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Wheat breeding in the hometown of Chinese Spring☆

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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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1. Introduction

Bread wheat (*Triticum aestivum*) is an allopolypoid 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 paring [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

also, however, suffers from a number of defects, namely its late maturity, small grain size, tendency to lodge and formation of geniculate culms (the latter results in a non-uniform height of ears at maturity, Fig. 1). Removing these defects by conventional breeding has not been straight-forward.

3. The landrace CDGT

3.1. The use of CDGT in wheat improvement in Sichuan

CDGT has been the most heavily used landrace in the breeding of current Sichuan varieties. It features in the pedigree of 29 commercially released varieties [7]. One of these varieties is Wuyi-mai (CDGT/Ardito//Fawn/Florence), released in 1951, which was used as a parent in the breeding of 27 commercially released varieties [7,22]. A theoretical 25% of the Wuyi-mai genome was inherited from CDGT (Fig. 2). The pedigree of Fan 6, a variety released in 1969, suggests that it has retained ~10% of the CDGT genome (Fig. 2). The development of Fan 6 has been recognized as a milestone for wheat breeding in Sichuan and surrounding provinces [23]. Some 29 commercially released varieties include Fan 6 in their pedigree [22,24]. According to Yen [25], the successful breeding of Fan 6 was achieved by combining "convergence crossing" with selection for dominant traits. Its pedigree comprises eight crosses, based on seven parents, made between 1960 and 1964 [26]. Each of the seven parents was selected on the basis of harboring a specific target trait(s). The crossing scheme resembles the recently described "multiparent advanced generation inter-cross" (MAGIC) design [27]. The major problem encountered in the scheme is the choice of selection criteria for the hybrid intermediaries. The approach taken was to base selection purely on the expression of dominant traits, which resulted in the stacking of over ten traits in a relatively short period of selection in rather small populations [25].

Due to hexaploidy the majority of common wheat genes are present in triplicate (one per homeolog). Although seldom 100% identical with respect to coding sequence, these homeoalleles typically share >97% homology with one another [28], with the result that a recessive allele at one (or even two) of the homeoloci is typically masked by the presence of a dominant allele present at one (or both) of the other homeoloci [29]. The consequence is that recessive alleles become fixed at a relatively low frequency, so that the outcome of breeding is primarily the selection of dominant gain-of-function alleles [30].

3.2. The continuing utilization of exotic parents post-Fan 6

Fan 6 proved to be a very productive parent in breeding programs based in the south western part of China: along with its derivatives, this variety has dominated wheat production in Sichuan since the late 1970s [24]. The variety Mianyang 11, which features Fan 6 in its pedigree, was released in 1976, becoming locally the most widely grown variety; it covered about 1.5 Mha in 1984 [23]. An analysis of commercially grown varieties released in Sichuan between the years 1984 to 2016 has shown that the grain yield achieved by varieties released from 1984 to 1990 (around 4.7 t ha^{-1}) was similar to that achieved by varieties released between 1991 and 2000, even though the more recently bred materials produced larger grains (Fig. 3). A later trial using a subset of the varietal set was able to confirm this conclusion [23]. A reason for the yield stasis between 1984 and 2000 may be the intensive use of Fan 6 as a crossing parent. However, during the 16 years since 2001, grain yield has increased. A set of 48 varieties released from 2011 to 2016 out-yielded the 1984–1990 set by around

Fig. 1 – The evolution of plant architecture from landrace to modern variety. A, Chinese Spring; B, a typical modern variety.

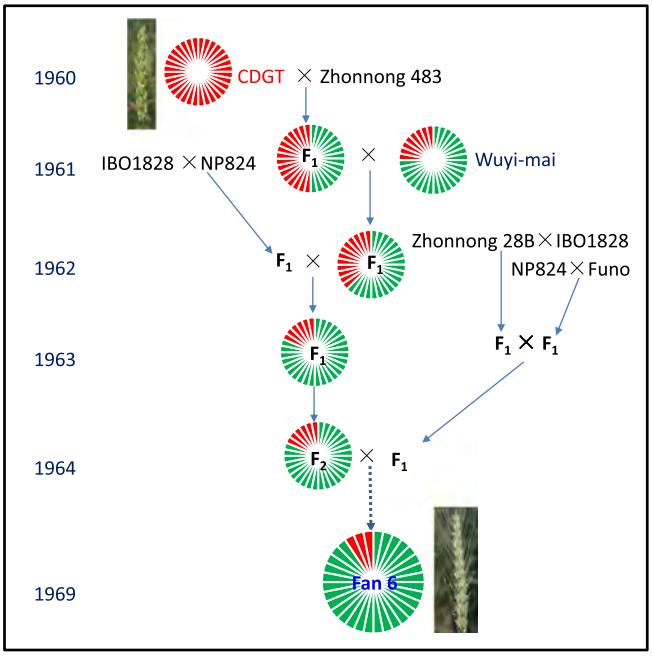

Fig. 2 – The breeding strategy used to derive the variety Fan 6. The seven parents comprised the landrace Cheng-du-guang-tou (CDGT, red) and six exotic wheat lines (shown in green). Three of the latter were bred elsewhere in China (Zhonnong 28B, Zhonnong 483, Wuyi-mai), two in Italy (IBO 1828, Funo) and one in India (NP 824). The pedigree of Zhongnong 483 is Jiang-dong-men × Florence (the latter is an Australian variety), while that of Wuyi-mai is CDGT/Ardito (Italy)//Fawn (Australia)/ Florence (Australia). Based on its known pedigree, 10% of the genetic background of Fan 6 was inherited from CDGT.

20%, mainly as a result of larger grain size. This increase has resulted from the use of exotic parents, and in particular, synthetic hexaploid wheats.

4. Synthetic hexaploid wheats

4.1. Synthetic hexaploid wheats as parents in Sichuan breeding programs

Synthetic hexaploid wheats are created by the whole genome doubling of hybrids between tetraploid wheat (usually *T. durum*) and *Ae. tauschii*, thereby somewhat duplicating the origin of bread wheat whose wheat parent was *T. dicoccum* [1,2] (Fig. 4). Chromosome doubling of the ABD hybrid is conventionally effected by colchine treatment, but is often more conveniently achieved by (as was the case in nature) spontaneous meiotic restitution [31,32]. The genetic base of bread wheat is thought to be rather narrow because the species evolved from a limited number of natural founder amphiploids, thereby excluding much of the genetic variation harbored by its progenitor species. Most synthetic hexaploids are fully crossable with bread wheat varieties, so that a relatively small number of *de novo* amphiploids can serve as a bridge to release novel genes into hexaploid germplasm. There is no major constraint to recombination between homologs in hybrids between a synthetic hexaploid and current wheat cultivars. >1000 synthetic hexaploids have been generated at CIMMYT in Mexico, mostly from crosses between either *T. durum* or *T. dicoccum* and *Ae. tauschii* [33,34]. Some locally produced synthetic hexaploids based on colchicine treatment were created during the 1990s [35,36], but the scale of effort was increased in later years once it was recognized that spontaneous chromosome doubling was a reasonably common event in tetraploid *Triticum* × *Ae. tauschii* hybrids [37–40].

4.2. Utilization of CIMMYT-derived synthetic hexaploid wheats in Sichuan

Two CIMMYT synthetic hexaploid selections, namely Syn769 (*T. durum* Decoy 1/*Ae. tauschii* 188) and Syn786 (*T. durum* Cereta/*Ae. tauschii* 783) were used to good effect in Sichuan wheat breeding programs [41]. The varieties Chuanmai 38, Chuanmai 42 and Chuanmai 43, released in 2003, 2003, and 2004, respectively, each included Syn769 in its pedigree, while Chuanmai 47 (released in 2005) was bred from a cross involving Syn786. Of these four varieties, Chuanmai 42 has proven to be the best performer with respect to yield, achieving a record return of >6 t ha^{-1} in a regional trial [41]. The variety has also become recognized as an outstanding crossing parent, with 12 commercially released varieties having been bred from it [42]. The similarly high yielding varieties Chuanmai 104 and Shumai 969 form notably large grains and tiller profusely. Varieties bred from synthetic hexaploids typically display high seedling vigor and are associated with a high level of canopy photosynthesis [43].

4.3. Utilization of Sichuan-derived synthetic hexaploid wheats in Sichuan

Synthetic hexaploids based on crosses with traditional tetraploid wheats (called Lánmài in Chinese) are attracting

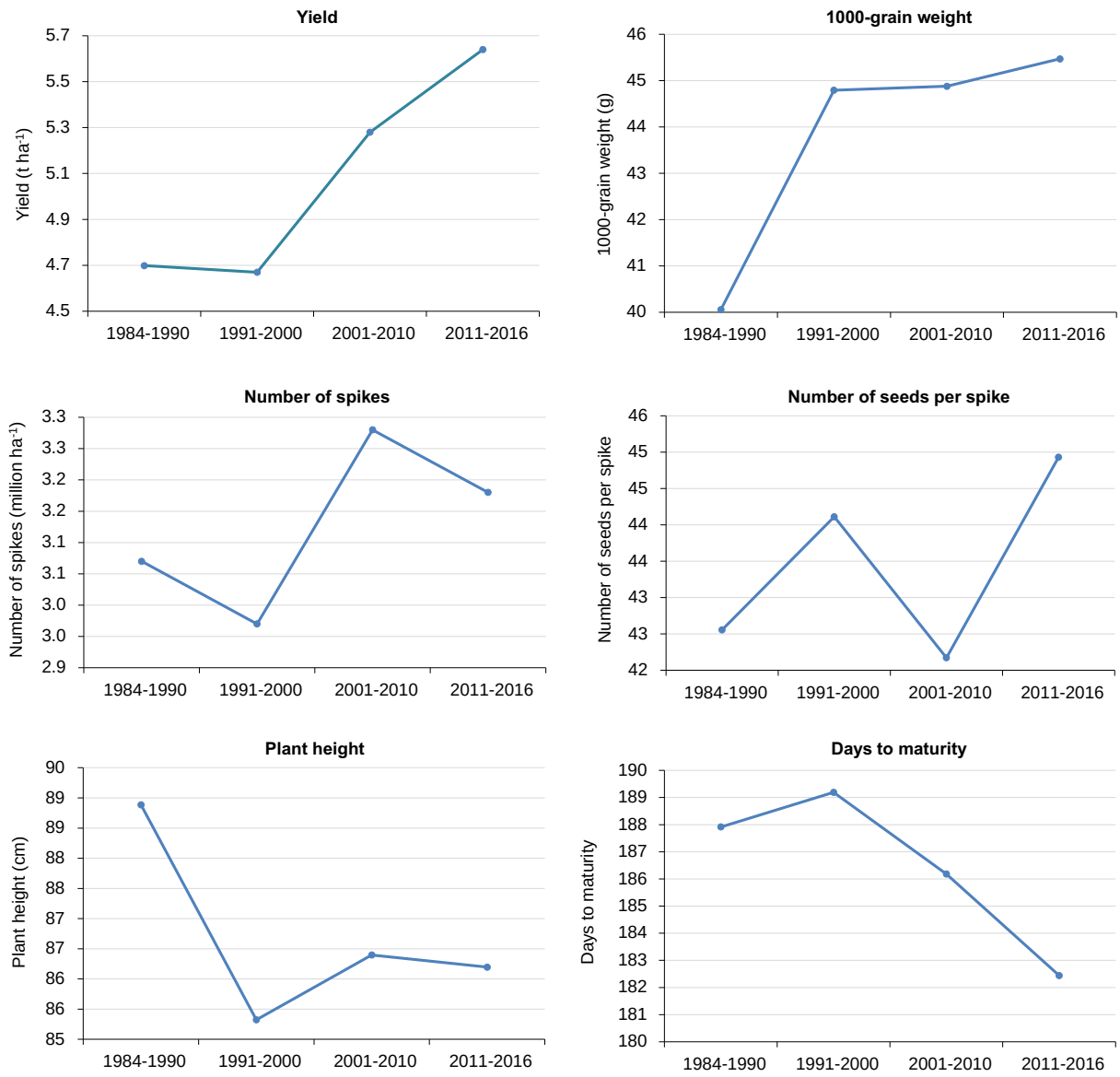

Fig. 3 – Trends in yield and related traits in wheat released in Sichuan since 1984. One hundred and ninety eight varieties were clustered according to year of release, including 23 from 1984 to 1990, 34 from 1991 to 2000, 93 from 2001 to 2010, and 48 from 2011 to 2016. Data obtained from Sichuan provincial regional trials.

a growing level of interest [44]. Lánmài plants form highly glaucous stems, leaves and ears, giving them a blue appearance (Fig. 4, left). The synthetic hexaploid line SHW-L1 (*T. turgidum* AS2255 × *Ae. tauschii* AS60) is a prominent example (Fig. 4). The multi-spikelet characteristic of AS2255 was inherited by the variety Shumai 969 (SHW-L1/Chuanmai 32//Chuanyu 16/3/Chuanmai 42), released in 2013. Despite its early maturity, Shumai 969 is a high yielding variety. An additional feature is that its flour produces strong dough, which is unusual for Sichuan-grown wheats. The Shumai 580 and Shumai 830 varieties bred from SHW-L1 are both excellent yielders and are expected to be released in 2017.

The positive contribution of synthetic hexaploid wheat to grain yield has been repeatedly demonstrated, most prominently by CIMMYT research, but also in Sichuan. As yet, the full potential of this gene pool is unknown, as its sampling has only just begun — there is no doubt that it will feature strongly as a donor of novel variation well into the foreseeable future. As yet, the identity of the genes responsible for the advances in yield achieved using synthetic hexaploid wheats is obscure. In addition to variation at the DNA sequence level that exists between synthetic hexaploids and standard bread wheat genotypes, the process of allopolyploidization used to create a synthetic is known to generate *de novo* variation in the form of epigenetic changes and mutations resulting from the remobilization of quiescent transposable elements [45–47]. Altered patterns of gene expression induced by these phenomena can have major effects on trait expression [48,49].

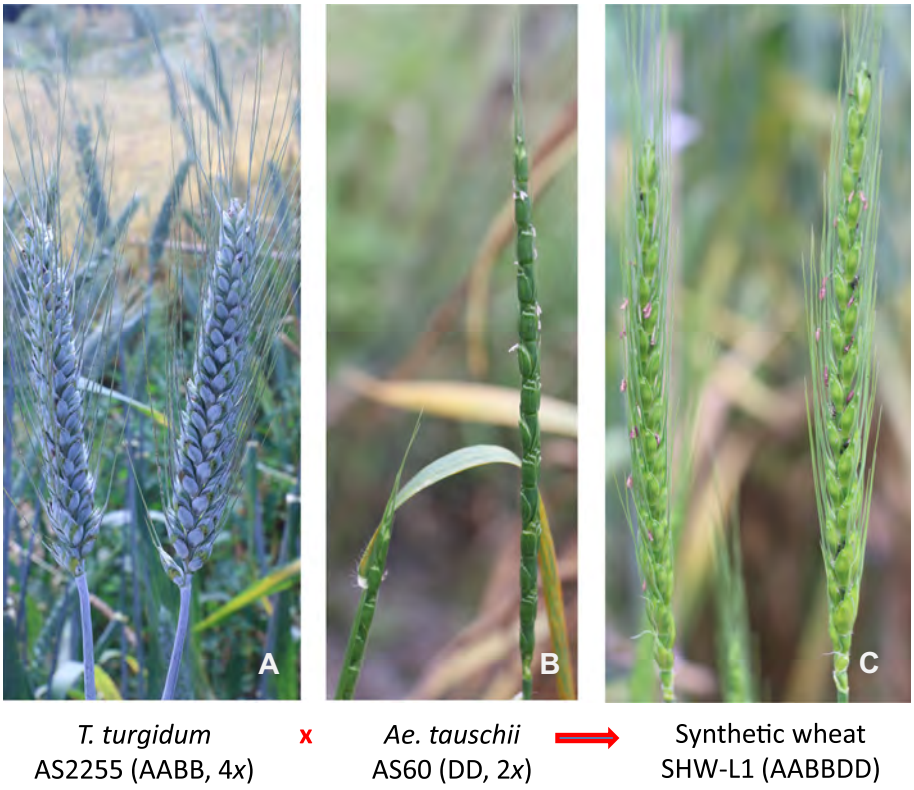

Fig. 4 – The parents of the synthetic wheat line SHW-L1. A, *T. turgidum* AS2255; B, *Ae. tauschii* AS60; C, SHW-L1.

5. Conclusions and future perspectives

5.1. *Improvements to CS-derived prebreeding materials*

Since CS and CDGT are quite closely related to one another, the successful use of CDGT for wheat improvement in Sichuan implies that CS-based materials could relatively easily be improved as well. As demonstrated by the variety Fan 6, it will probably require the replacement of most (in the case of Fan 6, ~90%) of the CS genome by alleles from elite lines to convert CS-based materials into commercial varieties. The process of allele replacement could be greatly accelerated through the use of genome-wide markers to perform background selection. The expectation is that a number of the CS-based pre-breeding materials will find their way into wheat breeding programs in this way.

5.2. *Re-capturing lost genetic variation from Sichuan landrace materials*

The effect of decades of breeding effort to improve Sichuan landrace materials has been to replace most of the CDGT alleles with exotic ones. As yet, it has not been established whether the landrace alleles that were retained are dispersed across the genome or whether they are concentrated in a small number of chromosomal regions. This question can now be relatively straightforwardly addressed through either large-scale single nucleotide polymorphism genotyping and/or genome-wide resequencing. The outcome of such analyses would be highly informative for designing optimal breeding strategies directed at the further improvement of Sichuan wheat.

The time is probably now ripe to consider revisiting landrace materials with a view to recovering some of the ~90% of their genetic variation that was lost through conventional breeding. It is known, for example, that landrace materials, including CS, harbor durable resistance gene *Lr34/Yr18* that protects against the damaging diseases leaf rust and stripe rust [50], whereas the resistances bred into modern varieties are typically overcome by the causative pathogens within a few years. Furthermore, landrace materials typically display a high level of resistance to preharvest sprouting [51], a character that is not a feature of many modern varieties, because it has never been strongly selected in breeding programs. To the best of our knowledge landrace germplasm from Sichuan has been scarcely accessed by breeders since the release of Fan 6. While in the past, many breeders have been reluctant to consider non-elite materials as crossing parents for fear of linkage drag, genomics technologies can in principle effectively and efficiently overcome this problem.

5.3. *Introgressing genes from the secondary gene pool*

Linkage drag remains a disincentive to using synthetic hexaploid wheats as breeding parents. However, as the pace quickens in relation to the identification of functionally important genes, directed transfer is becoming easier. A prominent role can be expected for marker assisted selection here, since it can be used in a backcrossing/top-crossing context both to achieve

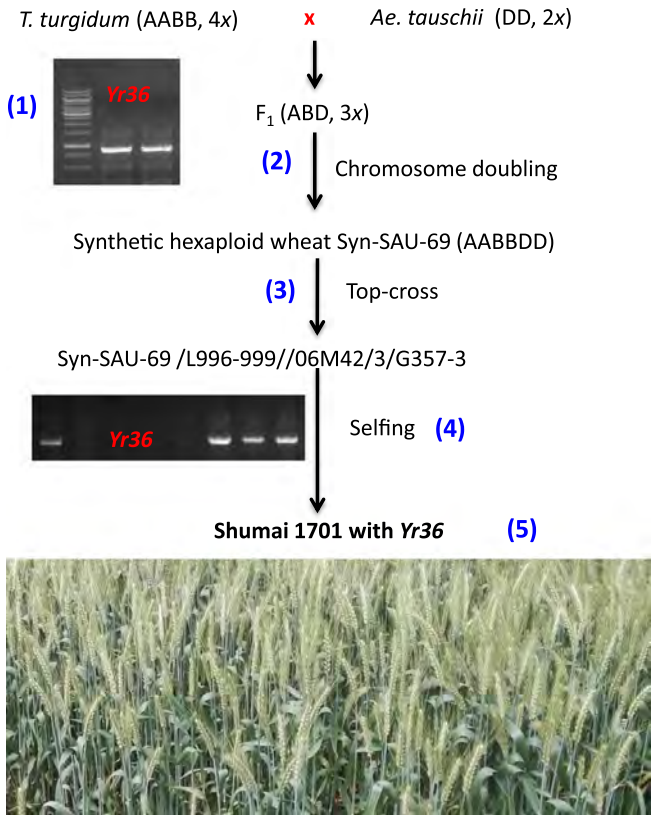

Fig. 5 – Strategy used to transfer *Yr36* from the tetraploid to the hexaploid level.

foreground selection to maintain a given target gene(s) and background selection to accelerate the process of replacing unwanted donor alleles by alleles from elite parents. While many agronomically important traits (notably yield and end-use quality) are not simply inherited, modern marker technologies are increasingly capable of handling multiple targets simultaneously in a cost- and time-effective manner. Working with synthetic wheats, we have been exploiting over 30 donors to introduce genes promoting disease resistance and stress tolerance, altering plant architecture, enhancing crop growth and improving end-use quality. The transfer of *Yr36*, a gene conferring resistance to stripe rust [52], to wheat in Sichuan is illustrated in Fig. 5.

1) Identification of tetraploid wheat PI415152 as a carrier of *Yr36* based on the *Yr36*-specific marker with 911 bp [53];
2) formation of the synthetic hexaploid wheat Syn-SAU-69 through a wide cross between PI415152 and *Ae. tauschii*, followed by spontaneous whole genome doubling;
3) improvement of the resulting synthetic hexaploid wheat by crossing with local lines;
4) fixation of *Yr36* by self-pollination;
5) selection of the elite bread wheat line Shumai 1701.

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REFERENCES

[1] H. Kihara, Discovery of the DD-analyser, one of the ancestors of *Triticum vulgare*, Agric. Hortic. 19 (1944) 889–890.
[2] E. McFadden, E. Sears, The artificial synthesis of *Triticum spleta*, Rec. Genet. Soc. Am. 13 (1944) 26–27.
[3] S.X. Huang, A. Sirikhachornkit, X.J. Su, J. Faris, B. Gill, R. Haselkorn, P. Gornicki, Genes encoding plastid acetyl-CoA carboxylase and 3-phosphoglycerate kinase of the *Triticum/Aegilops* complex and the evolutionary history of polyploid wheat, Proc. Natl. Acad. Sci. U. S. A. 99 (2002) 8133–8138.
[4] Y.Z. Zhang, The ancient crops in Xinjiang, Agric, Archaeol. (1) 3 (1983) 122–126 (in Chinese).
[5] X.S. Zeng, On the expansion of wheat in ancient China, J. Chin. Dietary Cult. 1 (2005) 99–133 (in Chinese with English abstract).
[6] A. Betts, P.W. Jia, J. Dodson, The origins of wheat in China and potential pathways for its introduction: a review, Quat. Int. 348 (2014) 158–168.
[7] S.B. Jin, Wheat varieties and their pedigrees in China, China Agriculture Press, Beijing, China, 1983 (in Chinese).
[8] C. Yen, M.C. Luo, J.L. Yang, The origin of the Tibetan weedrace of hexaploid wheat, Chinese Spring, Chengdu-guang-tou and other landraces of the white wheat complex from China, in:

T.E. Miller, R.M.D. Koebner (Eds.), Proceedings of the 7th International Wheat Genetics Symposium, July 13–19, 1988, Inst. Plant Science Research, Cambridge Laboratory, Trumpington, Cambridge, UK 1988, pp. 175–179.

[9] M.C. Luo, C. Yen, J.L. Yang, Crossability percentages of bread wheat landraces from Sichuan Province, China with rye, Euphytica 61 (1992) 1–7.

[10] Y.L. Zheng, M.C. Luo, C. Yen, J.L. Yang, Chromosome location of a new crossability gene in common wheat, Wheat Inf. Serv. 75 (1992) 36–40.

[11] D. Mettin, W. Bluthner, G. Schlegel, Additional evidence on spontaneous 1B/1R wheat-rye substitutions and translocations, in: E.R. Sears, L.M.S. Sears (Eds.), Proceedings of the Fourth International Wheat Genetics Symposium, August 6–11, 1973, College of Agriculture, University of Missouri, Agricultural Experiment Station 1973, pp. 179–184.

[12] F.J. Zeller, 1B/1R wheat–rye chromosome substitutions and translocations, in: E.R. Sears, L.M.S. Sears (Eds.), Proceedings of the Fourth International Wheat Genetics Symposium, August 6–11, 1973, College of Agriculture, University of Missouri, Agricultural Experiment Station 1973, pp. 209–221.

[13] P.D. Chen, L.L. Qi, B. Zhou, S.Z. Zhang, D.J. Liu, Development and molecular cytogenetic analysis of wheat-*Haynaldia villosa* 6VS/6AL translocation lines specifying resistance to powdery mildew, Theor. Appl. Genet. 91 (1995) 1125–1128.

[14] A.Z. Cao, L.P. Xing, X.Y. Wang, X.M. Yang, W. Wang, Y.L. Sun, C. Qian, J.L. Ni, Y.P. Chen, D.J. Liu, X.E. Wang, P.D. Chen, Serine/threonine kinase gene *Stpk-V*, a key member of powdery mildew resistance gene *Pm21*, confers powdery mildew resistance in wheat, Proc. Natl. Acad. Sci. U. S. A. 108 (2011) 7727–7732.

[15] R.W. Ward, Z.L. Yang, H.S. Kim, C. Yen, Comparative analyses of RFLP diversity in landraces of *Triticum aestivum* and collections of *T. tauschii* from China and Southwest Asia, Theor. Appl. Genet. 96 (1998) 312–318.

[16] E.R. Sears, T.E. Miller, The history of Chinese Spring wheat, Cereal Res. Commu. (1985) 261–263.

[17] W.O. Backhouse, Note on the inheritance of crossability, J. Genet. 6 (1916) 91–94.

[18] E.R. Sears, Cytogenetic studies with polyploid species of wheat. I. Chromosomal aberrations in the progeny of a haploid of *Triticum vulgare*, Genetics 24 (1939) 509–523.

[19] E.R. Sears, Genetic control of chromosome pairing in wheat, Annu. Rev. Genet. 10 (1976) 31–51.

[20] M. Liu, J. Stiller, K. Holušová, J. Vrána, D.C. Liu, J. Doležel, C.J. Liu, Chromosome-specific sequencing reveals an extensive dispensable genome component in wheat, Sci. Rep. 6 (2016) 36398.

[21] D.C. Liu, Y.L. Zheng, X.J. Lan, Utilization of wheat landrace Chinese Spring in breeding, Sci. Agric. Sin. 36 (2003) 1383–1389 (in Chinese with English abstract).

[22] Q.S. Zhuang, Chinese Wheat Improvement and Pedigree Analysis, China Agriculture Press, Beijing, 2002 (in Chinese).

[23] Y. Zhou, H.Z. Zhu, S.B. Cai, Z.H. He, X.K. Zhang, X.C. Xia, G.S. Zhang, Genetic improvement of grain yield and associated traits in the southern China winter wheat region: 1949 to 2000, Euphytica 157 (2007) 465–473.

[24] Y.D. Zhou, A survey of the Fan-6 and its sisters, excellent wheat germplasms for high yield and resistance to stripe rust, J. Sichuan Agric. Univ. 10 (1992) 682–688 (in Chinese with English abstract).

[25] C. Yen, History and prospect of study on wheat breeding of fifty years in Sichuan, J. Sichuan Agric. Univ. 17 (1999) 108–113 (in Chinese).

[26] C. Yen, Summary of wheat cross breeding in the past 20 years, Sichuan Agric. Sci. Technol. 4 (1973) 4–20 (in Chinese).

[27] B.E. Huang, A.W. George, K.L. Forrest, A. Kilian, M.J. Hayden, M.K. Morell, C.R. Cavanagh, A multiparent advanced generation intercross population for genetic analysis in wheat, Plant Biotechnol. J. 10 (2012) 826–839.

[28] C. Uauy, Wheat genomics comes of age, Curr. Opin. Plant Biol. 36 (2017) 142–148.

[29] P. Borrill, N. Adamski, C. Uauy, Genomics as the key to unlocking the polyploid potential of wheat, New Phytol. 208 (2015) 1008–1022.

[30] K.V. Krasileva, H.A. Vasquez-Gross, T. Howell, P. Bailey, F. Paraiso, L. Clissold, J. Simmonds, R.H. Ramirez-Gonzalez, X.D. Wang, P. Borrill, C. Fosker, S. Ayling, A.L. Phillips, C. Uauy, J. Dubcovsky, Uncovering hidden variation in polyploid wheat, Proc. Natl. Acad. Sci. U. S. A. 114 (2017) E913–E921.

[31] M. Hao, J.T. Luo, D.Y. Zeng, L. Zhang, S.Z. Ning, Z.W. Yuan, Z.H. Yan, H.G. Zhang, Y.L. Zheng, C. Feuillet, F. Choulet, Y. Yen, L.Q. Zhang, D.C. Liu, *QTug.sau-3B* is a major quantitative trait locus for wheat hexaploidization, G3-Genes Genomes Genet. 4 (2014) 1943–1953.

[32] D.C. Liu, H.G. Zhang, L.Q. Zhang, Z.W. Yuan, M. Hao, Y.L. Zheng, Distant hybridization: a tool for interspecific manipulation of chromosomes, in: A. Pratap, J. Kumar (Eds.), Alien Gene Transfer in Crop Plants, Vol. 1, Springer, New York 2014, pp. 25–42.

[33] A. Mujeeb-Kazi, V. Rosas, S. Roldan, Conservation of the genetic variation of *Triticum tauschii* Coss. Schmalh. *Aegilops squarrosa* auct. non L. in synthetic hexaploid wheats *T. turgidum* L. s. lat. × *T. tauschii*; $2n = 6x = 42$, AABBDD and its potential utilization for wheat improvement, Genet. Resour. Crop. Evol. 43 (1996) 129–134.

[34] S. Dreisigacker, M. Kishii, J. Lage, M. Warburton, Use of synthetic hexaploid wheat to increase diversity for CIMMYT bread wheat improvement, Crop Pasture Sci. 59 (2008) 413–420.

[35] X.J. Lan, D.C. Liu, Z.R. Wang, Inheritance in synthetic hexaploid wheat 'RSP' of sprouting tolerance derived from *Aegilops tauschii* Cosson, Euphytica 95 (1997) 321–323.

[36] L.Q. Zhang, D.C. Liu, Z.H. Yan, X.J. Lan, Y.L. Zheng, Y.H. Zhou, Rapid changes of microsatellite flanking sequence in the allopolyploidization of new synthesized hexaploid wheat, Sci. China C Life Sci. 47 (2004) 553–561.

[37] L.Q. Zhang, Y. Yen, Y.L. Zheng, D.C. Liu, Meiotic restriction in emmer wheat is controlled by one or more nuclear genes that continue to function in derived lines, Sex. Plant Reprod. 20 (2007) 159–166.

[38] L.Q. Zhang, D.C. Liu, Y.L. Zheng, Z.H. Yan, S.F. Dai, Y.F. Li, Q. Jiang, Y.Q. Ye, Y. Yen, Frequent occurrence of unreduced gametes in *Triticum turgidum–Aegilops tauschii* hybrids, Euphytica 172 (2010) 285–294.

[39] M. Hao, J.X. Chen, L.Q. Zhang, J.T. Luo, Z.W. Yuan, Z.H. Yan, B. Zhang, W.J. Chen, Y.M. Wei, H.G. Zhang, Y.L. Zheng, D.C. Liu, The genetic study utility of a hexaploid wheat DH population with non-recombinant A- and B-genomes, SpringerPlus 2 (2013) 131.

[40] J.T. Luo, M. Hao, L. Zhang, J.X. Chen, L.Q. Zhang, Z.W. Yuan, Z.H. Yan, Y.L. Zheng, H.G. Zhang, Y. Yen, D.C. Liu, Microsatellite mutation rate during allohexaploidization of newly resynthesized wheat, Int. J. Mol. Sci. 13 (2012) 12533–12543.

[41] W.Y. Yang, D.C. Liu, J. Li, L.Q. Zhang, H.T. Wei, X.R. Hu, Y.L. Zheng, Z.H. He, Y.C. Zou, Synthetic hexaploid wheat and its utilization for wheat genetic improvement in China, J. Genet. Genomics 36 (2009) 539–546.

[42] J. Li, H.S. Wan, W.Y. Yang, Synthetic hexaploid wheat enhances variation and adaptive evolution of bread wheat in breeding processes, J. Syst. Evol. 52 (2014) 735–742.

[43] Y.L. Tang, C.S. Li, X.L. Wu, C. Wu, W.Y. Yang, G. Huang, X.L. Ma, Accumulation of dry matter, canopy structure and photosynthesis of synthetic hexaploid wheat-derived high yielding varieties grown in Sichuan basin, China, Sci. Agric. Sin. 47 (2014) 844–855 (in Chinese with English abstract).

[44] D.C. Liu, M. Hao, A.L. Li, L.Q. Zhang, Y.L. Zheng, L. Mao, Allopolyploidy and interspecific hybridization for wheat improvement, in: A.S. Mason (Ed.), Polyploidy and Hybridization for Crop Improvement, CRC Press, Boca Raton, FL, USA 2016, pp. 27–52.

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[45] K. Kashkush, M. Feldman, A.A. Levy, Transcriptional activation of retrotransposons alters the expression of adjacent genes in wheat, Nat. Genet. 33 (2003) 102–106.
[46] X. Guo, F.P. Han, Asymmetric epigenetic modification and elimination of rDNA sequences by polyploidization in wheat, Plant Cell 26 (2014) 4311–4327.
[47] A.L. Li, S.F. Geng, L.Q. Zhang, D.C. Liu, L. Mao, Making the bread: insights from newly synthesized allohexaploid wheat, Mol. Plant 8 (2015) 847–859.
[48] C.W. Yang, L. Zhao, H.K. Zhang, Z.Z. Yang, H. Wang, S.S. Wen, C.Y. Zhang, S. Rustgi, D. von Wettstein, B. Liu, Evolution of physiological responses to salt stress in hexaploid wheat, Proc. Natl. Acad. Sci. U. S. A. 111 (2014) 11882–11887.
[49] Y. Han, M.M. Xin, K. Huang, Y.Y. Xu, Z.S. Liu, Z.R. Hu, Y.Y. Yao, H.R. Peng, Z.F. Ni, Q.X. Sun, Altered expression of *TaRSL4* gene by genome interplay shapes root hair length in allopolyploid wheat, New Phytol. 209 (2016) 721–732.
[50] W.X. Yang, F.P. Yang, D. Liang, Z.H. He, X.W. Shang, X.C. Xia, Molecular characterization of slow-rusting genes *Lr34/Yr18* in Chinese wheat cultivars, Acta Agron. Sin. 34 (2008) 1109–1113 (in Chinese with English abstract).
[51] J.R. Wang, Y.X. Liu, Y. Wang, Z.H. Chen, S. Dai, W.G. Cao, G. Fedak, X.J. Lan, Y.M. Wei, D.C. Liu, Y.L. Zheng, Genetic variation of *Vp1* in Sichuan wheat accessions and its association with pre-harvest sprouting response, Genes Genom. 33 (2011) 139.
[52] D.L. Fu, C. Uauy, A. Distelfeld, A. Blechl, L. Epstein, X.M. Chen, H. Sela, T. Fahima, J. Dubcovsky, A kinase-START gene confers temperature-dependent resistance to wheat stripe rust, Science 323 (2009) 1357–1360.
[53] C.L. Yuan, H. Jiang, H.G. Wang, K. Li, H. Tang, X.B. Li, D.L. Fu, Distribution, frequency and variation of stripe rust resistance loci *Yr10*, *Lr34/Yr18* and *Yr36* in Chinese wheat cultivars, J. Genet. Genomics 39 (2012) 587–592.