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The Archaeological Record of Wheat: From Neolithic Innovations to Modern Developments

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Abstract Wheat has played a fundamental role in human societal development, from its early domestication in the Neolithic era to its current status as a global staple crop. This study reviews the archaeological, genetic, and historical records of wheat, tracing its evolutionary journey over millennia. Beginning with its domestication in the Fertile Crescent, the research explores wheat's spread to Europe and Asia, its adaptability to diverse climates, and the technological innovations that shaped its cultivation. Special attention is given to wheat's role in ancient empires, the agricultural advancements that promoted its growth, and its integration into cultural and religious practices. The study also examines the impacts of modern developments, including the Green Revolution, genetic engineering, and precision agriculture. Finally, it addresses the contemporary challenges of wheat cultivation, particularly in the context of climate change and sustainability, while reflecting on wheat's ongoing importance to human health and global food security.

Keywords Wheat domestication; Archaeobotany; Neolithic agriculture; Wheat cultivation; Green revolution; Genetic engineering; Climate change adaptation

1 Introduction

Wheat has been a cornerstone of human civilization, playing a pivotal role in the development of societies from the Neolithic era to the present day (Toulemonde et al., 202). Its cultivation dates back approximately 12 000 years, marking the transition from nomadic lifestyles to settled agricultural communities (Velimirović et al., 2021). The domestication of wheat, along with barley, in the Near East during the early Holocene epoch, significantly influenced the socio-economic structures of ancient societies (Ghahremaninejad et al., 2021). The adaptability of wheat to various climates and its high nutritional value facilitated its spread from its origin in the Fertile Crescent to other parts of the world, making it one of the most important cereal crops globally (Sousa et al., 2021; Velimirović et al., 2021).

The domestication and cultivation of wheat were instrumental in the rise of early agricultural societies. In regions such as Mesopotamia, the cultivation of tetraploid wild emmer wheat around 4 000 B.C.E. supported the growth of the first civilizations (Velimirović et al., 2021). Similarly, in Iran, the domestication of wheat and barley around the 10th millennium BP led to significant advancements in agricultural techniques, irrigation, and storage, which in turn spurred the development of complex human societies (Sousa et al., 2021). The introduction of wheat to other regions, such as northern China, also marked a significant shift in subsistence economies, often in response to climatic changes (Cheung et al., 2019). These early agricultural innovations laid the foundation for modern agricultural practices and societal development.

This study will explore the historical significance of wheat cultivation, its impact on early agricultural societies, and the technological advancements that have shaped its production. By examining archaeological and archaeobotanical evidence from various regions, including the Near East, Europe, and Asia, the study highlights the evolutionary trajectory of wheat and its enduring importance as a staple crop. The study covers genetic, environmental, and socio-political factors influencing wheat cultivation, providing insights to inform future agricultural development strategies.

2 Early Domestication of Wheat (Neolithic Era)

2.1 Geographic origins and genetic evolution

The domestication of wheat is a pivotal event in human history, marking the transition from foraging to farming. Bread wheat (*Triticum aestivum*) originated approximately 8 500~9 000 years ago through hybridization between a domesticated tetraploid progenitor and Aegilops tauschii, the diploid donor of the D subgenome (Figure 1). This hybridization likely occurred in the Fertile Crescent, a region known for its rich biodiversity and favorable conditions for early agriculture. The genetic evolution of wheat was significantly influenced by allopolyploidy, which facilitated the acquisition of new traits and enhanced genetic diversity, enabling wheat to adapt to various climates and environments (Levy and Feldman, 2022). Additionally, the B subgenome's origin remains elusive, suggesting the involvement of an unknown or extinct species.

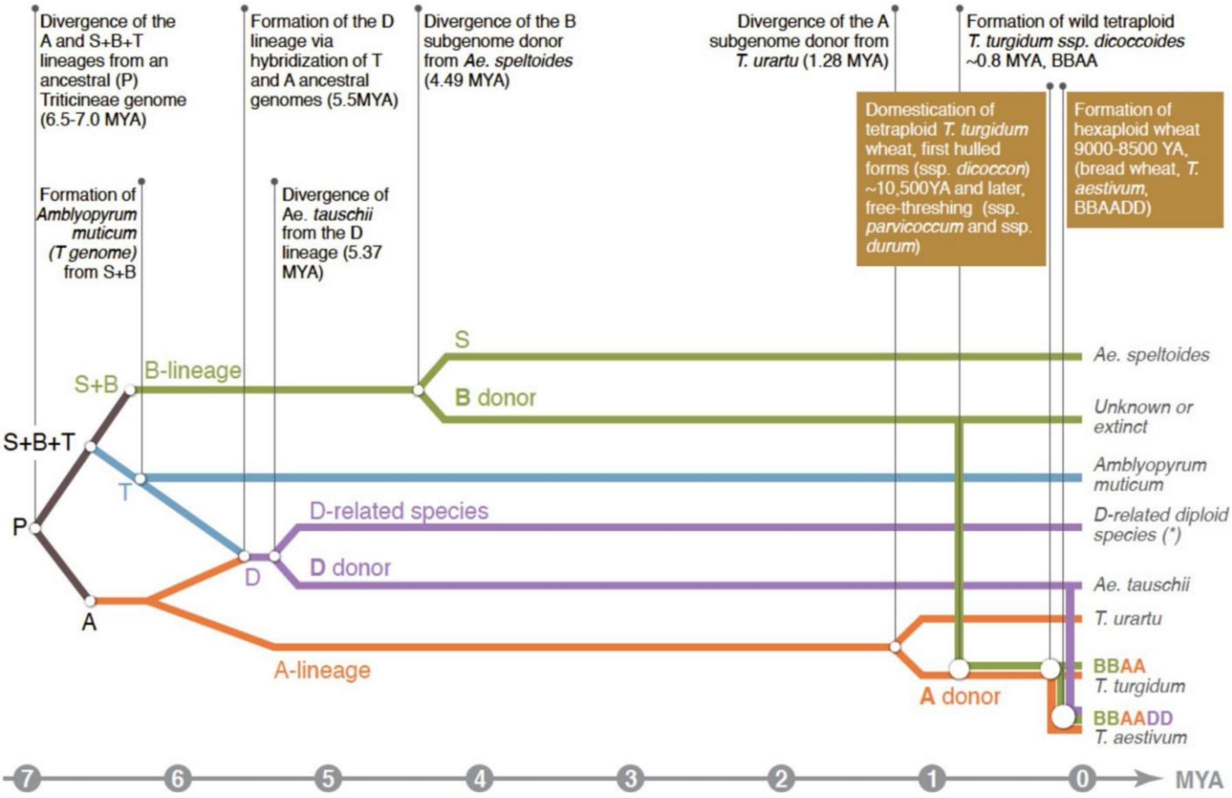


Figure 1 Phylogenetic representation of wheat evolution (Adopted from Levy and Feldman, 2022)

Image caption: Wheat evolution is shown starting ~7 MYA from a progenitor that gave rise to the (A), (B), and (D) lineages that merged to form bread wheat; The relative timing of the major speciation events is shown in the horizontal axis and described in the boxes above (Adopted from Levy and Feldman, 2022)

2.2 Archaeobotanical and DNA evidence

Archaeobotanical evidence from sites such as Gusir Höyük in Southeast Anatolia provides insights into the early domestication processes. This site, dating back to the 12th-late 11th millennia cal BP, shows selective use and management of cereal and legume crop progenitors, indicating a faster pace of wheat domestication than previously hypothesized (Kabukcu et al., 2021; Zhang, 2024). Similarly, microtexture analysis of sickle blades from Dja'de el-Mughara in the northern Levant reveals complex cereal harvesting strategies during the Early PPNB period, suggesting the exploitation of cereal populations at different domestication stages (Pichon et al., 2021). DNA evidence from ancient wheat samples, such as the 3 000-year-old Egyptian emmer wheat genome, further elucidates the domestication and dispersal history of wheat, highlighting genetic similarities with modern domesticated emmer and unique haplotypes absent in contemporary varieties (Scott et al., 2019).

2.3 Environmental and agronomic conditions

The environmental and agronomic conditions during the Neolithic era played a crucial role in the domestication of wheat. The Fertile Crescent's diverse ecogeographies provided a conducive environment for the cultivation and selection of wheat varieties with desirable traits. Early Neolithic farmers in regions like the Plain of Troyes in Champagne introduced staple crops such as emmer and einkorn, which were well-suited to the local conditions (Toulemonde et al., 2020). The resilience of pioneer crops, including bread wheat and naked barley, in high-altitude regions like the Central Tien Shan mountains, further underscores the adaptability of early domesticated wheat to various environmental stresses (Matuzevičiūtė et al., 2022). These conditions facilitated the development of unique landraces and the successful establishment of agriculture in diverse ecological niches.

The early domestication of wheat was a complex process influenced by genetic evolution, archaeobotanical evidence, and environmental conditions (Bohra et al., 2022). The Fertile Crescent served as the cradle of wheat domestication, with significant contributions from regions like Southeast Anatolia and the northern Levant. The adaptability of wheat to different climates and environments ensured its global spread and enduring significance in human agriculture.

3 Spread of Wheat Cultivation

3.1 Wheat's diffusion into europe and asia

The diffusion of wheat from its origin in the Fertile Crescent into Europe and Asia was a complex process influenced by various factors, including environmental conditions, trade routes, and social interactions. In Europe, the spread of wheat cultivation is closely linked with the broader Neolithic agricultural expansion. For instance, the introduction of broomcorn millet in Europe during the 2nd millennium BC marked a significant agricultural transformation, with wheat and barley being the primary crops before millet's introduction (Filipović et al., 2020). This period saw major societal and economic changes, particularly during the Bronze Age.

In Central Asia, the earliest evidence of southwest Asian grain crops, including wheat, dates back to the mid-third millennium BCE. Archaeobotanical remains from the Chap II site in Kyrgyzstan indicate that wheat, along with barley, was cultivated at high altitudes, suggesting an adaptation to local environmental conditions (Matuzevičiūtė et al., 2020). This early cultivation in Central Asia highlights the eastward spread of agricultural technologies and the dynamic interaction networks between highland and lowland farming societies.

3.2 Adaptation to local climates

Wheat's ability to adapt to diverse climatic conditions played a crucial role in its widespread cultivation. In northern China, the introduction of wheat and barley during the Neolithic period led to significant changes in the subsistence economy. Stable isotope analysis of human skeletal remains reveals a shift from a millet-based diet to a mixed diet that included wheat and barley around 4 500~4 000 BP, coinciding with a global climatic event (Cheung et al., 2019). This adaptation to local climates was further evidenced by the distinct cultivation strategies employed on the Loess Plateau, where ancient farmers used novel soil and water management techniques for wheat, contrasting with the pre-existing practices for barley (Li et al., 2022).

In the Gansu-Qinghai region of northwest China, the spatiotemporal distribution of wheat and barley during the Late Neolithic and Bronze Age was influenced by geographical factors such as proximity to rivers and suitable climatic conditions. Wheat sites were generally located at lower elevations and closer to water sources compared to barley sites, reflecting wheat's specific environmental requirements (Ma et al., 2022).

3.3 The role of trade and social networks

Trade and social networks were instrumental in the spread of wheat cultivation across different regions. The introduction of wheat into central China, for example, is thought to have resulted from interactions between China and Central Asia during the 3rd millennium BC. However, the role of wheat in subsistence farming in central China remained minimal until the later Bronze Age, suggesting a gradual integration facilitated by trade and cultural exchanges (Deng et al., 2019).

In southeastern Shandong Province, China, direct evidence of early bread wheat dating to 2 460~2 210 BC suggests multiple possible routes for wheat transmission, including the Eurasian Steppe route and potential ocean travel. This early introduction of wheat to the eastern Chinese coast highlights the role of trade networks in facilitating the spread of agricultural practices (Chen et al., 2020).

4 Wheat in Historical Civilizations

4.1 Role in ancient empires

Wheat has played a pivotal role in the sustenance and expansion of ancient empires. In central China, the introduction of wheat during the late Neolithic period marked a significant shift in agricultural practices, although its role in subsistence farming remained minimal until the later Bronze Age during the Zhou dynasty (Deng et al., 2019). The spread of wheat and barley from Central Asia to northern China around 4 500~4 000 BP coincided with a global climatic event, leading to a mixed subsistence economy and indicating the crop's importance in adapting to environmental changes (Cheung et al., 2019). In the Near East, wheat was one of the "Founder Crops" that underpinned early agricultural societies, contributing to the development of complex civilizations (Ulaş and Fiorentino, 2020).

4.2 Agricultural innovations in ancient civilizations

Ancient civilizations developed various agricultural innovations to cultivate wheat effectively. In southeastern Anatolia, traditional wheat cultivation practices observed today mirror those from 10 500 years ago, including the use of silos made from earth, stones, and tree branches, and manual harvesting techniques (Ulaş, 2020). At Göbekli Tepe, an Early Neolithic site in southeastern Turkey, extensive plant food processing tools such as grinding slabs and pestles were used for cereal processing, highlighting the sophistication of early agricultural practices (Dietrich et al., 2019). Additionally, the genetic diversity of modern bread wheats has been shaped by 10 000 years of hybridization, selection, and adaptation, reflecting the continuous improvement and innovation in wheat cultivation (Pont et al., 2019).

4.3 Wheat in cultural and religious practices

Wheat has also held significant cultural and religious importance throughout history. In ancient Eurasian agriculture, the "new" glume wheat (*Triticum timopheevii*) was a notable crop, present across western Asia and Europe during the Neolithic and Bronze Ages, and played a role in the cultural practices of these regions (Czajkowska et al., 2020). The processing of cereals at Göbekli Tepe, a site known for its monumental architecture and ritual significance, suggests that wheat was not only a staple food but also integral to the social and ceremonial activities of its builders (Dietrich et al., 2019). Furthermore, the ethnobotanical study in southeastern Anatolia indicates that women were central to wheat cultivation and processing, suggesting a deep-rooted cultural tradition of female involvement in agriculture (Ulaş, 2020).

Wheat has been a cornerstone of ancient civilizations, influencing their agricultural practices, economic stability, and cultural traditions. Its introduction and cultivation have been marked by significant innovations and adaptations, underscoring its enduring importance in human history.

5 Technological Innovations in Wheat Cultivation

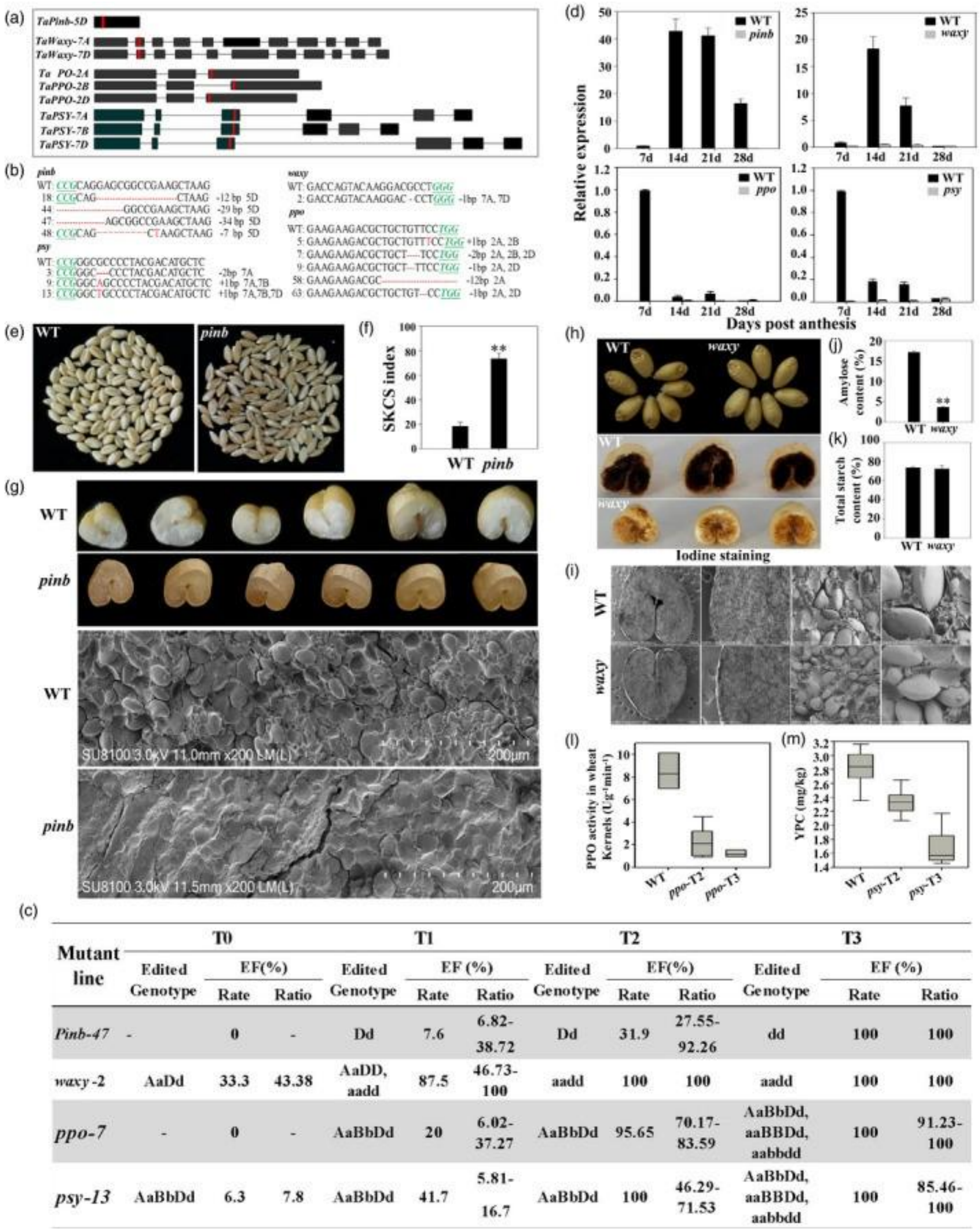
5.1 Mechanization and the agricultural revolution

The Agricultural Revolution marked a significant shift in wheat cultivation, characterized by the introduction of mechanized farming equipment. This period saw the development and widespread adoption of machinery such as the plow, seed drill, and combine harvester, which drastically increased the efficiency and scale of wheat production. These innovations reduced the labor intensity of farming and allowed for the cultivation of larger areas, leading to increased wheat yields and the ability to support growing populations.

5.2 Green revolution and genetic engineering

The Green Revolution, which began in the mid-20th century, introduced high-yielding wheat varieties and advanced agricultural practices, including the use of chemical fertilizers, pesticides, and irrigation techniques. These advancements significantly boosted wheat production and helped alleviate food shortages in many parts of the world. However, the Green Revolution also brought challenges such as environmental degradation and increased dependency on chemical inputs (Hamdan et al., 2022).

In the subsequent Gene Revolution, biotechnological advancements further transformed wheat cultivation. Techniques such as Marker-Assisted Selection (MAS), Genomic Selection (GS), and CRISPR-Cas9 genome editing have enabled precise modifications to wheat genomes, enhancing traits such as yield, disease resistance, and climate adaptability (Figure 2) (Abideen et al., 2023; Zhao, 2024). These genetic engineering methods hold promise for addressing the ongoing challenges of food security and environmental sustainability (Hamdan et al., 2022; Abideen et al., 2023).



Mutant line	T0			T1			T2			T3		
	Edited Genotype	EF(%)		Edited Genotype	EF (%)		Edited Genotype	EF(%)		Edited Genotype	EF (%)	
		Rate	Ratio		Rate	Ratio		Rate	Ratio		Rate	Ratio
Pinb-47	-	0	-	Dd	7.6	6.82-38.72	Dd	31.9	27.55-92.26	dd	100	100
waxy-2	AaDd	33.3	43.38	AaDD, aadd	87.5	46.73-100	aadd	100	100	aadd	100	100
ppo-7	-	0	-	AaBbDd	20	6.02-37.27	AaBbDd	95.65	70.17-83.59	AaBbDd, aaBBDd, aabbdd	100	91.23-100
psy-13	AaBbDd	6.3	7.8	AaBbDd	41.7	5.81-16.7	AaBbDd	100	46.29-71.53	AaBbDd, aaBBDd, aabbdd	100	85.46-100

Figure 2 Generation and Results of Wheat pinb, waxy, ppo, and psy Mutants Using CRISPR/Cas9-Mediated Gene Editing (Adapted from Zhang et al., 2021)

Image caption: The figure provides a detailed analysis of the mutations in the four target genes (pinb, waxy, ppo, and psy) across different generations (T0, T1, T2, and T3), focusing on editing efficiency (EE) and mutation rates (number of mutants/total plants); The study reveals a significant increase in editing efficiency with successive generations, reaching 100% in the T2 and T3 generations. Additionally, the expression levels of the target genes in the mutants were significantly reduced, becoming almost undetectable throughout grain development; The figure also illustrates the phenotypic changes in mutant grains, the endosperm structure as observed under scanning electron microscopy, and the notable differences in grain hardness, starch composition, and dough color between the mutants and wild-type wheat (Adapted from Zhang et al., 2021)

5.3 Current innovations: CRISPR and precision agriculture

Recent innovations in wheat cultivation include the application of CRISPR/Cas genome editing and precision agriculture techniques. CRISPR/Cas9 allows for targeted modifications in wheat DNA, enabling the development of varieties with improved traits such as enhanced nutritional content, resistance to pests and diseases, and better adaptability to changing climatic conditions (Chen et al., 2019). This technology represents a significant leap forward in plant breeding, offering the potential for rapid and precise genetic improvements (Chen et al., 2019; Abideen et al., 2023).

Precision agriculture, on the other hand, leverages advanced data collection and analysis tools to optimize farming practices. By utilizing technologies such as remote sensing, geophysical and geochemical mapping, and data analytics, farmers can manage crop and soil variability more effectively. This approach aims to increase yields, reduce input costs, and enhance environmental sustainability (Webber et al., 2019). The integration of precision farming with archaeological studies also presents new opportunities for understanding the historical impacts of agricultural practices on the environment.

6 Modern Developments in Wheat Cultivation

6.1 Sustainability challenges and climate change

Wheat cultivation faces significant sustainability challenges, particularly in the context of climate change. The loss of genetic variation due to modern breeding practices has reduced the resilience of wheat crops to environmental stresses. Ancient wheat varieties, such as those from the Caucasus, offer a reservoir of biodiversity that can be harnessed to improve sustainability and resilience in wheat production. These ancient varieties have shown higher protein content and antioxidant capacity compared to modern durum wheat, making them valuable for sustainable agriculture and healthy food production (Nocente et al., 2022). Additionally, the development of stress-tolerant wheat cultivars through molecular breeding, genetic engineering, and other advanced techniques is crucial for mitigating the adverse effects of abiotic stresses under changing climatic conditions (Hossain et al., 2021). Improved root systems tailored to specific agricultural environments can also enhance climate resilience by optimizing water and nutrient uptake (Ober et al., 2021).

6.2 Biotechnology in wheat breeding

Biotechnology plays a pivotal role in modern wheat breeding, offering tools to enhance yield, quality, and stress tolerance. Advances in genomics and quantitative genetics have provided unique opportunities to balance wheat quantity and quality, addressing both food security and environmental sustainability (Fradgley et al., 2023). Techniques such as exome sequencing have shed light on the genetic diversity and evolution of modern bread wheats, revealing considerable genetic variation that can be exploited for future breeding improvements (Pont et al., 2019). Moreover, the use of molecular breeding, speed breeding, and gene editing technologies like CRISPR-Cas has shown promise in developing wheat cultivars that are resilient to abiotic stresses, thereby ensuring sustainable production in the face of climate change (Hossain et al., 2021).

6.3 Global wheat trade and its impacts

The global wheat trade has significant implications for food security and economic stability. Wheat is a staple crop that provides a substantial portion of the world's carbohydrates and protein, with nearly 25% of global production being traded internationally (Langridge et al., 2022). The strategic importance of wheat has led to the establishment of initiatives like the Global Wheat Initiative, which aims to support the wheat research community in addressing production challenges through collaboration and resource sharing. However, the focus on high-yielding varieties for trade can sometimes lead to negative environmental impacts, as seen in the UK, where intensive cropping systems prioritize quantity over quality, resulting in sustainability issues (Fradgley et al., 2023). Innovations in wheat breeding and agronomy are essential to balance these trade-offs and ensure that global wheat production meets both demand and sustainability goals.

By addressing these modern developments in wheat cultivation, researchers and policymakers can work towards a more sustainable and resilient global wheat production system that can withstand the challenges posed by climate change and meet the nutritional needs of a growing population.

7 Wheat and Human Health

7.1 Nutritional composition of ancient vs. modern wheat

The nutritional composition of ancient and modern wheat varieties has been a subject of extensive research. Ancient wheat varieties, such as emmer, einkorn, spelt, and khorasan, have been found to possess a healthier nutritional profile compared to modern wheat. These ancient grains often exhibit higher levels of antioxidants and anti-inflammatory properties, which are beneficial for human health (Dinu et al., 2018; Spisni et al., 2019; Renzo et al., 2023). Studies have shown that ancient wheat varieties have a higher amylose/amylopectin ratio and a lower glycemic index, which can contribute to better metabolic health (Renzo et al., 2023). However, it is important to note that while ancient wheats may offer certain health benefits, the evidence is not conclusive enough to definitively state that they are superior to modern wheat in reducing chronic disease risk (Dinu et al., 2018).

7.2 The rise of gluten sensitivity

The prevalence of gluten-related disorders, including celiac disease (CD) and non-celiac gluten sensitivity (NCGS), has increased significantly in recent decades. Celiac disease is an autoimmune condition triggered by the ingestion of gluten in genetically susceptible individuals, leading to intestinal damage and various gastrointestinal and extra-intestinal symptoms (Potter et al., 2018; Sharma et al., 2020; Raju et al., 2023). Non-celiac gluten sensitivity, on the other hand, is characterized by gastrointestinal and non-gastrointestinal symptoms that improve upon the removal of gluten from the diet, despite the absence of celiac disease (Potter et al., 2018; Scherf, 2019; Sharma et al., 2020). The rise in gluten sensitivity has been partly attributed to changes in wheat breeding practices, which may have inadvertently increased the immunostimulatory potential of modern wheat varieties (Pronin et al., 2020). Additionally, the growing popularity of gluten-free diets, often without medical necessity, has further complicated the understanding and management of gluten-related disorders (Sabença et al., 2021; Raju et al., 2023).

7.3 Archaeological evidence of wheat in ancient diets

Archaeological evidence indicates that wheat has been a staple in human diets since its domestication in the Fertile Crescent around 9000 BC. The spread of wheat cultivation played a crucial role in the development of early agricultural societies. Ancient grains, including various wheat species, have been found in archaeological sites, providing insights into the dietary practices of ancient civilizations. These findings suggest that wheat was a significant source of nutrition and energy for ancient populations (Raju et al., 2023; Renzo et al., 2023). The study of ancient wheat varieties and their nutritional properties continues to offer valuable information on the evolution of human diets and the potential health benefits of these grains (Dinu et al., 2018; Renzo et al., 2023).

8 Concluding Remarks

The evolution of wheat from its Neolithic origins to its current status as a global staple crop is a testament to its adaptability and significance in human history. The synthesis of archaeological, genetic, and modern studies provides a comprehensive understanding of wheat's journey and its impact on civilization.

Archaeological evidence highlights the early domestication and spread of wheat. For instance, tetraploid wild emmer wheat was cultivated as early as 4 000 B.C.E. in Mesopotamia, marking the beginning of sedentary agricultural societies. The domestication of wheat, along with barley, was a cornerstone of the agricultural revolution in the Fertile Crescent, leading to significant changes in human societies. The spread of wheat to regions such as northern China around 4 500~4 000 BP, driven by climatic changes, further underscores its adaptability and importance.

Genetic studies have unraveled the complex ancestry and evolution of modern bread wheat. The hybridization events that led to the formation of hexaploid bread wheat (*Triticum aestivum*) around 8 500~9 000 years ago were crucial for its global expansion. Exome sequencing of a diverse panel of wheat genotypes has shed light on the genetic diversity and evolutionary history of modern bread wheat, providing insights into the allelic variants selected over millennia. The sequencing of ancient wheat genomes, such as the 3 000-year-old Egyptian emmer wheat, has revealed unique genetic traits and historical dispersal patterns, emphasizing the value of ancient DNA in understanding crop evolution.

Modern studies have focused on the physiological and nutritional differences between ancient, heritage, and modern wheat varieties. Research indicates that ancient and heritage wheat varieties may have different anti-inflammatory and antioxidant properties compared to modern cultivars, suggesting potential health benefits. The Green Revolution and subsequent agricultural advancements have dramatically increased wheat yields, transforming global agriculture and food security.

Wheat's historical significance in shaping human civilization is undeniable. From enabling the rise of early agricultural societies to becoming a staple food for billions, wheat has played a pivotal role in human development. Looking forward, the conservation and utilization of wheat's vast genetic diversity are crucial for addressing future challenges such as climate change and food security. Continued research and breeding efforts, informed by historical and genetic insights, will be essential for developing resilient and high-yielding wheat varieties that can sustain the growing global population.

In conclusion, the archaeological, genetic, and modern studies of wheat provide a holistic view of its evolution and underscore its enduring importance. As we face new challenges, the lessons from wheat's past will guide us in securing its future as a cornerstone of human civilization.

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Conflict of Interest Disclosure

The author affirms that this research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

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