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Transferring diversity of goat grass to farmers' fields through the development of synthetic hexaploid wheat

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Abstract

Crop wild relatives are important components of genebank collections. These genetic resources are unique reservoirs of useful alleles for crop improvement. To assess the impact of goat grass (*Aegilops tauschii*), The D genome donor of bread wheat, we analyzed the role of its derivatives in widening the genetic base for wheat breeding and the extent of adoption of derived varieties. Synthetic hexaploids (SHW), the result of crossing *Aegilops tauschii* with durum wheat, are used as a bridge to transfer desirable traits into modern bread wheat (*Triticum aestivum* subsp. *aestivum*) varieties. The collections of *Aegilops tauschii* from major genebanks were used extensively in pre-breeding to develop SHW. Our results show that 629 unique accessions from 15 countries were used to generate 1,577 primary SHW. This later represented 21% of the germplasm distributed by the CIMMYT genebank between 2000 and 2018, with more than 10,000 samples of SHW were distributed to 110 institutions in 40 countries. We observed substantial increase of synthetic hexaploids derived lines (SHDL) included in international nurseries. SHDL were screened for major diseases of wheat, mainly for *Septoria* and stem rust. So far, at least 85 varieties were selected from SHDL and released in 20 countries. The breeder survey we conducted indicated the highest scale of adoption in southwest China and India with 34% and 10% of the reported wheat area, respectively. In addition to having biotic resistance, these varieties demonstrate high yield potential, have good quality attributes, and are suitable for the development of biofortified wheat.

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Acronyms

CAIGE	CIMMYT Australia ICARDA Germplasm Evaluation
CIMMYT	Centro Internacional de Mejoramiento de Maíz y Trigo
CIS	Commonwealth of Independent States
CWR	Crop wild relatives
GRIN-Global	Germplasm Resource Information Network
ICARDA	International Center for Agricultural Research in the Dry Areas
IN	International nurseries
ITPGRFA	International Treaty on Plant Genetic Resources for Food and Agriculture
KSU	Kansas State University
MTA	Marker trait associations
NARS	National agricultural research systems
SHW	Synthetic hexaploids wheat
SHDL	Synthetic hexaploids derived lines
SSR	Simple sequence repeat
PPM	Parts per million

Contents

1	Introduction	5
2	Context	7
3	Data and methods	8
3.1	ICARDA/CIMMYT collections	8
3.2	<i>Aegilops tauschii</i> pre-breeding and development of SHW	9
3.3	Distribution of SHW by CIMMYT genebank	9
3.4	Incorporation of SHW derived lines in international nurseries	9
3.5	Variety releases from SHW	10
4	Results	10
4.1	<i>Aegilops tauschii</i> in genebank collections	10
4.2	<i>Aegilops tauschii</i> pre-breeding and development of SHW	11
4.3	Distribution of SHW by CIMMYT genebank	12
4.4	International nurseries (IN)	12
4.5	Variety release	13
5	Discussion	15
6	Conclusion	18
7	References	19
8	Tables	22
9	Figures	23
10	Annexes	33

1 Introduction

Changes in climate and human society pose immense challenges for food security and crop biodiversity. The world population is expected to reach 9.3 billion by the year 2050 and global food demand is expected to double by that time (Dempewolf et al. 2014; Zhang et al. 2017; Barrett 2010). As a consequence, agricultural systems are subject to ever-increasing pressure to supply more food under less optimal conditions. Wheat is among the four crops providing 75% of calories to the world population. More than 4.5 billion people obtain 21% of their calories and 20% of their protein from wheat (Ogbonnaya et al. 2013; Lobell et al. 2011).

Lobell et al (2011) reported that climate change slowed yield growth trends in wheat from 1980 to 2008. By 2080, climate change effects associated with the predicted increase of drought and extreme temperatures are expected to cause yield losses of 10 to 30% (Kumar et al. 2013). Diseases and insect pathogens also cause considerable yield loss, and new, more virulent races and biotypes¹ are threatening the wheat production (Bahrani and Joo 2011).

In many regions of the world, wheat yields are now reaching a plateau and this is assumed to be due to lack of genetic variation (King et al. 2018). Under stressed environments, yield annual genetic gain reaches only 0.3 to 0.5% while it should increase by 2% to meet future global demand (Velu and Singh 2013). Future enhancement of wheat production can be achieved through the increase of productivity per unit of area, but this will require the development of high-yielding, environmentally adapted wheat varieties with high tolerance to biotic and abiotic stresses (Zhang et al. 2017; Velu and Singh 2013; King et al. 2018).

Climate change and its deleterious effects require access to a large genepool including landraces² and crop wild relatives³ (CWR). Wheat wild relatives provide an important reservoir of genetic diversity distributed over a wide range of geographic conditions (Mickelbart et al. 2015). These wild relatives were successfully used to transfer resistance to the major diseases and insects of wheat. The survey conducted by (Hajjar and Hodgkin 2007) over 13 crops showed that CWR are used extensively as a source of resistance to pests and diseases. Eleven wheat wild relatives were used for disease and pest resistance. *Aegilops tauschii* is the donor of stem rust resistance genes *Sr33*, *Sr45*, and *Sr46* (Rouse et al. 2011). A high level of tolerance to drought, heat and salinity has been found in *T. dicoccum*, *T. diccoicoides*, *Aegilops tauschii*, *Aegilops geniculata*, *Aegilops speltoides*, *Aegilops searsii* and

¹ Biotypes: a group of organisms having an identical genetic constitution.

² A crop cultivar that has evolved through many years of farmer-directed selection and that is specifically adapted to local conditions; landraces are usually genetically heterogeneous.

³ The possible progenitors of the cultivated crops; they have a relatively close genetic relationship to a crop.

Aegilops biuncialis. *Triticum turgidum* subsp. *dicoccoides* was found to hold high genetic diversity for grain nutrients and protein content. Zinc and iron concentrations were twice as much in the wild accessions⁴ as in the accessions of cultivated genotypes (Chatzav et al. 2010; Dempewolf et al. 2017).

The survival of CWR in their natural habitats is subject to several threats including climate change and land reclamation and degradation. There is need to reduce the loss of biodiversity through promoting *in situ* conservation and sustainable use as per the targets of the convention on biological diversity (Ford-Lloyd et al. 2011).

At the same time, *ex situ* conservation in genebanks is needed to house and maintain this fundamental raw material in a form that can be directly accessed by plant breeders and researchers in the process of selection and crop improvement. Genebanks represent a wealth of genetic potential, genetic variation, and an insurance against future challenges (Xepapadeas et al. 2014). There are some 1750 genebanks in the world conserving around 7.4 million accessions. Genesys⁵ records 283,282 wheat accessions worldwide, of which 13,183 are wild relatives. CIMMYT and ICARDA hold 50% of the global wheat collection, with CIMMYT genebank being the largest for a single crop; it conserves more than 150,000 wheat accessions. Though the total economic value of these collections is virtually inestimable, we know that the greatest share of that value is derived from the use of its accessions mainly in wheat genetic improvement (Smale 2019 WP1). CWR accessions cannot be used by the breeders in their original wild form but must be pre-bred into germplasm that is then deployed to transfer valuable traits. In other words, a genetic “bridge” is needed to link conservation to use of CWR.

Wheat synthetic hexaploids⁶ (SHW) are the result of artificial crossing of the wild progenitor goat grass (*Aegilops tauschii* DD) to tetraploid wheat (*T. turgidum* ssp. *durum*, AABB). Mujeeb-Kazi (1995) described the procedure to develop SHW. The durum line is selected based on agronomic performance and is used as a female. After pollination using *Aegilops tauschii* selected for a certain trait (e.g. resistance to pests and diseases), the chromosomes of the F1 hybrid are doubled. The result is a primary SHW⁷.

⁴ Accession: A distinct, uniquely identifiable sample of seeds representing a cultivar, breeding line or a population, which is maintained in storage for conservation and use.

⁵ Genesys is an online platform where you can find information about Plant Genetic Resources for Food and Agriculture (PGRFA) conserved in genebanks worldwide. See <https://www.genesys-pgr.org/>.

⁶ Hexaploids are species that possess six homologous chromosome sets per cell

⁷ The development of SHW is based on the origin of the wild parents and the agronomic performance of the tetraploid parent. This approach was criticised for being random and not strategic. However, SHW exhibited traits that are not expressed in neither of the parents and vice versa, which justifies the way SHW are developed.

The SHW represents the ideal bridge for transferring desirable traits from either parent to adapted bread (common) wheat (*Triticum aestivum* subsp. *aestivum* AABBDD) and broadening the genetic base for plant breeding (Singh et al. 2018). CIMMYT used approximately 900 *Aegilops tauschii* accessions maintained in the genebank collections to produce approximately 1300 primary SHW between 1988 and 2010. In turn, the lines derived from SHW represent an importance source of untapped genetic variation for improved traits like high yield potential, tolerance to heat and drought and resistance to pests and diseases (Ogbonnaya et al. 2013).

Despite the increase in the number of publications citing many traits found in species of wild relatives, there is delayed recognition and a lack of information about the incorporation of these traits in released varieties of wheat (Hajjar and Hodgkin 2007; Zhang et al. 2017). In 2003, Carmona and Chuanmai were released in Spain and China, respectively. Both have synthetic hexaploid backgrounds obtained from CIMMYT. Since then, Li et al. (2018) reported 62 varieties registered in many countries.

Considering the points raised above, this study addresses the different components of wheat improvement using *Aegilops tauschii*. We first examined how the development of SHW mobilized *Aegilops tauschii* from the genebanks. We then assess the use of SHDL (synthetic hexaploids derived lines) by plant breeders. Finally, we provide survey estimates of adoption of derived varieties in farmers' fields.

2 Context

Access to diverse genetic resources allows plant breeders to select and improve crops for desirable characteristics, including productivity; it is estimated, for example, that half of the yield gains in cereals grown in the United States over time have been attributed to genetic improvement (Rubenstein et al. 2005). Since the 1990s, the number of citations for breeding use of CWR has grown substantially. However, there is limited information about the release of varieties with CWR in their genetic backgrounds and their impact in farmers' fields. It is also difficult to assess the economic value derived from CWR once their allelic variation is introduced into bred cultivars.

After sunflower, wheat is the second crop with the highest documented use of CWR. Most of those uses are associated with biotic resistance and abiotic tolerance (Dempewolf et al. 2017; Zhang et al. 2017). To date, Genesys records 5,876 accession of wheat wild relatives conserved at ICARDA (International Center for Agricultural Research in the Dry Areas) and CIMMYT (Centro Internacional de Mejoramiento de Maíz y Trigo). Gollin et al. (1998) showed that much of the value of large collections is derived from the shape of the probability distribution for traits. The rarer the trait, and the greater the economic size of the problem, the greater the payoff.

Aegilops tauschii is confirmed as the source of several economically important traits. Several researchers have studied the diversity of SHW and evaluated them with respect to agronomic performance and yield stability. Recently, Li et al. (2018) reported 62 wheat varieties derived from SHW in several countries. Previously, Ogonnaya et al. (2013) reported that lines derived from SHW represented 26% of all the lines made available by CIMMYT international nurseries.

Evaluating the impact of SHW highlights the contribution of CWR conservation and pre-breeding to variety releases. Analysis by component (i.e. conservation, pre-breeding, distribution and breeding, use in farmer's fields) widens our perspective about the role played by genebanks throughout the process of genetic improvement.

3 Data and methods

3.1 ICARDA/CIMMYT collections

SHW have been developed with the purpose of serving as a bridge to transfer desirable traits from either parent of common wheat into adapted varieties of bread wheat. *Aegilops tauschii* is the main source of many traits in SHW. CIMMYT and ICARDA are the two CGIAR centers working on wheat improvement. Their two genebanks conserve and supply germplasm to several national and international partners under the multilateral system of the ITPGRFA (International Treaty on Plant Genetic Resources for Food and Agriculture). Therefore, the analysis of their *Aegilops tauschii* collections is essential to address the availability of this raw germplasm.

Data on the number of accessions and passport information⁸ were compiled for CIMMYT and ICARDA collections of *Aegilops tauschii*. For ICARDA, the information was collected from the genebank database; data for CIMMYT was found in GRIN-Global (Germplasm Resource Information Network), which is the documentation system used by CIMMYT genebank. Genesys, a global portal for plant genetic resources, was also consulted to compare and complete some of information. The information collected included the accession number, country of origin, latitude and longitude based on the availability of georeferenced information. The georeferenced data was then used to plot the origins of the materials in the two collections in order to indicate the complementarity and level of duplication between the two collections. During a visit to Kansas State University (KSU), access to hard copy records of collecting missions allowed the identification of the country of origin for 54 *Aegilops tauschii* accessions used in the development of SHW.

⁸ Passport information: Basic information about the origin of an accession, such as details recorded at the collecting site, pedigree or other relevant information that assists in the identification of an accession.

3.2 *Aegilops tauschii* pre-breeding and development of SHW

We compiled data of the SHW developed by CIMMYT since 1986. The data included the year of development, the female parent, the male parent used for the crosses, and the full pedigree⁹ of the line. The CIMMYT genebank provided the accession number and passport data for the *Aegilops tauschii* accessions used in SHW crosses.

Our analysis focused on three aspects: the variation in the parents used for the development of SHW, the origin of these parents, and the evolution of SHW development over the years. Spatial analysis was performed to assess the trends in *Aegilops tauschii* parents and see which region is more represented in the SHW collection. We then sought the reasons behind the geographical distribution. GRIN Global, Genesys and reports provided by KSU were used to complete the passport data and related information for the accessions used in SHW development. The origins of 498 accessions were identified, while 131 remained with unknown country of origin. The online app Mapmaker¹⁰ was used to visualize the geographic distribution of *Aegilops tauschii* used in the crosses to develop SHW.

3.3 Distribution of SHW by CIMMYT genebank

Distribution is one of the core genebank activities. The first step toward making an impact is to make the germplasm available for potential users. We evaluated the direct distribution of SHW by the CIMMYT genebank from 2000, with a focus on external requests. The data collected consisted of the list of accessions distributed by year, country, institution and requestor. Once the 10,167 samples distributed externally were identified, we calculated the percentage of SHW in the total number of samples distributed and the number of samples received by each country and institution.

3.4 Incorporation of SHW derived lines in international nurseries

In order to assess the evolution of lines derived from synthetic hexaploid wheat in the international nurseries (IN), seven wheat IN were selected based on their importance to the wheat breeding programs. Data were available for all the years until 2018 for six of the nurseries; the International Septoria Observation Nursery (ISEPTON) was analyzed since the 10th nursery due to lack of data for the first nine years. Main IN included yield trials nurseries, elite spring wheat yield trials (ESWYT), semi-arid wheat yield trials (SAWYT), and high rainfall wheat yield trial (HRWYT). The other four nurseries for disease screening, scab resistance screening nursery (SRSN), and *Fusarium* head blight screening nursery (FHBSN), are complementary nurseries. Table 1 presents a summary of the years and the number of nurseries for each IN. We focus on the number of SHDL in each nursery, applying

⁹ Pedigree: The record of the ancestry of a genetic line or variety.

¹⁰ <https://www.darrinward.com/lat-long/>

this as an indicator of SHW use in the spring wheat breeding. International winter wheat¹¹ nurseries were analyzed for the last five years. Detailed results are not presented since no clear conclusion could be drawn from such a brief time period.

3.5 Variety releases from SHW

We assess the impact of SHW in farmers' fields by tracing the germplasm from release to adoption of wheat varieties. The list of bread wheat varieties grown worldwide was compiled from online databases¹², literature review, wheat breeders in national agricultural research systems (NARS), and national official sources. We started by collecting the lists of varieties for 92 countries available in Wheat Atlas. The list of varieties in each country was compiled with additional information on year, pedigree, growth habit, and any other information about the variety. Using the pedigree information, we identified the varieties which included SHW in their pedigree. Out of more than 6,900 varieties, we identified 86 varieties derived from a cross involving *Aegilops tauschii*. This included the first cultivar derived from direct cross of wheat to *Aegilops tauschii* in 1994, which was released in Armenia.

After the identification of the varieties with SHDL in their pedigrees, an expert consultation was conducted in order to assess the extent of adoption by farmers and trace back the way the candidate parents reached the NARS. The consultation involved 13 NARS breeders and CIMMYT representatives in countries where these varieties were released. A total of 62 varieties in 13 countries¹³ were included in this survey. The questionnaires were customized based on the country, the number of varieties, and available information about each variety. We collected information about the growing conditions, the area cultivated, the yield potential, use of SHW in NARS crosses, the traits associated with these varieties, and the expectation of their adoption in the next five years.

4 Results

4.1 *Aegilops tauschii* in genebank collections

Together, ICARDA and CIMMYT hold 1,570 accessions of *Aegilops tauschii* with country origins from Turkey to west of China. Iran and Azerbaijan are the most represented countries with 23% and 17% of the genebank holdings, respectively, coinciding with parts of the major areas of distribution of

¹¹ Winter wheat: wheat that requires vernalization to reach heading, the plants should go through cold winter temperatures (0°C to 5°C) for 30 to 60 days.

¹² e.g. <http://www.wheatpedigree.net/> and <http://wheatatlas.org/>

¹³ The countries included in the survey are: Afghanistan, Argentina, Australia, Bolivia, China, China, Ethiopia, India, Iran, Kazakhstan, Mexico, Pakistan, Turkey and Uruguay.

this species. A recent study by Singh et al. (2018) using genotypic data highlighted a high level of duplicates among *Aegilops tauschii* collections in Punjab Agricultural University (PAU), Wheat Genetic Resources Center (WGRC) at KSU, and CIMMYT genebanks. CIMMYT was found to have only 57% unique accessions. The level of duplicates among the three centers was estimated at 50%. The geographic distribution of georeferenced accessions at ICARDA and CIMMYT shows some redundancies in the two collections based on the collecting sites (Figure 1). Part of the duplication is linked to the germplasm exchange among the different genebanks. Instead, the level of duplication should be assessed in the global collection of *Aegilops tauschii* in order to locate gaps of less represented hotspots and identify unique accessions. The gap analysis conducted by the Global Crop Diversity Trust classified *Aegilops tauschii* as a species with low priority for collecting. However, any new assessments should take into consideration the current threats to the natural habitat of goat grass. It will be also rewarding to compile information on accessions held by other genebanks, mainly from India, Iran, Georgia and Russia. In addition, trait gap analysis is needed to better target adaptive traits in future collecting missions.

4.2 *Aegilops tauschii* pre-breeding and development of SHW

Our results show that 629 unique accessions of *Aegilops tauschii* were used to develop 1,577 primary SHW since 1986. These accessions originate from at least 15 countries represented in different proportion. In addition to *Aegilops tauschii*, CIMMYT is now using *Aegilops speltoides*, *Triticum urartu*, *Triticum monococcum* to enhance diversity and introduce new traits through the donors of A and B genome. Moreover, 185 tetraploid wheat parents (*Triticum turgidum* subsp. *durum* and *Triticum dicoccon*) were used with an average of 16 parents each year. The use of *Triticum dicoccon* in the development of SHW at CIMMYT started in 1998, and it resulted in the development of 99 primary SHW using 36 emmer parents. On average, 42 *Aegilops* accessions were used every year to produce around 62 SHW. Since 2013, more diversity is introduced as we observed the use of 105 tetraploid parents and 95 *Aegilops tauschii* accessions (Figure 2). Since 2008, the number of tetraploid parents used in the crosses has increased in comparison to the previous years.

In terms of origin, Iran is the first contributor to the development of SHW with 231 accessions of *Aegilops tauschii* followed by Afghanistan with 111 accessions (Figure 3). The two countries provided more than 54% of the total accessions used to create SHW. Azerbaijan has 44 accessions involved in the crosses, although the richness of genebank collections of accessions from Azerbaijan is not reflected in the development of SHW. The origin of the 131 *Aegilops tauschii* accessions is unknown (Figure 3). Mapping the geo-localized accessions allows us to visualize more clearly the regions that were extensively represented with respect to the intensity of use in pre-breeding (Figure 4).

4.3 Distribution of SHW by CIMMYT genebank

The analysis of SHW distribution by the CIMMYT genebank provides a clear view of the demand for this germplasm and the role of the genebank in supporting other institutions. Since the year 2000, CIMMYT has distributed 10,167 samples to 110 institutions in 40 countries; ICARDA received 988 samples representing nearly 10% of the total samples distributed (Figures 5 and 6). China comes as the first country to request SHW from CIMMYT with 1322 samples, followed by the United States of America with 957 samples, and the United Kingdom with 877 samples. This ranking is reflected in the number of institutions that received the material in each country. Fifteen institutions are from USA, followed by China with 13 institutions (Figure 5). Between 2000 and 2013, SHW represented, on average, 21% of the germplasm distributed externally by CIMMYT genebank.

At the regional level, Asia received 30% of the samples, followed by Europe and Latin America with 24% and 20%, respectively. The United Kingdom has worked closely with CIMMYT to include SHW in the improvement of winter bread wheat, as reflected on the number of SHW received from CIMMYT genebank. The exchange of germplasm under the CAIGE (CIMMYT Australia ICARDA Germplasm Evaluation) project allowed evaluating and screening a high number of SHDL for several traits. This evaluation data is publicly available, and its analysis could provide information on the contribution of SHDL to different traits.

4.4 International nurseries (IN)

The analysis of the distribution of IN provides an indication of the “internal” use of SHW, i.e. within the international research network including centers such as CIMMYT or ICARDA and national agricultural research systems (NARS). IN are the gateway of germplasm before its testing and proposal for release by NARS. Our study assessed 142 spring bread wheat IN for the number of SHW evaluated every year (Table 1). The results show that the first two lines derived from SHW were sent to the ESWYT nursery in 1996. Since then, 853 lines derived from crosses with *Aegilops tauschii* have been sent within the seven IN studied (Figure 7). More than 50% (446 lines) of these 853 are unique lines. It is noticeable that the presence of SHW in the IN has been increasing with more SHDL screened for disease resistance. In 2016, out of the 119 SHDL, 66 were screened for stem rust resistance – representing 40% of the total lines in STEMRSN for that year. In the last nine years, *Septoria* screening nursery received around 30% of the total SHDL screened for disease resistance.

Analyzing 22 years from ESWYT and SAWYT data revealed that SHW are used twice as often in SAWYT (17%, compared to 9% for ESWYT). SAWYT received 190 SHDL, with an average of eight lines per year, whereas 110 SHDL lines were sent to ESWYT with the average of five lines per year. In the 15th SAWYT, SHDL represented 46% of the total lines, a finding highlighted previously by

(Lage and Trethowan 2008), their analysis of the coefficient of parentage (CoP) showed that between the 5th and 15th SAWYT, the average CoP fell down from 75% to 19%. This suggests that the increase in numbers of SHDL was associated with an increase in the latent diversity conferred through parentage of the elite germplasm. The conclusion we draw from these findings is that SHDL attracted the interest of breeders to acquire them and use them in their programs.

As most SHW is developed using spring durum wheat as parents, the winter wheat IN were analysed separately to avoid any misleading conclusions. Our analysis of five years (2013–2018) of facultative¹⁴ and winter wheat IN showed less incorporation of SHDL in these nurseries than in the spring wheat IN. Since 2013, strictly winter wheat nurseries received only 19 lines out of the 76 sent for both facultative and winter wheat nurseries. However, we observed that there is growing use of *Aegilops speltoides* (the donor of the B genome to wheat) over the five-year period.

4.5 Variety release

Our investigation identified 86 bread wheat varieties derived from a cross with *Aegilops tauschii*. Voskehask, released in 1994 in Armenia, is included as the first identified variety that resulted from a direct cross of bread wheat with *Aegilops tauschii*. Since 2003, 85 varieties resulting from SHW were released in 21 countries. The analysis of pedigree showed that five accessions from China, Iran, and Russia contributed to the release of 22 cultivars in 13 countries.

Among countries included in the survey, China, India and Pakistan have the highest number of varieties released with 18, 10 and nine varieties, respectively (Annex 1).

The survey revealed that IN are the first source of germplasm for NARS, as more than 57% of candidate lines reached national programs through the IN. Except for Pakistan, the NARS in the surveyed countries are using SHW and their derived varieties in the breeding program. In China, the success of the cultivar Chuanmai 42 released in 2004 triggered the use of more SHW in the breeding program. Chuanmai 42 broke the yield record by surpassing the commercial check with 35% grain yield (Li, Wan, and Yang 2014), leading to more varieties released with SHW germplasm. High yield stability, good quality attributes, disease resistance and drought tolerance made Chuanmai 42 successful. Currently, our survey respondent reports that Chuanmai 42 is planted to over 100,000 hectares in southwest China. The wheat area in southwest China totals 2 million hectares; varieties derived from SHW currently occupy an estimated 34% of this area (689,000 ha). The leading varieties are Chuanmai 104 grown on 200,000 ha followed by Chuanmai 42, Shumai 969, and Mianmai 367 cultivated on 100,000 ha each (Figure 8). All of these cultivars are grown under irrigated conditions

¹⁴ Facultative wheat: wheat with partial sensitivity to vernalization. It requires short vernalization and it is less tolerant to cold than true winter wheat.

and their yield potential ranges from 8 t/ha to 9 t/ha. With the exception of Chuanmai 42, it is expected that each will be grown on larger areas in the future. Wheat area planted to Chuanmai 42 is decreasing although it is still used in the crosses by national breeders. The varieties released from 2011 to 2014 with Chuanmai 42 as a parent yield 8.5% higher than varieties released from 2006 to 2010. This variety is now playing a crucial role in enhancing the production of modern wheat in south west China (Li et al. 2014).

In India, the 10 cultivars derived from SHW are now grown on 3.15 million hectares, representing 10% of the total area cultivated by wheat. WH-1142 and MP 1203 are the two major varieties adopted on 1.5 million and 1 million hectares, respectively (Figure 9). Interestingly, WH-1142 wheat variety reached this area only four years after its release. WH-1142 is resistant to yellow rust, possesses high levels of protein (12.1%), iron (36.4 ppm), zinc (33.7 ppm), and has a good bread quality score. This variety is cultivated in the north west plains zone of India under restricted irrigation. MP1203 is grown in the central zone for late sowing under irrigation. The cultivar KRL 213 is adopted in the salt affected areas of the northern plains and covers around a hundred thousand hectares, while Zinc Sakhti, a biofortified variety, is desired for its bold attractive grains. These two varieties are expected to be grown on larger acreage in the next five years.

Relatively less information was gathered for Pakistan, Turkey and Argentina. In Pakistan, the yield potential reported by survey respondents ranged from 2.7 t/ha to 3.5 t/ha based on the growing conditions. SHW-derived varieties are in initial phases of diffusion and it is estimated that they currently occupy 12,180 hectares. Yakamoz and Altinbasak are two wheat varieties released for irrigated conditions in Turkey. Their yield potential ranges from 6.5 to 9.5 t/ha, Yakamoz is cultivated on 5000 hectares. SRM NOGAL was released in Argentina (2006) targeting 25% of the national area, it is now replaced by new varieties that are also derived from SHW according to the survey. Currently, BIOINTA-1006 released in 2009 is planted to 5 to 10% of the national area. Our survey revealed that SHDL represents 30 to 40% of the germplasm used in the national breeding program in Argentina. In China, by comparison, the number rises to 80%.

Out of all of the 45 varieties for which we received a survey response in seven countries, 93% were described as resistant to pests and disease. Yield potential and yield stability are the secondary traits for which these varieties are desired, as 38 of 45 have good yield potential and yield stability. An interesting finding is that end-use quality (i.e. high protein and micronutrients content) is a key trait in the varieties derived from SHW. Drought and heat tolerance are each reported in around 15% of the cases (Figure 10) whereas other abiotic stresses characterize 28% of the cultivars.

The rate of response to the survey was not high, yet it covered the countries where farmers are adopting synthetic-derived varieties. More data is needed from other countries in order to assess the use of SHW in contrasting environments.

5 Discussion

SHW illustrates the use of CWR in pre-breeding and the impact generated on breeding and variety release. The role of the genebank is crucial in this process as it protects against the loss of wild crop relatives in natural habitats, conserving and making them available in pre-bred germplasm to breeders and other users. The initial *Aegilops tauschii* accession used to develop SHW was obtained from several genebanks including CIMMYT genebank (Mujeeb-Kazi 1995). The trends in distribution of SHW by CIMMYT genebank is an indicator of the extensive use of SHW in research and breeding.

SHW shows also the importance of pre-breeding in linking the conservation to the use of CWR. The *Aegilops tauschii* collection has been well utilized in pre-breeding, although use aspect varies by geographical region. Accessions from some regions like Azerbaijan and Commonwealth of Independent States (CIS) are not yet used extensively in the development of SHW. This area holds high level of diversity in *Aegilops tauschii*, conserved in *ex situ* collection. Efforts should be implemented to identify the gaps in the global collection and fill them, as there is a high level of duplication within and between collections of *Aegilops tauschii*. As suggested by Dempewolf et al. (2014), such analysis should assess the vulnerability of goat grass natural habitat to prioritize the most endangered areas. Pre-breeding activities can be strengthened by the use of passport data and information available about CWR to target specific traits. Other wheat wild relatives are also essential to widen the genetic bases of the A and B genome for wheat. This is already reflected in the use of new species (*Aegilops speltoides*, *Triticum urartu*, *Triticum monococcum*) in CIMMYT pre-breeding program.

Contrary to the classic use of genebank germplasm, where the accession is used based on the identification of a specific trait, the development of SHW aims to bring the maximum allelic variation and introduce it to an adapted background. That is why the crosses are random and the selection of the parents is based on practical considerations such as crossability and pollen quality from the parents. Moreover, especially when it comes to abiotic stress tolerance, the performance of the SHW cannot be predicted based on the performance of the *Aegilops tauschii* or the tetraploid parent because some alleles¹⁵ from both parents are not detected in SHW. Performance may be due to epistatic gene interaction¹⁶, modified gene expression, and high genetic diversity in *Aegilops tauschii* which results

¹⁵ Allele: One, two, or more alternate forms of a gene occupying the same locus on a particular chromosome.

¹⁶ Epistatic gene interaction: The interaction of genes at different loci.

in phenotypic variation in the SHW (Dreisigacker et al. 2008). In another example – screening for Hessian fly resistance – SHDL derived from the same *Aegilops tauschii* accession showed differences in reaction to Hessian fly ranging from susceptible to resistant (Yu et al. 2012). Moreover, because of the winter and weedy growth habit of *Aegilops tauschii*, it is hard to grow and test it for several traits under field conditions.

With the combination of traits from both parents (*Aegilops tauschii* and tetraploid wheat), SHW represent the ideal material to increase both yield potential and diversity for several traits simultaneously (Dreisigacker et al. 2008). The use of simple sequence repeat (SSR) markers showed that breeding lines derived from SHW had higher diversity compared to the wheat of the Green Revolution. In fact, the level of diversity is close to that of landraces cultivated prior to the Green Revolution (Warburton et al. 2006). Ogonnaya et al. (2013) reported more than 42 mapping population for yellows rust, head scab, Hessian fly, drought tolerance, milling and baking quality, and other traits. They also reported more than 100 sources of useful genes for resistance to major pests and disease. Transferring these traits into released varieties is challenging because breeders are reluctant to the use of exotic germplasm as it is a long-term process. Additionally, necrosis of the F1 is a major limitation to the use of SHW by the breeders. Most of the SHW inherit *Ne1* dominant gene from durum wheat parent located on chromosome arm 5BL. When SHDL carrying this gene are crossed with bread wheat lines having another dominant gene *Ne2* located on chromosome arm 2BS, there is a problem of necrosis at the F1 progeny, which occurs in 1 to 50% of the cases (van Ginkel and Ogonnaya n.d.; Chu et al. 2006).

Despite these constraints, this study showed that SHW have found their way into breeders' collections and the IN results indicate that SHW were extensively explored for disease and pest resistance and agronomic performance. This finding is consistent with the survey results where 93% of the released varieties have been characterized by resistance to biotic stresses. Resistance to yellow rust, leaf rust, and *Septoria* is registered in most of the released varieties surveyed. More than 50% of the traits associated with the use of wheat wild relatives are resistance to pests and diseases as reported by Dempewolf et al. (2017).

In Morocco, Aguilal is the first SHW released in 1998 with resistance to Hessian fly and to UG99, but was susceptible to yellow rust new virulences. Kharoba, also derived from SHW, combines resistance to yellow rust, stem rust, and Hessian fly – the last one considered as the major pest for wheat production in Morocco (Elhaddoury et al. 2012). Chuanmai 42 inherited its resistance to stripe rust from the tetraploid durum parent (i.e. Decoy 1) of the SHW. Other SHW screened in China inherited their resistance to powdery mildew from the *Aegilops tauschii* parent (Chu et al. 2006). *Aegilops tauschii* is the donor of stem rust resistance genes *Sr33*, *Sr45*, and *Sr46*. Twelve *Aegilops tauschii*

accessions distributed across Azerbaijan, Iran, Turkmenistan, and Uzbekistan showed combined resistance to six different races of stem rust. This suggests that these countries could be the hotspot for resistance to *Pgt* races (Rouse et al. 2011). In another study, despite the durum parent was susceptible to tan spot, Hessian fly and *Stagonospora nodorum* blotch, the synthetics derived from this parent showed resistance to these pests and diseases. This indicates that the *Aegilops tauschii* parents are potential sources of resistance, the same lines inherited resistance to stem rust from the tetraploid parent (Friesen et al. 2008).

Yield potential and yield stability are ranked as the second most important trait in the released varieties; they are the first requirement for release and adoption by the farmers. Previous studies reported an increase of SHDL yield in comparison to the recurrent parents. This increase was mainly associated with an increase in seed weight, number of spikes per meter square, and the number of seeds per spike (Cooper et al. 2013; del Blanco et al. 2001). Chuanmai 104 and Chuanmais 64 inherited higher production of seed numbers per spike and higher thousand seed weight from Chuanmai 42 (Li et al. 2014). The findings indicate that a suitable breeding procedure can take advantage of the beneficial traits from SHW and overcome the undesirable ones coming mainly from the wild parent, the breeding procedure is described by Li et al. (2014) for the release of Chuanmai 42. Reaching a good yield stability is associated with the tolerance to drought, heat and to other abiotic stresses where wheat is grown under rainfed conditions, these traits were reported in 60% of the response in the survey.

Twenty-four marker trait associations (MTA) were identified on the D genome of SHW for several grain minerals, suggesting that *Aegilops tauschii* can be a source for biofortified wheat. Other MTAs were located on A and B genome, which means the cumulative effect of multiple alleles could be positive on nutritional quality of wheat grains (Bhatta et al. 2018). In Bolivia, for example, INIAF-Yesera is a biofortified bread wheat cultivar released in a participatory approach for its yield potential (3.6 t/ha), richness in protein, high micronutrients content, and good baking quality. The protein content of the INIAF-Yesera variety in dry base was 16.51%, which greatly exceeds the control of 11.28%, and the zinc and iron concentrations are 4.9 and 3.5 mg*100 g⁻¹, respectively. This result guarantees that the INIAF-Yesera variety meets the wheat requirements for good bread making. Zinc Sakhti, WB02 and HPBW-01 are also zinc biofortified wheat varieties released and adopted together over 250,000 hectares in India. The zinc concentration of Zinc Sakhti and WB02 is more than 14 ppm and 7 ppm, respectively. Zinc Sakhti was released in a participatory approach with farmers and it has early maturity (Singh and Govindan 2017). According to the conducted survey, the area grown by Zinc Sakhti is expected to increase in the next five years, it is grown in the north-eastern plain zones of India.

Thereby, SHW combine pest and disease resistance, yield potential and stability and furthermore quality attributes of wheat (i.e. protein content, micronutrients content and bread making quality). This makes the payoff related to the adoption even greater, as in addition to grain yield, quality traits are a necessary requirement to commercialize the grains. The level of variety adoption was different based on the local seed system in each country, e.g. China and India showed the highest level of variety adoption.

6 Conclusion

Throughout this study, we traced the path of the germplasm from the genebank until the variety release. We highlighted the importance of using wheat wild relatives in pre-breeding to ensure the incorporation of the beneficial traits into adapted background. The analysis of the distribution data and international nurseries showed the importance of SHW through the number of samples distributed from CIMMYT genebank which reached 10,167 samples since the year 2000. This distribution highlights the screening efforts of SHW to explore the potential traits. The international nurseries analysis provided evidence on the evolution of SHW in CIMMYT breeding program over time. The analysis of the performance and selections from the international nurseries could provide a better view of SHDL performance in comparison with the other elite lines. The analysis of the international nurseries was important because they are the first source of germplasm for NARS especially in countries that rely on the CGIAR centers as a main source of germplasm. Thus, any change in the type of germplasm will be translated on the variety release in those countries. The breeder survey demonstrated that, in addition to biotic resistance and agronomic performance, SHW derived varieties have good end use quality and improved nutritional traits.

CWR are an important component of genebank collections, containing a wide range of beneficial, economically important traits for crop improvement, including adaptive traits needed to cope with climate change effects. The utilization of CWR in crop improvement is limited by time and funding constraints, and the need to eliminate undesirable traits from the progeny. Due to their inherent long-term process, pre-breeding related projects should be strategic and designed to cope with future challenges. For example, our study identified varieties that are released from crosses made in 1987. Unless such pre-breeding programs are linked to genebank collections, CWR will remain underutilized. The case of *Aegilops tauschii* collections showed clearly how the pre-breeding program extensively used it in the development of SHW.

New genes for biotic resistance, abiotic tolerance, agronomic performance, and quality attributes were identified in SHW. Some of these traits are expressed only after combining both parents in SHW, meaning that these genetic resources can expand allelic variation. The use of SHW in breeding and

research has expanded over the last 20 years, as demonstrated by the increasing numbers of requests from the CIMMYT genebank. The role of CGIAR centers is clear – 35 varieties either are derived from an advanced line from CIMMYT or have at least one parent from CIMMYT. This underscores the need for well-informed use of resources to collect and conserve unique accessions.

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8 Tables

Table 1. Spring wheat international nurseries included for the use of synthetic hexaploids wheat.

International nursery Abbreviation	Name of international nursery	Period	IN included	Number of nurseries analyzed
ESWYT	Elite spring wheat yield trials	1979-2018	1 st -39 th	39
SAWYT	Semi-arid wheat yield trials	1992-2018	1 st -26 th	26
SRSN	Scab resistance screening nursery	1989-2009	1 st -12 th	12
HRWYT	High rainfall wheat yield trial	1992-2018	1 st -27 th	26
STEMRRSN	Stem rust resistance screening nursery	2006-2018	1 st -13 th	13
ISEPTON	International Septoria Observation nursery	1998-2018	10 th -28 th	18
FHBSN	Fusarium head blight screening nursery	2011-2018	13 th -20 th	8
Total				142

9 Figures

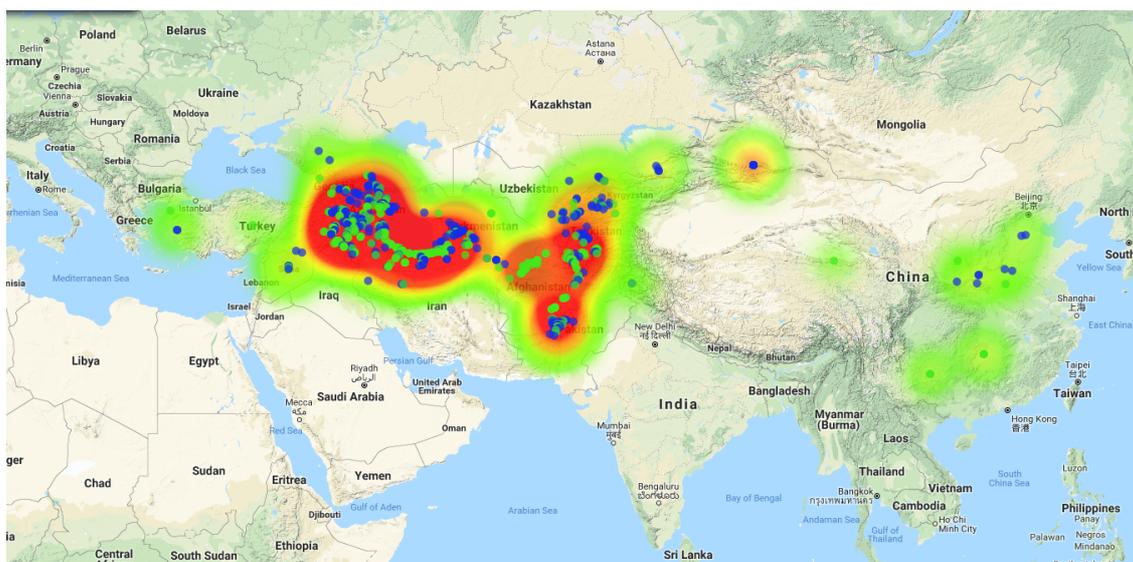


Figure 1. ICARDA and CIMMYT collection of *Aegilops tauschii* accessions. Blue dots represent ICARDA collection and green dots represents CIMMYT collection (Authors). Data sources: CIMMYT GRIN-Global, Genesys and ICARDA genebank database about *Aegilops tauschii* collection.

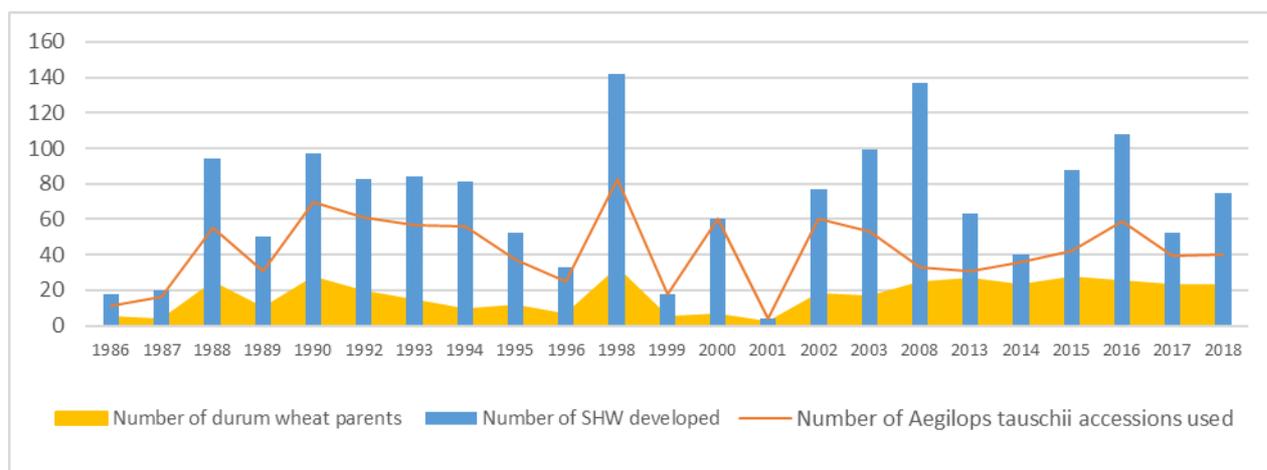


Figure 2. Number of SHW developed and parents used per year since 1986 (Authors). Based on the data provided by the Dr. Masahiro Kishi from the pre-breeding unit at CIMMYT.

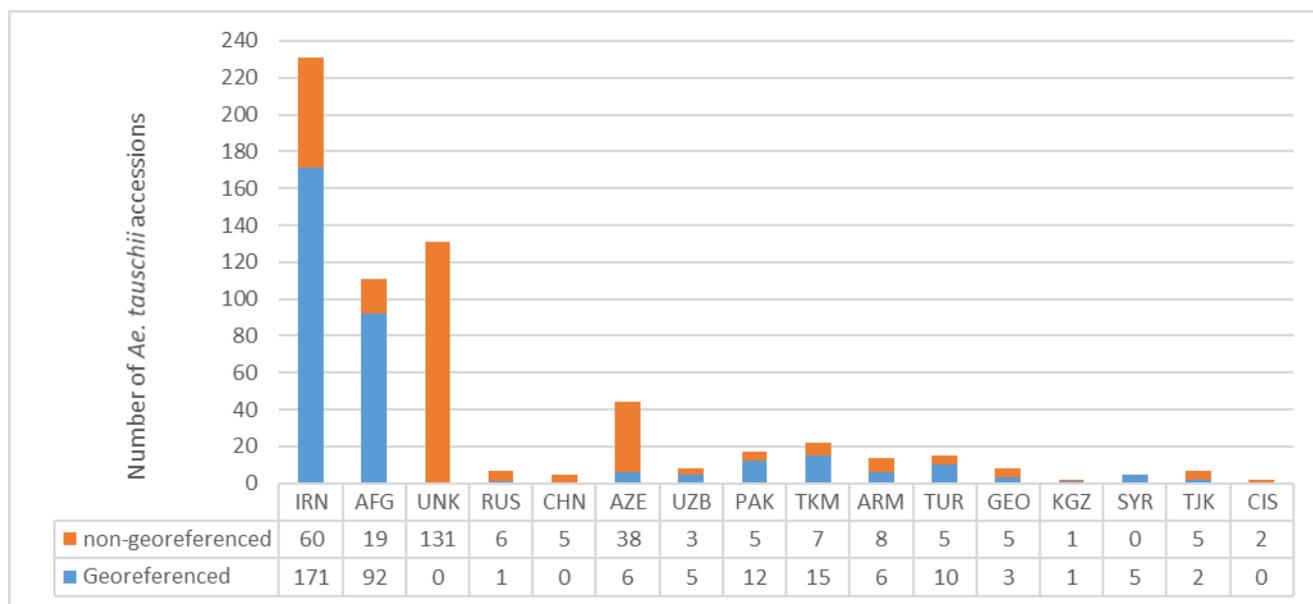


Figure 3. Country of origin for the *Aegilops tauschii* accessions used to develop SHW since 1986 (Authors). Data sources: List of primary synthetics provided by Dr. Masahiro Kishi from CIMMYT, CIMMYT GRIN-Global database.

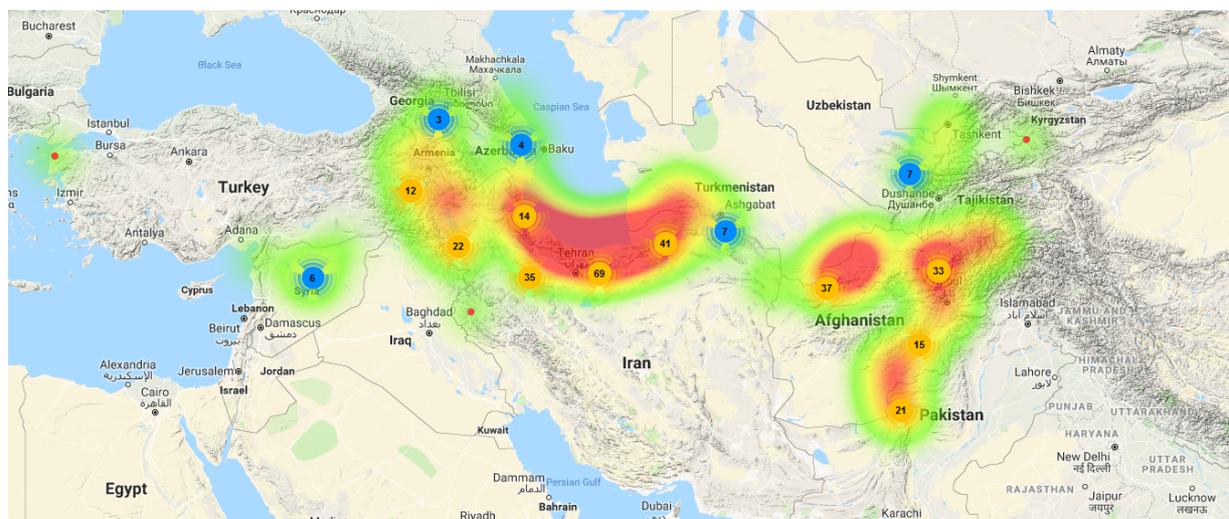


Figure 4. Geographic distribution of geolocalised *Aegilops tauschii* accessions used for the development of SHW by CIMMYT (Authors). Data sources: *Aegilops tauschii* Passport information from GRIN-Global and Genesys

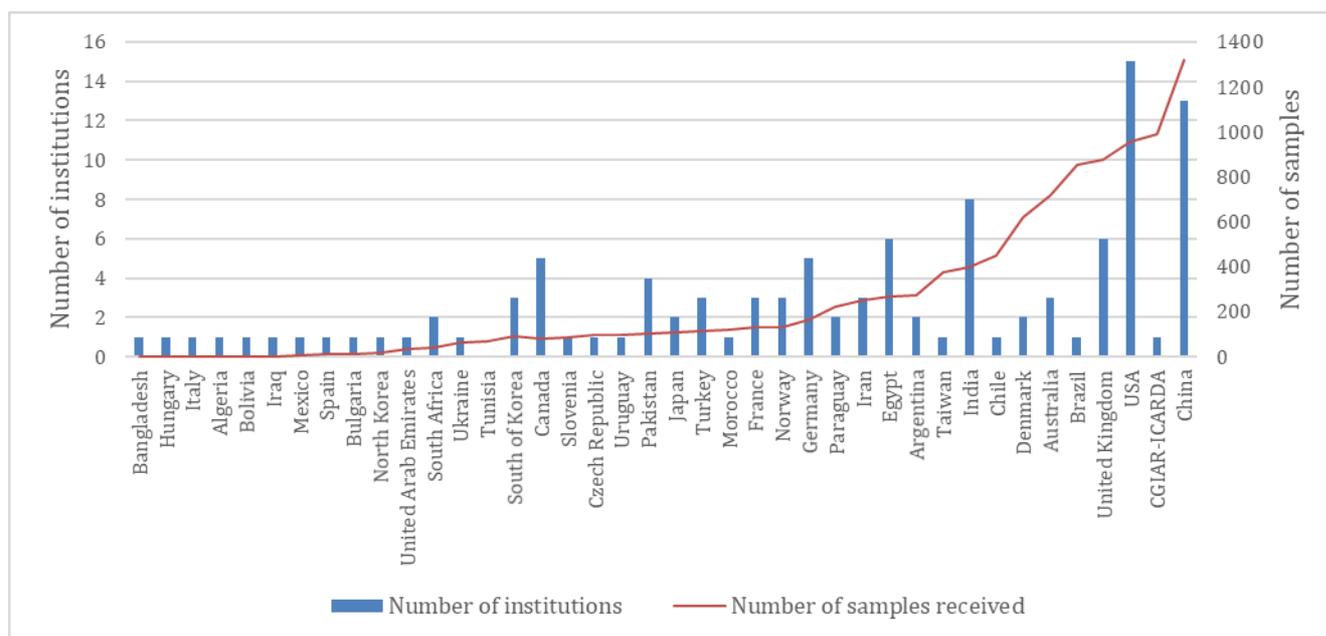


Figure 5. Number of samples and number of institutions in countries receiving SHW germplasm from CIMMYT genebank since 2000 (Authors). Data sources: Distribution data of SHW collected from CIMMYT GRIN-Global.

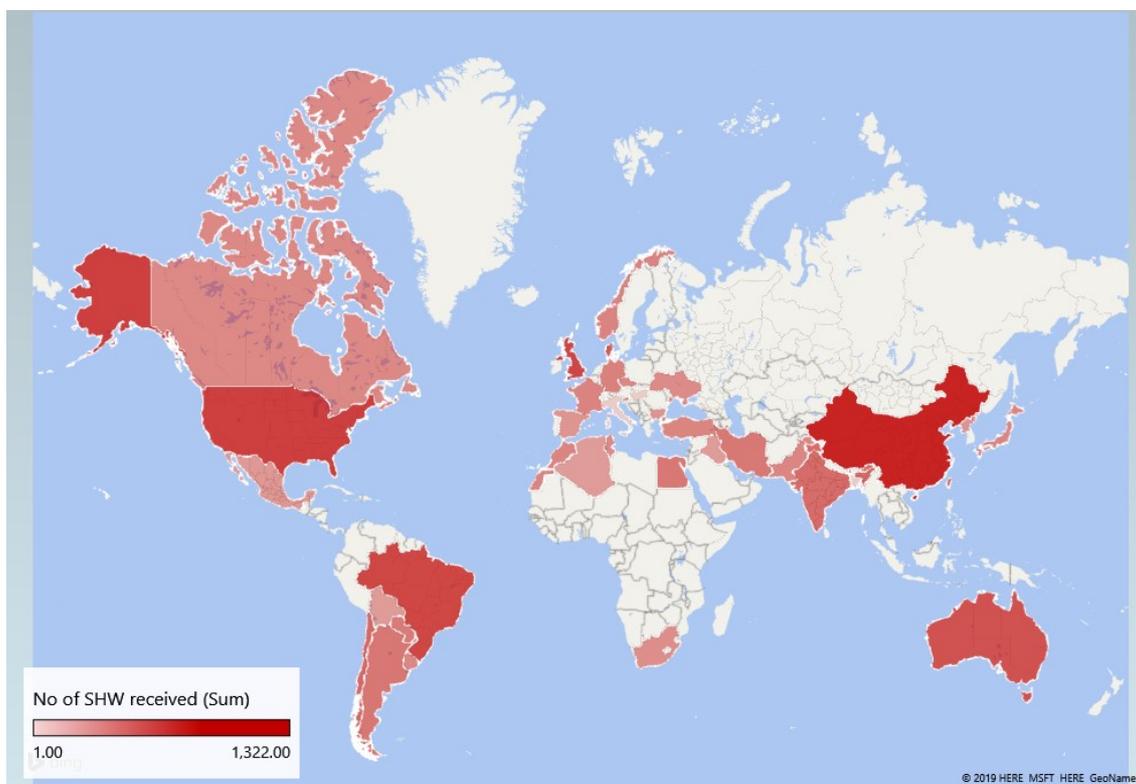


Figure 6. Samples of SHW distributed by CIMMYT genebank between 2000 and 2018 (Authors).

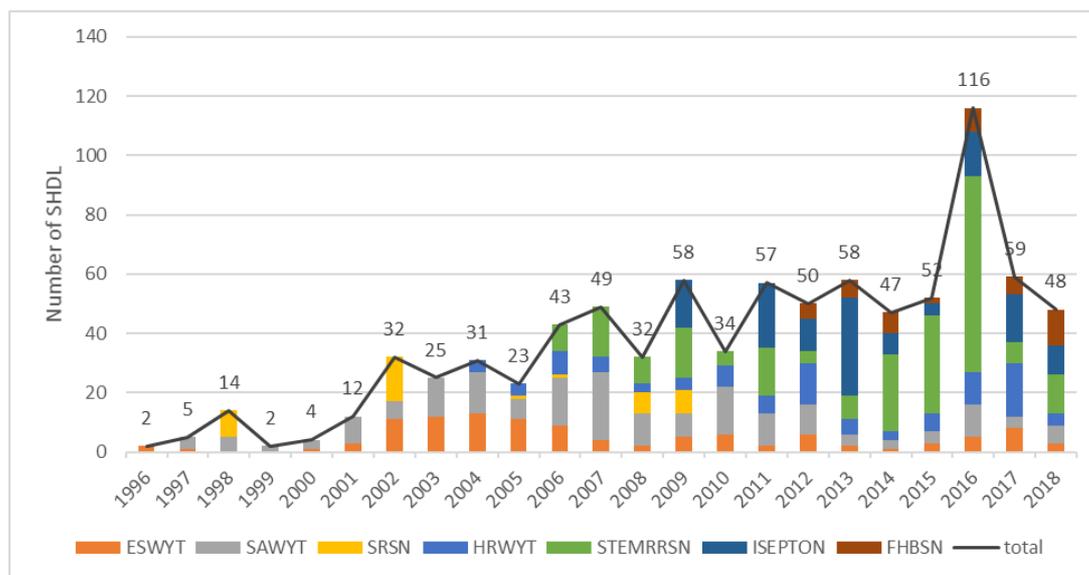


Figure 7. Evolution number of SHDL in seven spring wheat international nurseries (Authors). Data sources: List of international nurseries from CIMMYT International Wheat Improvement Network (<http://orderseed.cimmyt.org/iwin/iwinresults1.php?c=2010&o=BW>). Data provided by CIMMYT.

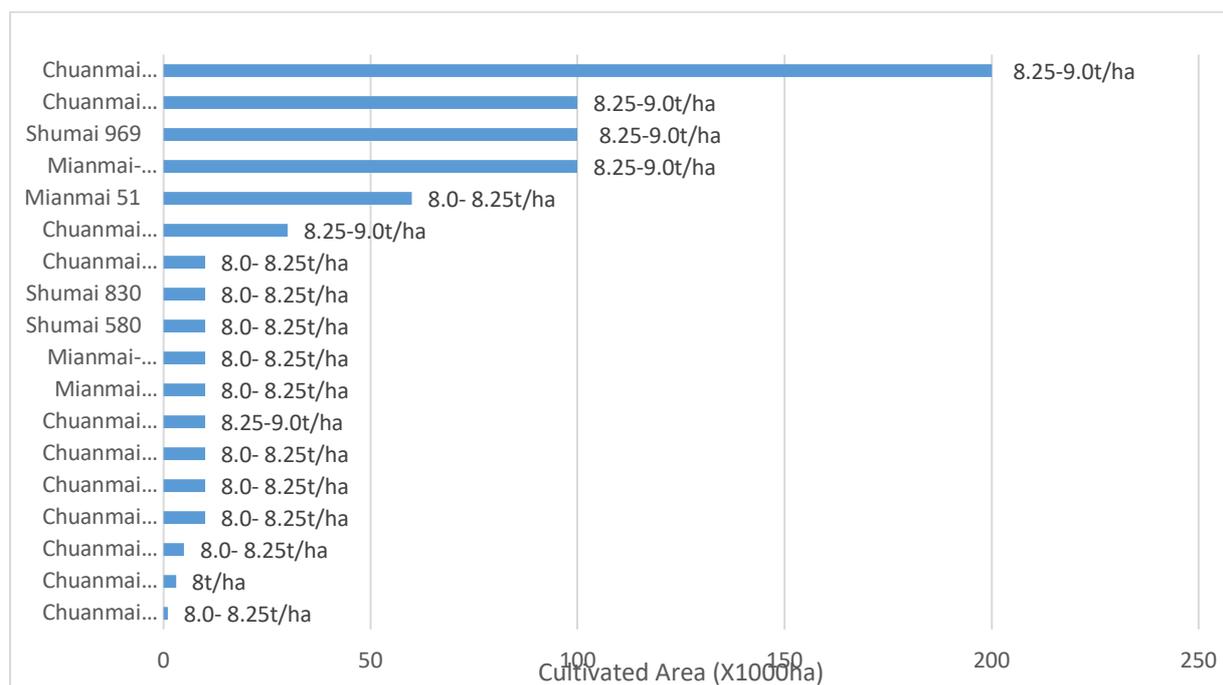


Figure 8. Area cultivated by varieties derived from SHW in China with the yield potential corresponding to each one (Authors). Based on the survey results.

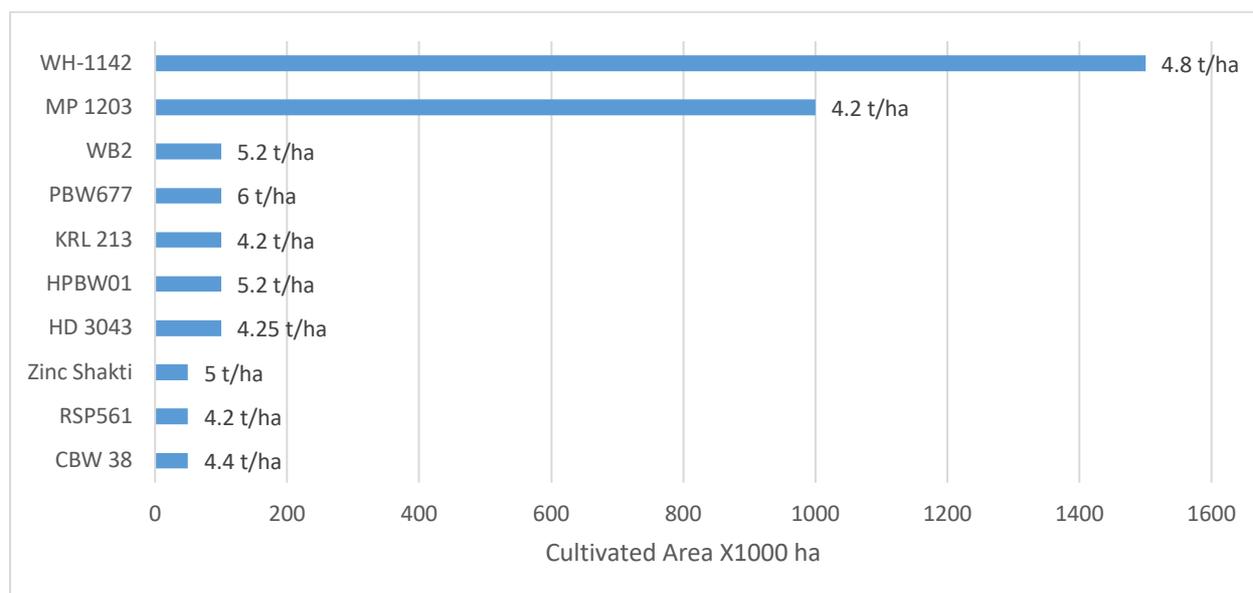


Figure 9. Area cultivated by varieties derived from SHW in India with the yield potential corresponding to each one (Authors). Based on the survey results

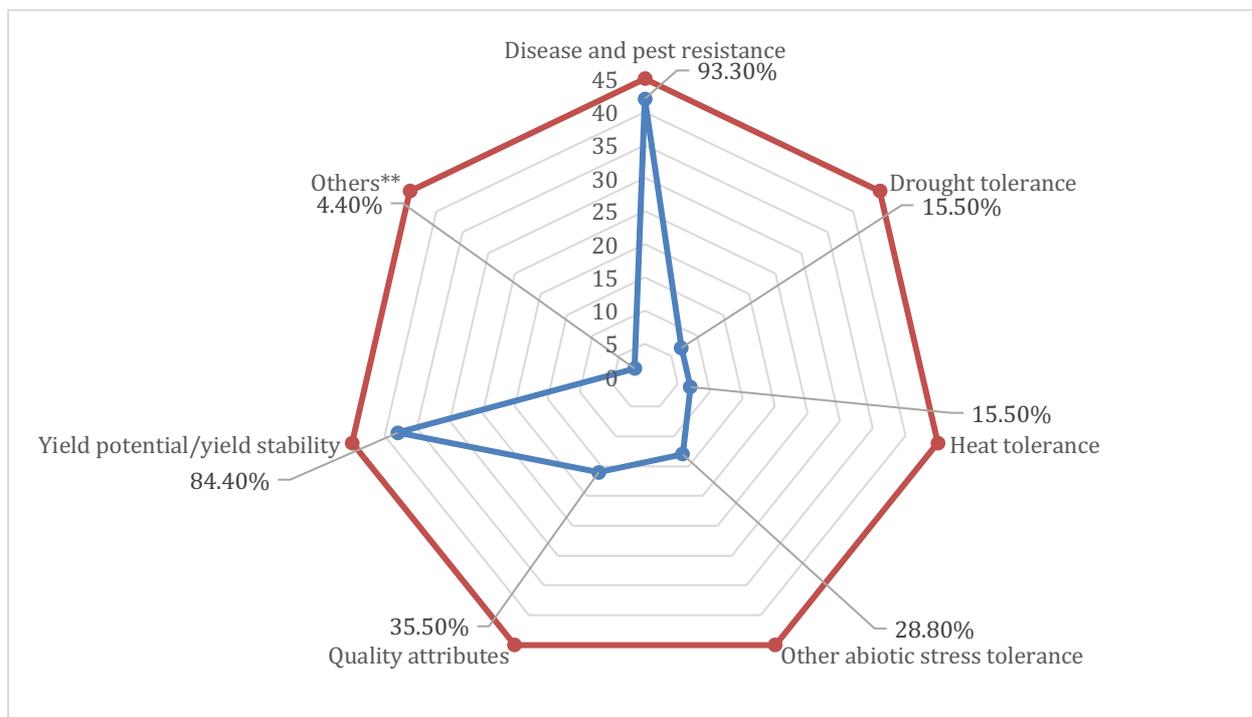


Figure 10. Radar plot for the importance of traits in SHW derived varieties. Based on the survey results.

10 Annexes

Annex 1. List of varieties derived from SHDL.

Country	Year	Name	Pedigree
Afghanistan	2008	Dorakshan-08	CNDO/R143//ENTE/MEXI_2/3/AEGILOPS SQUARROSA (TAUS)/4/WEAVER/5/2*KAUZ
Afghanistan	-	Croc-1	CROC_1/AE.SQ (205) KAUZ/3/PASTOR
Argentina	2006	Srm-Nogal	-
Argentina	2009	Biointa-1006	PGO//CROC_1/AE.SQUARROSA (224)/3/2*BORL95/4/BAV92/5/PASTOR
Argentina	2009	Klein-Leon	CHEN/AEGILOPS SQUARROSA (TAUS)
Argentina	2012	Biointa-3007-Bb	55.1744/7C//SU/RDL/3/CROW/4/MILAN/5/PGO/CHEN/AE.SQUARROSA (224)/3/WEAVER
Armenia	1994	Voskehask	AEGILOPS SQUARROSA/TRITICUM AESTIVUM
Australia	2003	Gba-Shenton	ALTAR 84/AE.SQUARROSA (219)//2*SERI
Australia	2003	Gba-Sapphire	3AG3/4*CONDOR//COOK*3/3/AEGILOPS SQUARROSA (TAUS)
Australia	2003	Gba-Combat	JANZ/AEGILOPS SQUARROSA (TAUS)//2*PWTH/3/CONDORS/2*OXLEY
Bolivia	2010	Motacu-Ciat	CROC-1/AE.SQ//OPATA/3/PASTOR
Bolivia	2012	Patuju-Ciat	MUNIA/3/RUFF/FGO//YAV79/4/CHEN/AE.SQ//BCN
Bolivia	2014	Bibosi-Ciat	CROC_1/AE.SQUARROSA (205)//BORL95/3/PASTOR
Bolivia	2014	Yesera	WHEAR/KUKUNA/3/C80.1/3*BATAVIA//2*WBILL1/4/T.DICOC CON PI94625/AE.SQUARROSA (372)//SHA4/CHIL/5/WHEAR/KUKUNA/3/C80.1/3*BATAVIA//2*WBILL1
Canada	-	Wft-1001	VORB/4/D67.2/PARANA 66.270//AE.SQUARROSA (320)/3/CUNNINGHAM
China	2003	Chuanmai 38	Syn-CD769/SW89-3243//Chuan 6415

China	2003	Chuanmai 42	Syn-CD769/SW89-3243//Chuan 6415
China	2004	Chuanmai 43	Syn-CD769/SW89-3243//Chuan 6415
China	2005	Chuanmai 47	Syn-CD786/Mianyang 26//Mianyang 26
China	2008	Chuanmai 51	174/183// Chuanmai 42
China	2009	Chuanmai 53	Chuanmai 43 /Miannong 4//Y- 314
China	2009	Chuanmai 56	Chuanmai 30/Chuanmai 42 or SW-3243/Chuanmai-42
China	2010	Mianmai-367	1275-1/ Chuanmai 43
China	2010	Chuanmai 58	CHUANMAI 42/03JIAN3// CHUANMAI 42
China	2012	Mianmai 51	1275-1/ Chuanmai 43
China	2012	Mianmai 228	1275-1/NEI-2938// Chuanmai 43
China	2012	Chuanmai 61	Zheng-9023/Jian 3//Jian 3/3/ Chuanmai 43
China	2012	Chuanmai 104	CHUANMAI42 /CHUANNONGMA I 16
China	2013	Mianmai-1618	1275-1/NEI-2938// Chuanmai 43
China	2013	Chuanmai 64	CHUANMAI 42 /CHUANNONGMAI 16
China	2013	Shumai 969	SHW-L1/SW-8188//Chuanyu- 18/3/Chuanmai-42
China	2017	Shumai 830	SHW-L1/Chuannong 16//Pm99915-1/3/Chuannong 24
China	2017	Shumai 580	SHW-L1/Chuanyu 17//Chuanyu 18/3/Chuanmai 107
Ethiopia	2012	Hidase	YANAC/3/PRL/SARA//TSI/VEE #5/4/CROC- 1/AE.SQUAROSA(224)//OPATT A
Ethiopia	2013	Nejmah-14	Skauz/BAV92/3/Croc_1/Ae. squarrosa (224)//Opata
Ethiopia	2016	Wane (ETBW 6130)	Ethiopia Sokoll/Excalibur
India	2008	Cbw 38	CANDO/R143//ENTE/MEXICAL I_2/3/AEGILOPS SQUARROSA (TAUS)/4/WEAVER/5/PASTOR/ 6/PASTOR
India	2009	Krl 213	CNDO/R143//ENTE/MEXI_2/3/ AEGILOPS SQUARROSA (TAUS)/4/WEAVER/5/2*KAUZ

India	2009	Mp 1203	FASN/2*EPOKA/3/CHEN/A.SQUARROSA/TA
India	2011	Hd 3043	PJN/BOW//OPATA*2//3/CROC_1/Ae.sq.(224)//OPATA
India	2014	Zinc Shakti	Croc_1/Ae. squarrosa (210)//Inqalab 91*2/Kukuna/3/PBW 343*2/Kukuna
India	2014	Wh-1142	CHEN/Ae.Sq.(TAUS)/FCT/3/2*WEAVER
India	2017	Hpbw01	T.DICOCCON CI9309/AE.SQUARROSA (409)//MUTUS/3/2*MUTUS
India	2017	Wb2	T.DICOCCONCI9309/AE.SQUARROSA (409)//MUTUS/3/2*MUTUS
India	-	Rsp561	HD2637/AE. CRASSA//HD2687
India	-	Pbw677	PFAU/MILAN/5/CHEN/AEGILOPS SQUARROSA(TAUS)//BCN/3/VEE#7/BOW/4/PASTOR
Iran	2018	Talaei	PASTOR//SITE/MO/3/CHEN/AEGILOPS SQUARROSA (TAUS)//BCN/4/WBLL1
Iran	2018	Tirgan	PFAU/MILAN/5/CHEN/AEGILOPS SQUARROSA (TAUS)//BCN/3/VEE#7/BOW/4/PASTOR
Kazakhstan	-	Avitsenna	PYN/BAU/3/CHEN/AEGILOPS SQUARROSA (TAUS)//BCN/6/SN64//SKE/2*ANE/3/SX/4/BEZ/5/SERI
Kenya	2016	Kenya Falcon	KSW/5/2*ALTAR 84/AE.SQUARROSA (221)//3*BORL95/3/URES/JUN/KAUZ/4/WBLL1
Kenya	2016	Kenya Pelican	KSW/5/2*ALTAR 84/AE.SQUARROSA (221)//3*BORL95/3/URES/JUN/KAUZ/4/WBLL1
Kenya	2016	Kenya Songbird	KSW/5/2*ALTAR 84/AE.SQUARROSA (221)//3*BORL95/3/URES/JUN/KAUZ/4/WBLL1
Kenya	2016	Kenya Hornbill	Pastor//HXL7573/2*BAU/3/So koll/WBLL1
Kenya	2016	Kenya Weaverbird	PRINIA/3/ALTAR84/AE.SQ//2*OPATA/4/CHEN/AEGILOPS SQUARROSA (TAUS)//BCN/3/BAV92

Mexico	1999	Crosbill	CANDO/R-143//ENTE/MEXICALI-2/3/TR.TA/4/WEAVER/5/2*KAUZ/6/FRET2
Mexico	2003	Fiscal	FALKE*2/BISHOFTU/3/CHEN/AE.SQ(TR.TA)//BACANORA-T-88
Mexico	2010	Tepahui-F2009	BETTY/3/CHEN/AE.SQ//2*OPATA
Mexico	2012	Maravillas-NI-M2012	T.DICOCCON PI94625/AE.SQUARROSA (372)//3*PASTOR
Mexico	2012	Conquista-NI-F2012	ELVIRA/5/CNDO/R143//ENTE/ MEXI75/3/AE.SQ/4/2*OCI
Mexico	2015	Bacorehuis F2015	ROLF07*2/5/REH/HARE//2*BCN/3/CROC_1/AE.SQUARROSA (213)//PGO/4/HUITES
Morocco	2010	Kharoba	ALTAR 84/AE.SQUARROSA (221)//PASTOR/3/K134(60)/V EERY//BOBWHITE/PAVON/4/T ILILA
Morocco	2017	Malika	---
Pakistan	2010	Kt 2009	ALTAR84/AE.SQUARROSA(219) 01//SERI
Pakistan	2013	Benazir-13	CHEN/AEGILOPS SQUARROSA (TAUS)//BCN/3/VEE#7/BOW/4 /PASTOR
Pakistan	2013	Pakistan-13	MEX94.27.1.20/3/Sokoll//Attila /3*BCN
Pakistan	2013	Lalma-13	PASTOR/3/ALTAR 84/AEGILOPS SQUARROSA (TAUS)//OPATA
Pakistan	2016	Borlaug 2016	Sokoll/3/Pastor//HXL7573/2*B AU
Pakistan	2016	Sindhu16	FLAKE*2/BISU/3/CHEN/AEGIL OPSSQAROSA(TASU)
Pakistan	2016	Ihsan16	PASTOR/3/ALTAR84/AE.SQ//O PATA
Pakistan	2017	Israr-Shaheed-2017	ESDA/ / ALTAR 84 / AE.AQUARROSA (211) /3/ ESDA/4/
Pakistan	2017	Wadaan-2017	YAV79//DACK/RABI/3/SNIPE/ 4/ AE. SQUARRO SA
Spain	2003	Carmona	-
Spain	2009	Trebuena	BCN/3/FGO/USA2111//AE.SQU ARROSA (658)/4/PRINIA
Spain	2010	Conil	CROC_1/AE.SQUARROSA (205)//BORL95/3/2*MILAN

Spain	2012	Marchena	CROC_1/AE.SQUARROSA (205)//BORL95/3/2*MILAN
Syrian Arab Republic	2014	Bouhouth-10	CHEN/AEGILOPS SQUARROSA (TAUS)//BCN/3/2*KAUZ
Tajikistan	2013	Zarnisor	CROC_1/AE.SQUARROSA (205)//BORL95/3/2*MILAN
Tajikistan	2013	Murodi	CHEN/AE.SQ//WEAVER/3/SSER I1
Tajikistan	2013	Sarvar	CHEN/AEGILOPS SQUARROSA (TAUS)//BCN/3/BAV92
Turkey	2013	Altinbasak	CHEN/AEGILOPS SQUARROSA (TAUS)//BCN/3/2*KAUZ
Turkey	2014	Yakamoz	BL 1496/MILAN/3/CROC_1/AE.SQ UARROSA (205)//KAUZ
Turkey	-	Doruk	CROC_1/AE.SQUARROSA(205)// KAUZ/3/LANG
Turkmenistan	2015	Davlatle	135U 6.1/5/CNDO/R143//ENTE/MEX I75/3/AE.SQ/4/2*OCI
United States	2008	Redwing	CMT SYNTHETIC/1065- 3//UCSR/PB775
Uruguay	2010	Genesis 2354	Uruguay —
Uruguay	2010	Genesis 2359	

Data sources: <http://www.wheatpedigree.net/>, <http://wheatatlas.org/>, and cited literature review.