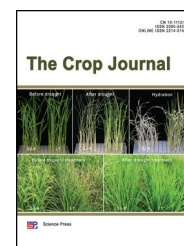
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## Wheat breeding in the hometown of Chinese Spring<sup>☆</sup>

Dengcai Liu<sup>\*</sup>, Lianquan Zhang, Ming Hao, Shunzong Ning, Zhongwei Yuan, Shoufen Dai, Lin Huang, Bihua Wu, Zehong Yan, Xiujin Lan, Youliang Zheng

Triticaceae Research Institute, Chengdu Campus of Sichuan Agricultural University, Wenjiang, 611130, Sichuan, China

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### ABSTRACT

The common wheat landrace Chinese Spring (CS) was made famous by the work of Ernie Sears, a great cytogenetist, who developed a number of CS-based aneuploid series that were used to identify individual wheat chromosomes. Based on this, a standard karyotype and nomenclature system was developed for wheat chromosomes that allowed wheat researchers to analyze and manipulate the wheat genome with unprecedented precision and efficiency. Nevertheless, not much is known about the utilization of CS at its hometown, Chengdu in Sichuan province, during early wheat breeding activity. In this review, we follow the speculation that CS is a selection from the Cheng-du-guang-tou (CDGT) landrace. We provide a description of how CDGT became a founder landrace for wheat breeding activities in early times. We show that CDGT-derived varieties were reinforced genetically by crosses to six more exotic parents. These varieties remained the major elite cultivar for several decades. Later, synthetic hexaploid wheats were introduced into the breeding program, firstly using those from CIMMYT and later using materials produced with local tetraploid wheat and goat grass. Finally, we discuss the strategies and future directions to improve wheat yield and resistance through an expanded genetic basis, especially by recapturing lost genetic variations from landraces and related wild species, a process that may set an example for wheat breeders in China and elsewhere.

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<sup>\*</sup> Corresponding author.

E-mail address: [dcliu7@sicau.edu.cn](mailto:dcliu7@sicau.edu.cn) (D. Liu).

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## 1. Introduction

Bread wheat (*Triticum aestivum*) is an allopolyploid species derived from two widely separated (in time) crosses: the first, which occurred about 0.5 million years ago, generated the AB tetraploid wild emmer (*T. dicoccoides*), and the second, occurring about 10,000 years ago, combined a domesticated form of emmer with the diploid goat grass D genome donor *Aegilops tauschii* to form the extant ABD hexaploid [1–3]. Despite its relatively recent origin, bread wheat is now one of the world's most important cereals, providing >20% of the calorific energy consumed by humans (<http://www.fao.org/faostat>). It arrived in north-western China from central Asia about 4500 years ago [4], and from there gradually spread across much of the country [5–7].

Chinese Spring (CS) is thought to be a Sichuan landrace. The wide application of this variety and its derived genetic stocks has greatly advanced wheat genetics, including the recent achievement of chromosome-by-chromosome genome sequencing of bread wheat. Sichuan province, located in southwestern China, experiences relatively low photosynthetic radiation, as well as high levels of humidity and temperature at the terminal growth stages of the wheat crop. Wheat landraces from Sichuan are collectively known as the Sichuan white wheat complex group, and they are characterized by the formation of multifloret spikelets and rounded glumes [8], and show a high level of crossability with cereal rye [9,10]. The application of directed improvement through breeding and selection in Sichuan has a history of over 70 years; the introduction of exotic germplasm has resulted in a declining contribution of Sichuan white to current commercial varieties. This review aims to highlight major features of the genetic improvements made to Sichuan wheat. While much of this improvement relates to the replacement of alleles in the wheat genome proper, there has also been a substantial impact of non-wheat germplasm, in the form of the two Robertsonian translocations, 1BL.1RS [11,12] and 6AL.6VS [13,14]. The intention is not to attempt a comprehensive review of the history of wheat breeding in Sichuan but rather to highlight the genomic changes that occurred in the shift from local landraces to modern varieties.

## 2. The variety CS

### 2.1. CS was a selection from a Sichuan white landrace

CS is familiar to the international wheat genetics community as it was used to derive a comprehensive set of aneuploids

representing all chromosomes and a range of derived cytogenetic stocks and intervarietal substitution lines. Yen et al. [8] were unable to distinguish CS from the Sichuan white landrace Cheng-du-guang-tou (CDGT) in a morphology-, physiology-, and cytogenetics-based comparison. The inferred close genetic relatedness between CS and CDGT was borne out by a genetic similarity analysis based on RFLP profiling [15]. The implication was that the geographical origin of CS was the region surrounding the city of Chengdu.

### 2.2. The contribution of CS to wheat cytogenetics

According to Sears et al. [16] CS (initially referred to as 'Chinese White') was taken from China to the UK by a missionary. Its ready crossability with cereal rye, reported by Backhouse [17], distinguished it from most European germplasm. The discovery of monosomic and trisomic plants among the offspring of two haploid progeny of a CS × cereal rye cross was the basis of the extensive series of aneuploids developed in a CS background [18]. This led naturally to the choice of CS as the target for induced mutagenesis, focusing *inter alia* on the genes that prevented homoeologous chromosome pairing [19]. Over the years, the CS-based aneuploidy sets were widely exploited for analyzing the mode of inheritance of both qualitative and quantitative traits and for transferring genes into wheat from its distant relatives. The CS aneuploids have retained their relevance to the present time in that they have been instrumental in the ongoing effort to acquire a chromosome-by-chromosome genome sequence of bread wheat (<https://wheat-urgi.versailles.inra.fr/>). Once established, the CS genome sequence will represent a scaffold around which the sequences of other wheat varieties can be conveniently acquired [20].

### 2.3. CS provided the means to develop chromosome engineering

The use of CS and its aneuploid and mutant derivatives for the purpose of alien introgression has, over the years, resulted in the development of a substantial number of pre-breeding lines. The impact on wheat improvement of most of these materials has been low, in part because the genetic background of CS is not well adapted outside its area of origin in Sichuan. In the local environment, CS harbors a number of breeder-relevant traits, including tolerance to moisture and nutritional stress, a high potential for tillering, the production of as many as six florets per spikelet, of 21–24 spikelets per ear on the leading tiller and a high level of floret fertility [21]. It

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