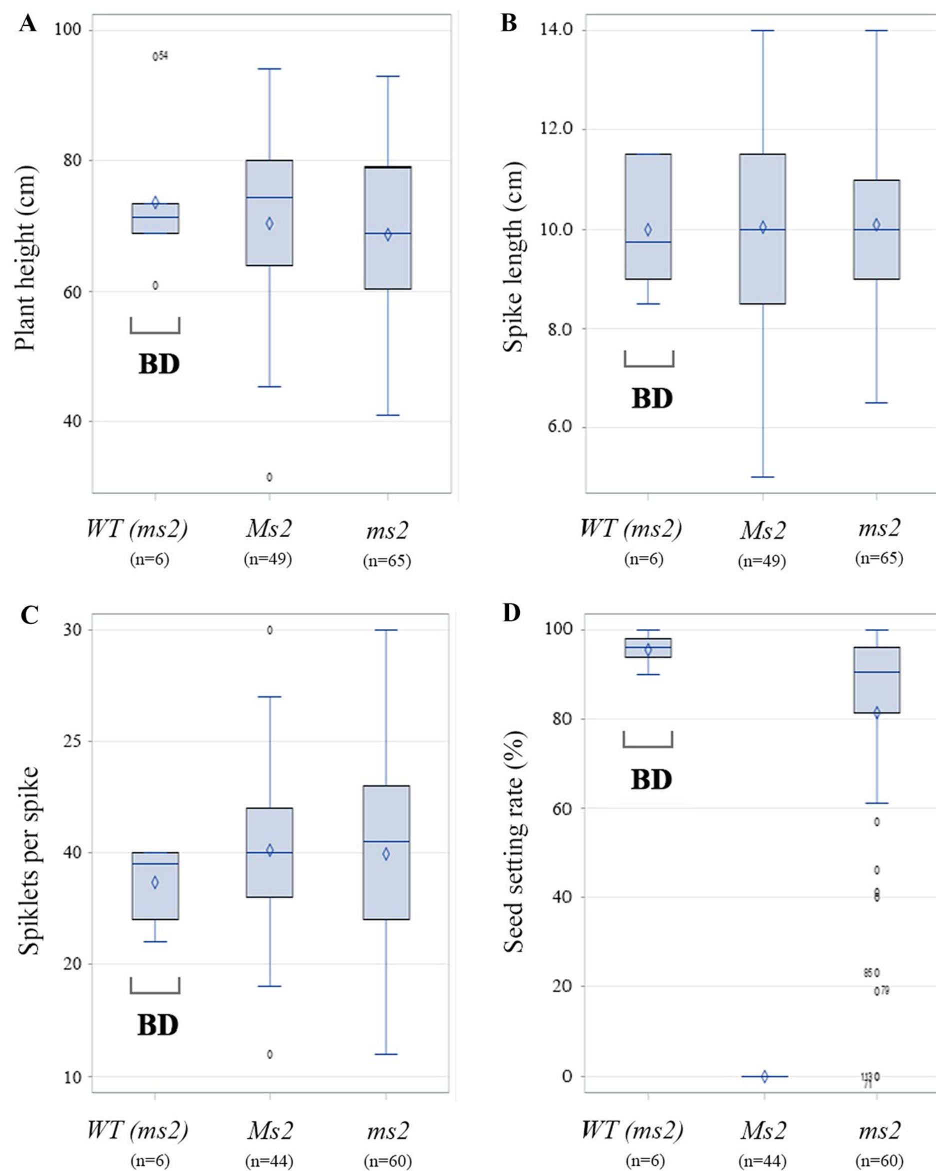

Fig. 2 Plant height and spike development in the T_2 transgenic 'Brundage'. Boxplots of the plant height (**a**), spike length (**b**), spikelets per spike (**c**), and the seed-setting rate (**d**). Transgenic plants segregated in the T_2 generation into the dominant *Ms2* group and the recessive *ms2* group. 'Brundage' (or BD) was included as the non-transgenic WT control, which contains only the recessive *ms2* gene. For each genetic group, the box plot depicts the range of values shown by the vertical lines, the interquartile range (25–75 percentile) shown by the shaded box, the group means shown by the diamond symbol, and the group medians shown by the horizontal lines within each box. Outliers were plotted separately as cycles on the chart

additional one by biolistic bombardment. BC_2F_1 generation and T_2 transgenic plants were investigated to illustrate the effect of *Ms2* on agronomic traits.

Plant height, spike length and spikelet numbers per spike are important traits that directly or indirectly contribute to yield potential. The yield components of wheat can be multifaceted (Slafer et al. 2014); however, grain number per spike is always an important parameter. In winter wheat, elite varieties showed on average 38% more yield compared to genetic resources, and this yield increase is mainly contributed by a 19% increase in grains per spike, but with limited gain (4%) in thousand grain weight (Philipp et al. 2018). Wheat yield largely depends on the final numbers of well-developed spikelets and grains per spike which are established prior to flowering (Würschum et al. 2018). In this study, both BC_2F_1 plants and transgenic plants together proved that the *Ms2* locus has no essential effect on plant height and spike-related traits, which provides a powerful breeding tool without masking the yield potentials in wheat breeding. Due to seed or space limitations, we did not include replication for each genotype; however, multiple backcross and transgenic lines unanimously agreed with each other, which served as a broad-sense replication within and between treatment groups.

The linkage of the dominant dwarfing gene *Rht-D1c* and the GMS gene *Ms2* (*RMs2*) (Liu and Yang 1991) is very useful for large-scale hybrid seed production, as this dwarfing gene helps the identification of tall male-fertile plants from dwarf male-sterile ones. However, our observations showed that the *Rht-D1c* gene had an adverse effect on natural seed-setting rate of the male-sterile spikes in an open pollination environment, as the

Ms2-positive BC_2F_1 plants had a 79% natural seed-setting rate, but the *RMs2*-positive ones had only a 60%. This difference probably due to the delayed anthesis (3–5 days) in *RMs2* lines. It has been reported that *Rht-D1c*genes have effects on wheat heading and flowering time under different backgrounds (Sun et al 2011). It might also come from the extreme dwarfing nature of the *Rht-D1c*; the dwarf plants may have less chance to capture pollen grains due to little air flow around the ground. Besides, the adverse effect of this dwarfing gene was also observed in non-male sterile background, as it significantly reduced grain yield (Alghabari et al. 2015) and root dry mass (Wojciechowski et al. 2009) as compared to various near-isogenic lines of winter wheat carrying various *Rht* alleles. Although the dwarf male-sterile wheat *RMs2* system has been widely used in wheat breeding programs in China, however, due to the above adverse effects of *Rht-D1c* dwarfing gene the *Ms2* system might be more practical for cross-pollination than the *RMs2* one.

In addition to its use as a recurrent selection tool in conventional breeding, the *Ms2* gene can also be designed for hybrid wheat breeding and hybrid seed production (Ni et al. 2017). To date, third-generation hybrid seed systems have been developed by integrating the use of male fertility/sterility genes and fluorescence marker genes in cereal crops (Chang et al. 2016; Zhang et al. 2018; Qi et al. 2020). A similar wheat hybrid system could also be developed by integrating the dominant *Ms2* gene and the natural blue aleurone gene (Li et al. 2017). There were breeders trying to create "Blue-AiBai" lines to stack *RMs2* and the blue aleurone gene via chromosome engineering. In 2004, Pu et al. reported a blue *RMs2* (collectively called *BRMs2*) carrying the blue aleurone gene and *RMs2* linkage on an additional chromosome. This monosomic wheat could be utilized in hybrid wheat breeding and hybrid seed production, but it has a main disadvantage that the inheritance of monosomic chromosome carrying the *BRMs2* is only around 22% (Pu et al. 2004). More efficient or high-throughput system could be developed by using cisgenics or transgenics methods to create *BRMs2* or the blue aleurone gene and *Ms2* linkage (*BMs2*). We think that last version, i.e., without the use of *Rht-D1c* gene, would be more economical solution for large-scale hybrid production due to the higher seed-setting rate on the male-sterile mother line.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s42976-021-00184-8.

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Authors' contributions DF conceived the project; FN, AC, and JW contributed ideas and resources, HZ, QH, FN, and BL performed the experiments; HZ, QH, and DF analyzed the data; HZ, DF, and AC wrote the paper; and all authors discussed the results and the paper.

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Availability of data and material All wheat lines tested in this study are used to demonstrate the research results, but they are not available for distribution.

Declarations

Conflict of interest The authors declare there is no competing interest.

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