

REVIEW

## A brief history of wheat utilization in China

Minxia LU<sup>1</sup>, Liang CHEN<sup>2</sup>, Jinxiu WANG<sup>3,4</sup>, Ruiliang LIU<sup>5</sup>, Yang YANG<sup>2</sup>, Meng WEI<sup>3,6</sup>,  
Guanghui DONG (✉)<sup>1,4</sup>

<sup>1</sup> MOE Key Laboratory of Western China's Environmental Systems/College of Earth & Environmental Sciences, Lanzhou University, Lanzhou 730000, China

<sup>2</sup> State Key Laboratory of Crop Stress Biology in Arid Areas/College of Agronomy, Northwest A&F University, Yangling 712100, China

<sup>3</sup> State Key Laboratory of Systematic and Evolutionary Botany/Institute of Botany, Chinese Academy of Sciences, Beijing 100093, China

<sup>4</sup> CAS Center for Excellence in Tibetan Plateau Earth Sciences, Chinese Academy of Sciences (CAS), Beijing 100101, China

<sup>5</sup> School of Archaeology, University of Oxford, 36 Beaumont Street, Oxford, OX1 2PG, UK

<sup>6</sup> University of the Chinese Academy of Sciences, Beijing 100049, China

**Abstract** Wheat is one of the most important crops in both China and the world, and its domestication can be traced back to ~10000 years ago. However, the history of its origin and utilization in China remains highly ambiguous. Drawing upon the most recent results of taxonomic, genetic, archeological and textual studies focused on the wheat in prehistory, this paper argues that wheat was not domesticated but introduced into China in the late fifth millennium BP. In the subsequent centuries, this exotic crop was quickly utilized as a staple food in northwest China. In contrast, it was not adopted as a staple in the Central Plains until the Han Dynasty (202 BCE–220 CE), which was mainly as a consequence of the living environment, population and innovations in food processing technology.

**Keywords** multidisciplinary evidence, prehistoric food globalization, wheat consumption, wheat domestication

### 1 Introduction

Wheat, rice and corn are the most important crops in the modern world. These three crops were initially domesticated in West Asia, East Asia and Central America, respectively<sup>[1–4]</sup>, and provide 60% of the entire human diet<sup>[5]</sup>. Of these, the cultivation of wheat covers probably the largest geographical area, mainly between 67° and 45° N around the Northern Hemisphere (Fig. 1(a)). However, archeological evidence suggests that wheat was cultivated only in Afro-Eurasia before 1000 BCE (before the

Common Era). Its first introduction into America was in the late 15th century<sup>[7]</sup>. The development and expansion of wheat has profoundly influenced the trajectory of human social evolution, as well as facilitated the emergence of the earliest civilizations in the old world, such as Mesopotamian, Egypt and India<sup>[8]</sup>.

Modern China is the largest producer of wheat across the world. The yield of wheat in China was 131 million tonne and the area of wheat cultivation was 24 million ha in 2018<sup>[9]</sup>. Wheat has also been crucial in the development of diet culture in ancient China. It was annotated as one of the five key crops in *Meng Zi* by Zhao Qi, viz., rice (*Oryza sativa*), foxtail millet (*Setaria italica*), broomcorn millet (*Panicum miliaceum*), soya (*Glycine max*) and wheat (*Triticum aestivum*). The initial use of wheat, nevertheless, has been the subject of a long-term debate. In the most recent scholarship, it is considered as an exotic crop that was introduced into China before the Shang Dynasty (~1600–1046 BCE) as attested by the inscription “来” (meaning: come or coming) on the oracle-bone inscriptions<sup>[8]</sup>, though some other scholars hold the view of independent local domestication within China<sup>[10–12]</sup>.

Previous research on the history of the utilization of wheat in China was primarily focused on the evidence from a single discipline<sup>[13–15]</sup>, such as archeology (Fig. 1(b)), historical philology, phytotaxonomy and genetics. In this paper, we provide a synthesis of data from a variety of spheres (taxonomic, genetic, archeological and historical studies) to illustrate the history of the domestication of wheat, its introduction into China, and the way in which it became one of the major Chinese staples in ancient China, which hopefully contributes to broader interests in the subject of east-west communication and the global history of agriculture.

Received March 5, 2019; accepted April 24, 2019

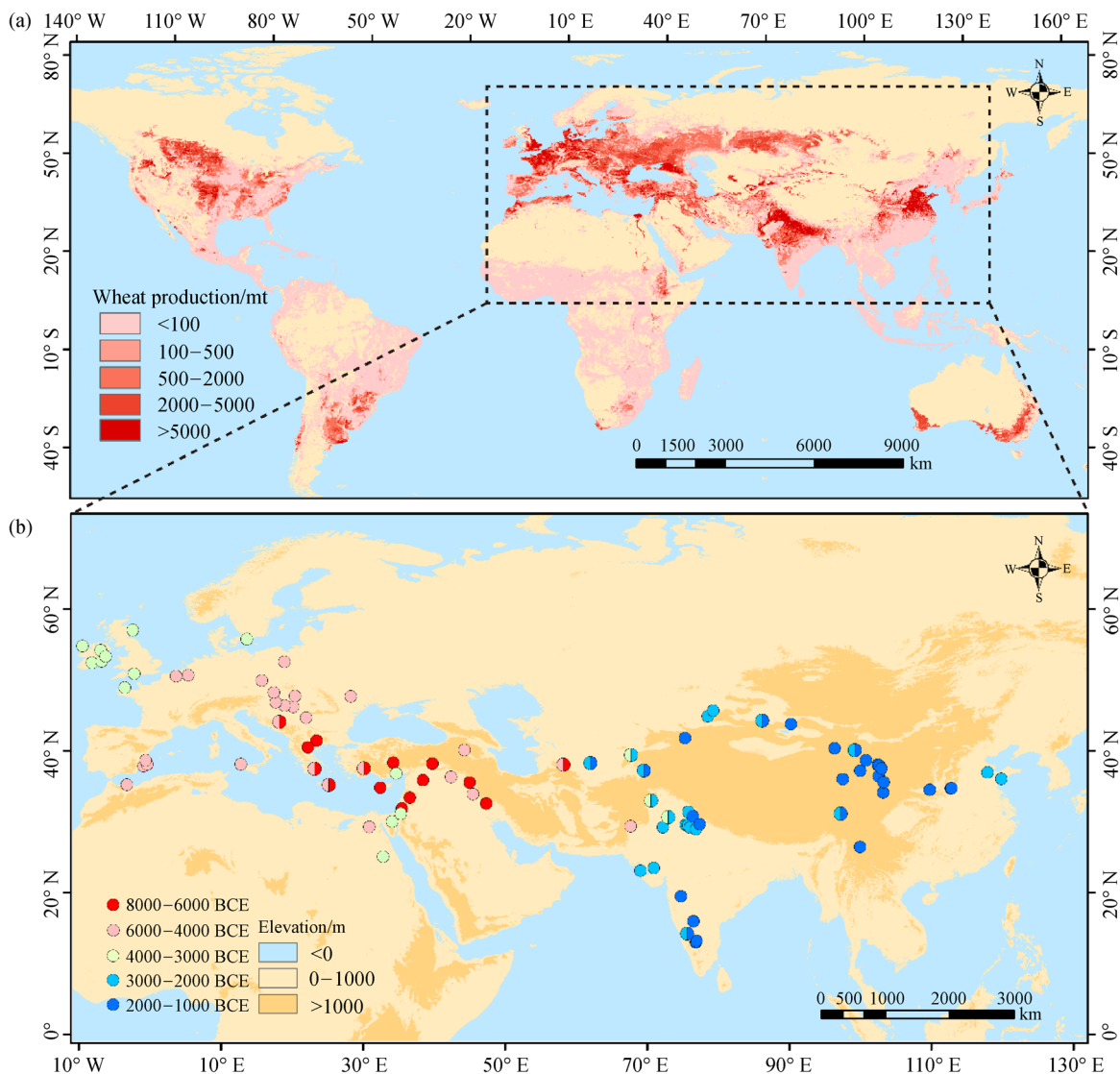
Correspondence: [ghdong@lzu.edu.cn](mailto:ghdong@lzu.edu.cn)

## 2 A brief history of the origin and dispersal of wheat across the world

### 2.1 Molecular biology and genomics: origin, evolution and spread of wheat

The domestication of animals and plants is a major milestone in the birth of modern agriculture and development of human civilization<sup>[16–18]</sup>. As one of the important staple foods, the domestication of wheat (*Triticum aestivum*) was essential to facilitate and sustain the development of human civilization<sup>[19]</sup>. Numerous studies have shown that the current widely planted hexaploid bread wheat was derived from a complex process believed to involve two polyploidization events between three diploid ancestors<sup>[20]</sup>. The first polyploidization event occurred between *Triticum urartu* (AA;  $2n = 2x = 14$ )

and an unknown close relative of *Aegilops speltoides* (BB;  $2n = 2x = 14$ ) and led to wild emmer wheat (*Triticum turgidum* subsp. *dicoccoides*, AABB;  $2n = 4x = 28$ ). After the domestication of wild emmer wheat, the second polyploidization event occurred between cultivated emmer wheat (*T. turgidum* subsp. *dicoccum*, AABB;  $2n = 4x = 28$ ) and *Aegilops tauschii* (DD;  $2n = 2x = 14$ ), eventually producing hexaploid common wheat (*Triticum aestivum*, AABBDD;  $2n = 6x = 42$ ). The current genetic and archeological evidence showed that the Fertile Crescent near the upper reaches of the Tigris and Euphrates Rivers in present-day southeastern Turkey and northern Syria was the area of origin of wheat and the cradle of modern agriculture<sup>[16]</sup>. About 12900–11700 years ago, Younger Dryas, which lasted for a thousand years with cool and dry climate conditions in the Fertile Crescent, promoted the domestication of wheat crops by the West



**Fig. 1** (a) Distribution of wheat production in the current world (source from IFPRI<sup>[6]</sup>); (b) spatiotemporal distribution of pre-1000 BCE sites with unearthed wheat remains in Afro-Eurasia.

Asians<sup>[21]</sup>. At inception, *T. monococcum* and *T. dicoccoides* were domesticated successively, and the domestication and cultivation of polyploid wheat were strengthened by the fact that polyploid wheat had stronger environmental tolerance (especially low temperature tolerance) and favorable harvest characteristics, including bare seeds and soft glumes. After about 1000 years of artificial selection, the *TtBtr1* gene, controlling shattering in wild emmer wheat, had been domesticated, and the cultivated emmer wheat produced<sup>[22]</sup>. Subsequently, about 8000 years ago, cultivated emmer wheat spread eastward to the Outer Caucasus between the northern part of the Iranian plateau and the southeastern part of the Caspian Sea, where the second hybridization event occurred between the cultivated emmer wheat and *A. tauschii*, forming the wild ancestor of hexaploid common wheat<sup>[18,20]</sup>.

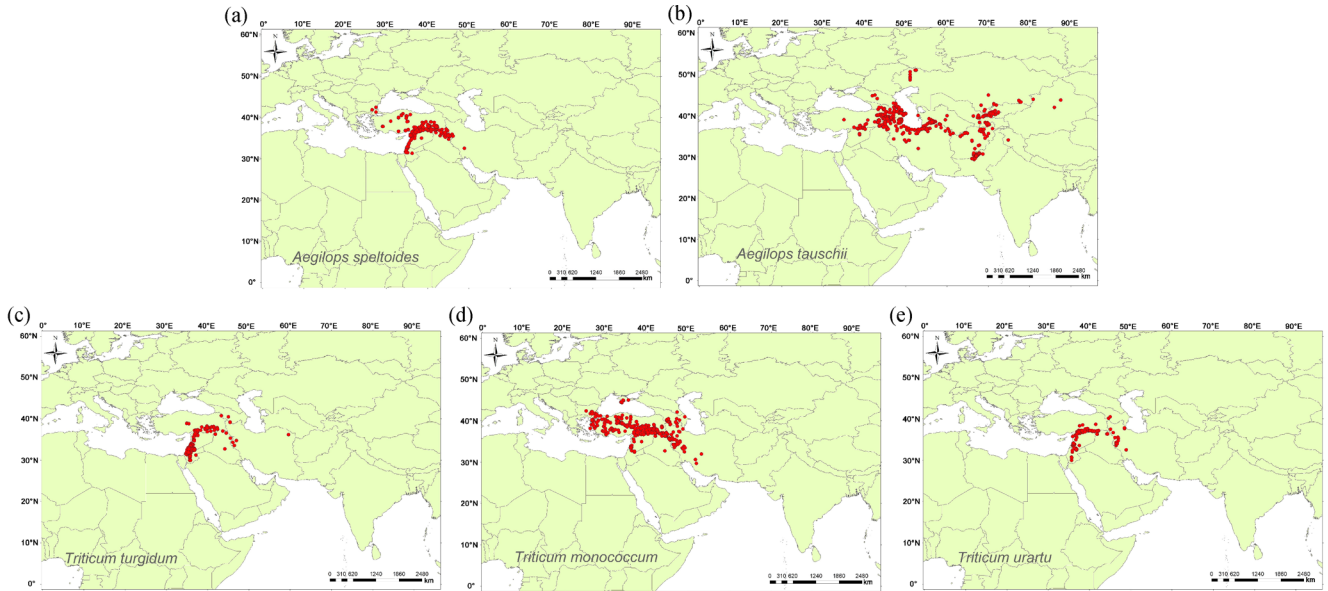
To understand the spread and evolution of wheat, genetic relationships among 477 *A. tauschii* and wheat accessions were studied with the *A. tauschii* 10K single nucleotide polymorphism array, which confirmed that *Aegilops* located in the southern and southwestern Caspian Sea was the donor of the D subgenome of hexaploid wheat<sup>[23]</sup>. The genetic diversity of 31 cultivated and 34 wild emmer wheat genotypes from Western Asia and its surrounding areas was analyzed by exome capture sequencing. The results showed that the cultivated emmer wheat germplasm from Turkey was distributed in all of the four subgroups (including Indian Ocean, Mediterranean, Eastern Europe and Caucasus). It was also found that the cultivated emmer wheat with the closest relationship with wild emmer wheat came from Turkey which was an important part of the Fertile Crescent. These findings confirmed that the Fertile Crescent was the center of origin and domestication of the cultivated emmer wheat<sup>[22]</sup>. The gradual eastward migration of hexaploid wheat, moving further away from the tetraploid center of origin, and the strong reproductive isolation between hexaploid wheat and *Aegilops*, made it difficult to transfer genes from *Aegilops* to bread wheat, which resulted in the lower diversity of the D subgenome of hexaploid wheat in East Asia<sup>[24,25]</sup>. Additionally, the results of whole genome resequencing have also confirmed the lower diversity of the D subgenome<sup>[26]</sup>. Moreover, investigations of the genetic diversity of 731 genotypes from China and West Asia (Iran and Turkey) indicated that Chinese wheat spread from the northwestern Caspian Sea region to south China, adapting during its agricultural trajectory to increasingly mesic and warm climatic areas<sup>[27]</sup>. In recent years, the rapid development of high throughput sequencing technology has completely changed the methods of wheat genomic research. In particular, the publication of the high-quality hexaploid wheat Chinese Spring reference genome sequence enabled the in-depth analysis of the domestication and global migration of hexaploid wheat<sup>[28]</sup>. Recently, cultivation and breeding history of bread wheat in China, which was analyzed by genome-wide resequencing,

revealed that the population structure was consistent with the geographic distribution of wheat: from its domestication area in the Fertile Crescent, hexaploid wheat spread westward to Europe and America, eastward to South and Central Asia and finally to East Asia, via separate routes<sup>[26]</sup>. The concentrated distribution of wild diploid wheat and wild emmer wheat in the Fertile Crescent, the archeological evidence of <sup>14</sup>C wheat grain residue and the evolutionary relationship of tetraploid wheat based on genome sequence, confirm that the Fertile Crescent is the center of origin of tetraploid wheat<sup>[16–18,20]</sup>. Furthermore, the extensive distribution of *A. tauschii* in the Outer Caucasus and the closer relationship between the hexaploid wheat and *A. tauschii* germplasm in that region suggested that the Outer Caucasus region was the center of origin of hexaploid wheat. Therefore, it is now widely believed that West Asia is the center of origin of hexaploid wheat. With the availability of the high-quality genome sequence of hexaploid wheat, more wheat lines of different ploidy levels worldwide should be selected to analyze their radiation and migration from the center of origin to the rest of the world.

## 2.2 Geographical distribution of the wild ancestors of domesticated wheat

Five wild species in two genera were directly involved in the origin of wheat, *T. monococcum*, *T. turgidum*, *T. urartu*, *A. speltoides* and *A. tauschii*. Both genera are members of the tribe Triticeae in the Poaceae<sup>[29]</sup>. Although they have been sometimes treated as independent genera, i.e., *Triticum* (6 species) and *Aegilops* (25 species), recent studies based on molecular evidence indicated that they appear more likely to be one genus, i.e., *Triticum*<sup>[30]</sup>. Both *Triticum* and *Aegilops* are herbs with one spikelet per node of rachis and the spikelets are not embedded in the rachis depression. The main differences between them are the ways in which their spikes fall and the morphology of their glumes. When mature, the spikes of *Triticum* often fall from the base as a whole, and the backs of the glumes are flat and not keeled. The spikes of the *Aegilops*, however, fall from the rachis section by section, and the glumes have one or two veins raised as keels<sup>[31]</sup>.

Based on the data from the GBIF (Global Biodiversity Information Facility)<sup>[32]</sup>, we obtained distribution maps of the five allied species of wheat (Fig. 2). Among the five species involved in the domestication of wheat, *A. tauschii* is widely distributed from eastern Europe to central Asia, the other four species are restricted to the Fertile Crescent (from central Iran to the east coast of the Mediterranean) (Fig. 2). *A. tauschii* is also reported to occur in Henan and Shaanxi Provinces of China<sup>[33]</sup>. This area is far away from the center of origin of the five species<sup>[34]</sup>. However, some scholars argued that *A. tauschii* in the area above was actually brought into China together with the introduction of wheat<sup>[33]</sup>. Thus, China is neither a center of wild



**Fig. 2** Distribution of the allied species of wheat (source from GBIF datasets<sup>[32]</sup>)

distribution of *Triticum* nor *Aegilops*. It lacks the five wild ancestors of the wheat, which are essential for the origin of the domesticated wheat.

### 2.3 Archaeological and historical evidence for wheat domestication and dispersal

Archaeobotanical studies provide additional detailed information for reconstructing the history of domestication and dispersal in antiquity (Fig. 1(b)). Remains of wild wheat and barley were identified from the Ohalo II site, which can be dated to 21000 BCE in the Fertile Crescent of West Asia<sup>[35,36]</sup>. The earliest bread remnants unearthed from northeastern Jordan date to around 12400 BCE<sup>[37]</sup>. However, the earliest definite domesticated einkorn wheat was recovered from Cafer Höyük and Çayönü Neolithic sites in the Levant areas around 8000 BCE<sup>[38]</sup>. These two crops were subsequently taken from their centers of domestication to the rest of Eurasia (Fig. 1(b)) and reached east Europe before 6500 BCE<sup>[39,40]</sup> and then other areas of Europe before 3000 BCE<sup>[41,42]</sup>.

Wheat was taken eastward to Iran and Turkmenistan before 5500 BCE<sup>[43,44]</sup>, and then Tajikistan, Afghanistan and the Indian subcontinent between 6000 and 3000 BCE<sup>[45–47]</sup>. Wheat was utilized in Kazakhstan in the central Eurasian Steppes between 3000 and 2000 BCE<sup>[48,49]</sup>. It was introduced further eastward to East Asia during the Longshan period (2600–2000 BCE). Charred remains of wheat from Zhaojiazhuang and Dinggong sites date to between 2500 and 2000 BCE<sup>[50,51]</sup>, while the earliest direct dates of wheat remains from west China was unearthed from Huoshiliang and Ganggangwa sites in the central Hexi Corridor<sup>[52,53]</sup>. The

timing and routes for introduction of wheat to China is still subject to debate<sup>[52,54]</sup>.

Archaeobotanical evidence suggests that wheat was definitely domesticated in West Asia (Fig. 1(b)), which is consistent with genetic studies. This western crop was first introduced into China during the late Neolithic Age and there is very little archaeobotanical evidence suggesting that wheat was independently domesticated in China. Although a few wheat remains have been occasionally unearthed from early Neolithic sites, such as Jiahu site (7000–5800 BCE) in Henan Province, the direct radiocarbon dates from these remains were younger than 1200 CE<sup>[55]</sup>. Clearly, these wheat remains were historical relics which were disturbed into stratum of the Jiahu culture. The same issue has also been reported from archaeobotanical studies of other Neolithic sites both in China and Europe<sup>[56,57]</sup>.

## 3 The brief history of wheat utilization in China

Before the introduction of wheat and barley, the spatial pattern of agriculture in late Neolithic China is featured by rainfed agriculture based on foxtail and broomcorn millet in the Yellow River valley, rice-based agriculture in the Yangtze River valley and mixed cultivation of millet and rice in transitional zone between these two areas<sup>[58]</sup>. Though wheat was introduced into the Shandong Peninsula during 2500–2000 BCE<sup>[50,51]</sup>, this exotic crop was likely to have been treated as a special item rather than a staple.

Remains of wheat and barley have been frequently

uncovered from Bronze Age sites in north China dating from 2000 BCE. However, the trajectories to adopt wheat as staple varied dramatically in different areas of China. In northwest China, wheat replaced millet crop as the primary crop around 1700 BCE in the Hexi Corridor<sup>[59]</sup> and might have become a staple food in Xinjiang from ~1800 BCE<sup>[60–62]</sup>. On the northeast Tibetan Plateau, however, barley became the most important staple after 1600 BCE<sup>[63]</sup>, especially in areas with an altitude above 2500 m.a.s.l (meters above sea level)<sup>[64]</sup>. Agricultural innovation dominated by cold-tolerant agro-pastoral production facilitated permanent settlement on the Tibetan Plateau<sup>[65]</sup>.

In the Central Plains, although wheat was introduced during the Xia Dynasty (~2000–1600 BCE) and became widely cultivated during the Shang Dynasty (~1600–1046 BCE)<sup>[66,67]</sup>, millet crops remained as the dominant staple in the area until the Zhou Dynasty (1046–221 BCE). This has been supported by the carbon isotopes of human bones unearthed from a variety of archeological sites<sup>[68–70]</sup>. Wheat was adopted as the staple in the Central Plains during the Han Dynasty (202 BCE–220 CE), which can be also detected from isotopic evidence, archaeobotanical analysis<sup>[27,71]</sup>, and historical documents such as *Han Shu* and *Hou Han Shu*.

Following the early introduction of wheat into pre-historic China, the cooking method for this kind of crop was the same as for millet and rice: people simply boiled the grain to make *maifan* (the aggregation of cooked wheat grains). However, this rough process was unable to separate the coat from the grain. As a result, mouthfeel would have been terrible and deglutination difficult. The invention and adoption of the stone mill helped people resolve this problem by turning the grains into powder, which has enriched the variety of wheat-based cuisines. In the Han Dynasty (202 BCE–220 CE), the widespread use of stone mills assisted Chinese people to use wheat more easily. Meanwhile, the development of water conservancy facilities and irrigation techniques helped to expand the scale of wheat cultivation<sup>[72]</sup>. During the Northern and Southern Dynasties (420–589 CE), the mastery of flour fermentation technology made wheat-based food even tastier<sup>[73]</sup>.

Apart from the development of wheat cultivation and processing techniques, the climate and the population were also vital factors during the intensification of wheat utilization in the Central Plains. From 2000 BCE, the Northern Hemisphere experienced a dramatic cooling period<sup>[74]</sup>. Unlike the Central Plains, the fluctuations of temperature in the northwest region of China had significantly affected the yield of millet farming. People were forced to cultivate more wheat and barley to adapt to the colder climate. However, in the Central Plains, higher-yield wheat became popular during the Han Dynasty due to the rapid growth of population, the shortage of food and the need to survive<sup>[75]</sup>.

## 4 Conclusions

Based on the comprehensive analysis of evidence from a range of disciplines, including genetic, taxonomic, archeological and historical literature, the history of the introduction of wheat and its utilization in China can now be better understood. Wheat was not an indigenous crop in China, but rather it was domesticated in West Asia around 8000 BCE. It was first introduced into China between 2500 and 2000 BCE and became one of the staples in the Hexi Corridor and Xinjiang after 1700 BCE. It remained a subsidiary crop in the Central Plains until the Han Dynasty (202 BCE–220 CE), when its use changed in response to the difference in susceptibility of traditional rainfed agriculture to cooling climate in these areas. Following the Song Dynasty (960–1279 CE), thanks to the improved food processing technology, wheat finally became the most favorite staple food in north China.

**Acknowledgements** This research was supported by the National Key R&D Program of China (2018YFA0606402), Strategic Priority Research Program of Chinese Academy of Sciences, Pan-Third Pole Environment Study for a Green Silk Road (Pan-TPE) (XDA2004010101), and the National Natural Science Foundation of China (31570334; 41620104007; 41825001).

**Compliance with ethics guidelines** Minxia Lu, Liang Chen, Jinxiu Wang, Ruiliang Liu, Yang Yang, Meng Wei, and Guanghui Dong declare that they have no conflicts of interest or financial conflicts to disclose.

This article is a review and does not contain any studies with human or animal subjects performed by any of the authors.

## References

1. Yan W M. The occurrence of agriculture and the origins of civilization. Beijing: *Science Press*, 2000 (in Chinese)
2. Zohary D, Hopf M, Weiss E. Domestication of plants in the old world: the origin and spread of domesticated plants in Southwest Asia, Europe, and the Mediterranean Basin. Oxford: *Oxford University Press*, 2012
3. Jones M K, Liu X Y. Origins of agriculture in East Asia. *Science*, 2009, **324**(5928): 730–731
4. Pankin A, von Korff M. Co-evolution of methods and thoughts in cereal domestication studies: a tale of barley (*Hordeum vulgare*). *Current Opinion in Plant Biology*, 2017, **36**: 15–21
5. Tilman D, Cassman K G, Matson P A, Naylor R, Polasky S. Agricultural sustainability and intensive production practices. *Nature*, 2002, **418**(6898): 671–677
6. IFPRI (International Food Policy Research Institute). Global spatially-disaggregated crop production statistics data for 2010 version 1.0. *Harvard Dataverse*, 2019, **V2**. doi: 10.7910/DVN/PRFF8V
7. Crosby A W. The Columbian exchange: biological and cultural consequences of 1492. Westport: *Greenwood Publishing Group*, 2003.
8. Zhao Z J. Research on the introduction of wheat into China-Archaeobotany. *Relics from South*, 2015, **3**: 44–52 (in Chinese)

9. National Bureau of Statistics (NBS). A statement from the National Bureau of Statistics on grain output in 2018. Available at NBS website on December 14, 2018
10. Cao L G. Problem on the origin of wheat in China. *Agricultural Archaeology*, 1983, **1**: 19–24 (in Chinese)
11. Chen E Z. Independent origin theory of Chinese hexaploid common wheat. *Agricultural Archaeology*, 1989, **1**: 74–84 (in Chinese)
12. Li F. Abriefly discussion on the origin and development of cultivated plants in China. *Agricultural Archaeology*, 1993, **1**: 49–55 (in Chinese)
13. Zeng X S. Discussion on the expansion of wheat in ancient China. *Chinese Cuisine Culture*, 2005, **1**(1): 99–133 (in Chinese)
14. Wei H Y, Li J, Peng Z S, Lu B R, Zhao Z J, Yang W Y. The exchange of agricultural technology between ancient China and the west revealed by DNA fingerprint relations of *Aegilops tauschii*. *Progress in Natural Science*, 2008, **18**(9): 987 (in Chinese)
15. Dong G H, Yang Y S, Han J Y, Wang H, Chen F H. Exploring the history of cultural exchange in prehistoric Eurasia from the perspectives of crop diffusion and consumption. *Science China: Earth Sciences*, 2017, **60**(6): 1110–1123
16. Lev-Yadun S, Gopher A, Abbo S. The cradle of agriculture. *Science*, 2000, **288**(5471): 1602–1603
17. Riehl S, Zeidi M, Conard N J. Emergence of agriculture in the foothills of the Zagros Mountains of Iran. *Science*, 2013, **341**(6141): 65–67
18. Salamini F, Özkan H, Brandolini A, Schäfer-Pregl R, Martin W. Genetics and geography of wild cereal domestication in the near east. *Nature Reviews Genetics*, 2002, **3**(6): 429–441
19. Heun M, Schäfer-Pregl R, Klawan D, Castagna R, Accerbi M, Borghi B, Salamini F. Site of einkorn wheat domestication identified by DNA fingerprinting. *Science*, 1997, **278**(5341): 1312–1314
20. Marcussen T, Sandve S R, Heier L, Spannagl M, Pfeifer M, Jakobsen K S, Wulff B B H, Steuernagel B, Mayer K F X, Olsen O A, Rogers J, Doležel J, Pozniak C, Eversole K, Feuillet C, Gill B, Friebe B, Lukaszewski A J, Sourdille P, Endo T R, Kubaláková M, Čihalíková J, Dubsá Z, Vrána J, Šperková R, Šimková H, Febrer M, Clissold L, McLay K, Singh K, Chhuneja P, Singh N K, Khurana J, Akhunov E, Choulet F, Alberti A, Barbe V, Wincker P, Kanamori H, Kobayashi F, Itoh T, Matsumoto T, Sakai H, Tanaka T, Wu J Z, Ogihara Y, Handa H, Maclachlan P R, Sharpe A, Klassen D, Edwards D, Batley J, Lien S, Caccamo M, Ayling S, Ramirez-Gonzalez R H, Clavijo B J, Wright J, Martis M M, Mascher M, Chapman J, Poland J A, Scholz U, Barry K, Waugh R, Rokhsar D S, Muehlbauer G J, Stein N, Gundlach H, Zytnicki M, Jamilloux V, Quesneville H, Wicker T, Faccioli P, Colaiacovo M, Stanca A M, Budak H, Cattivelli L, Glover N, Pingault L, Paux E, Sharma S, Appels R, Bellgard M, Chapman B, Nussbaumer T, Bader K C, Rimbart H, Wang S C, Knox R, Kilian A, Alaux M, Alfama F, Couderc L, Guilhot N, Viseux C, Loaec M, Keller B, Praud S. Ancient hybridizations among the ancestral genomes of bread wheat. *Science*, 2014, **345**(6194): 1250092
21. Moore A M T, Hillman G C, Legge A J, Huxtable J. Village on the Euphrates: from foraging to farming at Abu Hureyra. Oxford: *Oxford University Press*, 2000
22. Avni R, Nave M, Barad O, Baruch K, Twardziok S O, Gundlach H, Hale I, Mascher M, Spannagl M, Wiebe K, Jordan K W, Golan G, Deek J, Ben-Zvi B, Ben-Zvi G, Himmelbach A, MacLachlan R P, Sharpe A G, Fritz A, Ben-David R, Budak H, Fahima T, Korol A, Faris J D, Hernandez A, Mikel M A, Levy A A, Steffenson B, Maccaferri M, Tuberosa R, Cattivelli L, Faccioli P, Ceriotti A, Kashkush K, Pourkheirandish M, Komatsuda T, Eilam T, Sela H, Sharon A, Ohad N, Chamovitz D A, Mayer K F X, Stein N, Ronen G, Peleg Z, Pozniak C J, Akhunov E D, Distelfeld A. Wild emmer genome architecture and diversity elucidate wheat evolution and domestication. *Science*, 2017, **357**(6346): 93–97
23. Wang J, Luo M C, Chen Z, You F M, Wei Y, Zheng Y, Dvorak J. *Aegilops tauschii* single nucleotide polymorphisms shed light on the origins of wheat D-genome genetic diversity and pinpoint the geographic origin of hexaploid wheat. *New Phytologist*, 2013, **198**(3): 925–937
24. Dvorak J, Akhunov E D, Akhunov A R, Deal K R, Luo M C. Molecular characterization of a diagnostic DNA marker for domesticated tetraploid wheat provides evidence for gene flow from wild tetraploid wheat to hexaploid wheat. *Molecular Biology and Evolution*, 2006, **23**(7): 1386–1396
25. Dvorak J, Luo M C, Akhunov E D. N.I. Vavilov's theory of centres of diversity in the light of current understanding of wheat diversity, domestication and evolution. *Czech Journal of Genetics and Plant Breeding*, 2011, **47**: S20–S27
26. Chen H F, Jiao C Z, Wang Y, Wang Y G, Tian C H, Yu H P, Wang J, Wang X F, Lu F, Fu X D, Xue Y B, Jiang W K, Ling H Q, Lu H F, Jiao Y L. Comparative population genomics of bread wheat (*Triticum aestivum*) reveals its cultivation and breeding history in China. *bioRxiv*, 2019 (preprint). doi:10.1101/519587
27. Zhou L G, Garvie-Lok S J, Fan W Q, Chu X L. Human diets during the social transition from territorial states to empire: stable isotope analysis of human and animal remains from 770 BCE to 220 CE on the Central Plains of China. *Journal of Archaeological Science: Reports*, 2017, **11**: 211–223
28. International Wheat Genome Sequencing Consortium. Shifting the limits in wheat research and breeding using a fully annotated reference genome. *Science*, 2018, **361**(6403): eaar7191
29. Mayer K F X, Rogers J, Doležel J, Pozniak C, Eversole K, Feuillet C, Gill B, Friebe B, Lukaszewski A J, Sourdille P, Endo T R, Kubaláková M, Čihalíková J, Dubsá Z, Vrána J, Šperková R, Šimková H, Febrer M, Clissold L, McLay K, Singh K, Chhuneja P, Singh N K, Khurana J, Akhunov E, Choulet F, Alberti A, Barbe V, Wincker P, Kanamori H, Kobayashi F, Itoh T, Matsumoto T, Sakai H, Tanaka T, Wu J Z, Ogihara Y, Handa H, Maclachlan P R, Sharpe A, Klassen D, Edwards D, Batley J, Olsen O A, Sandve S R, Lien S, Steuernagel B, Wulff B, Caccamo M, Ayling S, Ramirez-Gonzalez R H, Clavijo B J, Wright J, Pfeifer M, Spannagl M, Martis M M, Mascher M, Chapman J, Poland J A, Scholz U, Barry K, Waugh R, Rokhsar D S, Muehlbauer G J, Stein N, Gundlach H, Zytnicki M, Jamilloux V, Quesneville H, Wicker T, Faccioli P, Colaiacovo M, Stanca A M, Budak H, Cattivelli L, Glover N, Pingault L, Paux E, Sharma S, Appels R, Bellgard M, Chapman B, Nussbaumer T, Bader K C, Rimbart H, Wang S C, Knox R, Kilian A, Alaux M, Alfama F, Couderc L, Guilhot N, Viseux C, Loaec M, Quesneville H, Keller B, Praud S. A chromosome-based draft sequence of the hexaploid bread wheat (*Triticum aestivum*) genome. *Science*, 2014, **345**(6194): 1251788

30. Fuller D Q, Lucas L. Wheats: origins and development. *Encyclopedia of Global Archaeology*, 2013: 7812–7817
31. Guo B Z. Gramineae. In: Editorial Committee of Flora of China, Chinese Academy of Sciences, ed. *Flora of China*, 2nd ed. Beijing: Science Press, 1987, 38–51 (in Chinese)
32. GBIF. GBIF occurrence download. March 25, 2019. doi: 10.15468/dl.nbp9if
33. Yan J, Yang J L, Cui N R. The *Aegilops tauschii* Cosson from Yi-Li, Xinjiang, China. *Acta Agronomica Sinica*, 1984, (1): 1–8 (in Chinese)
34. Zohary D, Hopf M. Domestication of plants in the Old World: the origin and spread of cultivated plants in West Asia, Europe and the Nile Valley. Oxford: Clarendon Press, 1994
35. Kislew M E, Nadel D, Carmi I. Epipalaeolithic (19,000 BP) cereal and fruit diet at Ohalo II, Sea of Galilee, Israel. *Review of Palaeobotany and Palynology*, 1992, 73(1–4): 161–166
36. Weiss E, Wetterstrom W, Nadel D, Bar-Yosef O. The broad spectrum revisited: evidence from plant remains. *Proceedings of the National Academy of Sciences of the United States of America*, 2004, 101(26): 9551–9555
37. Arranz-Otaegui A, Gonzalez Carretero L, Ramsey M N, Fuller D Q, Richter T. Archaeobotanical evidence reveals the origins of bread 14,400 years ago in northeastern Jordan. *Proceedings of the National Academy of Sciences of the United States of America*, 2018, 115(31): 7925–7930
38. Weiss E, Zohary D. The Neolithic Southwest Asian founder crops: their biology and archaeobotany. *Current Anthropology*, 2011, 52 (S4): S237–S54
39. Perlès C. The early Neolithic in Greece: the first farming communities in Europe. Cambridge: Cambridge University Press, 2001
40. Greenfield H J, Greenfield T L J, Jezik S. Subsistence and settlement in the Early Neolithic of temperate SE Europe: a view from Blagotin, Serbia. *Archaeologia Bulgarica*, 2014, 18(1): 1–33
41. Robinson D E. Neolithic and Bronze Age agriculture in southern Scandinavia—recent archaeobotanical evidence from Denmark. *Environmental Archaeology*, 2003, 8(2): 145–165
42. Collard M, Edinborough K, Shennan S, Thomas M G. Radiocarbon evidence indicates that migrants introduced farming to Britain. *Journal of Archaeological Science*, 2010, 37(4): 866–870
43. Hovsepyan R, Willcox G. The earliest finds of cultivated plants in Armenia: evidence from charred remains and crop processing residues in pisé from the Neolithic settlements of Aratashen and Aknashen. *Vegetation History and Archaeobotany*, 2008, 17(1): 63–71
44. Harris D R. Origins of Agriculture in Western Central Asia: an environmental-archaeological study. Philadelphia: University of Pennsylvania Press, 2010
45. Tengberg M. Crop husbandry at Miri Qalat Makran, SW Pakistan (4000–2000 BC). *Vegetation History and Archaeobotany*, 1999, 8 (1–2): 3–12
46. Fuller D Q. Agricultural origins and frontiers in South Asia: a working synthesis. *Journal of World Prehistory*, 2006, 20(1): 1–86
47. Spengler R N, Willcox G. Archaeobotanical results from Sarazm, Tajikistan, an Early Bronze Age Settlement on the edge: agriculture and exchange. *Environmental Archaeology*, 2013, 18(3): 211–221
48. Spengler R, Frachetti M, Doumani P, Rouse L, Cerasetti B, Bullion E, Mar'yashev A. Early agriculture and crop transmission among Bronze Age mobile pastoralists of Central Eurasia. *Proceedings of the Royal Society B: Biological Sciences*, 2014, 281(1783): 20133382
49. Doumani P N, Frachetti M D, Beardmore R, Schmaus T M, Spengler R N III, Mar'yashev A. Burial ritual, agriculture, and craft production among Bronze Age pastoralists at Tasbas (Kazakhstan). *Archaeological Research in Asia*, 2015, 1: 17–32
50. Jin G Y, Wang H Y, Yan S D, Liu C J, Lan Y F, Tong P H. Carbonized plant remains in Zhaojiazhuang site of Longshan culture, Jiaozhou County, Shandong Province. In: Center of Science for Archaeology, Institute of Archaeology, Chinese Academy of Social Sciences, ed. *Science for Archaeology* (3). Beijing: Science Press, 2011, 36–53 (in Chinese).
51. Long T W, Leipe C, Jin G Y, Wagner M, Guo R Z, Schröder O, Tarasov P E. The early history of wheat in China from <sup>14</sup>C dating and Bayesian chronological modelling. *Nature Plants*, 2018, 4(5): 272–279
52. Dodson J R, Li X Q, Zhou X Y, Zhao K L, Sun N, Atahan P. Origin and spread of wheat in China. *Quaternary Science Reviews*, 2013, 72: 108–111
53. Dong G H, Yang Y S, Liu X Y, Li H M, Cui Y F, Wang H, Chen G, Dodson J, Chen F H. Prehistoric trans-continental cultural exchange in the Hexi Corridor, northwest China. *The Holocene*, 2018, 28(4): 621–628
54. Dong G H. A new story for wheat into China. *Nature Plants*, 2018, 4 (5): 243–244
55. Zhang J Z, Chen Z J, Lan W L, Yang Y Z, Luo W H, Yao L, Yin C L. The new progresses of the paleoethnobotanical studies of Jiahu site in Wuyang, Henan. *Archaeological*, 2018, (4): 100–110 (in Chinese)
56. Motuzaite-Matuzeviciute G, Staff R A, Hunt H V, Liu X Y, Jones M K. The early chronology of broomcorn millet (*Panicum miliaceum*) in Europe. *Antiquity*, 2013, 87(338): 1073–1085
57. Liu X Y, Lister D L, Zhao Z J, Staff R A, Jones P J, Zhou L P, Pokharia A K, Petrie C A, Pathak A, Lu H L, Matuzeviciute G M, Bates J, Pilgram T K, Jones M K. The virtues of small grain size: potential pathways to a distinguishing feature of Asian wheats. *Quaternary International*, 2016, 426: 107–119
58. Zhang J Z, Chen C F, Yang Y Z. Origins and early development of agriculture in China. *Journal of National Museum of China*, 2014, 1: 6–16 (in Chinese)
59. Zhou X Y, Li X Q, Dodson J, Zhao K L. Rapid agricultural transformation in the prehistoric Hexi Corridor, China. *Quaternary International*, 2016, 426: 33–41
60. Yang R P, Yang Y M, Li W Y, Abuduresule Y, Hu X J, Wang C S, Jiang H E. Investigation of cereal remains at the Xiaohu cemetery in Xinjiang, China. *Journal of Archaeological Science*, 2014, 49: 42–47
61. Zhou L G, Garvie-Lok S J. Isotopic evidence for the expansion of wheat consumption in northern China. *Archaeological Research in Asia*, 2015, 4: 25–35
62. Zhang Q C, Zhu H. Carbon and nitrogen stable isotope analysis of the human bones from the Gumugou cemetery in Xinjiang: a

- preliminary exploration of the early population dietary in Lop Nur. *Western Regions Studies*, 2011, **3**: 91–96
63. Ma M M, Dong G H, Jia X, Wang H, Cui Y F, Chen F H. Dietary shift after 3600 cal yr BP and its influencing factors in northwestern China: evidence from stable isotopes. *Quaternary Science Reviews*, 2016, **145**: 57–70
  64. Dong G H, Ren L L, Jia X, Liu X Y, Dong S M, Li H M, Wang Z X, Xiao Y M, Chen F H. Chronology and subsistence strategy of Nuomuhong Culture in the Tibetan Plateau. *Quaternary International*, 2016, **426**: 42–49
  65. Chen F H, Dong G H, Zhang D J, Liu X Y, Jia X, An C B, Ma M M, Xie Y W, Barton L, Ren X Y, Zhao Z J, Wu X H, Jones M K. Agriculture facilitated permanent human occupation of the Tibetan Plateau after 3600 B.P. *Science*, 2015, **347**(6219): 248–250
  66. Lee G A, Crawford G W, Liu L, Chen X C. Plants and people from the Early Neolithic to Shang periods in North China. *Proceedings of the National Academy of Sciences of the United States of America*, 2007, **104**(3): 1087–1092
  67. Zhang J N, Xia Z K, Zhang X H. Research on charred plant remains from the Neolithic to the Bronze Age in Luoyang Basin. *Chinese Science Bulletin*, 2014, **59**(34): 3388–3397
  68. Hou L L, Hu Y W, Zhao X P, Li S T, Wei D, Hou Y F, Hu B H, Lv P, Li T, Song G D, Wang C S. Human subsistence strategy at Liuzhuang site, Henan, China during the proto-Shang culture (~2000–1600 BC) by stable isotopic analysis. *Journal of Archaeological Science*, 2013, **40**(5): 2344–2351
  69. Cheung C, Jing Z C, Tang J G, Weston D A, Richards M P. Diets, social roles, and geographical origins of sacrificial victims at the royal cemetery at Yinxu, Shang China: new evidence from stable carbon, nitrogen, and sulfur isotope analysis. *Journal of Anthropological Archaeology*, 2017, **48**: 28–45
  70. Zhou Y, Chen Z X, Cheng M P, Chen J, Zhu T T, Wang R, Liu Y, Qi P, Chen G, Jiang Q, Wei Y, Luo M C, Nevo E, Allaby R G, Liu D C, Wang J R, Dvorák J, Zheng Y L. Uncovering the dispersion history, adaptive evolution and selection of wheat in China. *Plant Biotechnology Journal*, 2018, **16**(1): 280–291
  71. Hou L L, Wang N, Lü P, Hu Y W, Song G D, Wang C S. Transition of human diets and agricultural economy in Shenmingpu site, Henan, from the Warring States to Han Dynasties. *Science China: Earth Sciences*, 2012, **55**(6): 975–982
  72. Wei S. A historical research on large area planting of wheat in Han Dynasty of China—Consult with Sadao Nishijima. *Agricultural History of China*, 1988, (4): 22–30 (in Chinese)
  73. Wang L H. The vicissitude of food culture in middle ancient north China. Beijing: *China Social Sciences Press*, 2001 (in Chinese)
  74. Bond G, Showers W, Cheseby M, Lotti R, Almasi P, deMenocal P, Priore P, Cullen H, Hajdas I, Bonani G. A pervasive millennial-scale cycle in North Atlantic Holocene and glacial climates. *Science*, 1997, **278**(5341): 1257–1266
  75. Peng W. Once more discussion on wheat extension in Han Dynasty. *Researches in Chinese Economic History*, 2010, (4): 63–71 (in Chinese)