Development and Utilization of Introgression Lines Using Synthetic Octaploid Wheat (Aegilops tauschii × Hexaploid Wheat) as Donor

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As the diploid progenitor of common wheat, Aegilops tauschii Cosson (DD, 2n = 2x = 14) is considered to be a promising genetic resource for the improvement of common wheat. In this work, we demonstrated that the efficiency of transferring A. tauschii segments to common wheat was clearly improved through the use of synthetic octaploid wheat (AABBDDDD, 2n = 8x = 56) as a “bridge.” The synthetic octaploid was obtained by chromosome doubling of hybrid F1 (A. tauschii T015 × common wheat Zhoumai 18). A set of introgression lines (BC1F8) containing 6016 A. tauschii segments was developed and displayed significant phenotype variance among lines. Twelve agronomic traits, including growth duration, panicle traits, grain traits, and plant height (PH), were evaluated. And transgressive segregation was identified in partial lines. Additionally, better agronomic traits could be observed in some lines, compared to the recurrent parent Zhoumai 18. To verify that the significant variance of those agronomic traits was supposedly controlled by A. tauschii segments, 14 quantitative trait loci (QTLs) for three important agronomic traits (thousand kernel weight, spike length, and PH) were further located in the two environments (Huixian and Zhongmou), indicating the introgression of favorable alleles from A. tauschii into common wheat. This study provides an ameliorated strategy to improve common wheat utilizing a single A. tauschii genome.

Keywords: wheat, Aegilops tauschii, quantitative trait loci, agronomic traits, introgression lines

INTRODUCTION

Wheat (Triticum aestivum L.) is one of the most important cereal crops, accounting for 20% of the calories consumed by humans (Brenchley et al., 2012). Based on hybridization among varieties, many wheat varieties have now been bred through modern cultivation procedures and it should be noted that the process of wheat breeding has been greatly accelerated by the utilization of core collection in China. However, the genetic background of wheat varieties is becoming increasingly consistent, due to their derivation from only a few core collections (Tian et al., 2005; Hao et al., 2006; Xiao et al., 2012), which is currently leading to an increasingly severe risk of abiotic and biotic stress. It has long been realized that the exploration and utilization of desirable genes from wild relatives is an effective approach to improving the genetic background of common wheat.
A. tauschii for transferring some superior genes of \( L_2 \) and \( L_3 \) through advanced backcross population or introgression lines with some of the QTLs being located on the D genome identified and located numerous QTLs from synthetic hexaploid wheat. It is also believed that the genetic variation type of \( A. tauschii \) transfer genes into common wheat via recombination and becomes a potential donor for the improvement of common wheat.

In addition, many other wild relatives, including 6VS of *Dasypyrum villosum* (Chen et al., 2013), 2S of *Aegilops speltoides* (Klindworth et al., 2012), 7Ag of *Thinopyrum ponticum* (Niu et al., 2014), and 6P of *Agropyron cristatum* (Luan et al., 2010; Ye et al., 2015; Zhang et al., 2015), have also been further utilized for the improvement of common wheat.

*Aegilops tauschii* Cosson (DD, \( 2n = 2 \times = 14 \)) is an annual, self-pollinated plant with a high level of genetic variability for disease resistance, productivity traits, and abiotic stress resistance (Singh et al., 2012). It is naturally distributed in central Eurasia, spreading from northern Syria and Turkey to western China. In China, it is mainly distributed in the Yili area of Xinjiang and the middle reaches of the Yellow River (including Shanxi and Henan provinces; Wei et al., 2008). Concerning its genetic background, *A. tauschii* can be subdivided into two phylogenetic lineages, designated as L1 and L2, which are broadly affiliated with *A. tauschii* ssp. *tauschii* and *A. tauschii* ssp. *strangulata*, respectively (Dvorak et al., 1998; Mizuno et al., 2010; Wang et al., 2013). Most of the exploited *A. tauschii* is generally derived from Transcaucasia and northern Iran, since it is believed that the *A. tauschii* in these regions (mainly from the L2 lineage) is involved in the origin of wheat D genome (Wang et al., 2013). By contrast, little is known about the genetic and phenotypic characteristics of *A. tauschii* (mainly L1 lineage) from the eastern and southern populations (i.e., those from Syria, Afghanistan, Pakistan, Central Asia, and China) (Matsuoka et al., 2009). Owing to the long genetic distance between L1 and L2, it is therefore believed that the genetic variation type of *A. tauschii* (L1 lineage) is more abundant than that of the wheat D genome (Lubbers et al., 1991; Dvorak et al., 1998, 2012; Wang et al., 2013). Therefore, like many wild crop progenitors, *A. tauschii* is considered to be a promising gene donor for the improvement of common wheat (Kilian et al., 2011).

As the diploid progenitor of common wheat, it is convenient to transfer *A. tauschii* genes into common wheat via recombination between homologous chromosomes. In addition, it is also possible that undesirable gene linkages can be easily broken by repeated backcrossing with common wheat (Gill and Raupp, 1987). To date, synthetic hexaploid wheat (tetraploid wheat × *A. tauschii*) has mainly been exploited as a “bridge” for transferring some superior genes of *A. tauschii* into common wheat (Miranda et al., 2007). Many previous researchers have identified and located numerous QTLs from synthetic hexaploid wheat with some of the QTLs being located on the D genome through advanced backcross population or introgression lines (ILs; Pestsova et al., 2006; Kunert et al., 2007; Naz et al., 2008; Yu et al., 2014). In addition, the desirable traits of *A. tauschii* may also be transferred to common wheat through direct crossing. Gill and Raupp (1987) proposed the first systematic direct gene transfer protocol. Wheat genomes A, B, and D could be improved concurrently through the hybridization of synthetic hexaploid wheat with common wheat. In comparison, unique advantages have been found in the hybridization of *A. tauschii* with common wheat, because this provides a strategy to transfer desired D genome regions (carrying target alleles) without disrupting adaptive allelic combinations (located in the A and B genomes). However, this method has drawn little attention (Fritz et al., 1995; Cox et al., 2006; Olson et al., 2013) due to the high sterility in the hybrid \( F_1 \) generation, caused by distant hybridization and extremely low ripening rates resulting from the backcross of the hybrid \( F_1 \) with the recurrent parent.

Fortunately, the above-mentioned challenge could be overcome through the use of the synthetic octaploid wheat (AABBDDDDD, \( 2n = 8 \times = 56 \)), obtained by chromosome doubling of hybrid \( F_1 \) (*A. tauschii* × hexaploid wheat), although this has seldom been reported in the literature. In addition, *A. tauschii* from the same region has been generally regarded as more suitable for hybridization with common wheat, compared to strains from other areas, due to its broad ecological adaptation to the native area (Matsuoka et al., 2009). In this work, a series of ILs (BC1F3) was developed through the media of synthetic octaploid wheat, obtained by direct crossing of common wheat and *A. tauschii* from the same region in China. Various agronomic traits of these ILs were extensively investigated and analyzed. In addition, 14 major QTLs for three important agronomic traits, which were derived from *A. tauschii*, were successfully identified in the two environments.

**MATERIALS AND METHODS**

**Plant Materials**

The diploid *A. tauschii* ssp. *tauschii* accession T015 (\( 2n = 14 \), DD) was originally derived from Henan province. Zhoumai 18 (\( 2n = 42 \), AABBDD), a type of control variety of cultivar registered in Henan province, was applied as the recurrent parent in this study.

**Production of \( F_1 \) Hybrids Between Common Wheat and *A. tauschii***

Based on the traditional breeding method, *A. tauschii* accession T015 and Zhoumai 18 were directly crossed and the hybrid \( F_1 \) seeds were taken away 16 days after pollination. The method of embryo removal was reported by Sirkka and Immonen (1993). Seeds were surface sterilized for 8 min with 0.1% HgCl\(_2\) and rinsed three times in 20 mL ddH\(_2\)O. All handling of seeds and embryos was undertaken under sterile conditions in a laminar flow hood. Embryos were removed from the seeds and transferred to the endosperm of barley; the barley embryos were removed and the scutellums of the hybrid embryos were put in their place. An embryo culture media was used containing...
a mixture of 4.1 g/L Murashige and Skoog salts (Murashige and Skoog, 1962) with 3% sucrose and no hormone at pH 5.8. The hybrid embryos were incubated in darkness at 25°C for 2 weeks and developed etiolated seedlings with roots, and then the hybrid seedlings were cultivated at 21°C in a 16 h photoperiod (50 μmol/m²·s¹, fluorescent light) over the summer.

**Chromosome Doubling Treatment and Population Construction**

The method of chromosome doubling was reported by Taira et al. (1991). The hybrid F₁ seedlings were transferred to the greenhouse in September and were grown for 8 weeks at 21 ± 4°C with 10 h of supplemental light. The F₁ plantlets with well-formed tillers were uprooted from the soil and divided into two parts. One part was replanted as a control without treatment, and the other part was washed in running water. The roots of each plant were then cut back to a 4–5 cm length, and immersed in beakers containing a 0.5% (w/v) colchicine solution of pH 7.0, supplemented with a 1.5% (v/v) solution of dimethyl sulfoxide (DMSO). Treatments were conducted for a 16 h period at room temperature. After the treatment, the roots were thoroughly washed in running water for 24 h. All the plants were transplanted into a greenhouse until flowering and seed formation.

The following year, emasculated florets of Zhoumai 18 were pollinated by synthetic octaploid wheat to produce 10 BC₁F₁ seeds. Afterward, the entire BC₁F₁ seeds were cultivated and self-fertilized to acquire BC₁F₂ generation. About 400 seeds of BC₁F₂ were randomly selected, followed by further successive self-fertilization for six times to generate a BC₁F₈ population (Figure 1), in which 379 plants were randomly selected for genotyping and phenotyping in the present study. This population and Zhoumai 18 were cultivated in the 2015–2016 crop season, on the wheat breeding farms of the Huixian and Zhongmou, respectively. Seeds were sown at a distance of 10 cm between plants, and a 30 cm gap between rows, and were grown under consistent field conditions. The recurrent parent Zhoumai 18 was planted as a control.

**Chromosome Karyotype and FISH of Synthetic Octaploid Wheat**

The seeds of synthetic octaploid wheat were germinated at 25°C for 2–3 days. About 2 cm long root tips were treated for karyotyping chromosome preparation. Chromosome preparation and FISH were performed according to the method described by Andres and Kuraparthy (2013). The synthetic oligonucleotides pAs-1 and pSc119.2-1 were marked by 6-carboxytetramethylrhodamine (Tamra) and Alexa Fluor-488-dUTP, respectively (Tang et al., 2014). For sample examination, a drop of pre-mixed DAPI solution (Sangon Biotech, Shanghai, China) was deposited on each slide, and chromosomes were observed by an Olympus BX63 fluorescence microscope (Olympus Corporation, Tokyo, Japan).

**Investigation of Agronomic Traits**

Twelve agronomic traits, including days to heading (DH), days to flowering (DF), plant height (PH), spike length (SL), spikelets (SPI), spikelet density (SPI), grain number main spike (GNS), thousand kernel weight (TKW), grain length (GL), grain width (GW), grain perimeter (GP), and grain length/grain width (GL/GW), were scored by the method described in Li and Li (2006). PH was recorded just before harvest. DH and DF were noted in the field. After harvest, GNS, SL, and SPI were determined from three main spikes per line, while TGW, GL, GW, and GP were determined from three to five plants.

**Map Construction and QTL Analysis**

DNA was extracted from the fresh leaves of ILs and Zhoumai 18 in 2014 using the method described by Olson et al. (2013). The genetic map was constructed based on the physical positions of simple sequence repeat (SSR) markers from wheat D genome¹. PCR reactions for SSR were performed using the method described by Röder et al. (1998). SSR markers were anchored and grouped into the seven A. tauschii chromosomes through sequence alignment between the primers and reference genome (ALB78 accession; Zhao et al., 2017). The calculation of segment lengths and genome ratios followed the method described by Liu et al. (2006). The QTLs for agronomic traits were identified using QTL IciMapping Ver 4.0 (Meng et al., 2015). RSTEP-LRT-ADD mapping (stepwise regression-based likelihood ratio test for additive QTL) was adopted and a significant threshold of likelihood of odds (LOD) was estimated by running 1000 permutations with a type I error of 0.05.

**Statistical Analysis**

All statistical analyses were performed on IBM® statistics 19 (SPSS Inc.), including frequency distribution, correlation coefficient (Pearson correlation), and analysis of variance (ANOVA). ANOVA-general linear model (GLM) was performed to determine the significance of differences between the genotypes of the lines and environments. Genotype-by-environment (G × E) interactions were also analyzed using ANOVA-GLM.

¹http://wheat.pw.usda.gov/cgi-bin/GG3/
RESULTS

Development of Introgression Lines Through Synthetic Octaploid Wheat

The ripening rates of reciprocal crosses exhibited significant differences utilizing A. tauschii T015 and Zhoumai 18 as parents (Table 1). Altogether 73 caryopses were obtained by pollinating 118 emasculated florets of A. tauschii T015, with a ripening rate of 61.9%. In contrast, no caryopses were obtained by pollinating 212 emasculated florets of Zhoumai 18. Caryopses collected 16 days after pollination were dissected, and not all of them were found to contain normal embryos (well-developed primordium and scutellum), and about 37.0% contained embryos. Moreover, the embryos were always found floating in a watery endosperm. The normal embryos on the endosperm of barley could germinate and grow into seedlings (Figure 2A). Some of the normally developed seedlings were backcrossed with Zhoumai 18 as the female parent, without obtaining any seed. The other seedlings were treated via colchicine to generate amphidiploid seeds (Figure 2B). Though these seeds were not full, they could grow normally, exhibiting a chromosome number of 56 in their root tip cells (Figure 2C). Except for the prominent characteristics of A. tauschii in glume color and hardness, the developed synthetic octaploid wheat showed an analogous phenotype with its male parent (Figure 2D). In total, 10 BC1F1 seeds were obtained through pollinating 16 emasculated florets of Zhoumai 18 with synthetic octaploid wheat as the male parent. Afterward, these BC1F1 plants successively self-fertilized for eight generations to generate 379 ILs (BC1F8), in which their phenotypic traits were stabilized after several generations, with no phenotype segregation found in each line, implying the cytogenetical stability of these lines. Furthermore, the chromosome karyotypes of the root tip cell were observed in four selected lines with good agricultural traits, and the number of chromosome in each line was determined to be 42 (Supplementary Figure S1).

Numbers and Positions of Introgessed A. tauschii Segments

To identify the distribution of chromosome segments from A. tauschii in the wheat D genome, 379 BC1F8 lines were successfully genotyped using SSR markers. Altogether 261 SSR markers were selected to construct a genetic map from the GrainGene 2.0 database. Polymorphism was detected in 130 SSR markers between A. tauschii T015 and Zhoumai 18, and 62 of these were established to be polymorphic in ILs, accounting for 47.7%. The numbers of polymorphic markers on each chromosome were found rather even, with an average value of 8.9 per chromosome. Excluding three unidentified markers, a physical map was constructed based on the 127 polymorphic SSR markers between parents, which displayed heterogeneous distribution on seven linkage groups of D genome, with a total length of 3954.48 Mb (Figure 3). The physical map illustrates that these polymorphic markers in different chromosomes, or different chromosome regions, exhibit uneven distribution. For example, some markers are concentrated in the same region with a minimum gap of only 0.11 Mb. However, huge distances were also found for some other markers. For instance, the distance between Xgwm157 and Xgwm30.1 on chromosome 2D was determined to be 307.9 Mb.

Since each line may contain more than one chromosome segment, altogether 6016 segments from A. tauschii were determined in ILs. Specifically, these ILs contained 5120 homozygous and 896 heterozygous segment (Supplementary Table S4), with an average of 13.51 homozygous and 2.37 heterozygous segments in each line. The number of segments ranged from 1 to 25 in each line, and only a single introgressed segment was observed in one line. Using the physical positions of the SSR markers, the size of each introgressed segment, the number of unique segment, and the ratios accounting for the whole donor genome were estimated (Table 2). The sizes of the introgressed segments ranged from 1.3 to 238.9 Mb, with an average size of 33.45 Mb in homozygous and 31.46 Mb in heterozygous segments. In addition, the distribution of chromosome segments from A. tauschii exhibited clear differences in the wheat D genome, and A. tauschii segments in each line were counted and graphed in Supplementary Table S1 and Supplementary Figure S2. Typically, the introgression fragments from 1D of A. tauschii showed the least 651 fragments, only accounting for 10.8%, and those from 4D of A. tauschii possessed the most 1086 fragments, accounting for 18.5%. These results clearly reveal that the chromosome segments of A. tauschii have been transferred into common wheat by the “bridge” of synthetic octaploid wheat, which effectively broadens the genetic basis of common wheat.

TABLE 1 | Crossing/backcrossing outcomes for A. tauschii/SOW x T. aestivum.

| Cross patterns | T015 x Zhoumai18 | Zhoumai18 x T015 | Backcross of hybrid F1 with Zhoumai18 (♂) | Backcross of SOW with Zhoumai18 (♀) |
|----------------|------------------|------------------|------------------------------------------|----------------------------------|
| No. of florets pollinated | 118 | 212 | 224 | 16 |
| No. of caryopses formed | 73 | 0 | – | – |
| No. of embryos formed | 27 | 0 | – | – |
| No. of crossed seeds formed | – | – | 0 | 10 |

SOW, synthetic octaploid wheat.
Phenotypic Variation of Introgression Lines

Some typical traits of *A. tauschii* could be observed in partial lines of ILs. For instance, the glume of some lines exhibited enhanced hardness and deepened color. Consequently, owing to the hardened glume, the spike threshing became difficult in the former trait. Meanwhile, a negative correlation was found between SL and SPI. Genetic correlations were calculated among lines for the agronomic traits in the population (*Supplementary Tables S2, S3*). In Huixian, the two traits of DH and DF showed significant positive correlation with each other (*r* = 0.860, *p* < 0.01), and were also positively correlated with SL and SPI. Meanwhile, a negative correlation was found between these two traits and PH, TKW, GNS, and SD. Among the panicle traits, SL and SPI displayed a positive correlation (*r* = 0.158, *p* < 0.01), and SD was observed to be negatively correlated with the former trait (*r* = −0.843, *p* < 0.01). As for the grain traits, TKW demonstrated a positive correlation with GL, GW, GP, and GL/GW. Concerning the trait of PH, it was found to be negatively correlated with GNS, SPI, and SD, but positively correlated with SL, TKW, GL, GW, GP, and GL/GW. Observations from the Zhongmou environment showed analogous correlations to those in Huixian, with the exception of a positive correlation between growth duration and GNS (*r* = 0.114, *p* < 0.01), and the negative correlation between TKW and GL/GW.

QTL Analysis of Partial Agronomic Traits in Introgression Lines

To elucidate the significant changes in the 12 traits mentioned above, supposedly controlled by *A. tauschii* segments, QTLs for three important agronomic traits (TKW, SL, and PH) of them were further identified (*Table 5*). The TKW is an important factor affecting yield. Three major QTLs for TKW, designated *QTKW.At-2D*, *QTKW.At-4D*, and *QTKW.At-6D*, were detected on the chromosomes 2D, 4D, and 6D, based on ICIM analysis, respectively (*Figure 5*), and the *QTKW.At-2D* could be detected in both the Huixian and Zhongmou areas. As clearly shown in *Table 5*, the positive alleles of additive effect were derived from *A. tauschii*, further revealing the huge value of genes from *A. tauschii* as a wild wheat resource (Singh et al., 2012). The *QTKW.At-2D* displayed the similar phenotypic variance values (PVEs) of 9.24 and 9.19% in Huixian and Zhongmou, corresponding to the additive effect of the values 1.22 and 1.35 g.
FIGURE 3 | Physical map constructed based on the 127 polymorphic SSR markers between parents. Polymorphic markers in the advanced backcross population are highlighted in red. The unit of distance is megabasepairs (Mb).

TABLE 2 | The size of introgressed segments detected in the ILs and cumulative proportion in the donor genome.

| Chr. | Polymorphic markers | Unique segments | No. of segments | Average length (Mb) | No. of segments | Average length (Mb) | Maximum chromosome coverage (%) |
|------|---------------------|-----------------|-----------------|--------------------|-----------------|--------------------|-------------------------------|
| 1D   | 7                   | 9               | 981             | 17.53              | 105             | 12.48              | 20.44                         |
| 2D   | 12                  | 20              | 560             | 19.87              | 502             | 12.14              | 47.55                         |
| 3D   | 7                   | 11              | 665             | 42.16              | 49              | 27.89              | 30.38                         |
| 4D   | 11                  | 21              | 914             | 58.64              | 65              | 71.92              | 55.52                         |
| 5D   | 8                   | 8               | 733             | 20.11              | 64              | 28.62              | 27.91                         |
| 6D   | 9                   | 16              | 619             | 59.86              | 32              | 50.26              | 48.05                         |
| 7D   | 8                   | 9               | 648             | 15.98              | 79              | 16.93              | 23.75                         |
| Total| 62                  | 94              | 5120            | 33.45              | 896             | 31.46              | 36.23                         |

Spike length is one of the significant spike traits for the improvement of common wheat. Altogether six major QTLs for SL, designated QSL.At-2D.1, QSL.At-2D.2, QSL.At-3D, QSL.At-4D, QSL.At-5D, and QSL.At-7D were detected in Huixian and Zhongmou (Figure 5), and QSL.At-2D.1, QSL.At-2D.2, QSL.At-4D, and QSL.At-7D were detected in both locations. QSL.At-3D was only detected in Zhongmou, whereas QSL.At-4D was observed in Huixian. Among these major QTLs, the PVEs of QSL.At-2D.1 on chromosome 2D were the highest, and could explain 12.88 and 8.04% of the phenotypic variance in Huixian and Zhongmou corresponding to the additive effect of the values 0.35 and 0.30 cm.

The PH is also an important agronomic trait, and four major QTLs for PH, designated as QPH.At-2D, QPH.At-3D, QPH.At-4D, and QPH.At-5D hereafter (Figure 5), were observed in both Huixian and Zhongmou. The other QTL of QPH.At-1D was only detected in Huixian. Among them, the QPH.At-4D on chromosome 4D provided the highest explanation for the phenotypic variances in Huixian and Zhongmou, 27.55 and 17.22%, respectively. Moreover, the PVEs of QPH.At-2D and QPH.At-5D were also relatively high in both places, and could explain 13.95 and 8.92% of the mean phenotypic variance, corresponding to the mean additive effect of the values of 4.33 and 4.12 cm, respectively.
TABLE 3 | Twelve agronomic traits measured from the recurrent parents and the introgression lines in Huixian and Zhongmou.

| Traits | Location | Parent | Introggression lines |
|--------|----------|--------|----------------------|
|        |          | Zhoumai 18 | Mean | SD | Min–Max | C.V(%) | Skewness | Kurtosis |
| DH     | ZM       | 195.00 | 197.37 | 2.50 | 191.00–206.33 | 1.26 | 0.12 | 0.04 |
|        | HX       | 187.56 | 188.20 | 1.78 | 180.00–194.00 | 0.95 | −0.15 | 1.32 |
| DF     | ZM       | 197.88 | 200.89 | 2.27 | 195.75–208.50 | 1.13 | 0.22 | −0.12 |
|        | HX       | 193.94 | 193.94 | 1.82 | 189.00–199.00 | 0.94 | 0.22 | −0.15 |
| SL     | ZM       | 9.27   | 9.98  | 1.06 | 6.95–13.58   | 10.60 | 0.15 | 0.44 |
|        | HX       | 8.77   | 9.77  | 0.97 | 7.10–12.87   | 9.91  | 0.26 | 0.35 |
| SPI    | ZM       | 23.25  | 21.95 | 1.25 | 18.50–26.00  | 5.70  | 0.17 | 0.51 |
|        | HX       | 21.02  | 21.56 | 1.20 | 18.00–25.33  | 5.55  | 0.07 | 0.37 |
| GNS    | ZM       | 59.33  | 54.40 | 7.29 | 34.75–78.00  | 13.40 | 0.19 | −0.003 |
|        | HX       | 55.33  | 53.10 | 6.39 | 32.30–73.50  | 12.03 | 0.09 | 0.13 |
| SD     | ZM       | 24.73  | 22.24 | 2.65 | 15.84–32.37  | 11.93 | 0.54 | 0.71 |
|        | HX       | 26.14  | 22.26 | 2.38 | 16.26–33.02  | 10.71 | 0.54 | 0.93 |
| PH     | ZM       | 76.55  | 75.24 | 11.89 | 46.65–113.45 | 15.81 | 0.40 | 0.19 |
|        | HX       | 78.86  | 77.19 | 11.76 | 53.60–118.63 | 15.24 | 0.72 | 0.65 |
| TKW    | ZM       | 49.54  | 47.99 | 4.42 | 33.81–60.96  | 9.22  | −0.13 | 0.005 |
|        | HX       | 48.63  | 48.27 | 4.01 | 37.48–59.02  | 8.31  | 0.08 | −0.16 |
| GL     | ZM       | 5.96   | 6.58  | 0.38 | 5.51–7.55    | 5.82  | −0.10 | −0.21 |
|        | HX       | 5.98   | 6.44  | 0.40 | 5.46–7.41    | 6.27  | −0.14 | −0.48 |
| GW     | ZM       | 3.18   | 3.37  | 0.20 | 2.89–3.96    | 5.96  | −0.004 | −0.28 |
|        | HX       | 3.27   | 3.28  | 0.20 | 2.80–3.78    | 5.97  | −0.05 | −0.75 |
| GP     | ZM       | 15.25  | 16.85 | 0.97 | 14.30–19.53  | 5.74  | −0.16 | −0.32 |
|        | HX       | 15.46  | 16.44 | 1.03 | 13.98–18.73  | 6.29  | −0.18 | −0.71 |
| GL/GW  | ZM       | 1.89   | 1.97  | 0.09 | 1.71–2.25    | 4.62  | 0.11 | 0.09 |
|        | HX       | 1.84   | 1.98  | 0.09 | 1.70–2.28    | 4.71  | 0.19 | 0.49 |

DH, day to heading; DF, day to flowering; PH, plant height; SL, spike length; SPI, spikelets; SD, spikelet density; GNS, grain number main spike; TKW, thousand kernel weight; GL, grain length; GW, grain width; GP, grain perimeter; GL/GW, grain length/grain width; ZM, Zhongmou; HX, Huixian.

TABLE 4 | F values of ANOVA-GLM for genotype and environment as well as their interaction in the introgression lines.

| Traits | Genotype (G) | Environment (E) | G x E interaction |
|--------|--------------|-----------------|-------------------|
|        | df | F | df | F | df | F |
| DH     | 378 | 117.52** | 1 | 28967.90** | 378 | 21.36** |
| DF     | 378 | 82.00** | 1 | 28120.59** | 378 | 20.77** |
| PH     | 378 | 69.01** | 1 | 148.59** | 378 | 5.22** |
| SL     | 378 | 22.86** | 1 | 132.51** | 378 | 1.77** |
| SPI    | 378 | 6.53** | 1 | 72.11** | 378 | 1.44** |
| GNS    | 378 | 14.69** | 1 | 2.26NS | 378 | 1.02NS |
| SD     | 378 | 4.72** | 1 | 16.68** | 378 | 2.76** |
| GP     | 378 | 11.67** | 1 | 338.57** | 378 | 5.30** |
| GL/GW  | 378 | 15.45** | 1 | 537.04** | 378 | 6.05** |
| GL     | 378 | 11.08** | 1 | 188.98** | 378 | 4.87** |
| GW     | 378 | 14.54** | 1 | 20.97** | 378 | 7.15** |
| TKW    | 378 | 36.77** | 1 | 38.03** | 378 | 12.33** |

NS, not significant; **significant difference at P < 0.01.

FIGURE 4 | The various phenotype traits from the introgression lines. (A) Plant height of partial strains. Scale bars = 8 cm. (B) Spike length of partial strains. Scale bars = 2 cm. (C) Thousand kernel weight of partial strains. Scale bars = 5 mm. (D) Grain length of partial strains. Scale bars = 5 mm. (E) Grain width of partial strains. Scale bars = 5 mm.

DISCUSSION

Direct introgression from diploid species into hexaploid wheat has been explored as a possible applied plant-breeding technique for the rapid introgression of useful traits. Gill and Raupp (1987) reported that a total of 219 hybrid embryos were obtained by the hybridization of hexaploid wheat “Wichita” or “Newton” with 31 accessions of A. squarrosa (2n = 14) as male parent, but only 24 F1 hybrids were grown to maturity. Another work of direct crossing between T. aestivum and A. tauschii was reported by Sehgal et al. (2011). Their results showed that
These results suggest that the hybrid F1 from distant hybridization. Moreover, the untreated tillers produced an average of 0.47 backcross seeds per 100 florets, while the colchicine treated tillers could produce an average of 14.9 backcross seeds per 100 florets pollinated (with a range of 8.33–26.88 seeds). In this work, the backcross of synthetic octaploid wheat as male parent with the recurrent parent Zhoumai 18 resulted in a ripening rate of 62.5%. Therefore, only direct crosses with A. tauschii as the male parent were adopted for gene transfer (Cox et al., 2006), and using synthetic octaploid wheat as the male parent could obviously enhance backcross ripening rates with the recurrent parent. Specifically, the hybrid F1 was obtained by A. tauschii as the female parent and was then doubled to generate the synthetic octaploid wheat. In addition, compared with single gene transfer, the development of ILs can incorporate more than one useful gene and was then doubled to generate the synthetic octaploid wheat. In addition, compared with single gene transfer, the development of ILs can incorporate more than one useful gene.

### TABLE 5 | Analysis of putative QTLs for partial agronomic traits in ILs.

| Trait | QTL | Environment | Marker | Position (Mb) | LOD | PVE (%) | Add |
|-------|-----|-------------|--------|--------------|-----|---------|-----|
| TKW   | QTKW-At-2D | Huixian | Xcdf53 | 2D (26.2) | 7.05 | 9.24 | 1.22 |
|       |       | Zhongmou  |        |              | 7.02 | 9.19 | 1.35 |
|       |       | Combined  |        |              | 8.48 | 10.69 | 1.28 |
|       | QTKW-At-4D | Huixian | Xwmc48a | 4D (71.1) | 3.11 | 3.60 | 1.37 |
|       |       | Zhongmou  |        |              | 3.12 | 3.90 | −0.88 |
|       |       | Combined  |        |              | 3.12 | 3.90 | −0.88 |
|       | QTKW-At-6D | Zhongmou | Xcdf13a | 6D (16.6) | 17.89 | 12.61 | 4.25 |
| PH    | QPH-At-2D | Huixian | Xgwm296 | 2D (20.0) | 18.61 | 13.29 | 4.41 |
|       |       | Zhongmou  |        |              | 21.12 | 13.95 | 4.33 |
|       |       | Combined  |        |              | 21.12 | 13.95 | 4.33 |
|       | QPH-At-3D | Huixian | Xbarc323 | 3D (602.1) | 3.55 | 2.60 | −2.01 |
|       |       | Zhongmou  |        |              | 5.17 | 3.82 | −2.46 |
|       |       | Combined  |        |              | 5.35 | 3.63 | −2.29 |
|       | QPH-At-4D | Huixian | Xwmc48a | 4D (71.1) | 34.72 | 27.55 | 11.09 |
|       |       | Zhongmou  |        |              | 22.37 | 17.22 | 8.87 |
|       |       | Combined  |        |              | 32.40 | 23.86 | 9.99 |
|       | QPH-At-5D | Huixian | Xbarc144 | 5D (562.8) | 15.17 | 10.75 | 4.73 |
|       |       | Zhongmou  |        |              | 10.36 | 6.83 | 3.73 |
|       |       | Combined  |        |              | 14.10 | 8.92 | 4.12 |
| SL    | QSL-At-2D.1 | Huixian | Xcdf53 | 2D (26.2) | 14.19 | 12.88 | 0.35 |
|       |       | Zhongmou  |        |              | 10.48 | 8.04 | 0.30 |
|       |       | Combined  |        |              | 13.29 | 10.46 | 0.32 |
|       | QSL-At-2D.2 | Huixian | Xgwm296 | 2D (20.0) | 7.92 | 6.08 | 0.24 |
|       |       | Zhongmou  |        |              | 18.68 | 13.71 | 0.40 |
|       |       | Combined  |        |              | 14.25 | 9.81 | 0.31 |
|       | QSL-At-5D | Huixian | Xbarc144 | 5D (562.8) | 4.49 | 3.47 | 0.22 |
|       |       | Zhongmou  |        |              | 5.27 | 3.59 | 0.24 |
|       |       | Combined  |        |              | 5.63 | 3.80 | 0.23 |
|       | QSL-At-7D | Huixian | Xbarc126 | 7D (91.3) | 8.02 | 6.27 | 0.25 |
|       |       | Zhongmou  |        |              | 7.22 | 5.11 | 0.24 |
|       |       | Combined  |        |              | 7.61 | 5.11 | 0.22 |
|       | QSL-At-3D | Zhongmou | Xgwm161b | 3D (8.1) | 4.27 | 3.33 | −0.19 |
|       |       | Xgwp342   | 4D (451.6) | 3.67 | 3.71 | −0.29 |

LOD, likelihood of odds; PVE, phenotypic variance explained by each QTL; Add, additive effect. Positive values of Add indicate the effects increasing trait values by A. tauschii alleles.
It is well known that polyploids are more prone to receive portions of alien chromosomal introgression from related weedy species compared to diploids. Despite their overall inferior agronomic performance, wild and weedy species are likely to contain genetic factors that can increase the yield of modern varieties. In other words, quantitative traits of modern varieties may be improved using wild and weedy species (Frey et al., 1984). The 1RS arm in the translocation line 1BL/1RS wheat, for example, carries a battery of resistance traits and adaptation to abiotic stresses, as well as high-yield traits (Friebe et al., 1996; Sharma et al., 2011). In the process of improving common wheat by utilizing the desirable genes of *A. tauschii*, the yield, kernel weight, protein concentration, and kernel hardness were evaluated, based on 147 BC$_2$F$_1$-derived families from crossing between elite common wheat lines and *A. tauschii* (Fritz et al., 1995). The results indicated that introgression of *A. tauschii* germplasm into the wheat genome had fewer effects on agronomic performance, compared to the extreme phenotypic differences between the two species. Variability for yield and protein was actually lower among strains carrying larger estimated amounts of *A. tauschii* segments. Thus, *A. tauschii* has been deemed to have a relatively neutral impact on the agronomic and quality traits of wheat but to serve as a source of important resistance genes. To date, many resistance genes of *A. tauschii* have been transferred into common wheat through the use of synthetic hexaploid wheat as a “bridge” (Naz et al., 2008; Dunckel et al., 2015; Wang et al., 2016). Through a doubled haploid (DH) population derived from synthetic-derived bread wheat line SYN1 and FHB-susceptible line Ocoroni, Zhu et al. (2016) identified a major QTL of Fusarium head blight (FHB) resistance on chromosome 2D, accounting for 25% of the phenotypic variation explained. Liu et al. (2006) investigated nine agronomic traits of 97 ILs containing Am3 chromosome segments, in which the Am3 was synthesized by the crossing of *Triticum carthlicum* with *A. tauschii*. The phenotype traits from ILs showed obvious change, and some strains displayed better agronomic traits than the recurrent parent. In this work, the agronomic traits among lines also showed significant variation. Although most of the strains were similar to the recurrent parent Zhoumai 18, some of them demonstrated apparent transgressive segregation (Table 3). In addition, 14 quantitative trait loci (QTLs) among three important agronomic traits (TKW, SL, and PH) were further located in the Huixian and Zhongmou, confirming the introgression of favorable alleles from *A. tauschii* into common wheat.

Genetic correlations between traits are due to linkage and/or pleiotropy and indicate the magnitude and direction of correlated response to selection, as well as the relative efficiency of indirect selection (Holland, 2006). When traits are highly correlated, plant breeders can select for the trait with higher heritability and simultaneously indirectly select for the other trait. The genetic correlation of agronomic traits of 188 recombinant inbred lines (RILs) from the spring wheat “Louise” × “Penawawa” were analyzed by Carter (2011), who found that flowering date and PH, as well as maturity date and PH, were moderately correlated. PH was positively correlated to grain yield, with taller plants having higher grain yield potential. Kumar et al. (2007) reported that grain yield was significantly correlated to SL in two mapping populations. In this work, PH was found to be negatively correlated with GNS, SPI, and SD, but positively correlated with SL, TKW, GL, GW, GP, and GL/GW. Similarly, TKW and SL showed significant positive correlation.
Plenty of studies have attempted to map QTL for grain yield and yield components of wheat under non-stress conditions (Kato et al., 2006; Börner et al., 2002; Huang et al., 2004, 2006; Mccartney et al., 2005; Marza et al., 2006; Narasimhamoorthy et al., 2006; Kuchel et al., 2007; Kumar et al., 2007; Cuthbert et al., 2008; Heidari et al., 2011). However, it is still necessary to confirm the role of important markers associated with grain yield across different genetic backgrounds and environments. Huang et al. (2003) reported detecting a major QTgw.ipk-2D on chromosome 2DL with a boundary from Xgwm539 to Xgdm6 in a BC2F2 population derived from a cross between the common wheat and the synthetic wheat. This QTL could explain 15.4% of the phenotypic variation. Crossa et al. (2007) used two linear mixed models to assess marker-trait associations. They identified significant associations between grain yield and the DArT markers wPt-4413 on chromosome 2D. Using association mapping, Edae et al. (2014) detected one stable QTL for grain yield on chromosome 2DS, under both irrigated and rain-fed conditions. The QTL associated with the DArT marker wpt6531 is about 8 cm away from the wpt4144 marker, which was associated with yield in the study of Crossa et al. (2007). Using two different RILs populations, Kumar et al. (2007) identified one QTL for grain yield on chromosome 2D with a boundary from Xgwm261 to Xcdo1379. In addition, Narasimhamoorthy et al. (2006) detected a QTL for grain yield linked to Xgwm261. Interestingly, according to the linkage map of Crossa et al. (2007), the SSR markers (Xgwm261) were linked to the DArT marker wPt-4413, spanning 3.2 cM. Four QTLS for TKW (Huang et al., 2004, 2006; Cuthbert et al., 2008) were identified close (from 1.7 cM for Xgwm296 to 7.9 cM for Xwmc601) to the DArT marker wPt-4413 on chromosome 2D, according to the linkage map of Crossa et al. (2007). Azadi et al. (2015) identified that two QTLS (QTgw.abrii-2D1 and QTgw.abrii-2D3) were also close to the DArT marker wPt-4413. In the present study, one major QTL for TKW, designated QTKW.At-2D, was detected on the Xcfd53 of chromosome 2D in the Huixian and Zhongmou environments (Table 3). The QTL (QTKW.At-2D) was also close to the DArT marker wPt-4413 according to the linkage map of Crossa et al. (2007). Identification of this QTL for grain yield/TKW at the same position suggests a possible pleiotropic QTL and also indicates that this region may play an important role in improving grain yield. When averaged across two environments, this QTL could explain 10.69% of the phenotypic variation, corresponding to the additive effect values of 1.28. The Xcfd53 was associated with positive effects on TKW. Typically, the accession 150679, containing the above-mentioned marker, showed TKW values of 59.02 and 60.96 g in the two districts, providing high increments of 22.2% and 24.4% compared with Zhoumai 18, respectively. These results reveal that favorable alleles from A. tauschii can improve important agronomic traits of an elite wheat variety, even though A. tauschii itself is inferior to the cultivated variety in the phenotypic traits.

CONCLUSION

A set of ILs containing only A. tauschii segments was established by using synthetic octaploid wheat (AABBDDDD, 2n = 8x = 56) as a “bridge.” This bridge was obtained by the chromosome doubling of hybrid F1 (A. tauschii T015 × common wheat Zhoumai 18). The agronomic traits among lines also showed significant phenotype variation. For every trait, some lines displayed better performance than the recurrent parent. In addition, 14 QTLS for three important agronomic traits (TKW, PH, and SL) were further located in Huixian and Zhongmou regions, respectively.

AUTHOR CONTRIBUTIONS

SL and CS conceived and designed the study. DZ, YZ, XZ, LL, CZ, JL, and GS generated the data and performed the analysis. DZ and YZ contributed reagents, materials, and analysis tools. DZ, YZ, SL, and CS wrote and revised the paper. All authors read and approved the final manuscript.

FUNDING

This work was supported by the National Natural Science Foundation of China (Grant Nos. 31401379 and 31571649) and Project of Major Science and Technology in Henan Province (Grant No. 161100110400), and Project of Science and Technology Department of Henan Province (Grant No. 172102110004).

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fpls.2018.01113/full#supplementary-material

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Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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