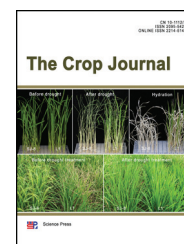


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# Current advances in genome sequencing of common wheat and its ancestral species

Xiaoli Shi<sup>a</sup>, Hong-Qing Ling<sup>a,b,\*</sup>

<sup>a</sup>State Key Laboratory of Plant Cell and Chromosome Engineering, Institute of Genetics and Developmental Biology, Chinese Academy of Sciences, Beijing 100101, China

<sup>b</sup>College of Life Sciences, University of Chinese Academy of Sciences, Beijing 100049, China

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## ABSTRACT

Common wheat is an important and widely cultivated food crop throughout the world. Much progress has been made in regard to wheat genome sequencing in the last decade. Starting from the sequencing of single chromosomes/chromosome arms whole genome sequences of common wheat and its diploid and tetraploid ancestors have been decoded along with the development of sequencing and assembling technologies. In this review, we give a brief summary on international progress in wheat genome sequencing, and mainly focus on reviewing the effort and contributions made by Chinese scientists.

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\* Corresponding author at: Institute of Genetics and Developmental Biology, Chinese Academy of Sciences, Beijing 100101, China.

E-mail address: [hqling@genetics.ac.cn](mailto:hqling@genetics.ac.cn) (H.-Q. Ling).

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## 1. Introduction

Common wheat (*Triticum aestivum* L.), one of the important staple food crops in the world, feeds >30% of the human population [1]. The world annual production of wheat is >620 million metric tons (<http://www.fao.org/3/a-i4691e.pdf>). China is the largest wheat producer and consumer. The Chinese annual wheat production is about 100 million tons [2]. Wheat production needs to be constantly increased in order to satisfy the food demands of the increasing world. Accurate sequencing and assembly of wheat genomes are helpful for basic research and genetic improvement of wheat cultivars [3].

The different ecotypes of common wheat (such as winter wheat and spring wheat) adapt well to a wide range of climates. Wheat is an allohexaploid (AABBDD) that arose from two wide hybridization events. The first occurred 0.5–3.0 million years ago between two diploid ancestral species carrying the A (*T. urartu*) and B (an unknown species) genomes and after chromosome doubling formed wild tetraploid wheat (*Triticum turgidum* ssp. *dicoccoides*, AABB). This species was domesticated to cultivated emmer (*T. turgidum* ssp. *dicoccum*, AABB) [4]. The second hybridization took place about 9000 years ago between cultivated emmer and diploid goat grass (*Aegilops tauschii*, DD) to form allohexaploid common wheat [5]. Compared with other major crops the common wheat genome is very large in size (~17 gigabases, Gb) with each subgenome being approximately 5.5 Gb [6] and complex in composition, of which >80% is made up of repetitive sequences. Therefore, sequencing and assembly of the entire wheat genome was very challenging. During the past several years many effort was made in this area, and a series of draft and near completed genome/chromosome assemblies for common wheat and its diploid and tetraploid progenitors have been generated in succession [7–16]. In this review, we mainly focus on contributions made by Chinese scientists in the area of wheat genome sequencing following a brief summary of international achievements.

## 2. International progress in wheat genome sequencing

In order to decode the mystery of the wheat genome and to expedite molecular breeding in wheat, a group of scientists and breeders initiated the International Wheat Genome Sequencing Consortium (IWGSC) in 2005. To overcome the difficulties caused by genome size and complexities, the 21 chromosomes of common wheat landrace Chinese Spring were separated by flow cytometric sorting. Bacterial artificial chromosome (BAC) libraries and physical maps were then constructed for each chromosome or chromosome arm. Chromosome sorting, DNA isolation and BAC library construction for each chromosome arm were performed in the laboratory of Prof. Jaroslav Dolezel at the Institute of Experimental Botany in the Czech Republic. Subsequent physical map construction and BAC sequencing were assigned to different laboratories of the International Wheat Genome Sequencing Consortium (IWGSC). Numerous projects by different groups were undertaken to produce reference

sequences of single chromosome or chromosome arms. Chromosome 3B was the first chromosome to be sorted successfully due to its large size. A 3B physical map was generated using BAC clones originating from the purified 3B chromosome in 2008 [17]. BAC clones were selected by a minimal tiling path (MTP) approach and sequenced. The final pseudomolecule of 3B was 774 megabases (Mb) in length and carried 5326 protein-coding genes [13]. Currently, all chromosomes/chromosome arms of Chinese Spring have been sorted and their physical maps have been constructed (<http://www.wheatgenome.org/Projects/IWGSC-Bread-Wheat-Projects>). Sequences of many chromosomes, or parts thereof, are publicly available, including 1AS, 1BS, 3DS, 5DS, 7DS, 1AL, 1BL, 4A, 5A, 6A, 6B, and 7B [16,18–29].

In addition to the chromosome-based BAC-by-BAC sequencing strategy of IWGSC, Hall and colleagues in the UK applied a whole genome shotgun sequencing strategy with 454 pyro-sequencing technology to sequence Chinese Spring, and produced a five-fold coverage genome sequence of Chinese Spring in 2012. Based on the assemblies of 5.42 Gb, they predicted 94,000 to 96,000 genes, and assigned two-thirds of them to the three subgenomes (A, B, and D). The authors indicated that gene families were pronouncedly reduced in common wheat compared to the diploid progenitors, [7]. Two years after the first wheat genome release, IWGSC published a chromosome-based draft sequence of Chinese Spring [1]. Compared to the whole genome shotgun sequencing strategy, this approach differentiated the highly conserved gene copies in each chromosome.

The 21 chromosomes of Chinese Spring were isolated by flow cytometric sorting and sequenced by a chromosome-based shotgun sequencing strategy using Illumina technology to yield 10.2 Gb of genome sequence. Abundant gene losses and duplications were observed by intra- and inter-specific comparisons, indicating that the wheat genome was somewhat dynamic in evolution [1]. In 2017, Clark et al. [11] published an improved genome sequence of Chinese Spring. They used precisely sized mate-pair libraries and an optimized algorithm to generate a new assembly representing >78% of the genome, much higher than the scaffold proportion (~49%) produced previously by IWGSC. Genome-wide sequence rearrangements were revealed based on comparative analysis of the data. Zimin et al. [12] reported a more complete wheat genome assembly. The final sequences were generated by combining next generation (short Illumina reads) and third generation sequencing data (long Pacific Biosciences reads). >15 Gb of final assembly representing >90% of the Chinese Spring genome was created by merging two sets of sequences assembled using the MaSuRCA [30] and FALCON assemblers [31]. This is the most complete wheat genome sequence published by far. Recently, IWGSC announced that they have completed a high quality sequence of Chinese Spring (IWGSC v1.0) and released the genomic data for public access (<http://www.wheatgenome.org/News/Latest-news/RefSeq-v1.0-URGI>).

In addition to sequencing Chinese Spring at the genome and single chromosome level, sequencing of wild emmer, the tetraploid ancestor of common wheat, was reported in July 2017 [10]. A software package DenovoMAGIC2 (NRGene, NesZiona, Israel) was applied to perform the scaffold

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