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Malting Barley: The Botanical Evolution and Domestication History from Wild Grain to Brewing Staple

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Abstract Barley (*Hordeum vulgare*), an ancient grain crop, originally grew in the wild and has undergone long-term domestication to become an essential crop in modern agriculture. Widely cultivated across the globe, barley plays a critical role in beer brewing, where its ability to serve as a fermentable sugar source makes it indispensable in the brewing process. This study explores the botanical evolution and domestication history of barley from its wild grain origins to its foundational role in modern beer brewing. The specific objectives include analyzing barley's morphological characteristics, ecological adaptability, and domestication process, investigating the selection of Malting Barley varieties and their specialized applications in brewing, and further revealing barley's cultural and historical impact on agriculture and brewing. The research shows that barley's morphological structure and genetic traits have undergone significant changes during its domestication, particularly in terms of adaptability and yield performance. Additionally, specific barley varieties have shown enhanced enzyme activity and saccharification efficiency, providing better raw material for beer brewing. By gaining a deeper understanding of barley's biological traits and its domestication history, this study will provide a scientific basis for the improvement and breeding of Malting Barley. In the context of global climate change, improving barley's stress resistance and brewing quality holds substantial agricultural and economic value. Moreover, this research highlights barley's profound influence on human society, culture, and economic development.
Keywords Malting Barley; Barley domestication; Brewing process; Genetic improvement; Stress resistance

1 Introduction

Barley (*Hordeum vulgare*) is one of the oldest cultivated grains, with a history that dates back to the Neolithic revolution approximately 10 000 years ago. It is a crop of significant botanical and agricultural importance, being the fourth most important cereal crop globally after wheat, rice, and maize (Nevo, 2013; Tyagi et al., 2020; Wu, 2024). Barley's adaptability to a wide range of environmental conditions, from extreme latitudes and altitudes to various climates and soils, underscores its ecological versatility and resilience (Nevo, 2013). This adaptability has allowed barley to thrive in regions where other crops might fail, making it a crucial staple in diverse agricultural systems (Nevo, 2013; Dawson et al., 2015).

Barley plays a pivotal role in agriculture not only as a food source but also as a key ingredient in the brewing industry. Its use in beer brewing dates back thousands of years, and it remains the primary grain used in the production of malt, which is essential for brewing beer (Mrízová et al., 2014; Tyagi et al., 2020). The genetic diversity and adaptability of barley have made it a valuable crop for both traditional and modern agricultural practices. Its ability to be used as animal feed, human food, and a brewing staple highlights its multifaceted utility (Baik and Ullrich, 2008; Nevo, 2013; Mrízová et al., 2014).

Understanding the evolution of barley from its wild progenitor, *Hordeum spontaneum*, to its domesticated form, *Hordeum vulgare*, is crucial for several reasons. The domestication process involved significant genetic changes, such as the loss of seed shattering, increased seed size, and the development of a non-brittle rachis, which made barley more suitable for cultivation and harvesting (Badr et al., 2000; Wang et al., 2019). Exploring these evolutionary changes provides insights into the genetic and ecological factors that have shaped barley's development and its current genetic diversity (Pankin et al., 2018; Wang et al., 2019). This knowledge is essential for improving barley varieties to meet future agricultural challenges, including climate change and food security (Dawson et al., 2015; Pankin et al., 2018).

This study explores the close relationship between barley and beer brewing by examining its botanical characteristics, ecological adaptability, and domestication history. By investigating the genetic and phenotypic changes that occurred during barley's domestication, we can better understand how this ancient grain became the foundation of modern brewing. The study focuses on various aspects of barley's evolution and its significance in both agriculture and brewing. It delves into the genetic adaptations that have enabled barley to thrive in diverse environments, the historical and archaeological evidence of its domestication, and the ongoing efforts to conserve and improve barley genetic resources for future agricultural applications. Understanding the botanical and genetic traits of barley will help enhance its brewing performance through breeding and biotechnology, and address the agricultural challenges posed by climate change.

2 Botanical Characteristics of Barley: Morphology and Growth Environment

2.1 Morphological structure and developmental traits of barley

Barley (*Hordeum vulgare* L.) exhibits distinct morphological traits that are crucial for its identification and cultivation. The spike, a key feature, can be categorized into two-rowed or six-rowed types, which significantly influence grain yield and quality. The spikelets, arranged along the central rachis, can develop into either fertile or sterile forms, impacting the overall grain production. The grain itself is typically elongated with a husk that remains attached, although some varieties, known as "naked barley," have a hull-less grain. The root system of barley is fibrous and extensive, allowing efficient nutrient and water uptake, which is essential for its growth in various soil types (Terzi et al., 2017; Youssef et al., 2020).

Barley's performance varies across different ecological environments. In temperate regions, barley thrives due to its adaptability to cooler climates and shorter growing seasons. In contrast, in arid and semi-arid regions, barley's deep root system and efficient water use enable it to survive and produce yields under drought conditions. This adaptability is further enhanced by genetic variations that allow barley to modify its growth patterns and physiological responses to suit diverse environmental conditions (Terzi et al., 2017; Youssef et al., 2020).

2.2 Ecological adaptability and environmental adaptation mechanisms of barley

Barley's global distribution is a testament to its remarkable ecological adaptability. Through genetic adaptation and selective breeding, barley has developed mechanisms to survive and reproduce in a wide range of environments. Key adaptive traits include early flowering time, which allows barley to complete its life cycle before the onset of adverse conditions, and reduced seed dormancy, which ensures rapid germination and establishment. These traits are controlled by complex genetic networks that have evolved over millennia, enabling barley to expand its ecological niche (Wang et al., 2019).

Malting Barley is specifically bred for certain characteristics that make it suitable for brewing, including tolerance to various climatic conditions such as salinity and drought, which are crucial for maintaining consistent grain quality and yield. For instance, the application of ascorbic acid (AsA) has been shown to improve barley's tolerance to salinity stress by regulating morphophysiological traits and reducing oxidative stress, thus ensuring stable grain production even under adverse environmental conditions (Figure 1). Studies have indicated that under salt stress, as the salt concentration increases, the sodium content in barley roots and stems increases significantly, while calcium and potassium levels decrease notably. However, the application of ascorbic acid, especially at higher concentrations (AsA 60), alleviated the negative effects of salt stress on calcium and potassium uptake to some extent and reduced sodium accumulation. This suggests that ascorbic acid may enhance barley's adaptability to saline conditions by regulating ion balance. These findings provide potential strategies for improving salt tolerance in crops such as barley, helping them achieve better growth and productivity in saline soils and other harsh environments. This adaptability is crucial for meeting the brewing industry's demands, where consistent grain quality is essential for producing high-quality beer (Hassan et al., 2021).

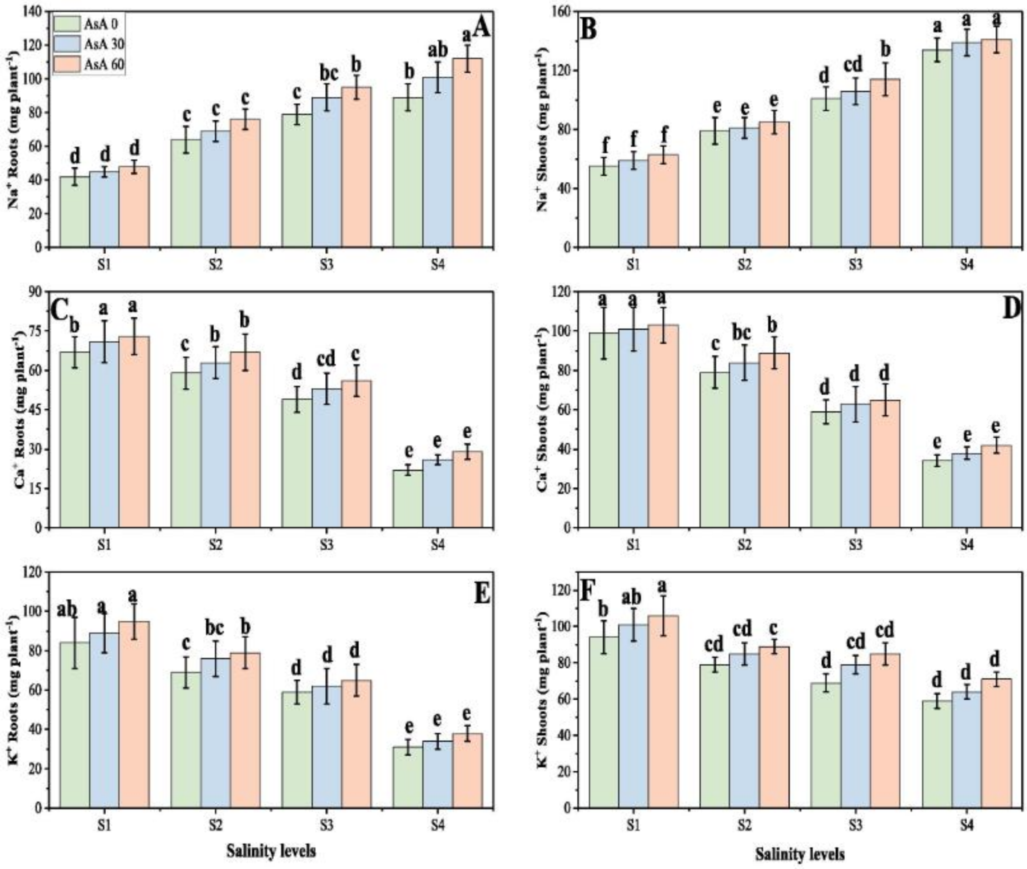

Figure 1 Effects of different ascorbic acid concentrations on sodium, calcium, and potassium content in roots and stems of barley (*H. vulgare*) under various salinity levels (Adapted from Hassan et al., 2021)

Image caption: The figure illustrates the impact of different salinity levels (S1: 0 mM; S2: 50 mM; S3: 100 mM; S4: 150 mM) and three ascorbic acid treatments (AsA 0: 0 mM, AsA 30: 30 mM, AsA 60: 60 mM) on sodium (Na^+), calcium (Ca^{2+}), and potassium (K^+) accumulation in the roots and stems of barley; The bar charts represent the content of these ions in the roots and stems; Different letters indicate significant differences among the treatment groups ($P<0.05$); The experiment was analyzed using a two-way analysis of variance (ANOVA) to assess treatment differences, with an HSD test used to determine significant differences (Adapted from Hassan et al., 2021)

3 Domestication of Barley: From Wild Grain to Modern Food Crop

3.1 The domestication process of barley

Barley (*Hordeum vulgare*) was one of the first crops to be domesticated by humans, with evidence suggesting that this process began around 10 000 years ago in the Fertile Crescent, a region that includes parts of modern-day Israel, Jordan, Lebanon, Syria, southeastern Turkey, and western Iran (Badr et al., 2000; Ozkan et al., 2002; Mascher et al., 2016). Genetic and archaeobotanical studies have pinpointed the Upper Jordan Valley as a significant area for the early domestication of barley, with ancient barley grains showing close genetic affinity to modern landraces from the Southern Levant and Egypt (Mascher et al., 2016). This region's wild barley populations, particularly those from Israel and Jordan, are genetically similar to the earliest domesticated forms, supporting the hypothesis that this area was a primary center of barley domestication (Badr et al., 2000).

The domestication process involved a gradual transition from wild barley (*Hordeum spontaneum*) to cultivated forms, marked by significant genetic changes. Archaeobotanical evidence indicates that the domestication of barley was a protracted process, taking thousands of plant generations to complete (Allaby et al., 2017). This extended period of pre-domestication cultivation suggests that early human groups experimented with barley cultivation long before the crop became fully domesticated (Allaby et al., 2010). The genetic evidence from ancient barley grains and modern landraces highlights the continuity and stability of barley cultivation in the region over millennia, with minimal lineage turnover (Mascher et al., 2016).

3.2 The history of genetic improvement

One of the most critical traits selected during the domestication of barley was the development of non-shattering spikes, which allowed for more efficient harvesting by preventing the mature grains from dispersing naturally (Fuller, 2007; Pourkheirandish et al., 2015). This trait evolved through mutations in specific genes that controlled the brittleness of the rachis, the part of the plant that holds the grains. In wild barley, the rachis is brittle, causing the grains to shatter and disperse, while in domesticated barley, mutations led to a tough, non-brittle rachis that retained the grains on the plant (Pourkheirandish et al., 2015). These genetic changes were crucial for the transition from wild to cultivated barley, as they enabled early farmers to harvest and store the grains more effectively.

The genetic improvement of barley also included the development of six-rowed barley from the ancestral two-rowed form. This change, controlled by a specific gene, resulted in a significant increase in the number of seeds per spike, thereby enhancing the crop's yield (Pourkheirandish and Komatsuda, 2007). The identification and study of these domestication genes have provided valuable insights into the mechanisms by which wild barley was transformed into a staple food crop. The evolution of these traits was not uniform across all regions; instead, it occurred through multiple independent events, reflecting the diverse selection pressures and cultivation practices of early agricultural societies (Pourkheirandish et al., 2015).

3.3 The role of barley in early agriculture

Barley played a pivotal role in the development of early agricultural societies in the Near East and beyond. As one of the founder crops of Neolithic agriculture, barley was integral to the transition from hunter-gatherer lifestyles to settled farming communities (Piperno et al., 2004; Mascher et al., 2016). The crop's adaptability to different environmental conditions and its relatively short growing season made it a reliable food source for early farmers. Archaeobotanical evidence from various sites in the Fertile Crescent and surrounding regions indicates that barley was widely cultivated and used in diverse ways, including as a staple food and for brewing beer (Piperno et al., 2004; Leipe et al., 2017).

The spread of barley cultivation from its center of origin in the Fertile Crescent to other parts of the world was facilitated by its versatility and the development of different barley phenotypes suited to various climates and agricultural practices. For instance, the Okhotsk culture in northern Japan utilized barley as part of a mixed subsistence strategy that included hunting, fishing, and gathering, highlighting the crop's importance in diverse cultural contexts (Leipe et al., 2017). The historical significance of barley is further underscored by its role in the diets and economies of ancient civilizations, where it was used not only for food but also for brewing, which became a central aspect of many cultures (Piperno et al., 2004).

In summary, the domestication and genetic improvement of barley were crucial developments in the history of agriculture, enabling the crop to become a staple food source for early human societies. The selection of key traits such as non-shattering spikes and the evolution of six-rowed barley significantly enhanced the crop's utility and productivity, facilitating its widespread adoption and cultivation across different regions and cultures.

4 Varietal Selection and Brewing Traits of Malting Barley

4.1 Major malting barley varieties

Barley varieties are primarily categorized into two-row and six-row types, each with distinct applications in beer brewing. Two-row barley is predominantly used in large-scale beer production due to its higher starch content and lower protein levels, which contribute to a cleaner and more efficient fermentation process (Figure 2) (Kim et al., 2013; Doe, 2019). In contrast, six-row barley, which is more commonly used in smaller-scale brewing operations such as microbreweries, has a higher protein content that can enhance the body and foam stability of the beer but may also introduce more haze and off-flavors if not managed properly (Kim et al., 2013; Kim et al., 2014). The choice between two-row and six-row barley often depends on the desired characteristics of the final product and the specific brewing techniques employed.

Figure 2 Beer (left) and *Thunder* winter two-row malting barley (right) (Adapted from Doe, 2019)

The morphological differences between two-row and six-row barley also play a role in their brewing applications. Two-row barley typically has larger and more uniform kernels, which facilitate more consistent malting and mashing processes. Six-row barley, on the other hand, has smaller and more variable kernels, which can lead to challenges in achieving uniform malt quality (Figure 3) (Jeanty et al., 2023). Despite these challenges, six-row barley varieties like Dahyang have been found to produce beers with high sensory preferences, indicating their potential suitability for certain brewing contexts (Kim et al., 2013; Kim et al., 2014).

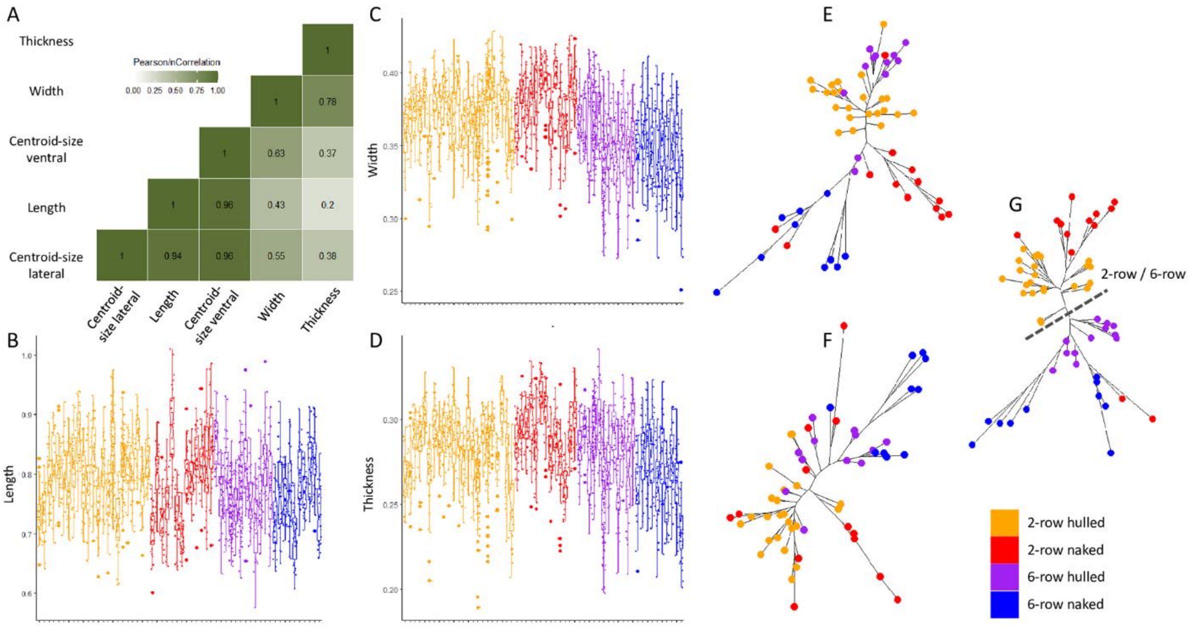

Figure 3 Overall morphological differences between two-row and six-row barley (Adapted from Jeanty et al., 2023)

Image caption: A: Correlation of length, width, thickness, and two central dimensions (VV and VL views); B, C, and D: Box plots of grain length, grain width, and grain thickness for different varieties; E and F: Morphological difference networks for side view and ventral view of the grains; G: Combined morphological information from both views; colors distinguish hulled two-row (orange), hull-less two-row (red), hulled six-row (purple), and hull-less six-row (blue) barley varieties (Adapted from Jeanty et al., 2023)

4.2 Selection criteria for brewing barley

The selection of barley for brewing is guided by several key quality indicators, including protein content, enzyme activity, and saccharification efficiency. Protein content is a critical factor as it influences the clarity, stability, and flavor of the beer. Lower protein levels are generally preferred for producing clear and stable beers, while higher protein levels can enhance foam stability and mouthfeel but may also lead to haze formation (Gupta et al., 2010; Fox and Bettenhausen, 2023). Enzyme activity, particularly of amylases, is essential for the conversion of starches into fermentable sugars during the mashing process. High levels of α-amylase and β-amylase are desirable as they ensure efficient starch breakdown and optimal sugar availability for fermentation (Gupta et al., 2010).

Saccharification efficiency, which measures the effectiveness of converting starches into fermentable sugars, is another crucial criterion. This efficiency is influenced by the barley's enzymatic profile and the presence of non-starch polysaccharides such as β-glucans and arabinoxylans, which can impede the mashing process if not adequately broken down (Gupta et al., 2010). Therefore, selecting barley varieties with high enzymatic activity and low levels of non-starch polysaccharides is essential for achieving high saccharification efficiency and producing high-quality wort (Gupta et al., 2010; Fox and Bettenhausen, 2023).

4.3 Selection for specific traits

The development of barley varieties suitable for beer fermentation involves targeted selection and breeding to enhance specific traits. Breeding programs focus on improving traits such as kernel uniformity, enzyme activity, and disease resistance to ensure consistent malt quality and brewing performance (Ramsay et al., 2011). For instance, the selection of barley with high levels of α-amylase and β-amylase is prioritized to enhance starch conversion during mashing, while breeding for lower protein content helps in producing clearer beers with better stability (Gupta et al., 2010).

Genetic studies have identified key genes, such as VRS1 and INTERMEDIUM-C (INT-C), that control important traits in barley, including row number and spikelet fertility. These genes have been manipulated through breeding to develop varieties with desirable characteristics for brewing (Ramsay et al., 2011). For example, the VRS1 gene is responsible for the two-row or six-row phenotype, and its alleles can be selected to produce barley with the preferred row type for specific brewing applications (Palmer et al., 2009; Ramsay et al., 2011). Additionally, the INT-C gene, an ortholog of the maize domestication gene TEOSINTE BRANCHED 1, has been shown to modify lateral spikelet fertility, further influencing the yield and quality of barley for brewing (Ramsay et al., 2011). Through such targeted breeding efforts, barley varieties with optimized traits for beer fermentation are continuously developed to meet the evolving needs of the brewing industry.

5 Application of Malting Barley in the Brewing Process: Saccharification and Fermentation

5.1 Role in the saccharification process

Barley serves as a crucial starch source in the brewing process. During saccharification, the starches present in barley grains undergo biochemical transformations to produce fermentable sugars. The malting process activates various enzymes, such as α-amylase and β-amylase, which break down the starches into simpler sugars. These enzymes play a pivotal role in converting the complex carbohydrates in barley into maltose and other fermentable sugars, which are essential for the subsequent fermentation process (Gupta et al., 2010; Kok et al., 2018). The structural characteristics of barley starch, including its chain-length distributions and molecular size distributions, significantly influence the efficiency of saccharification and the quality of the resulting wort (Yu et al., 2020).

5.2 Contribution to the fermentation process

The fermentable sugars derived from barley during saccharification are vital for the fermentation process. These sugars are metabolized by yeast to produce alcohol, carbon dioxide, and various flavor compounds. The type and concentration of fermentable sugars influence the flavor, texture, and alcohol content of the final beer product. For instance, maltose, the primary sugar produced during saccharification, is readily fermentable by yeast and contributes to the beer's alcohol content and overall flavor profile (Kok et al., 2018; Yu et al., 2020). Additionally, the presence of non-fermentable dextrins, which are also products of starch hydrolysis, can affect the mouthfeel and perceived fullness of the beer (Yu et al., 2020).

5.3 The role of barley enzymes in fermentation

Barley enzymes, particularly α-amylase and β-amylase, are integral to the saccharification of malt. α-Amylase breaks down starch molecules into smaller dextrins, while β-amylase further hydrolyzes these dextrins into maltose. These enzymatic activities are crucial for producing a wort rich in fermentable sugars, which are necessary for efficient yeast fermentation (Gupta et al., 2010; Kok et al., 2018). The activity of these enzymes can be influenced by the malting and mashing conditions, which in turn affect the overall efficiency of the brewing process and the quality of the beer (Kok et al., 2018). Understanding the molecular interactions between starch and amylolytic enzymes can help brewers optimize the brewing process to achieve desired beer qualities (Yu et al., 2020).

Additionally, proteases play a crucial role in beer brewing. Proteases break down proteins in malt, generating amino acids and small peptides that not only provide essential nutrients for yeast but also improve the foam stability and flavor of the beer (Benešová et al., 2018). Different proteases exhibit varying activity levels under different temperature and pH conditions, and brewers must skillfully manage these factors to optimize brewing efficiency and the quality of the final product. By leveraging the enzymatic potential of barley, brewers can enhance the mashing and fermentation processes, ultimately producing high-quality beer with desirable sensory attributes and nutritional characteristics.

6 Cultural and Historical Impact of Barley in Agriculture and Brewing

6.1 The historical role of barley in different cultures

Barley (*Hordeum vulgare*) is one of the oldest cultivated crops, with its domestication dating back approximately 10 000 years in the Fertile Crescent (Badr et al., 2000; Mascher et al., 2016). This cereal grain played a crucial role in the transition from hunter-gatherer societies to agrarian communities, serving as a staple food source and a key agricultural product (Pourkheirandish and Komatsuda, 2007; Pourkheirandish et al., 2015). Archaeological evidence indicates that barley was a founder crop in Neolithic agriculture, contributing significantly to the development of early agrarian societies in the Near East (Mascher et al., 2016; Riehl, 2019). Its adaptability to diverse climates and environments allowed it to spread globally, reaching the New World after 1492 and achieving widespread cultivation by the 1950s. Barley’s resilience to arid and saline conditions, as well as its suitability for cooler climates, made it a versatile crop for various ancient civilizations, including those in Mesopotamia and Egypt, where it was integral to daily diets and economic productivity (Riehl, 2019).

6.2 The cultural connection between barley and beer brewing

The cultural significance of barley extends beyond its role as a food crop; it has been intrinsically linked to the production of beer, one of the oldest fermented beverages. Evidence of beer brewing dates back to at least 13 000 years ago, with the Natufian people in the Near East using barley to produce beer for ritual feasting (Liu et al., 2018). This early use of barley for brewing highlights its importance in social and ceremonial contexts. In ancient Mesopotamia and Egypt, beer was a staple in the diet and a significant aspect of daily life, with its production becoming a major sector of economic activity (Riehl, 2019). The development of beer brewing techniques evolved over millennia, from simple fermentation processes to more sophisticated methods, eventually leading to the diverse and complex beer production practices seen today. The genetic and morphological evolution of barley, including traits such as grain retention and increased seed yield, facilitated its use in brewing and contributed to the growth of beer culture (Pourkheirandish and Komatsuda, 2007; Haas et al., 2019).

6.3 The economic and social status of barley

Barley has long been a vital economic resource, both as a food crop and as a raw material for various industries. Historically, it has been used for baking, cooking, and as animal feed, with a significant portion of modern barley production still dedicated to livestock. However, its role in the brewing industry has elevated its economic importance. The cultivation of barley for beer production has driven agricultural practices and breeding programs aimed at improving its processing characteristics, nutritional value, and stress tolerance. The economic impact of barley extends to its contributions to cardiovascular health and diabetes control, due to its beneficial micronutrients (Riehl, 2019). Additionally, the genetic diversity and adaptability of barley have made it a valuable crop for addressing global agricultural challenges, such as climate change and food security (Wang et al., 2015; Milanesi et al., 2021). The ongoing research and development in barley genetics continue to enhance its economic viability and social significance in both traditional and modern contexts.

7 Future Directions and Research

7.1 Development of new barley varieties

The development of new barley varieties is crucial for enhancing the quality and sustainability of beer production. Modern breeding technologies, such as genome editing and marker-assisted selection, play a pivotal role in this process. For instance, the use of new breeding technologies (NBTs) can facilitate the re-domestication of crop wild relatives (CWR), which harbor beneficial traits that are often difficult to incorporate into conventional breeding programs (Chen, 2024). By leveraging genebank collections and digital sequence information, re-domesticated barley can be produced with improved characteristics while retaining the resilience and adaptation of the original material (Hanak et al., 2023). Additionally, the evaluation of genetic resources from currently available germplasm has shown that modern Australian barley varieties exhibit higher genetic diversity than historical cultivars, indicating the potential for developing new and improved varieties tailored to local environments (Hill et al., 2021).

7.2 Addressing the challenges of climate change

Climate change poses significant challenges to barley production, necessitating the development of climate-resilient crops. Barley serves as an excellent model for understanding agricultural responses to climate change due to its historical adaptation to diverse environments. Extensive collections of landraces and wild barley accessions provide a rich source of new alleles relevant to climate-smart agriculture. Genomic and analytical tools, along with specialized populations and transgenics, facilitate the exploration and capture of this genetic variation, laying the foundation for developing climate-resilient barley varieties (Dawson et al., 2015). Moreover, the sustainability of producing malting barley in the face of climate change can be enhanced by exploring the feasibility of breeding perennial malting barley, which offers ecosystem services and resilience to environmental stresses (Doe, 2019). The conservation and utilization of wild barley, which harbors immense adaptive abiotic and biotic resistances, are also imperative for barley improvement in the context of global warming (Nevo, 2013).

7.3 Application of biotechnology in barley improvement

Biotechnology, particularly gene-editing technologies, holds significant promise for barley improvement. Proteomics and metabolomics have been employed to study how proteins in barley respond to adverse environmental conditions and how they are impacted during food processing, including malting and brewing. These technologies can inform breeding programs aimed at enhancing the nutritional value and broadening the application of barley in new food and beverage products (Bahmani et al., 2021). Additionally, the application of mass spectrometry-based proteomics has revealed insights into the brewing process, such as the identification of key enzymes and their roles in fermentability, which can guide the optimization of brewing performance (Kerr et al., 2023). The integration of genomics, proteomics, and other "omics" technologies can thus drive the development of superior barley varieties with enhanced brewing performance and environmental adaptability.

By focusing on these future directions, researchers can address the challenges posed by climate change, improve the quality and sustainability of Malting Barley, and harness the potential of biotechnology to drive innovation in barley breeding and brewing.

8 Concluding Remarks

The evolutionary history of barley (*Hordeum vulgare*) from a wild grain to a cornerstone of modern beer brewing is a testament to the intricate interplay between natural selection and human intervention. Barley was first domesticated around 8000 BCE in the Fertile Crescent, specifically in regions such as Israel and Jordan, where wild barley (*Hordeum spontaneum*) was prevalent. The domestication process involved significant genetic changes, including the loss of seed shattering, reduced seed dormancy, and increased seed size and number, which were crucial for its cultivation and utility.

Barley's domestication was not a singular event but rather a complex process involving multiple genetic pathways and selective sweeps across different regions of the Fertile Crescent. This led to the development of various domestication traits such as a non-brittle rachis, a six-rowed spike, and a naked caryopsis, which were essential for its adaptation to agricultural practices. The genetic diversity observed in wild barley populations, particularly in the Levant, underscores the importance of these regions as centers of barley domestication and diversification.

The significance of barley extends beyond its agricultural value. As one of the earliest domesticated cereals, barley played a pivotal role in the development of early agricultural societies and has been a staple in human diets for millennia. Its adaptability to diverse climates and environments has made it a resilient crop, capable of thriving in conditions where other cereals might fail. This adaptability is particularly relevant in the context of climate change, where barley serves as a model for developing climate-resilient crops.

In the realm of brewing, barley's biochemical properties, such as its starch, protein, and polyphenol content, have made it the preferred grain for malting and brewing. The evolution of brewing techniques and the selection of barley varieties with desirable traits have further cemented its status as a fundamental ingredient in beer production. The cultural significance of barley is also noteworthy, with historical records indicating its use in brewing beer in ancient civilizations such as Mesopotamia and Egypt, where it was an integral part of daily life and economy.

In conclusion, the journey of barley from a wild grain to a brewing staple is a remarkable narrative of domestication, adaptation, and cultural integration. Its importance in agriculture, brewing, and cultural history cannot be overstated, as it continues to be a vital crop with significant economic and nutritional value. The ongoing research and breeding programs aimed at improving barley's resilience and quality will ensure its continued relevance in the face of global challenges.

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Conflict of Interest Disclosure

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

References

Allaby R., Brown T., and Fuller D., 2010, A simulation of the effect of inbreeding on crop domestication genetics with comments on the integration of archaeobotany and genetics: a reply to Honne and Heun, Vegetation History and Archaeobotany, 19: 151-158. https://doi.org/10.1007/S00334-009-0232-8

Allaby R., Stevens C., Lucas L., Maeda O., and Fuller D., 2017, Geographic mosaics and changing rates of cereal domestication, Philosophical Transactions of the Royal Society B: Biological Sciences, 372(1735): 20160429. https://doi.org/10.1098/rstb.2016.0429

Badr A., Mller K., Schafer-Pregl R., Rabey E., Effgen H., Ibrahim S., Pozzi C., Rohde W., and Salamini F., 2000, On the origin and domestication history of Barley (*Hordeum vulgare*), Molecular Biology and Evolution, 17(4): 499-510. https://doi.org/10.1093/oxfordjournals.molbev.a026330

Baik B., and Ullrich S., 2008, Barley for food: characteristics, improvement, and renewed interest, Journal of Cereal Science, 48, 233-242. https://doi.org/10.1016/J.JCS.2008.02.002

Bahmani M., O'Lone C., Juhász A., Nye-Wood M., Dunn H., Edwards I., and Colgrave M., 2021, Application of mass spectrometry-based proteomics to barley research, Journal of Agricultural and Food Chemistry, 69: 8591-8609. https://doi.org/10.1021/acs.jafc.1c01871

Chen F.P., 2024, Genetic diversity and adaptability analysis of wild rice germplasm resources, Rice Genomics and Genetics, 15(2): 58-68. https://doi.org/10.5376/rgg.2024.15.0007

Dawson I., Russell J., Powell W., Steffenson B., Thomas W., and Waugh R., 2015, Barley: a translational model for adaptation to climate change, The New Phytologist, 206(3): 913-931. https://doi.org/10.1111/nph.13266

Doe J., 2019, Sustainable malting barley and climate change, CSA News, 64(11): 12. https://doi.org/10.2134/csa2019.64.s053

Fox G., and Bettenhausen H., 2023, Variation in quality of grains used in malting and brewing, Frontiers in Plant Science, 14: 1172028.. https://doi.org/10.3389/fpls.2023.1172028

Fuller D., 2007, Contrasting patterns in crop domestication and domestication rates: recent archaeobotanical insights from the old world, Annals of Botany, 100: 903-924. https://doi.org/10.1093/aob/mcm048

Gupta M., Abu-Ghannam N., and Gallaghar E., 2010, Barley for brewing: characteristic changes during malting, brewing and applications of its by-products, Comprehensive reviews in Food Science and Food Safety, 9(3): 318-328. https://doi.org/10.1111/J.1541-4337.2010.00112.X

Haas M., Schreiber M., and Mascher M., 2019, Domestication and crop evolution of wheat and barley: genes, genomics, and future directions, Journal of Integrative Plant Biology, 61(3): 204-225. https://doi.org/10.1111/jipb.12737

Hanak T., Janjić J., Hay F., and Brinch-Pedersen H., 2023, Genome editing to re-domesticate and accelerate use of barley crop wild relatives, Frontiers in Sustainable Food Systems, 7: 1331577.
https://doi.org/10.3389/fsufs.2023.1331577

Hassan A., Amjad S., Saleem M., Yasmin H., Imran M., Riaz M., Ali Q., Joyia F.M., Ahmed S., Ali S., Alsahli A., and Alyemeni M., 2021, Foliar application of ascorbic acid enhances salinity stress tolerance in barley (*Hordeum vulgare* L.) through modulation of morpho-physio-biochemical attributes, ions uptake, osmo-protectants and stress response genes expression, Saudi Journal of Biological Sciences, 28: 4276-4290.
https://doi.org/10.1016/j.sjbs.2021.03.045

Hill C., Angessa T., Zhang X., Chen K., Zhou G., Tan C., Wang P., Westcott S., and Li C., 2021, A global barley panel revealing genomic signatures of breeding in modern *Australian cultivars*, The Plant Journal : for Cell and Molecular Biology, 106(2): 419-434.
https://doi.org/10.1111/tpj.15173

Jeanty A., Bouby L., Bonhomme V., Balfourier F., Debiton C., Dham C., Ivorra S., Ros J., and Evin A., 2023, Barley systematics and taxonomy foreseen by seed morphometric variation, PLOS ONE, 18(5): e0285195.
https://doi.org/10.1371/journal.pone.0285195

Kerr E., Fox G., and Schulz B., 2023, Proteomics and metabolomics reveal that an abundant α-glucosidase drives sorghum fermentability for beer brewing, Journal of Proteome Research, 22(11): 3596-3606.
https://doi.org/10.1021/acs.jproteome.3c00436

Kim J., Kim J., Choi E., Lee S., Kwon Y., Hong K., and Kim W., 2014, Multivariate analysis for feasibility of Korean six-row barleys for beer brewing, Journal of The Institute of Brewing, 120: 371-378.
https://doi.org/10.1002/JIB.168

Kim J., Kim J., Lee S., Hong K., Kwon Y., Park J., and Kim W., 2013, Characterization of fermentation kinetics of beer made of korean 6 row-barley, Food Engineering Progress, 17: 189-197.
https://doi.org/10.13050/FOODENGPROG.2013.17.3.189

Kok Y., Ye L., Muller J., Ow D., and Bi X., 2018, Brewing with malted barley or raw barley: what makes the difference in the processes?, Applied Microbiology and Biotechnology, 103: 1059-1067.
https://doi.org/10.1007/s00253-018-9537-9

Leipe C., Sergusheva E., Müller S., Spengler R., Goslar T., Kato H., Wagner M., Weber A., and Tarasov P., 2017, Barley (*Hordeum vulgare*) in the Okhotsk culture (5^{th}-10^{th} century AD) of northern Japan and the role of cultivated plants in hunter-gatherer economies, PLoS ONE, 12(3): e0174397.
https://doi.org/10.1371/journal.pone.0174397

Liu L., Wang J., Rosenberg D., Zhao H., Lengyel G., and Nadel D., 2018, Fermented beverage and food storage in 13,000 y-old stone mortars at Raqefet Cave, Israel: Investigating Natufian ritual feasting, Journal of Archaeological Science: Reports, 21: 783-793.
https://doi.org/10.1016/J.JASREP.2018.08.008

Mascher M., Schuenemann V., Davidovich U., Marom N., Himmelbach A., Hübner S., Korol A., David M., Reiter E., Riehl S., Schreiber M., Vohr S., Green R., Dawson I., Russell J., Kilian B., Muehlbauer G., Waugh R., Fahima T., Krause J., Weiss E., and Stein N., 2016, Genomic analysis of 6 000-year-old cultivated grain illuminates the domestication history of barley, Nature Genetics, 48: 1089-1093.
https://doi.org/10.1038/ng.3611

Milanesi C., Vignani R., Scali M., Faleri C., Donne M., Cresti M., and Costantini L., 2021, A comparison of aleurone cells in centenarian African and contemporary barley seeds to identify the geographic origin, Comptes Rendus Palevol, 20(43): 887-896.
https://doi.org/10.5852/cr-palevol2021v20a43

Mrízová K., Holásková E., Öz M., Jiskrová E., Frébort I., and Galuszka P., 2014, Transgenic barley: a prospective tool for biotechnology and agriculture, Biotechnology Advances, 32(1): 137-157.
https://doi.org/10.1016/j.biotechadv.2013.09.011

Nevo E., 2013, Evolution of wild barley and barley improvement, In: Zhang G., Li C., and Liu X., (eds) Advance in Barley Sciences, Springer, Dordrecht, pp.1-23.
https://doi.org/10.1007/978-94-007-4682-4_1

Palmer S., Moore J., Clapham A., Rose P., and Allaby R., 2009, Archaeogenetic evidence of ancient nubian barley evolution from six to two-row indicates local adaptation, PLoS ONE, 4(7): e6301.
https://doi.org/10.1371/journal.pone.0006301

Pankin A., Altmüller J., Becker C., and Korff M., 2018, Targeted resequencing reveals genomic signatures of barley domestication, The New Phytologist, 218: 1247-1259.
https://doi.org/10.1111/nph.15077

Piperno D., Weiss E., Holst I., and Nadel D., 2004, Processing of wild cereal grains in the Upper Palaeolithic revealed by starch grain analysis, Nature, 430: 670-673.
https://doi.org/10.1038/nature02734

Pourkheirandish M., Hensel G., Kilian B., Senthil N., Chen G., Sameri M., Azhaguvel P., Sakuma S., Dhanagond S., Sharma R., Mascher M., Himmelbach A., Gottwald S., Nair S., Tagiri A., Yukuhiro F., Nagamura Y., Kanamori H., Matsumoto T., Willcox G., Middleton C., Wicker T., Walther A., Waugh R., Fincher G., Stein N., Kumlehn J., Sato K., and Komatsuda T., 2015, Evolution of the grain dispersal system in barley, Cell, 162: 527-539.
https://doi.org/10.1016/j.cell.2015.07.002

Pourkheirandish M., and Komatsuda T., 2007, The importance of barley genetics and domestication in a global perspective, Annals of Botany, 100: 999-1008.
https://doi.org/10.1093/aob/mcm139

Ramsay L., Comadran J., Druka A., Marshall D., Thomas W., Macaulay M., MacKenzie K., Simpson C., Fuller J., Bonar N., Hayes P., Lundqvist U., Franckowiak J., Close T., Muehlbauer G., and Waugh R., 2011, Intermedium-c, a modifier of lateral spikelet fertility in barley, is an ortholog of the maize domestication gene Teosinte branched 1, Nature Genetics, 43: 169-172.
https://doi.org/10.1038/ng.745

Ozkan H., Brandolini A., Schäfer-Pregl R., and Salamini F., 2002, AFLP analysis of a collection of tetraploid wheats indicates the origin of emmer and hard wheat domestication in southeast Turkey, Molecular Biology and Evolution, 19(10): 1797-801 .
https://doi.org/10.1093/oxfordjournals.molbev.a004002

Riehl S., 2019, Barley in archaeology and early history, Oxford Research Encyclopedia of Environmental Science, 10: 1093
https://doi.org/10.1093/acrefore/9780199389414.013.219

Terzi V., Tumino G., Pagani D., Rizza F., Ghizzoni R., Morcia C., and Stanca A., 2017, Barley developmental mutants: the high road to understand the cereal spike morphology, Diversity, 9: 21.
https://doi.org/10.3390/D9020021

Tyagi V., Jacob S., Gupta K., and Brahmi P., 2020, Status of introduction and conservation in barley (*Hordeum vulgare* L.), Journal of Cereal Research, 12(1): 13-18.
https://doi.org/10.25174/2582-2675/2020/83213

Wang Y., Ren X., Sun D., and Sun G., 2015, Origin of worldwide cultivated barley revealed by NAM-1 gene and grain protein content, Frontiers in Plant Science, 6: 803.
https://doi.org/10.3389/fpls.2015.00803

Wang Y., Ye H., Liu L., Wu J., Ru W., and Sun G., 2019, Molecular insights on the domestication of barley (*Hordeum vulgare* L.), Critical Reviews in Plant Sciences, 38: 280 - 294.
https://doi.org/10.1080/07352689.2019.1658856

Wu W.C., 2024, Predicting wheat response to drought using machine learning algorithms, Plant Gene and Trait, 15(1): 1-7.
https://doi.org/10.5376/pgt.2024.15.0001

Yu W., Zhai H., Xia G., Tao K., Li C., Yang X., and Li L., 2020, Starch fine molecular structures as a significant controller of the malting, mashing, and fermentation performance during beer production, Trends in Food Science and Technology, 105: 296-307.
https://doi.org/10.1016/J.TIFS.2020.09.010

Youssef H., Allam M., Boussora F., Himmelbach A., Milner S., Mascher M., and Schnurbusch T., 2020, Dissecting the genetic basis of lateral and central spikelet development and grain traits in intermedium-spike barley (*Hordeum vulgare* Convar. Intermedium), Plants, 9(12): 1655.
https://doi.org/10.3390/plants9121655