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History and current value of ancient barley (*Hordeum vulgare* L.) – a review

Ancient barley (*Hordeum vulgare* L.) varieties were not subjected to modern breeding. They were well adapted to their environment but lost importance over time due to the development and cultivation of higher-yielding varieties. This contributed to a loss of plant genetic resources. However, in the context of climate change and a growing population, as well as increasing consumer interest in new and high-quality products, these ancient barley varieties are receiving renewed attention. This review provides a history of ancient barley varieties, as well as an overview of the available data regarding their suitability for malting and brewing. It also briefly discusses the challenges and opportunities associated with integrating these ancient barley varieties into our current food system, as well as their potential as plant genetic resources. Ancient barley varieties are mainly considered a valuable pool of genetic resources for incorporating beneficial traits, such as resistance to diseases and pests, into modern cultivars. Whereas limited data are available regarding their malting and brewing performance and their potential to produce beers with specific sensory profiles. They currently play only a minor role as a raw material in the modern malting and brewing industry.

Descriptors: Ancient barley, barley history, brewing, malting

1 Introduction

The current malting and brewing industry relies heavily on modern bred barley varieties. Over the last decades, breeding programmes have mainly focused on improving yield, malt quality parameters or disease resistance, rather than on positive or unique flavour attributes of barley genotypes [1, 2]. These modern varieties replaced and eliminated previously used and well-adapted varieties. As a result, improved cultivars now draw on a relatively narrow gene pool [3]. To avoid further loss of plant genetic resources, efforts have been made to preserve the genetic diversity of barley and other cereals in gene banks, making them accessible to various stakeholders [4]. This review shows how and to what extent these previously used barley varieties are currently studied. It will also provide an overview of these varieties' potential value and applications in the malting and brewing industry. It also provides an

overview of their malt quality and brewing performance compared with modern barley varieties, and discusses the knowledge gaps and challenges associated with their use and valorisation.

2 Plant genetic resources

Intensive breeding started with the so-called Green Revolution during the 1940s to 1960s [5]. Prior to that, seed diversity was maintained by farmers through so-called on-farm seed saving, in which part of the harvest was used for food or feed, while another part was used as seed for the next growing season. This resulted in crop varieties which were well adapted to the respective local growing conditions and maintained seed diversity [6, 7], because the selection process of early farmers was based on phenotypic selection of plant species and genotypes with favourable traits for cultivation but also for human nutrition [7, 3]. But with modern selective breeding programmes, which focused on high yields, uniformity and processing efficiency, together with a worldwide change in agricultural practices in terms of higher levels of industrialisation, monocultures, as well as ultra-processed foods, these well-adapted varieties lost importance, resulting in a loss of genetic diversity [6, 8, 9]. The beginning of modern, intensive breeding programmes was based on the findings of Gregor Mendel, who defined "heritable characteristics", which were the basis for a better understanding of genetic principles of inheritance. The application of "Mendel's Laws" [10] occurred after its rediscovery in 1900, because Mendel's research was not available to plant breeders and biologists during the 19th century, and the concept of natural selection by Darwin was the basis for modern plant breeding [11]. The application of these concepts in plant breeding resulted in improved cultivars [10] with high productivity and quality, as well as greater resistance to diseases and pests [10, 12]. The productivity of modern barley cultivars increased annually by approximately 1–2 % over the last

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few decades, due to genetic breeding progress combined with more efficient disease and insect control, as well as improved fertilisation systems and agricultural production technologies. Modern barley varieties are characterised by high yields and improved malting quality, as well as significantly enhanced agronomic traits like resistance to lodging, resistance to virus diseases like soil-borne yellow mosaic viruses, and fungal pathogens like powdery mildew (*Bumeria Graminis*), leaf rust (*Puccinia hordei*) or scald (*Rhynchosporium secalis*) [1]. These improved cultivars replaced and eliminated the previously used well-adapted varieties [3]. But these positive traits and high yields are mainly achieved when these varieties are provided with ideal growth conditions, including sufficient fertilisation and adequate provision of pesticides and sufficient precipitation [5]. But, human caused climate change and global warming will increase the pressure of abiotic stress in every region across the globe, like increased intensities and frequencies of drought, heat waves, heavy precipitation, flooding/waterlogging or storms, soil salinity and marginal soils. The severity of these events depends on geographic location [13, 14, 15]. Under these less favourable growing conditions, modern bred barley varieties are often not able to cope with abiotic stress [12]. In a botanical sense, the term “variety” is used to differentiate plants from the same species which differ in some structural aspects, and these differences will persist throughout succeeding generations. Varieties have, within some measurable time, a common ancestry. Nevertheless, the term is often used in a much broader sense [16]. Modern breeding resulted in the cultivation of cultivars with a very narrow genetic base, which made them more vulnerable to new diseases or pests [3, 17]. The loss of landrace diversity was primarily due to replacement with modern cultivars, but other drivers, such as demographic or environmental factors, were also reported [18]. As early as 1999, the Food and Agriculture Organisation (FAO) stated that since the 1900s, around 75 % of plant genetic diversity has been lost because farmers have started to rely on modern bred varieties [19]. But the empirical basis for the reported value of 75 % is debated [18]. Van de Wouw et al. (2010) reported only a significant reduction of 6 % of crop diversity between 1950 and 1960, while overall no significant reduction of genetic diversity was observed. But the meta analysis only focused on modern cultivars released between 1900 and 2000 and did not include historical landraces and varieties released before 1900 [20]. Genetically uniform and higher-yielding varieties replaced local varieties and landraces over time. As a result, only 12 plants, together with five animal species, generate 75 % of the world’s food. Around 60 % of the calories and proteins obtained by humans derive from the three crops: rice, maize and wheat [19]. To avoid further loss of plant genetic resources, there is an urgent need for conservation [21]. Therefore, an International Treaty on Plant Genetic Resources for Food and Agriculture (ITPGRFA) was developed, under which contracting parties agreed on conserving, characterising, as well as evaluating plant genetic resources. This treaty involves conserving genetic resources in nature (*in situ*), in farmers’ fields (on farm) as well as in gene banks (*ex situ*). This binding international agreement entered into force in 2004 and aims to promote the sustainable use of plant genetic resources to ensure food security and appropriate adaptation to climate change. This treaty should further ensure contracting parties’ access to resources, as well as an equitable sharing of benefits [22]. The Kunming-Montreal Global Biodiversity Framework from 2022, similarly incorporates these aspects. It will contribute to achieving

the 2030 Agenda for Sustainable Development. “It will place biodiversity, its conservation, the sustainable use of its components and the fair and equitable sharing of the benefits arising out of the utilization of genetic resources, at the heart of the sustainable development agenda, recognizing the important linkages between biological and cultural diversity” [23]. Genetic resources are defined by the Convention on Biological Diversity (CBD) as “genetic material of actual or potential value” [24]. According to the ITPGRFA the term *in situ* conservation refers to “the conservation of ecosystems and natural habitats and the maintenance and recovery of viable populations of species in their natural surroundings and, in the case of domesticated or cultivated plant species, in the surroundings where they have developed their distinctive properties”. The term *ex situ* conservation is defined as “the conservation of plant genetic resources for food and agriculture outside their natural habitat” [22]. The term habitat refers to “the place or type of site where an organism or population naturally occurs” [24]. *In situ* and *ex situ* conservation are the two most important strategies for conserving plant genetic resources [7]. According to CBD (1992), it is important that *in situ* and *ex situ* conservation are not strategies that function as alternatives or in opposition to each other. They should rather work as two strategies which complement each other, both aiming at conservation, and being a safety back-up for the other [25].

One option for *ex situ* conservation is to preserve seeds in so-called gene banks that have been established around the world over the last few years. So far, over 5.9 million accessions are conserved under medium- and long-term storage conditions. These accessions are mainly stored as seeds in over 850 national gene banks in 116 countries, as well as four regional and 13 international gene banks. At the end of 2022, around 41 % of all *ex situ* conserved accessions were duplicated for safety reasons. The majority of these safely duplicated accessions – over one million – were brought to the Svalbard Global Seed Vault in Norway, which opened in 2008, as long-term safety storage for seeds [26]. “Gene banks should promote the availability of genetic resources for uses including research, breeding, education, farming and repatriation” [4]. To ensure that genetic resources, which are used for food as well as agriculture, can be used in the future, it is necessary to put national legislation in place which ensures the protection of these endangered genetic resources. Suitable national legislation ensures that they can be used and managed by local communities, but also indigenous people. Appropriate national legislation will ensure that these often disadvantaged sections of the population will also receive their fair share of the benefits from the use of genetic resources [19]. For instance, the European Union (EU) Biodiversity Strategy for 2030 highlights the benefits of biodiversity conservation, noting that it has “potential direct economic benefits for many sectors of the economy” and that “biodiversity is also crucial for safeguarding EU and global food security” [27].

It is also necessary to set suitable agricultural policies in place, which will provide incentives for those who will use genetic resources in a sustainable way. They will also ensure a better interlink between *in situ* and *ex situ* conservation [19]. Also, Salgotra and Chauhan (2023) highlight the importance for national and international communities to maintain genetic diversity, the conservation of plant genetic resources as well as their sustainable use, by implementing appropriate policies and frameworks [17].

3 Terms and definitions

The use of ancient barley, but also other cereal varieties, in our current food system is challenging due to various factors. An important one is the inconsistent use of terminology for description and classification. Terms like ancient, heirloom, heritage or landrace are often found in scientific literature [6, 28, 29]. Sometimes the term underutilised crop or forgotten crops can also be found [6, 30]. These terms refer to varieties which have been of great importance for humankind for a long time, but are now neglected by modern agriculture. The term also includes former varieties that are not well researched and undervalued in disciplines like education, regulatory frameworks and trade systems. Despite this, they may possess a valuable nutritional profile and beneficial traits in terms of climate resilience [30]. Ancient cereals are defined by Giambanelli et al., (2013), as “populations not subject to any modern breeding or selection, and sometimes retaining characters of wild ancestors, such as individual variability, height, brittle rachis, low harvest index and, in some taxa, hulled kernels” [31]. Up to now, there is no clear scientific way to differentiate modern cereal varieties from ancient ones, but often ancient cereal varieties are defined as those planted and processed before the start of the Green Revolution in the 1960s [32]. Sometimes the term ancient cereals also includes early domesticated cereals like einkorn (*Triticum monococcum*), emmer (*Triticum dicoccum*), spelt (*Triticum spelta*), and Khorasan wheat or even pseudocereals like quinoa (*Chenopodium quinoa* Willd.) or buckwheat (*Fagopyrum esculentum* Moench.) [8, 33, 34]. The term heirloom cultivar also lacks a clear scientific definition. The term covers old, non-hybrid cultivars with an open-pollinating nature which are often handed down from generation to generation. These cultivars are often quite variable and therefore not used in large-scale agriculture, where uniformity is desired [35]. The term landrace has been defined in various ways: According to Schmidt et al. (2023), landraces are defined as “genotypes of traditionally domesticated crops that are locally adapted, selected from diverse environments, and maintained by farmers over generations” [12]. Following Camacho Villa et al. (2005), landraces have a historical origin, a recognised identity, and high genetic diversity. Landraces are well adapted to their environment and have not experienced intentional or structured genetic selection. The authors used the following definition: “dynamic population(s) of a cultivated plant that has historical origin, distinct identity and, as well as often being genetically diverse, locally adapted and associated with traditional farming systems”. Landraces were well adapted to local conditions, due to the fact that traditionally farmers kept seed quite diverse, as on-farm seed saving was common practice. Accordingly, several landraces were lost as modern breeding programs expanded, resulting in an erosion of the crop gene pool [21]. While modern bred barley varieties are characterised by higher yields when grown under ideal conditions, landraces are often quite well adapted to local climatic conditions, for instance irregular rainfall, or their resistance to specific pests and diseases makes these varieties still interesting for farmers who do not solely focus on yield maximisation, but also on maintaining and enriching local culture [36]. Due to their high-level adaptation to marginal soils, landraces are still grown in some regions and for niche markets [21].

Wild relatives are defined by Choudhary et al. (2017) as an “organism which is taxonomically related to a domesticated organism”.

Wild relatives are further characterised by the authors as “the progenitors of crops as well as other species which are more or less closely related to them” [37]. The crop wild relative for barley is *Hordeum spontaneum* (C. Koch) Thell. [38, 39]. In recent years, interest in wild relatives has increased, as they are considered a valuable source of traits such as disease and pest resistance that can be incorporated into modern cultivar development [37].

According to Boukid et al. (2018), modern varieties are “the result of the continued modern breeding progress, aiming to select homogeneous lines with stable and improved characters [...] these varieties are cultivated worldwide ensuring higher productivity than landraces” [34].

4 Barley history

Cereal-based food products are an important part of our diet, as they serve as a valuable source of constituents such as protein, dietary fibre and bioactive compounds [40]. Barley (*Hordeum vulgare* L.) is, after corn (*Zea mays*), wheat (*Triticum aestivum*) and rice (*Oryza sativa*), the fourth most relevant cereal in the world. Around 142 million tons of barley were harvested in 2024 worldwide [41].

Barley belongs to the *Poaceae* family, the tribe *Triticeae* and the genus *Hordeum* [42, 43]. It can be cultivated in high-elevation, high-latitude regions with short growing seasons [44]. Due to its great adaptability, cold and rainy climate zones with long daylight hours, but also warmer and drier climate zones, are suitable [45]. Barley is self-pollinating, but natural cross-pollination might occur, too [43]. Compared with wheat, domesticated barley is characterised by a shorter vegetative cycle and higher stress tolerance to salinity and aridity. Due to a greater tillering ability and a below-ground root system, barley is more competitive with weeds than wheat species [42].

The majority of barley, i.e. more than two-thirds of today's production, is used as animal feed or a feed ingredient [46]. Barley is also an important raw material for the malting and brewing industries today. The same holds for distillers [44, 47]. Barley serves as a main food source in extreme climates, for instance in the Himalayan region or even in Ethiopia or Morocco nowadays, and it is very likely that barley was first utilised as human food [48]. Newman and Newman (2008) stated that in ancient times barley was one of the most important food grains. It can be assumed that the kernels were eaten raw, with the hull still attached to the grain. After discovering that removing the hull of hulled barley and soaking and/or cooking improved texture and flavour, early humans learned about fermentation and the production of alcoholic beverages. Barley became an essential dietary constituent of the working class in Europe. However, this changed around the beginning of the 20th century due to the growing wheat industry, which led to bread and breakfast cereal products with a more appealing sensory profile than those from barley [43]. Barley was a main ingredient for unleavened bread and porridge eaten by the ancient Greek population [49]. Löscher et al. (2014) used stable isotope analysis and trace element studies on remains of a gladiator cemetery discovered in Ephesus (Turkey), dating back to the 2nd or 3rd century before Christ (BC), to

show that gladiators consumed C3 plants like wheat and barley as staple foods [50].

Barley is considered one of the first domesticated plants. Its first domestication most likely occurred in the Fertile Crescent about 10,000 years BC [48, 51–54]. But its exact domestication location has been debated intensely [39, 53]. According to Lev-Yadun et al. (2009), the first domestication of barley and other Neolithic founder crops, such as einkorn wheat, took place in the Jordan Valley and adjacent areas of the southern Levant, in present-day Israel and Jordan. But based on genetic, botanical, and archaeological evidence, a smaller core area within the Fertile Crescent can be seen as the cradle of agriculture. This area covers the upper reaches of the Tigris and Euphrates rivers in today's southeast Turkey/northern Syria [54]. Badr et al. (2000) concluded that, with a high probability, the southern part of the Fertile Crescent, i.e. an area in Israel and Jordan, was the area where wild barley was domesticated [38]. Mascher et al. (2016), who sequenced the genome of 6,000-year-old barley grains retrieved from the Yoram Cave in the Judean Desert in Israel, confirmed these findings. The authors further showed that these 6,000-year-old grains differed genetically from the wild forms found in that region today. But genetic overlap with domesticated barley varieties used in that region today is also evident. The authors further assumed that immigrants arriving in that region did not bring crops from their homelands but rather cultivated local, well-adapted varieties [55]. Populations from western Iran contributed germplasm to cultivated barley on its way to the Himalayas as well [38]. Harlan and Zohary (1996) stated that barley and wheat do not have their primary habitats in the same region. As barley is more drought-tolerant, it is expected that barley was also cultivated further down the arc of the Fertile Crescent into the steppes, deserts, as well as along the wadis [56]. Following Morell and Clegg (2007), wild barley from the Fertile Crescent largely contributed to the genetic diversity of nowadays European and American barley cultivars. In contrast, wild barley from Central Asia contributed to some extent to the genetic diversity of barley cultivated from Central Asia to the Far East. The authors concluded that barley was not only domesticated in the Fertile Crescent, instead domestication of barley must have occurred outside of the Fertile Crescent, too. [57]. It is very likely that Tibet is a second domestication centre for barley [58]. Recent data from Guo et al. (2025) showed that the largest contribution of wild barley populations to the gene pool of cultivated barley came from the southern and northern Levant as well as Central Asia, while those from the Syrian Desert and northern Mesopotamia contributed to a lower extent [9]. Modern, cultivated barley (*Hordeum vulgare* L. ssp. *vulgare*) originates from its wild ancestor *Hordeum spontaneum* (C. Koch) Thell and is morphologically quite similar to its wild progenitor [38, 39]. The cultivation of barley extends back to 5,000 BC in Egypt, 3,500 BC in Mesopotamia, 3,000 BC in north-western Europe, and 2,000 BC in China [59]. With increased trade and the movement of civilisation towards Europe, barley was cultivated there as well [43].

A very important trait in the domestication of barley was the non-brittle rachis, because spikes remained longer on the plant after maturation, enabling a more efficient harvest with lower grain loss compared to barley with a brittle rachis [60]. In barley with a brittle rachis, the spikelets of the ears fall apart at ripening, caused by

fragmentation of the rachis (shattering or disarticulation), while in domesticated forms the seeds are held together by a tougher rachis. The rachis is considered the backbone of the ear, which bears lateral spikelets. The spikelet can be defined as the part of the ear that contains 1–4 seeds and their surrounding glumes, which can be seen as leaf-like structures [53]. Pourkheirandish et al. (2015) identified two recessive alleles, *btr1* and *btr2*, which are responsible for suppressing the development of expanded cells in the separation zones, which results in a non-brittle rachis. Based on the results of their study, the authors conclude that *btr1*-type barley emerged earlier and in the southern Levant, while *btr2*-type barley appeared later and in the northern part of the Levant region. So, they emerged independently in both time and location [61].

Another important trait for barley domestication was the development of six-row spikes, which resulted in a three times higher number of kernels compared to two-row barley [60]. Wild barley, *Hordeum spontaneum* (C. Koch) Thell, the progenitor of cultivated barley, was two-rowed [43, 62]. Six-row barley emerged as a result of mutation during domestication [60]. The *vrs1* gene is responsible for the six-row spike in barley. Results of phylogenetic analysis indicated that six-rowed barley had multiple independent origins across different regions and time periods. This might be caused by farmers, who selected the higher-yielding six-row barley for further breeding [62].

The presence of awns, which contribute to photosynthesis [63], was preserved during barley domestication. While wild barley was characterised by long awns, domesticated barley has shorter awns [39]. Wild forms are also characterised by smaller seeds [53], as well as a higher level of dormancy [64]. Seed dormancy refers to a physiological condition of the viable seed, which prevents germination in situations where favourable germination conditions are given [53]. The application of fertilisers and pesticides led to heavy spikes and large kernels, but the stalks of the ancient cultivars were not strong enough to support them, resulting in lodging [65, 66]. Lodging results in a lower harvest index and a higher risk of fungal infections and pre-harvest germination [66, 67], thereby reducing grain and malt quality. Therefore, breeding for lodging resistance was one of the main focuses of breeding programs. To avoid this risk, breeding incorporated dwarfing mutant alleles to achieve more robust and shorter stalks. Several semi-dwarfing genes are used in barley breeding; one of them is the *sdw1/denso* locus, which leads to a decrease in plant height but also an increased time to heading, late maturity, as well as decreased thousand-kernel weight [68].

5 Barley classification

There are various ways for barley classification and differentiation:

Based on spike morphology and number of fertile spikelets present at each node of the rachis, two *Hordeum* subspecies can be differentiated [69]:

Two-row barley (*Hordeum vulgare* subsp. *distichum*), where only the central spikelet is fertile, and six-row barley (*Hordeum vulgare* subsp. *vulgare*, also called *Hordeum hexastichum*), where also the lateral spikelets are fertile [69, 70]. In two-rowed barley, all kernels

are quite symmetrical. A variation in size can be found between the larger kernels in the middle of the spike and the smaller ones at the base and tip of the spike. Two-rowed barley varieties usually have higher numbers of tillers per plant and large, heavier seed than that of six-rowed varieties, which have, in contrast, more seeds per spike. One-third of the kernels in six-row barley are asymmetrical, i.e. twisted. These twisted kernels are generally smaller and weigh 13–20 % less than the symmetrical kernels [43]. In Europe, two-row barley is mainly used for malting and brewing [42, 45, 71]. Also, the Bavarian Purity Law, which approved malted barley as the only cereal source for beer brewing, increased the breeding of barley in terms of starch content and enzymatic potential [45]. However, outside of Europe, barley with multiple rows is used for malting because of its higher protein content and enzymatic power, which will make the use of larger quantities of adjuncts in brewing easier [71, 72].

Two-row barley can further be categorised into two different groups: First, *Hordeum vulgare* ssp. *distichum erectum* barley varieties where the spike stands erect while it is maturing. The spike of these upright barley varieties is also dense and wide and the individual kernels are arranged close together. Second, *Hordeum vulgare* ssp. *distichum nutans* varieties, where the ear bends so that it hangs during maturation. These varieties are also characterised by long, narrow spikes and individual kernels that are arranged less closely to each other [72]. In former times, also *Hordeum zeocriton* L. varieties were also found, which were called “fan barley” or “peacock barley”, due to their pyramidal-shaped ears. As early as 1902, it was described as being out of general cultivation [16].

Two different types of barley are available: winter barley and spring barley. Winter barley is sown in autumn, as it requires vernalization, which refers to the need for a cold stimulus for initiating floral development [42, 71], but this is not required for spring barley, which is mainly used as a raw material for malting, brewing and distilling. Nevertheless, modern breeding has resulted in two-row winter barley varieties deemed suitable for malting, but how many of these varieties will be available in the coming years also depends on policy decisions [72, 73].

Spring barley is characterised by a particularly wide ecological range of adaptation to growing conditions [74], especially to northern regions, where the conditions are too harsh for the cultivation of winter barley varieties [69]. A high leaf formation rate and rapid grain development, together with comparatively low water demand, enable the realisation of acceptable yields even under short growing periods and restricted water availability. Spring barley is also able to tolerate frost up to -6°C during the tillering stage. The reduced transpiration rate through the leaf surface, compared with other cereal species, accounts for the low water requirement of spring barley. The yield potential of spring barley is strongly determined by the duration of the growing season [74]. Overall, spring barley varieties have a shorter growth cycle than winter barley and they provide lower yields than winter barley varieties [69]. Under a vegetation period of 110 days, grain yields of approximately 6 tons (t) per hectare (ha) are feasible, while a vegetation period of 140 days might result in grain yields of up to 8 t / ha. The length of the growing season is determined by the sowing date. This means an earlier sowing results in a longer vegetation period. Temperature, water stress, and nutrient supply will also influence the length of the

growing season. Temperatures of 35°C or above induce premature ripening, which leads to a shorter growing season. Water stress accelerates senescence, while nutrient deficiencies accelerate the development process during the stem elongation and grain filling phase [74]. According to Friedt (2011) modern spring barley varieties in Europe trace back to European landraces from the south of Germany i.e. Bavaria as well as Moravia (today Czech Republic), Sweden and United Kingdom. First cycles of cross-breeding focused on hybridisation among landraces, which resulted in early spring barley varieties like “Isaria” in 1924 [1].

Barley can also be divided into two different forms: hulled barley and hull-less (naked) barley. Hulled barley has an outer husk attached to the grain, which is not the case for hull-less barley [70]. In naked barley varieties, the hull easily separates from the grain kernel during harvest and further processing. Naked barley can be used as a whole grain for human consumption with higher flavour and nutritional value [75]. Both, two-row and the multiple-row barley produce hulled and naked varieties [42]. Cultivation of hull-less barley was common in Europe, but in the post-Roman period the number of sites where naked barley was cultivated decreased significantly. Naked barley varieties were replaced by hulled barley and today the cultivation of naked barley plays only a very minor role in Western Europe, while it is still quite common in the eastern part of Eurasia [76]. On the Tibetan Plateau, predominantly in Bhutan, Nepal, as well as China, naked barley is one of the most primary crops used for human consumption in form of noodles, steamed bread or beer, but it also plays an important role as animal feed [77]. Whether hulled or naked barley was cultivated may depend on ancient agricultural technology. While threshing naked barley might be less labour-intensive, hulled barley may be more resistant to pests and damage during storage [42].

Barley can be differentiated in terms of the composition of the grain, which also determines its processing capabilities and areas of application. Normal, waxy, high-amylose starch types, barley with high lysine or β -glucan content [48, 70]. The term waxy barley refers to the appearance of the endosperm, which can be described as soft, white and mealy. Waxy barley has a low amylose content of less than 10 % and a high amylopectin content, while non-waxy barley has an amylose content of 17 - 24 % [78, 79] containing starch with the normal ratio of 3:1 of amylopectin to amylose, i.e. amylopectin is 72–78 % of the major starch type, while amylose makes up the remaining 22–28 % [43]. Waxy barley is further characterised by higher β -glucan content than normal barley [80–82], as well as higher levels of soluble fibre and protein. There are also differences in the physicochemical properties of non-waxy barley starch and waxy barley starch. The latter has a higher gelatinisation temperature and swelling power, solubility and pasting viscosity [79].

β -glucans are a family of non-starch polysaccharides [83] which can also be found in yeast, fungi and marine algae [84]. Barley has, on average, a ten times higher β -glucan content compared to wheat varieties [85]. β -glucans are partially soluble in aqueous solutions, and they consist of high-molecular-weight linear chains of β -glucosyl residues polymerised through both β -(1,3) and β -(1,4) linkages. While high β -glucan contents are not favoured when barley is used as a raw material for brewing, as higher levels of β -glucan in malt will lead to lower malt extract values [43]. Higher β -glucan content in

barley provides viscous extracts, which can lead to filtration problems [86]. However, high β -glucan content is desirable when using barley as a food ingredient due to its health benefits. β -glucan forms a viscous solution within the human digestive tract, which slows the absorption of glucose after a meal, and it helps to maintain a good ratio of glucose to insulin in the blood [87]. Incorporating barley in food products, especially baked goods, might be beneficial, as the European Food Safety Authority (EFSA) and the U.S. Food and Drug Administration (FDA) have approved health claims for β -glucan and soluble fibre from barley in terms of lowering blood cholesterol and reducing the risk of coronary disease [88, 89].

β -glucan content in barley can be influenced by air temperature and precipitation, where rain during the flowering and grain-filling phase leads to a lower β -glucan content [90]. Also, Güler (2003) reported that irrigation tends to reduce barley β -glucan content. Lower temperatures during the tillering and stem elongation phases and higher temperatures during the grain-filling phase resulted in higher β -glucan content. β -glucan content was not influenced by higher mineral fertiliser rates. So, β -glucan can be obtained by low-input or organic production and does not require intensive conventional production systems [91]. Barley genotype has an influence on β -glucan content, too [90]. In contrast, Güler (2003) showed that high levels of nitrogen treatment resulted in higher β -glucan content in barley [91].

Commercially grown barley varieties do not contain pigments other than carotenoids [92], as a light-yellow grain colour is generally preferred for malting, brewing, and food purposes [93]. But there are also varieties with purple or blue colouring, caused by the accumulation of flavonoid compounds in the grain. These flavonoid pigments accumulate in vacuoles of plant cells as well as tissues [94]. Coloured ancient grains get their colour from two different types of pigments: Red to bluish coloured anthocyanins and black allomelanins. Accumulation of anthocyanins in the aleurone layer of the grain results in a blue colour of the grain [95]. Anthocyanins are among the most abundant secondary plant metabolites. They are responsible for the characteristic colour of numerous fruits and vegetables, as well as the autumn colour of numerous deciduous tree species [96–99]. Anthocyanins play an important role primarily in red wine production, but also in red juices [100].

Due to their antioxidant and presumably even anticarcinogenic as well as anti-inflammatory effects, anthocyanins are considered to be beneficial to health and have increasingly been the focus of scientific and medical investigations in recent years [101]. However, anthocyanins may only be beneficial, if the food contains a relevant amount. Their use as natural colourants for food is also a conceivable way of replacing synthetic food colourings [101, 102]. Like all known melanins, the allomelanin detected in barley is completely insoluble in water and organic solvents [97, 103]. Due to that allomelanin cannot be exploited in the beverage sector.

6 Ancient barley varieties for malting and brewing

Mikyška et al. (2022) compared the malting and brewing characteristics of Czech historic malting barley varieties with modern

varieties. Pilot malting and brewing trials (50 l) were conducted. For brewing, a single-decoction protocol was used to produce Czech (Pilsner) pale lager beer. Malt analysis showed that malt from ancient Czech barley varieties had high nitrogen content (12.45–13.89 %) and low extract (75.2–78.6 %). Based on the Kolbach index (37.4–40.9 %) and friability value (46.2–57.7 %), proteolytic and cytolytic modification were also lower than in modern bred barley varieties [104]. A low protein modification may not provide yeast with sufficient assimilable nitrogen compounds, which might lead to low yeast propagation as well as the development of undesired fermentation by-products, such as diacetyl. Low cytolytic modification can slow lautering and filtration, reduce brewhouse yield, and increase haze formation in beer [105]. Especially in modern brewhouses where mashing in directly at temperatures above 60 °C is common, a homogeneous and complete degradation of cell walls and a suitable level of protein modification is required, as in modern brewhouses, mashing often focuses on amylolysis. Adjusting the mash program in terms of temperature and rests is not practicable in large-scale industrialised breweries, as it makes the brewing process less efficient and disrupts the original, often very tight, production schedule [105, 106]. Because of their low cytolytic and proteolytic modification, the ancient Czech barley varieties studied were recommended for regional microbreweries rather than large-scale industrial breweries [104]. Olšovská et al. (2018) studied the malting and brewing characteristics of the ancient Czech spring barley variety Proskovcuv hanacky. Pilsner type malt was produced using floor malting. The malt was characterised by high protein content and very low cytolytic modification. Friability value varied only around 48 %. Also, a higher proportion of partially unmodified kernels (22.5 %) and glassy kernels (4.2 %) was found, which might have been caused by a low germination rate and lower cytolytic enzyme activity. A high content of β -glucans (500 mg/ l) in wort was found, too [107]. Finding higher β -glucan content in ancient barley varieties is feasible, as breeding programs focused, among others, on reducing β -glucan content in malting barley [106]. High levels of β -glucan are problematic when available as a gel, as it may cause filtration problems. Especially high mashing in temperatures above 60 °C may cause the release of β -glucan still bound in the cell walls due to the enzyme β -glucan solubilase. This high-molecular β -glucan cannot be further decomposed because the responsible enzyme, endo- β -glucanase, is already inactivated at temperatures above 52 °C, resulting in higher β -glucan content in wort and beer [105]. The malt also showed low proteolytic modification, as indicated by a low Kolbach index of 28.6 % [107], while the desired range lies between 38 and 42 % [105]. Malt from the ancient Czech spring barley variety Proskovcuv hanacky had a quite low relative extract at 45 °C of 29.7 % and a low amylolytic modification, shown by a final attenuation degree of only 74.6 %. Starch degradation was clearly affected by the high content of nitrogenous substances in malt [107]. Well-modified malt should have a final attenuation degree above 81 % [105]. The wort was described as opalescent, turbid and pale in colour, with a pH at the upper limit for pale malt. The authors therefore concluded that in terms of today's malt quality requirements and brewing process efficiency, the ancient Proskovcuv hanacky variety cannot be considered as an ideal variety [107]. Tucker et al. (2024) assessed the malt quality of two vintages of European-derived barley varieties. Malt was produced using a micro-malting system. The ancient varieties studied did not show malting quality profiles aligned

with the standards of modern Canadian malting barley. Some ancient barley varieties had (substantially) higher protein content, while others showed lower or comparable values. Ancient varieties generally had lower fine grind extract and a lower α -amylase activity [108]. Because this study did not focus on malt quality and brewing performance, no brewing trials were conducted. Yahiaoui et al. (2014), who compared Spanish barley landraces with modern bred varieties, reported higher thousand kernel weights for the landraces tested, and comparable results for malt extract and grain protein, which might also provide a rough indication of their malting quality potential. But due to low replication of these measurements, further research is needed to verify these results [109]. Likewise, to the previous study, no brewing trials were conducted. Psota (2008) studied ancient Czech barley varieties with respect to their malting quality. Varieties permitted in 1900–1977 were characterised by significantly the lowest friability and homogeneity values compared to all other tested sets of varieties. They had significantly higher levels of glassy and partly unmodified kernels than the other tested sets. Wort from ancient barley varieties had significantly the highest β -glucan content, viscosity and haze at 15 °C and 90 °C, compared to all other sets of varieties incorporated. The ancient varieties studied had a significantly lower extract content and final attenuation. Despite the fact that the set of ancient varieties covered a time span from 1900 to 1977, i.e. also varieties which underwent first breeding efforts, their malt quality can be described as inferior, indicating a low cytolytic modification and wort quality [110]. Despite analysing the malt quality of these varieties, no brewing trials were conducted. Gothard et al. (1983) studied the malting quality of barley varieties introduced in England and Wales between 1880 and 1980. Chevalier barley, introduced in 1880, and Plumage, introduced in 1889, had quite high nitrogen content and low Kolbach indexes, which indicated a lower proteolytic activity during modification, so less of the protein matrix surrounding the starch granules in the endosperm will be degraded, which allows the starch to be less easily degraded during mashing. The older varieties also showed lower hot water extract rates than the varieties introduced later. When combined with the greater yield that was found in the later introduced varieties, the mean extract yield of barley varieties introduced between 1953 and 1980 was 48.7 % higher than that of earlier varieties [111].

Considering the brewing trial results, Mikyška et al. (2022) found lower extract yield than in modern bred barley varieties. The extract yield in the wort of the brewing trials corresponded to the extract determined in malt. The low malt extract resulted in a lower extract yield of the final beer. Mashing in at a lower temperature (37 °C, 10 min.) and a rest of the mash at 52 °C for 20 min., which is supposed to promote proteolysis and degradation of non-starch polysaccharides, did not improve the extractability of the under-modified malt. During fermentation and maturation, ancient and modern barley varieties showed no differences, but ancient varieties were characterised by slower filtration rates. Beers from malt of ancient Czech barley varieties did not differ significantly in foaming ability, foam stability, or polyphenol content. The authors concluded that brewing with these ancient barley varieties was possible without further implications [104]. However, processability of barley and barley malt became increasingly important for the modern, highly industrialised malting and brewing industry to ensure efficient, cost-effective processing [106]. Ancient barley varieties may often fail to

meet these requirements. Lager beer brewed with ancient spring barley variety Proskovcuv hanacky, using a two-mash decoction process, was characterised by a relatively low alcohol content, a high content of dextrins, β -glucans, arabinoxylans and polyphenols. Overall analytical characteristics of a beer from under-modified malt. The beers also had a high iodine number of 2.5, indicating low efficiency in enzymatic starch degradation [107]. High iodine figures might also lead to turbidity in the filtered beer [105]. High levels of non-starch carbohydrates such as β -glucan, arabinoxylans, and pentosans are a result of low cytolytic modification. The high content of unfermented maltose was probably due to a slow main fermentation [107]. It must also be stated that beers were produced by two different breweries using different mashing methods, which might also have influenced the quality of the final beer. According to Mikyška et al. (2023), the mashing process, especially double or triple decoction, significantly increases flavonoid content in beer, which may affect the sensory stability of the final beer [112]. A selection of malt and brewing analyses of ancient barley varieties reported and discussed above is provided in Table S1 and Table S2 in comparison to data from modern bred barley varieties. Based on the data summarised above, it can be stated that ancient barley varieties are rarely studied regarding their suitability for malting and brewing. Comparing results is also challenging, as for malting different methods such as floor malting [107] or laboratory small-scale malting [104] were used. Sometimes the malting method is not clearly specified [110]. To better understand an ancient barley variety's performance in the malthouse, further studies using standardised malting trials are required. In a subsequent step, malting parameters such as steeping time and temperature, aeration, and/or germination time have to be adjusted for each ancient barley variety to ensure a sufficient level of modification and also to reduce malting loss. As stated by Mikyška et al. (2022), adjusting malting parameters can improve cytolytic, proteolytic and amylolytic modification [104]. Higher malt quality will also improve brewhouse efficiency and flavour stability [106]. Results presented are mainly based on base malts from ancient barley varieties. However, it might also be relevant to study the suitability of ancient barley varieties for the production of speciality malts, with the risk of losing their variety-specific sensory profile.

Most studies on ancient barley varieties did not investigate different growing sites [104, 107] nor different harvests [104], which also influence malt quality. This omission often reflects the limited availability of seed from ancient barley varieties for multi-year trials across different environments. Often a small sample of seeds is obtained from a collection of genetic resources and has to be propagated over several years until enough seed is available [107]. This already requires substantial resources and financial investment.

It should also be noted that data on the brewing performance of ancient barley varieties are very limited, as studies on ancient barley varieties often do not include malting and brewing trials. When brewing trials are conducted, researchers use different process parameters, such as mashing methods [104, 107], making comparisons more challenging. For future research, it is recommended to use, in a first step, the same process parameters to understand the brewing performance of each ancient variety. In a subsequent research project, different mashing methods should be tested, and the brewing process has to be adjusted for each

ancient barley variety's needs. A well-adjusted brewing process will increase processability, yield and even the sensory profile of beer from ancient barley varieties. Based on the data given, ancient barley varieties might not be suitable for modern, highly efficient brewing processes, where high mashing in at temperatures above 60 °C are common [105, 106]. If process parameters are adjusted, and when promising results are obtained at the laboratory scale, this could justify further investigation into scale-up, as this may also change processability and quality of the final product. Brewing trials with ancient barley varieties have mainly used lager-type beers [104, 109], but no information is available on their suitability for other beer styles. Future studies should explore a broader range of beer styles, potentially extending beyond the German Purity Law, to broaden raw material selection and to further investigate the potential of ancient barley varieties. Brewing outside the German Purity Law might also allow ancient barley varieties to be used as adjuncts. However, the feasibility will require further investigation. It might also be worth to investigate if dark-coloured ancient barley varieties might be exploited for producing beer with a red hue.

Research on the sensory profile of beer brewed with ancient barley varieties is also quite limited: Czech (Pilsner) pale lager beers brewed with ancient Czech barley varieties and beer brewed with modern Czech barley varieties were characterised by descriptive analysis of a trained panel. The panel also assessed the overall impression of the beer. Beers from the ancient Czech barley varieties Stupický staročeský and Diamant had a slightly lower, but not significantly lower, overall sensory impression. Overall, beers brewed with ancient Czech barley varieties had a comparable sensory quality to beers brewed with modern bred barley varieties. All beers were described as having medium bitterness and palate fullness, weak sweetness and astringency. Beer brewed with malt from ancient barley variety Stupický staročeský was slightly more astringent. A more intense perfume flavour was found in beer brewed with the ancient barley varieties Chlumecký and Opavský Kneifel and a more intense grainy flavour was found in beer brewed with malt from Opavský Kneifel. Some, but not all, assessors reported a more intense warty flavour for beers brewed with ancient barley varieties. However, cluster analysis differentiated their sensory profile from that of beer brewed with modern barley varieties [104]. Olšovská et al. (2018) conducted sensory analysis of the two pale lager beers brewed with malt from ancient spring barley variety Proskovcuv hanacký. However, these beers were not tasted in comparison to beer brewed with malt from a modern Czech barley variety. Beers were described by a medium palate fullness, medium bitterness and medium bitter aftertaste. A weak astringency, despite a high polyphenolic content of 288 mg / l, as well as a weak sweetness were attributed. Both had a medium sourness, with slightly higher values for beer brewed at Břevnov brewery. Both beers showed a fruity and yeasty aroma. The authors described perfume notes for the aroma and flavour of the beers. All notes were characteristic of a bottom-fermented pale lager beer. However, both beers showed a specific off-flavour that the authors did not further describe. The overall impression of both beers was described as medium (5) on a 9-point scale [107]. Sensory results of this study must be interpreted with caution, as beers were brewed at two different breweries using different brewing processes. For better comparison, a standardised brew-

ing process should be applied. This would help attribute sensory differences to variety rather than brewing-process differences. In contrast, a brewing process not well adjusted to the respective variety might also negatively affect the sensory profile of the final beer. For better comparability, future research should also include modern barley varieties.

It is often stated, that ancient barley varieties like Maris Otter, Schooner or Golden Promise have a specific sensory profile [113, 114]. Herb et al. (2018) even stated that the influence has a genetic basis. However, these results are based on micro-malting and nano-brewing trials, resulting in beer with low quality, as malting was not adjusted to each variety [113]. Some research focused on Maris Otter, a winter two-row barley variety selected from the cross of Proctor and Pioneer and released in the United Kingdom (U.K.) in 1966, but is nowadays rarely grown due to its poor agronomic performance [2]. While it occupied most of the English winter barley crop area well into the 1970s, it was suitable for cultivation in continental Europe, due to its lower winter hardiness [71]. Stewart et al. (2023), who tested the sensory profile on unboiled wort produced with pale malt from heritage barley varieties Maris Otter and Schooner in comparison to modern barley varieties, showed that the two heritage varieties were described as having higher overall flavour complexity, nutty/biscuit aroma, and sweetness intensity compared to the other varieties tested [114]. However, this study did not include brewing trials to assess whether these beneficial attributes transfer to the final beer. Further research is needed to determine whether these aroma and flavour characteristics transfer to the final beer. Also, Windes et al. (2021) identified some influence of barley genotype on beer flavour, using hot steep extracts and lager beer [115]. If further research data verifies that ancient barley varieties can bring in a unique and specific flavour profile, it may help maltsters and brewers to consistently target desired flavours in the final beer or even in whisk(e)y [114]. For studying the flavour profile of ancient barley varieties, hot steep extracts seem quite helpful [115]. Further research is also needed to determine whether the flavour profiles found in hot steep extracts transfer to the final product, or whether brewing parameters like hop addition or fermentation might mask the influence of barley variety. Scientific verification of a unique sensory profile will help brewers to differentiate beer brewed with ancient barley varieties from standardised, mainstream beers. An objective description of the final beer's sensory characteristics will be helpful to understand the influence of barley genotype. Descriptive analysis data can also be linked with consumer acceptance data to identify which attributes contribute to beer liking. The current literature also shows a lack of consumer studies on beer brewed with ancient barley varieties. Further research should therefore address how consumers respond to beer brewed with ancient barley varieties. Incorporating ancient barley varieties as a raw material for brewing or even distilling may become more relevant as consumers today seek new flavours in beer and higher-quality products [116]. It is also relevant to understand their willingness to buy and whether they would pay higher prices for these beers. A higher willingness to buy might offset the likely higher production costs of beer brewed with ancient barley varieties. It may also be relevant to research consumers' interest in beer brewed with ancient barley varieties and which attributes they associate with it; attributes that might help brewers to market their products successfully.



Fig. 1 Yeast Bread with 20 % barley flour of coloured ancient barley variety Schwarze Criewen (left), and sourdough bread with hull-less coloured barley variety Weihenstephaner Schwarze Nackte (right)

7 Ancient barley varieties for baking

In the past, flatbread made with barley flour was a staple food in Scandinavian countries, especially in rural areas [43]. Nowadays, barley plays a minor role in the food industry, especially in industrialised countries. Barley has lower gluten and higher dietary fibre content than wheat, resulting in lower-quality bread and other baked goods [117]. However, the EFSA and the FDA approved health claims for barley glucan and soluble fibre from barley for lowering blood cholesterol and reducing the risk of coronary disease [88, 89]. As a result, interest has increased in using barley as an ingredient in healthy food products with nutritional benefits [117], especially in baked goods, because of its beneficial constituents [88, 89, 118]. Shape and pore structure of bread with 10 % barley flour addition were comparable to bread made with 100 % wheat flour. Higher percentages decreased water absorption and stability, resulting in a denser crumb and larger, more non-uniform pores [119]. Gill et al. (2002) reported that substituting wheat flour with barley flour reduced loaf volume and changed bread colour as well as texture [120]. Results of a one-year field trial with heirloom hull-less barley varieties showed a wide protein content (11.5 - 16.8 %), making these varieties more suitable for the baking industry rather than for brewing. But for more consistent results, long-term trials are required [75]. Black-coloured heirloom barley varieties had higher protein contents and might be more suitable for the baking industry, where higher protein contents are desired, than for animal feed, as the authors recommended [121].

Barley flour as a substitute for wheat flour in bread might increase the final product's antioxidant potential, depending on barley variety and the baking process [118]. Flour from ancient blue or black coloured barley varieties might also increase the antioxidant potential of the products, as the blue colour of the grain is caused by an accumulation of anthocyanins in the aleurone layer of the grain [95]. Ancient coloured barley varieties can be used as a colouring agent, too. Small-scale baking trials with standardised tin-loaf bread showed that adding 20 % of flour from coloured

barley variety Schwarze Criewen resulted in grey-coloured bread (see fig. 1 left). The baking process did not reduce the colour. The addition of whole-grain flour from the ancient hull-less barley variety Weihenstephaner Schwarze Nackte resulted in a sourdough bread with an intense brown/grey colour (see fig. 1, right). Further research is needed to exploit the potential of ancient barley varieties as a colouring agent, possibly replacing vegetable carbon (E153), an insoluble black pigment produced by carbonising vegetable materials at high temperatures [122]. This could offer a clean-label option. Consumers' increased awareness of health and well-being drives their preference for clean-label products [123].

In the Mediterranean region, cuttlefish (*Sepia officinalis*) melanin has been used to colour bread and pasta specialities for centuries [124]; its use as a food colourant requires molluscs to be labelled as an allergen [125]. This can be avoided with coloured ancient barley varieties. Valorising ancient barley varieties not solely for brewing, but also as a raw material for the baking industry will give producers an additional sales channel, thereby minimising their risk. As ancient barley varieties are a more expensive raw material for brewers, due to lower yields [104, 121, 126] and lower malt quality [104, 107], it might be worth exploring the potential of their by-products such as barley rootlets and brewers' spent grain (BSG) for the baking industry. BSG, the largest and nutritionally valuable by-product generated in the brewing industry, is characterised by a high fibre and protein content [127]. Rootlets are rich in essential amino acids, especially lysine, the typically limiting essential amino acid of cereals. This makes them a valuable raw material by increasing a product's protein and β -glucan content. Adding up to 10 % of dried rootlets did not significantly compromise on bread texture and sensory profile [128]. Valorising by-products provides maltsters and breweries with an opportunity to generate additional revenue [127, 128] and contribute to overall sustainability by reducing resource consumption and environmental impact. However, BSG has to be preserved, typically by drying. Currently, no regulatory guidelines exist regarding the preservation of BSG for application in human food [127].

8 Ancient barley varieties agronomic performance

Ancient barley varieties often inherit specific agronomic traits that are not found in modern bred barley varieties. For instance, some are resistant to fungal diseases or are able to tolerate low temperatures or drought [107]. Marečková et al. (2011) reported barley landraces having a richer root system for more efficient nutrient uptake, predominantly nitrogen, and higher stress resistance. Barley landraces have the ability to tiller, which helps to suppress weeds and are characterised by a shorter vegetation period [126]. Stølen and Andersen (1978) showed that the Scottish Landrace Bere had higher tolerance to soils with high acidity, due to a single major gene Pht mapped on chromosome 4H [129]. Martin et al. (2023) further reported the ability of some Bere accessions to grow on marginal soils deficient in manganese, while they grow poorly on well-fertilised soil. Bere is also characterised by a higher tolerance to salinity stress [28]. The six-row barley also has an early heading date, reflecting a short growth cycle. Also, for the Scottish landrace Bere, a plant height of up to 120 cm has been reported, which makes this variety prone to lodging, limiting the feasibility of mechanical harvesting, potentially to the point of impracticability. This might have been one factor contributing to its decline in importance over time [36]. A high plant height which in turn resulted in lodging were reported for ancient Czech barley varieties, too [104]. Brown et al. (2017) studied the Scottish barley variety Bere to determine whether it has enhanced micronutrient efficiencies in the field. Bere is considered as one of the most ancient landraces in Scotland, which is still cultivated. Based on the results of their study, Bere genotypes have a superior ability to accumulate manganese, zinc and copper compared to elite and other heritage lines when they were planted on marginal soils with limited plant-available micronutrients. This might have resulted in a selection pressure for traits involved in micronutrient efficiency. The identification and use of those genes and phenotypes from ancient germplasms would be beneficial for breeders in developing barley varieties with greater micronutrient efficiency [29]. Cope et al. (2022) reported that some landraces showed higher salinity tolerance compared to modern bred barley varieties. The authors showed differences in root growth, where Bere was characterised by quicker and larger root growth at all salinity levels tested. Nevertheless, studies along the whole cropping lifecycle are still necessary to get a better understanding of how tolerant these varieties are. Salinity tolerance will be a trait relevant in the future as higher salinity levels are expected due to higher salt levels in groundwater caused by higher sea levels and an increased application of brackish water for irrigation [130]. Chapagain et al. (2014) studied the root architecture of heirloom barley cultivars in comparison to modern bred varieties. Their results indicated that heirloom barley varieties are better adapted to low phosphorus and/or drought conditions which are often found in low input or organic production, as some heirloom varieties have finer and longer roots as well as a higher shoot to root ratio. If these traits could be integrated into modern barley varieties, this might improve their suitability for drought conditions and also might improve nutrient uptake efficiency [131]. Chapagain and Riseman (2012), who compared the agronomic performance of commercial and heirloom barley cultivars in Canada, concluded that there were significant differences in terms of plant height, spike length, and seed weight to volume ratio. However, there were

significant differences in terms of yield (2.9 to 5.8 t / ha) between the heirloom cultivars. The authors further concluded that overall heirloom varieties performed well under organic farming conditions and referred to the potential value of heirloom barley cultivars in terms of yield and disease resistance [121]. Dwivedi et al. (2019) pointed out that ancient varieties often perform better under organic and more sustainable farming practices [35]. Yahiaoui et al. (2014) assessed the agronomic performance of Spanish barley landraces in ten field trials in typical barley growing regions over three years. The authors showed that landraces were characterised by later flowering date, higher plant height, and a greater tendency to lodging. The most relevant trait of some landraces was higher grain yield at low-production sites, which might reflect their ability to fill grain under stressful conditions [109]. The grain yield of ancient Czech barley varieties was on average 1.2 t/ha lower compared to current varieties [104]. Marečková et al. (2010) reported a substantially lower yield of landraces and older varieties (2.96 to 4.84 t / ha) compared to modern breeding lines (5.98 to 7.14 t/ha), and they had a pronounced tendency to accumulate nitrogenous substances in the grain (12.5–16.7 %) compared to standard and modern breeding lines (10.5–11.6 %). In terms of agronomic parameters [126]. Tucker et al. (2024) stated later heading dates for the majority of ancient barley varieties compared to the modern varieties. The ancient varieties also showed lower yield compared to the modern varieties, which might also be caused by the poor adaptation to the Canadian environment. On average the ancient barley varieties showed lower thousand kernel weights than the modern varieties [108]. Bahrman et al. (1999) studied twenty-six old French six-row winter barley varieties regarding their resistance to barley mild mosaic virus. Results of mechanical inoculation tests showed full resistance of seven old varieties. The authors used molecular, biochemical and morphological data. DNA molecular markers were more suitable to differentiate and discriminate between varieties than biochemical or morphological ones [132]. Aikasalo (1988) showed that Finnish landraces were well adapted to the short growing season, especially with Olli, a very early landrace [133]. Riggst et al. (1981) showed in field trials that incorporated most of the important spring barley varieties grown in Britain between 1880 and 1980, that grain yield was higher in most modern barley varieties. While the ancient barley variety Chevalier, introduced prior to 1900, was characterised by a grain yield of 4.61 t/ha, varieties introduced in 1980, such as Triumph, already had a grain yield of 6.68 t/ha. The genetic gain in yield was 0.39 % per year over the 100-year period. Between 1953 and 1980 the genetic gain in yield was higher, representing 0.84 % per year. The authors further found longer straw in the older variants. While Chevalier was 98.1 cm, Triumph was characterised by much shorter plant height, i.e. 69.8 cm. Also, fewer of the tillers they produced survived to give ears. Further, the time from sowing to ear emergence was almost ten days longer [134].

9 Ancient barley varieties for breeding

While little data are available regarding the use of ancient barley varieties for malting and brewing, ancient barley varieties are considered as a valuable pool of genetic resources which have to be preserved and exploited, as they might be a valuable source for incorporating their beneficial traits like resistance against diseases and pests

into modern cultivars [17, 21, 37, 133]. Advances in genomics and recombinant DNA technology make this considerable pool of genetic resources more accessible. While it is easier to transfer single gene traits from landraces germplasm to modern cultivars, most of the desirable traits characteristic of landraces are complex and therefore more complicated to express in different genetic backgrounds [135]. By transferring the large genetic and phenotypic diversity of wild relatives and barley landraces into elite germplasm, modern agriculture might be able to ensure food security on increasingly marginal soils and among the progressively noticeable impacts of climate change [12]. Tucker et al. (2024) studied European-derived ancient barley varieties regarding their suitability as a germplasm source to achieve greater resistance against Fusarium Head Blight, caused by *Fusarium graminearum*, a global pathogen found not only in barley but also in other cereals, resulting in lower grain yield [108]. Most *Fusarium* species causing Fusarium Head Blight produce mycotoxins like Deoxynivalenol (DON) in the infected grains, which is toxic to humans [136]. Tucker et al. (2024) identified several resistant varieties like 'Chevallier Chile', 'Domen', 'Hannchen', or 'Heils Franken', which could function as parents in breeding programs to develop Fusarium Head Blight resistant malting barley varieties [108]. Mamo and Steffenson (2015) studied Ethiopian and Eritrean barley landraces using whole-genome association mapping for resistance to Fusarium Head Blight. The authors identified one common resistance quantitative trait locus on one barley chromosome, significantly associated with both Fusarium Head Blight severity and DON concentration, and on another chromosome, a quantitative trait locus associated with DON concentration, which might be integrated into breeding programs [136]. D'Souza et al. (2025) screened barley landraces for their resistance, to net form net blotch, a fungal disease in barley that reduces the photosynthetic area of leaves, which leads to significant yield loss. Resistance was investigated at different Zadok's stages, i.e. at approximately Z17 (seedling, encompassing early tillering), Z30 (stem elongation), and Z70 (heading, encompassing flowering to early seed development). The authors identified key regions on six of the seven chromosomes with different expression profiles and levels of resistance [137]. Daba et al. (2019) screened, amongst others, Ethiopian landraces for resistance to scald, a fungal disease caused by *Rhynchosporium secali*, and found that a large proportion were resistant [138]. While substantial research has been done to determine the genetic basis of agronomic and malt quality traits, research on which genes contribute to beer flavour remains scarce [47, 2, 114]. This aspect should be investigated further. If empirical evidence supports the contribution of barley genotype to beer flavour, this factor should be considered in further breeding programs, too.

10 Challenges and opportunities for ancient barley varieties

It is worth noting that valorising ancient barley varieties can be challenging, but also offers opportunities. As shown above, research in this area, especially regarding their exploitation as a raw material for malting and brewing, remains limited. Cultivating ancient barley varieties can be challenging for several reasons: before barley and other cereal varieties can be placed on the market, they must be registered in the common catalogue of varieties of agricultural plant species. For this registration, a variety must show distinctness,

uniformity and stability, the so-called DUS criteria. Approval of a variety will be granted by the Community Plant Variety Office (CPVO) after fulfilling the test protocol. The approval remains valid for ten years following its issuance [139, 140]. However, several ancient cereals typically lack the traits needed to meet the DUS criteria. Selling seeds from a variety not approved by the CPVO and not listed on the national list is not permitted. However, it is common for farmers to exchange their farm-reproduced seeds. In Europe, several seed exchange networks like Garden Organic, Irish Seed Savers or ProSpecieRara are trying to conserve ancient varieties, but focus on fruit and vegetables, rather than field crops [7]. Since 2008, the EU has provided some exceptions. With Commission Directive 2008/62/EC, a legal framework was created, which permits EU member states to provide exceptions from standard seed marketing legislation in order to support the legal conservation and cultivation of threatened, naturally adapted landraces and varieties. EU member states must officially identify the region(s) where each variety was historically grown and adapted. Afterwards, seeds of a conservation variety may be produced only in the previously identified region of origin. To maintain the emphasis on genetic resource conservation, the directive restricts the quantities of each conservation variety that may be marketed [141]. "However, being mainly concerned with seed trading, it is unlikely that the Directive will be of great help in preserving all the diversity maintained up to now in Europe [...] and the 'loose' wording of the Directive may result in quite different national interpretations" [7].

It is important to work with ancient barley varieties that are well adapted to the conditions of their respective regions [142]. The selection of suitable varieties should be based on several field trials in various locations to rule out environmental effects. Agronomic parameters such as disease tolerance, yield potential, as well as their compatibility with modern machinery and production methods should be examined [33]. Using ancient barley varieties might also be challenging, as farmers have lost knowledge of how to grow them. Low-input or organic farming may be an option when cultivating ancient barley varieties, as some ancient varieties seem to grow well under these conditions [131]. It is also important to ensure that farmers receive guaranteed purchase prices through cultivation contracts [33] between farmers and maltsters. Higher yield variability may compromise continuous supply of grain from ancient barley varieties in the required quantity and quality, compared to modern bred barley varieties. Overall, the availability of smaller quantities of grain from ancient barley, especially when crop failure occurs, may also limit the use of alternative suppliers, as they may be unavailable. This reduces the predictability and reliability of raw-material supply for all stakeholders along the value chain. Working with ancient barley varieties might open niche markets for farmers, maltsters and brewers. It might help to diversify their product portfolio [36]. Another central aspect of a long-term, successful production chain is ensuring farmers are supplied with high-quality seed. As smaller quantities are needed, large-scale breeding companies are not interested. So, integrating small, family-owned breeding companies into the value chain is relevant. These small-scale breeders might see potential in supplying a niche market [33]. The same holds for seed multipliers. Seed multiplication seems to be a bottleneck for production chains with ancient barley varieties. It is important to ensure that enough high-quality seed is available. Using seed multipliers from different

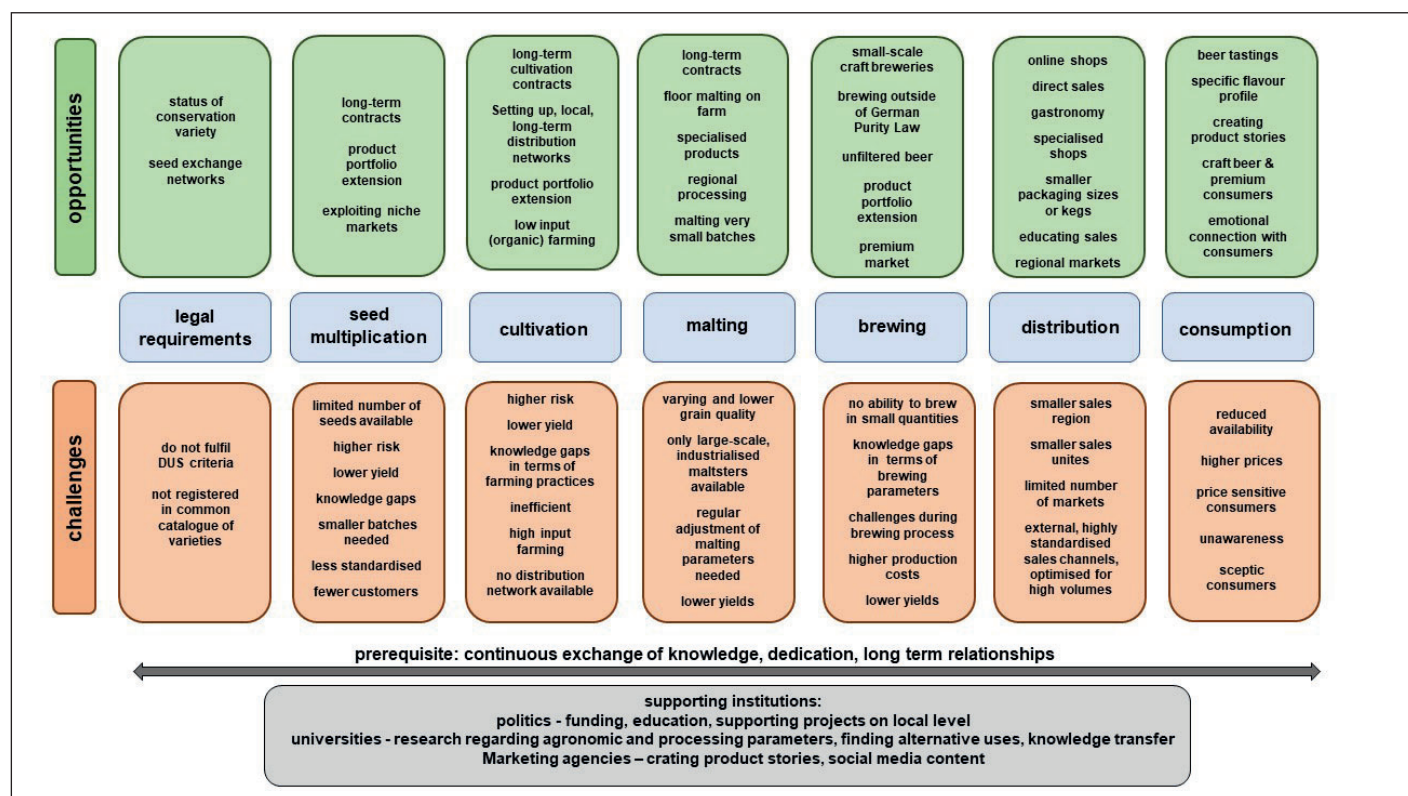


Fig. 2 Condensed overview: challenges and opportunities when using ancient barley (*Hordeum vulgare* L.) varieties for malting and brewing (integration and extension from Halland et al. (2020) [142], Lara (2025) [6], Longin and Würschum (2016) [33])

regions might balance the risk of crop failure, which can lead to insufficient seed supply. Sourcing seeds of ancient barley from an alternative seed multiplier, as it is feasible for modern bred barley, is often not possible. In modern, highly industrialised agricultural systems, not many seed multipliers are able to provide farmers with such small quantities and varieties that are not easy to cultivate.

Another relevant aspect is the strongly industrialised, large-scale malting and brewing industry, which is not adapted to these small-scale processes. There is a strong need to set up small-scale value chains with maltsters who are capable of malting smaller batches. Ideally, malthouses should be capable of processing a delivered batch of ancient barley into malt, while maintaining batch identity throughout the malting process. To overcome this issue, it might be an option to use floor malting, which is more labour-intensive but offers the opportunity to malt on a much smaller scale [142]. On-farm malting allows farmers to capture a larger share of the value added within their own agricultural operations. However, malting ancient barley varieties requires highly skilled and experienced maltsters who are able to adjust the malting process to each variety. Further research is needed to get a better understanding of how the malting process can be adjusted to improve malt quality of each ancient barley variety. Better modified malts from ancient barley varieties will reduce malting loss and improve processability and the quality of the final beer. It also requires small-scale breweries who are able to brew in smaller batches and with processes well-adjusted to each ancient barley variety. How the brewing process can be adjusted to each ancient barley variety should be investigated in further research studies. The same applies to testing the suitability of ancient barley varieties for different beer styles, maybe also for brewing outside of the German Purity Law. Brewing with ancient

barley varieties requires experience and dedication of the team working in the brewhouse. Further research should aim to exploit the sensory potential of each variety. Little information is available on the sensory profile of beer brewed with ancient barley varieties and consumers' perception and response towards those products. This indicates another research gap. As some of the ancient barley varieties are coloured, and their colour can be used for baked goods (fig. 1), it should be explored whether these varieties can be used for brewing beer with a red hue. Producing red-hued beer from dark-coloured ancient barley varieties will give brewers an opportunity to differentiate themselves from competitors. Using ancient barley varieties for malting and brewing requires consumers willing to pay higher prices for beers brewed with these varieties, as production costs are often higher due to lower grain yields [109, 126, 134, 143]. Longin and Würschum (2016) recommend analysing whether an ancient variety has health-promoting effects, which might also be exploited and advertised. However, it must be taken into consideration, that health benefits of alcoholic beverages may not be advertised in most countries. According to Regulation (EC) No. 1924/2006, beverages containing more than 1.2 % by volume alcohol are not allowed to bear health claims within the EU [144]. Consequently, ancient barley varieties' potential health benefits may be better exploited in non-alcoholic applications, given the legal restrictions on health claims for alcoholic beverages. Some consumers increasingly seek new, healthy food alternatives with an interesting sensory profile; reintroducing ancient cereals might meet these needs. Researchers should also examine traditional recipes and production methods, as they might attract consumers and increase their willingness to pay higher prices for these artisanal products [33]. Consumers are willing to pay higher prices for craft beer, which is often perceived as being of higher quality than

commercial beer, especially if organic raw materials are used. Craft beer consumers also prefer beer brewed locally by independent breweries [145-147]. Marketing beer brewed with ancient barley varieties as craft beer is an interesting option to explore in further studies, as craft beer consumers have higher purchasing power [116], which can help cover higher production costs and smaller margins. Hempel et al. (2025) conducted an online survey on bread made from heritage cereals, highlighting the importance of implementing target-specific communication strategies. For bread made with heritage cereals, some consumers were motivated by hedonic values when purchasing, so aspects such as taste and well-being should be prioritised. The other consumer group, mainly older people, associates heritage cereals with supporting the local economy [148]. Also, Dwivedi et al. (2019) referred to the potential of using ancient varieties for promoting local and more sustainable food systems [35] and a country's history in malting and brewing [107]. Another important aspect is the education of the brewery's sales force, as they are responsible for conveying the brewery's and the product's story to buyers and customers [149]. This may be especially important for beer brewed with ancient barley varieties, as their characteristics may need clear communication to consumers. Using direct sales or online commerce can also ensure personal interaction with consumers and easier access to the final product [146]. It might also be beneficial to sell beer brewed with ancient barley varieties as premium products to cover higher production costs. Beer brewed with ancient barley varieties may also extend and diversify a (craft) brewery's existing product portfolio [107]. Mikyška et al. (2022) did not recommend ancient barley varieties for large-scale industrial breweries [104]. Using malt derived exclusively from ancient barley varieties may pose risks for brewers, for instance, insufficient resource availability and lower, more inconsistent malt quality. A brief overview regarding the challenges and opportunities along the whole value chain, when ancient barley varieties are used for malting and brewing, is given in figure 2. It also shows that reintroducing and exploiting ancient barley varieties "must go beyond isolated efforts and must be embedded within broader, cross-sectoral strategies" [6]. Such an approach requires dedicated stakeholders along the whole value chain. It will also require close cooperation with political stakeholders and academia, as well as marketing agencies, to help access, inform, and educate consumers [142]. Developing market infrastructure and networks will be crucial to conserve and valorise ancient barley varieties [36].

One positive example of successful conservation and reutilisation is the Scottish barley landrace Bere, because of its broad versatility. Bere can be used as a raw material for beer brewing, distilling, as well as for flour production [142]. This flour is used to bake beremeal bannocks, a flatbread, bread, and biscuits [28]. Bere flour has significant concentrations of iodine, iron,

magnesium and phosphorus. However, results must be verified with data from different growing sites and vintages [150]. Because Bere has a very high plant height, its straw is often sold as an additional by-product. Intense collaboration and cross-disciplinary activities led to increased interest in Bere and the development of a regional long-term value chain [28]. Alignment and knowledge across disciplines such as agronomy, plant physiology, food science, innovation, marketing, and economics are relevant when reintroducing an ancient barley variety and exploiting its potential in our modern food system. Emphasis should be placed on knowledge transfer among the partners involved [142].

Overall, it can be stated that reducing ancient cereal varieties to a mere gene pool for the enhancement of modern breeding lines is an overly simplistic interpretation of their potential value, because "the loss of these crops is not only a nutritional or ecological issue, but it also represents a gradual erosion of food cultures, farming practices, knowledge systems [...] that have evolved over generations" [6]. Also, Dwivedi et al. (2019) refer to the culinary quality and unique flavour profile associated with ancient varieties and may "represent an important aspect of heritage" [35]. It might also be worth assessing potential alternative applications for ancient barley varieties (fig. 3). For instance, coloured ancient barley varieties could be used as a food colouring agent for bread or pasta, or as a raw material for the extraction of anthocyanins, allomelanin, or β -glucan. But further research is needed to exploit the technological possibilities of extracting anthocyanins, allomelanin or β -glucan from these dark coloured barley varieties. Adding barley flour, by-products from the malting and brewing industry, or extracted β -glucan from ancient barley varieties could be an important opportunity to develop products with an approved health claim. Especially as these varieties are often characterised by a higher β -glucan content compared to modern barley varieties [107]. But further studies are required to see how they might function as a raw material for the baking industry. Additional research is needed to determine whether they have the same composition or even more beneficial ingredients than modern barley varieties. Ancient barley varieties might also be used in the production of

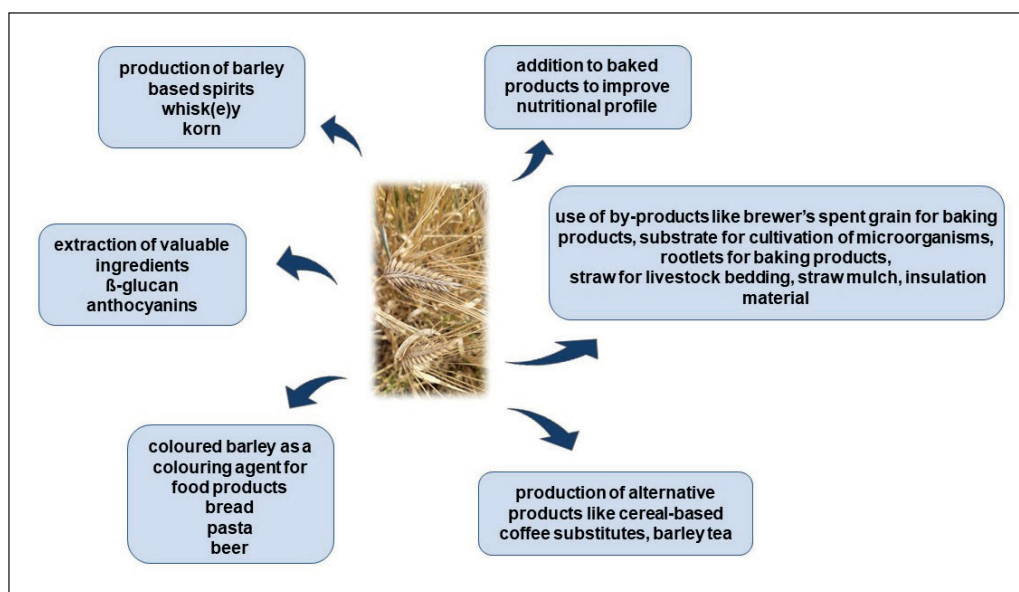


Fig. 3 Alternative applications and areas of use for ancient barley (*Hordeum vulgare* L.) varieties

grain-based spirits like whisk(e)y, as they can easily be marketed as (local) premium products, resulting in higher profit margins, as done with the Scottish ancient barley variety Bere, “especially when a ‘grain to glas’ approach has been adopted [28]. Exploring alternative uses, such as cereal-based coffee alternatives or barley tea, is also an interesting topic for further research. As ancient barley varieties are characterised by greater plant height than modern varieties [36, 104], their straw might be an interesting by-product. It can be used as livestock bedding [28] or as thermal insulation material, where barley straw tends to be more favourable than wheat straw, especially when treated with boric acid to improve mould resistance, too [151]. The application of straw mulch for instance in vineyards, seems to be very effective in reducing soil erodibility and surface runoff [152]. Another option is to valorise by-products like BSG or rootlets from ancient barley varieties as an ingredient in the baking industry for natural product fortification. BSG has been studied as a growth medium for microorganisms like lactic acid bacteria. By selling BSG, brewers could gain an additional source of income, compensating for the higher production costs of brewing with ancient barley varieties. It may also be worth studying whether BSG composition differs and is more valuable than BSG from modern barley varieties, for instance, as ancient barley varieties are often characterised by a higher β -glucan and protein content [104, 107].

However, extensive research is needed to successfully reintroduce and exploit ancient cereal varieties. They might remain only a valuable genetic resource for modern breeding and a raw material for a niche market, but they might also, as Mahon et al. (2016) stated, maintain and enrich local culture [36].

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Conflicts of interest

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CRedit Authorship contribution

Doris Häge: conceptualisation, writing (draft and review), visualisation

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Supplementary materials

Table S1: Summary table key malt quality parameters of ancient vs more recent barley varieties

		Introduction/ registration	Raw protein content (%)	Sorting ^{1st} grade (%)	Friability (%)	Glassiness (%)	Diastatic power (WK)	Total nitrogen of malt (%)	Kolbach index	Sacchari- fication time (min.)
Ancient barley varieties	Proskovcuv hanacky	-	-	76.1 ^[107]	48.1 ^[107]	4.2 ^[107]	205 ^[107]	-	28.6 ^[107]	23 ^[107]
	Chlumecký	1902	14.9 ^[104] 10.7 ^[110]	-	48.8 ^[104] 69 ^[110]	0.5 ^[104] 0.4 ^[110]	306 ^[104]	2.21 ^[104]	39.8 ^[104] 39.3 ^[110]	10 ^[104]
	Stupický staročeský	1919	13.4 ^[104]	-	57.7 ^[104]	0.1 ^[104]	410 ^[104]	1.99 ^[104]	37.4 ^[104]	10 ^[104]
	Opavský Kneifel	1926	14.7 ^[104]	-	46.2 ^[104]	0.3 ^[104]	194 ^[104]	2.22 ^[104]	38.0 ^[104]	10 ^[104]
	Chevalier barley	1880	-	-	-	-	-	-	29.7/31.5 * ^[111]	-
	Plumage	1900	-	-	-	-	-	-	26.6 28.7 * ^[111]	-
	Dregerův Imperial	1900	11.3 ^[110]	-	62 ^[110]	0.6 ^[110]	-	-	39.4 ^[110]	-
	Hanácký Kargyn	1919	11.1 ^[110]	-	73 ^[110]	0.4 ^[110]	-	-	42.4 ^[110]	-
	Bere	-	12.8 ^[108]	-	-	-	247 ^[108]	-	-	-
More recent barley varieties	Barke	1996	10.2 ^[153]	94 ^[153]	91 ^[153]	-	-	-	44.5 ^[153]	-
	Scarlett	1996	10.3 ^[153] 10.9 ^[110]	95 ^[153]	87 ^[153]	0.3 ^[110]	299 ^[110]	-	47.9 ^[153] 41.8 ^[110]	-
	Malz	2002	10.7 ^[110] 10.8 ^[154]	-	85 ^[110]	0.3 ^[110]	272 ^[110] 286.5 ^[154]	50.3 ^[154]	40.7 ^[110] 50.3 ^[154]	-
	Marthe	2006	11.7 ^[110]	-	90 ^[110]	0.2 ^[110]	442 ^[110]	-	47.4 ^[110]	-
	Quench	2006	10.3 ^[110]	-	95 ^[110]	0.2 ^[110]	339 ^[110]	-	45.4 ^[110]	-
	Petrus	2013	12.9 ^[104]	-	80.0 ^[104]	0.0 ^[104]	445 ^[104]	1.91 ^[104]	45.2 ^[104]	10 ^[104]
	Francin	2014	12.0 ^[104]	-	77.1 ^[104]	0.5 ^[104]	356 ^[104]	1.84 ^[104]	41.2 ^[104]	10 ^[104]

* two different growing sites, WK= Windisch-Kolbach, - no data available

Table S2: Summary table of beer quality parameters of ancient vs more recent barley varieties

		Introduction/ registration	Apparent extract (%)	Real extract (%)	Apparent attenuation (%)	Alcohol by volume	pH	Bitterness units (IBU)	Colour (EBC)
Ancient barley varieties	Proskovcuv hanacky	-	3.88 / 3.96 * ^[107]	5.53 / 5.54 * ^[107]	67.4 / 68.9 * ^[107]	4.37 / 4.59 * ^[107]	4.53 / 4.75 * ^[107]	28.4 / 31.5 * ^[107]	11.9 / 13.2 * ^[107]
	Chlumecký	1902	2.83 ^[104]	4.62 ^[104]	76.7 ^[104]	4.95 ^[104]	4.87 ^[104]	28 ^[104]	9.2 ^[104]
	Stupický staročeský	1919	1.99 ^[104]	3.88 ^[104]	83.1 ^[104]	5.20 ^[104]	4.64 ^[104]	28 ^[104]	7.1 ^[104]
	Opavský Kneifel	1926	2.20 ^[104]	3.95 ^[104]	80.4 ^[104]	4.79 ^[104]	4.62 ^[104]	27 ^[104]	7.3 ^[104]
More recent barley varieties	Petrus	2013	1.90 ^[104]	3.97 ^[104]	85.0 ^[104]	5.73 ^[104]	30 ^[104]	30 ^[104]	9.6 ^[104]
	Francin	2014	2.84 ^[104]	4.73 ^[104]	77.5 ^[104]	5.23 ^[104]	30 ^[104]	30 ^[104]	7.8 ^[104]

* two different breweries, - no data available