



Research article

The transfer to and functional annotation of alien alleles in advanced wheat lines derived from synthetic hexaploid wheat

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ABSTRACT

The abundant genetic diversity in synthetic hexaploid wheat (SHW) can achieve breakthroughs in wheat genetic improvement, but little is known of the genetic mechanisms involved. In this study, three populations of advanced lines (totaling 284 individuals), derived from three top-crosses of SHW-L1 with different common wheat cultivars, followed by ten generations of artificial selection, were used to evaluate the transfer of alien alleles with 24872 Diversity Arrays Technology (DArT) markers. Only 1824, 1786 and 1514 DArT markers were needed to distinguish the alleles from SHW-L1 and the other common wheat parent in the populations SCPD, SS7M and SSYZ, respectively. The data clearly showed that all the advanced lines contained alien alleles from SHW-L1. The lowest percentage of alien alleles was 6.97% in an advanced line in population SSYZ, while the biggest was 30.41% in a SCPD advanced lines. The percentages of alien alleles at each locus ranged from 0% to 100% in all three populations. Forty-four alien alleles did not exist in all advanced lines, while two alien alleles were present in all advanced lines. Two of the 100% alien alleles were associated with thousand-grain weight and leaf rust resistance. Thirteen alien alleles were associated with grain yield, grain thickness and width, thousand-grain weight, grain weight/ear, plant height, grain weight, grain number, powdery mildew resistance, spikelet number per spike or yellow rust resistance. The research provided direct evidence of the existence of alien alleles in advanced lines and detected a number of valuable alleles related to wheat yield or disease resistance. More research is needed to analyze the functional mechanisms of these alleles, and to use these materials and alleles in wheat improvement.

1. Introduction

Wheat is the world's most widely grown crop, and, by 2050, wheat production needs to increase by a rate of 2% every year to meet the demands of the increasing world population, a target which is a huge challenge for wheat breeders (Hawkesford et al., 2013). Incorporation of genetic diversity from wild wheat relatives into elite common wheat (*Triticum aestivum* L., $2n = 6x = 42$, AABBDD) cultivars has long been recognized as an important means of improving wheat productivity and securing global wheat supply (Godfray et al., 2010).

Common wheat originated from the cross between *Triticum turgidum* L. ($2n = 4x = 28$, AABB) and *Aegilops tauschii* Coss. ($2n = 2x = 14$, DD). Since only a small number of *Triticum turgidum* and *Aegilops*

tauschii accessions were involved in the formation of common wheat, a large number of genetic variants in populations of the two progenitor species were excluded from common wheat populations (Salamini et al., 2002). Productivity traits such as abiotic and biotic stress resistance/tolerances, as well as novel grain quality traits, have been discovered in the progenitor species (Peng et al., 2011). By mimicking the origin of common wheat, artificial allohexaploid wheat lines (synthetic hexaploid wheat [SHW]) have been generated in the laboratory (Mujeebkazi et al., 1996; Ogbonnaya et al., 2013; Zhang et al., 2010), providing materials containing the genetic diversity of *T. turgidum* and *Ae. tauschii* which was lost during the origin, domestication, and improvement of modern common wheat populations. Gene transfers from the progenitor species into common wheat can be then made by

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homologous recombination, using synthetic wheat as a bridge (Gill et al., 1987). Usually, synthetic wheats have poor agronomic value, generally being tall, difficult to thresh, and with grains frequently being of poor quality (Trethowan and Mujeeb-Kazi, 2008). Some negative traits are controlled by several genetic loci, and are very hard to eliminate in simple crosses with artificial selection. To overcome these shortcomings, adapted cultivars or elite lines have been used in multi-top-crosses to ensure that the negative alleles were effectively eliminated in breeding programs (Liu et al., 2016). Numerous commercial cultivars have been released in a number of countries since the first documented release of the first commercial SHW “Chuanmai 42” in China, which was obtained by crossing a SHW from CIMMYT with locally adapted cultivars (Li et al., 2014). Some elite synthetic-derived lines have been shown to yield up to 8%–35% more grain than the best local controls (Dreccer et al., 2007; Ginkel and Ogonnaya, 2007; Ogonnaya et al., 2013; Yang et al., 2009). Although SHWs have been successfully used in commercial breeding, little is known of the genetic basis for their commercial success, such as which alien regions or alleles exist in the elite SHW-derived cultivars (lines) after the top-cross and artificial selection.

In addition to the applications of SHWs in wheat breeding programs, the high level of genetic polymorphism between SHWs and common wheat cultivars makes SHW lines useful for gene mapping investigations. A large number of genes/QTLs have been mapped using SHW-derived genetic populations (Börner et al., 2015). However, the mapping population used was usually generated by a simple cross, and contained the wild traits from SHWs, which masked the accurate identification of genes/QTLs and thus limits the utilization of SHWs in wheat molecular breeding. In order to avoid the impacts of wild traits, we derived 284 advanced F₁₀ lines in three breeding populations developed according to normal breeding and selection procedures. They were derived from top-crosses between synthetic hexaploid wheat SHW-L1 and three common wheat cultivars. These lines and their parents were genotyped with DArT markers to reveal the SHW-derived genetic variations and to identify important alien alleles for further gene identification and molecular breeding.

2. Materials and methods

2.1. Plant materials

A total of 284 F₁₀ advanced spring wheat lines and their parents were used in this study (Table 1). They all had a common parent, the synthetic hexaploid wheat SHW-L1, which was synthesized from a cross between *T. turgidum* line AS2255 and *Ae. tauschii* accession AS60 (Zhang et al., 2004). All these lines were developed from a top-cross of

SHW-L1 with three common wheat cultivars, followed by three backcrosses and subsequent self-pollination, with selection against undesirable agronomic traits and disease resistance at each generation. They were classified into three populations according to their pedigrees (Table 1). SHW-L1 has many poor agronomic traits, such as late heading and wild characters from the diploid grass parent *Ae. tauschii*, but beneficial traits include a long spike (Yu et al., 2014). Because it is difficult to overcome all of the poor agronomic traits from a single cross or backcross using a single common wheat parent, SHW-L1 was top-crossed to three different wheat parents. Moreover, single spike was artificially selected at each generation to obtain plants with desirable agronomic traits (including plant height, spike length, spikelets, grain number per spike, thousand-grain weight) in Xining (101°74'E, 36°56'N), Qinghai, China, according to the selection requirements for local commercial cultivars. The plant region existed some main abiotic and biotic stresses, including drought, cold, and rust. Any of the 284 SHW-L1-derived lines which were discarded had clearly negative agronomic traits and exhibited a higher or similar yield potential compared to local commercial cultivars.

2.2. DNA extraction and DArT genotyping

Leaf tissues from each advanced line of the three populations and from the parents were collected and stored at –80 °C. Genomic DNA was extracted using the CTAB method (Yan et al., 2002). A wheat DArT-sequence array consisting of 24,872 random sequences was used (<http://www.triticarte.com.au>). Procedures for the hybridization of the genomic DNA to the DArT-sequence array, image analysis and polymorphism scoring were as described as described by Akbari et al. (2006).

2.3. Evaluating the genetic variation in advanced lines

A total of 24,872 markers had reproducibility values > 95%. Taking into account information such as the chromosome location, the minor allele frequency (> 5%), and the percentage of missing data (< 10%), 10,469 markers remained for further analysis. The markers differentiating specific for SHW-L1 and the common wheat parents were selected as diagnostic markers in order to detect alien alleles in the advanced lines.

3. Results

3.1. The genotypes of the advanced lines and their parents

The remaining 10,469 DArT markers, covering the framework

Table 1
Plant materials used in the experiment.

| Code | Description | Lines | Traits | | | | |
|------------|---|-------|--------|----|-----|-----|-----|
| | | | PHT | SL | SPI | GNS | TKW |
| SCPD | SHW-L1/CN16//Pm99915-1/3/03-DH1959 | 112 | | | | | |
| SS7M | SHW-L1/SY95-71//700-011689/3/MY68942 | 125 | | | | | |
| SSYZ | SHW-L1/SY95-71//Yu98767/3/ZL-21 | 47 | | | | | |
| SHW-L1 | Synthetic hexaploid wheat (AS2255/AS60), 2n = 6x = 42, AABBDD | 1 | 125 | 13 | 20 | 60 | 40 |
| SY95-71 | <i>Triticum aestivum</i> L. 2n = 6x = 42, AABBDD | 1 | 90 | 10 | 19 | 56 | 42 |
| Yu98767 | <i>Triticum aestivum</i> L. 2n = 6x = 42, AABBDD | 1 | 85 | 12 | 20 | 58 | 46 |
| ZL-21 | <i>Triticum aestivum</i> L. 2n = 6x = 42, AABBDD | 1 | 82 | 10 | 18 | 52 | 40 |
| 700-011689 | <i>Triticum aestivum</i> L. 2n = 6x = 42, AABBDD | 1 | 85 | 11 | 19 | 58 | 38 |
| MY68942 | <i>Triticum aestivum</i> L. 2n = 6x = 42, AABBDD | 1 | 80 | 12 | 19 | 55 | 54 |
| CN16 | <i>Triticum aestivum</i> L. 2n = 6x = 42, AABBDD | 1 | 77 | 10 | 18 | 48 | 50 |
| Pm99915-1 | <i>Triticum aestivum</i> L. 2n = 6x = 42, AABBDD | 1 | 80 | 12 | 19 | 51 | 48 |
| 03-DH1959 | <i>Triticum aestivum</i> L. 2n = 6x = 42, AABBDD | 1 | 83 | 10 | 18 | 55 | 45 |
| Sum | | 293 | | | | | |

Note: SL: spike length; SPI: spikelets; GNS: grain number per spike; TKW: thousand-grain weight.

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