

Review

Wild and Traditional Barley Genomic Resources as a Tool for Abiotic Stress Tolerance and Biotic Relations

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Abstract: Barley (*Hordeum vulgare* L.) is one of the main crops cultivated all over the world. As for other cereals, throughout the centuries barley was subjected by human breeding to genetic erosion phenomena, which guaranteed improved yields in organized (and then mechanized) agriculture; on the other hand, this selection weakened the ability of barley to survive under adverse environments. Currently, it is clear that climate change requires an urgent availability of crop varieties able to grow under stress conditions, namely limited irrigation, salinity, high temperatures, and other stresses. In this context, an important role could be played by wild relatives and landraces selected by farmers, particularly in specific field areas and/or climatic conditions. In this review, we investigated the origin of barley and the potentialities of wild varieties and landraces in different contexts, and their resilience to abiotic stress. The data obtained from Next Generation Sequencing technologies were examined to highlight the critical aspects of barley evolution and the most important features for abiotic stress tolerance. Furthermore, the potential of appropriate mycorrhiza is discussed under the view of the essential role played by these symbioses in field crops. The abilities of specific barley wild varieties and landraces may represent novel opportunities and suggest innovative strategies for the improvement of abiotic tolerance in crops and particularly in barley.

Keywords: *Hordeum vulgare* ssp. *vulgare*; *Hordeum vulgare* ssp. *spontaneum*; Poaceae; landraces; mycorrhiza; crop adaptation; fungal symbiosis



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1. Introduction

Environmental factors such as drought, salinity, nutrients starvation, and extreme temperatures are critical factors for agricultural production. Therefore, one of the most important challenge for plant researchers is the improvement of crops’ tolerance to stress conditions. [1]. In particular, drought has reduced the yields of most cultivated cereals, and specifically barley; as an example, European barley production has fallen by 3.8% due to temperature increase and rainfall trends in the decade 1989–2009 [2].

The Green Revolution (1940–1960) greatly enhanced agricultural productivity [3]. Crops were selected in order to increase the efficiency of fertilizers and irrigation, defining new strategies for controlling plant pathogens and parasites, thus guaranteeing better and higher yields [4]. On the other side, the massive changes introduced in agricultural techniques have also induced genetic erosion due to the loss of genomic variability [3]. Modern high-performance varieties currently cultivated have been selected for their improved yields under controlled growth conditions of fertilization, pesticides, supply, and irrigation. As consequence, this has caused a loss of genetic diversity with respect to landraces cultivated for centuries by farmers. Traditional landraces acquired a wide genetic diversity during domestication [3], when favorable alleles were selected and fixed [5].

Landraces are generally described as the traditional varieties selected by farmers throughout centuries; these have shown the ability to tolerate environmental changes,

maintaining unaltered yields, thus highlighting specific characteristics that differentiate them from commercial, high-yield varieties selected by private companies and public research centers [3,6–8].

Among major crops, barley is the fourth most cultivated cereal, representing one of the main sources of carbohydrates in developing countries (FAOstat 2019–9), where it represents one of the main resources grown by small farmers in many arid areas [6,9–12].

As shown in Figure 1A, Russia was the major producer of barley in 2018 (almost 2.0×10^7 tons), followed by France, Germany, Australia, and Canada. A trend of the yield increases between 2010 and 2018 can be observed (Figure 1B).

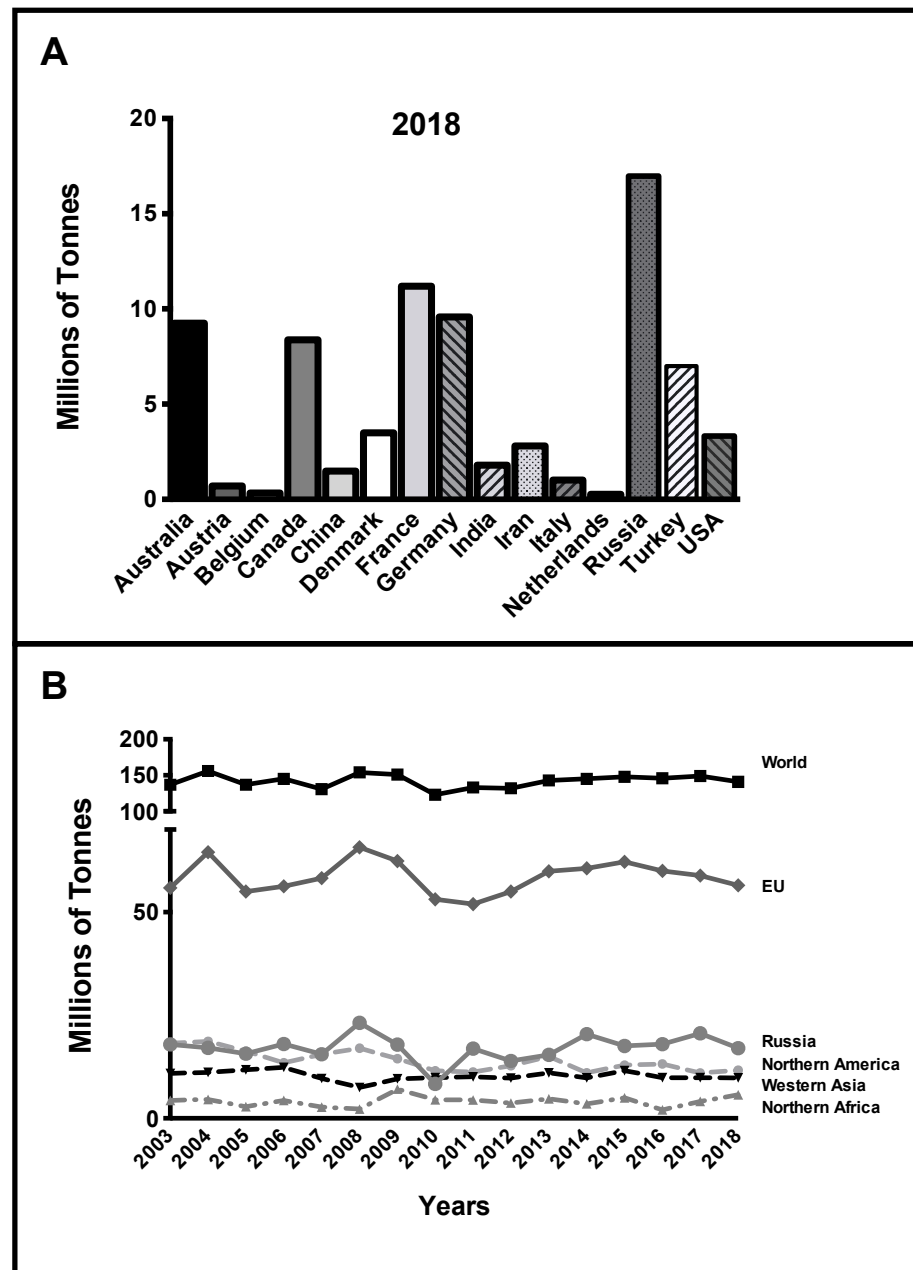


Figure 1. (A) Barley production in different countries in 2018. (B) Evolution of barley production from 2003 to 2018 in different countries and macro-areas. The figure was obtained from data present in the FAO database [6] (<http://www.fao.org/faostat/en/#home>, accessed on 1 November 2021).

Many studies have shown that, even if barley cultivars guarantee a higher yield performance under optimal growth conditions, traditional landraces can exceed selected

genotypes yields up to 20% upon stress conditions [5]. These properties could be due to both their metabolic and biochemical flexibilities and molecular peculiarities [13–15]. It is worth pointing out that the identification of novel alleles, particularly from unexploited genotypes, is a central challenge for researchers, in order to improve crop productivity in vulnerable environments, thus possibly providing new tools to increase crop yields [16].

The focus of this review is to provide an analysis of traditional barley landraces, ecotypes, and wild relatives properties under abiotic stress. Genomic, transcriptomic, biochemical, and physiological resources will be investigated, also keeping in mind the geographical and evolutionary origin of genus *Hordeum*. Furthermore, the perspective of the use of appropriate mycorrhiza in order to improve yields and stress resilience will be examined.

2. Barley: Origin, Geographic Evolution, and Relation with Wild Relatives

Barley is one of the oldest domesticated cereals, possibly the first crop cultivated by humankind [17,18]. This cereal is cultivated from the Arctic Circle to equatorial latitudes; therefore, barley's ability to grow in stressful environments will increase its importance in the coming years.

The history of barley domestication started in the Fertile Crescent, at least 10,000 years ago, selecting the current cultivated crop from a wild progenitor, *Hordeum vulgare* L. ssp. *spontaneum* [19,20].

The genus *Hordeum* comprises about 30 species both perennial and annual, distributed all over the world [21].

The genus is characterized by one-flowered spikelets, borne three together on each rachis. It should be noted that the two lateral spikelets are generally sterile in wild species; another property on *Hordeum* genus is the presence of a reduced glume on the dorsal side of spikelets.

Barley genome is about 5.1 Gb, showing abundance of repetitive elements [22]. Different authors reported genetic erosion processes, by comparing wild and domesticated barleys, thus highlighting a severe reduction (about 50%) of diversity [23,24]. Probably, this condition derived by reduced allelic re-assortment during meiosis and restricted recombination in the pericentromeric regions, possibly caused by an intensive and stringent selection by breeders [25].

A principal-components analysis (PCA) recently made partitioned 228 accessions into two distinct groups, representing 91 wild varieties (*Hordeum vulgare* ssp. *spontaneum*) and 137 landraces (*Hordeum vulgare* ssp. *vulgare*) [26]. Genome-wide analysis indicated that rare SNPs variants were more common in wild varieties, carrying on average over 5000 private alleles, while domesticated landraces showed less than 430 private alleles. Therefore, this large genetic variation observed in wild barley could represent a promising genetic pool to be studied and utilized for crop improvement in the next decades. Landraces, and possibly all cultivated, selected genotypes, exhibited a very low variation in private alleles, in order to obtain higher yields in farmer-assisted cultivated fields. On the other hand, domestication obviously resulted in a loss of diversity, as a consequence, further improvement of these varieties with respect to wild relatives is limited [26].

A number of barley varieties (both wild and selected) genomes have been recently sequenced. It is worth noting that a 4.28 Gb genome has been indicated for the wild barley WB1 (*Hordeum vulgare* ssp. *spontaneum*) [27], and a 3.89 Gb genome for the Tibetan barley "qingke" [28].

Hordeum vulgare ssp. *spontaneum* group exhibited a genetic diversity largely related to geographic distribution. This can be observed by ordering different samples along the Fertile Crescent and connecting these with accessions from Central Asia. The geographic correlation is more pronounced in *Hordeum vulgare* ssp. *vulgare* [26].

Barley landraces can be divided in two groups, distinguished by structure of inflorescence, containing two or six rows of grains, respectively. This feature has been recently used to define cultivated barley as two species, *Hordeum distichum* L. and *Hordeum hexastichum*

L., obviously descending from *H. vulgare* ssp. *spontaneum* (originally presenting two-rows of grains). Interestingly, these changes occurred during—or soon after—domestication, when mutations arose in a single gene, SIX-ROWED SPIKE 1 (*HvVRS1*) [29].

The critical sweeps characterizing two key loci namely *nonbrittle rachis 1* and 2 (*Btr-1*, *Btr-2*) have been analyzed and multiple novel candidate genes for domestication were identified [30]. Among these, interesting candidates are involved in light signaling regulation, circadian clock, and carbohydrate metabolism. It is worth noting that modifications in genes related to circadian clock are common during the breeding and selection of modern crops, thus suggesting a convergent evolution during domestication. Examples are *EID1* (an F-box protein functioning as a negative regulator of phytochrome-A in tomato (*Solanum lycopersicum*)); or SUPPRESSOR of PHYTOCHROME A (*SPA*) and *CUL4* in *Arabidopsis thaliana*, which are all components of the E3 ubiquitin ligase COP1-CUL4-SPA complex, the main regulator of photomorphogenesis in higher plants [30–32].

Genomic and geographic analyses delineated the occurrence of three different clusters in the genetic pool of wild barley: (i) Levant and Southern Turkey cluster, (ii) Southeastern Turkey cluster, and (iii) Eastern and Middle Asian cluster. Among these, the Levant cluster showed the highest diversity in wild *Hordeum vulgare* ssp. *spontaneum* gene pool [18]. Also, genomic analysis of wild barley accessions revealed the presence of 57.8 single nucleotide variants (SNVs) unique in these genotypes. This evidence suggested a huge loss of genetic diversity when comparing modern vs. wild barleys. These results also confirm that wild barley has a larger gene pool than cultivated varieties, thus indicating that many genetic resources for barley improvement are present and still unexploited [26,27]. Moreover, a genotyping approach on accessions from Anatolia identified further loci involved in the adaptation of barley to adverse environments: a calmodulin like protein (CML), a member of the heat shock protein 40 kDa (HSP40), an adenine nucleotide alpha hydrolases-like protein, and the transcriptional co-repressor SEUSS [20]. Beneficial effects by these alleles were proposed for flooding tolerance, leaf senescence, and scavenging of reactive oxygen species [20].

Possibly, modern barley originated in the Near East Fertile Crescent, which is commonly recognized as a major evolutionary center for this crop [19,33], but a theory for a mosaic origin of barley genome has been recently proposed [24]. Several authors recognized Tibet as a secondary but crucial center of diversification for the modern barley [24,34].

Particularly, the annual barley (*Hordeum vulgare* L.) of the Qinghai-Tibet plateau is considered one of the ancestors of cultivated barley [35]. It has been recently reported the transcript sequencing of 9 *Hordeum vulgare* ssp. *vulgare* and 12 *H. Hordeum vulgare* ssp. *spontaneum* genotypes, thus identifying 8177 and 7913 SNVs from Near East barleys and Tibetan barleys, respectively. The authors proposed a Fertile Crescent derivation for chromosomes 1 H, 2 H, and 3 H and a Tibet origin for chromosomes 4 H, 5 H, 6 H, and 7 H. This hypothesis was reinforced by the genomic characterization of the six-rowed wild barley *Hordeum agriocrithon* Åberg [36].

Zeng et al. [37] refused this hypothesis, by sequencing 177 barley genomes, prevalently from Tibet. They suggested a phylogenetic origin from eastern domesticated barley, refusing a parental role for Tibetan barley. To support their thesis, the authors analyzed five genes involved in key traits of domestication, namely *btr1–2*, *sixrowed spike* (*vrs1* and *int-c*), and *naked caryopsis* (*nud*). Tibetan barley showed a sharing of these haplotypes with modern barley genotypes, thus sustaining the hypothesis that barley domestication has originally occurred in the Fertile Crescent [33,37]. Despite of a possible ambiguous relationship between cultivated and Tibetan barleys, genome sequencing clearly indicated a specific and useful adaptation to environmental stress by Eastern barleys. Particularly, these varieties have been predicted to show enhanced phenylpropanoid and flavonoid biosynthesis, essential for the accumulation of sunscreen molecules protecting against ultraviolet radiation, and for plant hormone signal transduction [28].

Therefore, peculiar characteristics from different geographic origins could be investigated and analyzed to identify particular genes and traits by conventional and specific -omics approaches.

Table 1 shows different genotypes, both landraces and wild relatives, described as tolerant to environmental perturbations, by physiological and/or molecular adaptations.

Table 1. List of abiotic stress tolerant genotypes discussed in this review.

Genotypes Name	Germplams Type	Geographic Origin	Abiotic Stress Relation	Physiological and/or Molecular Peculiarity	References
<i>Arta</i>	Landrace	Syria	Drought and Heat tolerant	Reduced impact of drought to photosynthesis; reduced proteomic effects upon drought; reduced effects of heat on plant growth	[38]
<i>B1K2</i>	Wild barley ecotype	Israel	Drought tolerant	Higher RWC; improved WUE	[39]
<i>B1K30</i>	Wild barley ecotype	Israel	Drought tolerant	Reduced water loss and transpiration	[39]
<i>Batini</i>	Landrace	Oman	Abiotic stress tolerant	Enhanced protein folding regulation	[15]
<i>L118</i>	Double haploid line	Tibet	Low phosphorus tolerant	Increased shoot DW and root length upon low P condition	[40]
<i>L130</i>	Double haploid line	Tibet	Low phosphorus tolerant	Increased shoot DW and root length upon low P condition	[40]
<i>L138</i>	Double haploid line	Tibet	Low phosphorus tolerant	Increased shoot DW and root length upon low P condition	[40]
<i>SBCC073</i>	Landrace derived inbred	Spain	Drought and Heat tolerant	Improved regulation of secondary metabolism	[41]
<i>Himalaya 10</i>	Inbred line	Tibet	Drought tolerant	Increased accumulation of hormones of ABA; efficient ROS detoxification	[42]
<i>XZ147</i>	Wild barley ecotype	Tibet	Drought tolerant	Improved regulation of hormones and H ₂ O ₂ homeostasis	[43]
<i>XZ149</i>	Wild barley ecotype	Tibet	Low nitrogen tolerant	Less reduced shoot DW and increased root DW upon N deprivation; enhanced molecular regulation of N transporter and hormone biosynthesis-related genes	[44]
<i>XZ16</i>	Wild barley ecotype	Tibet	Salt and Aluminum tolerant	Improved regulation of ions transport and location	[45]
<i>XZ166</i>	Wild barley ecotype	Tibet	Salt tolerant	Presence of specific allele of HvCBL8 (calcium-sensor calcineurin B-like)	[46]
<i>XZ26</i>	Wild barley ecotype	Tibet	Low phosphorus tolerant	Increased plasticity of root system	[40]
<i>XZ29</i>	Wild barley ecotype	Tibet	Aluminum tolerant	Increased accumulation of hormones (ABA, ethylene)	[47]
<i>XZ5</i>	Wild barley ecotype	Tibet	Drought and aluminum tolerant	Increased accumulation of hormones (ABA, ethylene); improved molecular regulation of cell wall modification, antioxidant process, and root hair development; increased shoot dry weight, photosynthesis rate, and WUE upon drought	[45,47,48]
<i>Z772</i>	Accession	Tibet	Drought tolerant	Enhanced molecular regulation of protein folding complexes, photosynthetic complex, and wax biosynthesis	[49]

Abbreviations: ABA = Abscissic acid; DW = Dry weight; RWC = Relative water content; SA = Salicylic acid; WUE = Water use efficiency.

3. Omics Approach of Barley Genotypes Identified Peculiar Genes Involved in Abiotic Stress Tolerance

Traditional agricultural practices and modern breeding programs originated over 800 landraces and over than 100 QTLs associated with stress-sensitive traits [39,50–52]. These elite barley cultivars reported limited genetic variability when compared to wild progenitors, thus indicating the wild varieties and traditional landraces as a primary—and still unexplored—source of genes for genetic improvement [27,53,54].

Different wild barley genotypes exhibited interesting potential to improve drought tolerance [39,50,51]. Bedada et al. [39] identified genes expressed under drought conditions, studying two wild barley varieties from a collection of *Hordeum vulgare* ssp. *spontaneum* ecotypes [55]. In particular, B1K2 and B1K30 (from Negev Desert and Mediterranean area, respectively) showed 839 and 881 transcripts related to drought stress. The most abundant stress-related gene families were zinc-finger proteins (185 in B1K2; 241 in B1K30), ABC transporters (104 in B1K2; 93 in B1K30), and heat shock proteins (HSPs) (61 in B1K2; and 63 in B1K30).

In barley, changes in HSPs following growth and stress conditions, and the occurrence associated to different genotypes has been described over 30 years ago [56]. Accordingly, peculiar roles of HSP70 proteins have recently been analyzed in tolerant landraces, such as Batinì from MENA region, demonstrating a rapid up-regulation under drought stress and salinity [14].

The genomic resources from Tibetan barley varieties and other genotypes could represent a useful resource to design new breeding strategies to counteract environmental stress, increase tolerance against pathogens, and improve grain qualities. Recently, genes identified in Tibetan genotypes of *Hordeum vulgare* ssp. *spontaneum* have been used for biotechnology approaches. *HsCBL8* (calcium-sensor calcineurin B-like) and *HsCIPKs* (CBL-interacting protein kinase) were overexpressed in rice, contributing to an improved tolerance to salinity [46].

Southern Asia represents one of the environments for barley diversification, producing a number of typical ecotypes in geographic areas such as China or Tibet [35,37]. Particularly, the Qinghai-Tibetan region offered the perfect background to develop landraces tolerant to different adverse conditions [43]. Accessions reported to be tolerant upon abiotic stress included XZ5, XZ147, XL, and Z772 for drought [43,45,48,49,57]; XZ166 for salinity [46]; X16 and XZ29 for aluminum [45,47]; and XZ149 for low nitrogen [44].

Tibetan varieties analyzed upon drought using -omics approaches were Z772, XL, XZ5, and Himalaya 10 [42,47,49,57]. These genotypes were analyzed using three different experimental strategies to induce stress: (i) dry dishes; (ii) hydroponic culture using PEG; (iii) irrigation deprivation in greenhouse. These studies identified comprehensive catalogues of candidate genes able to improve drought tolerance. Tibetan barley Z772 after 1 h and 5 h of dehydration stress, showed 5439 and 7203 up-regulated genes, respectively; the number of down-regulated genes was 1143 after 1 h and 1662 after 5 h. The XL genotype showed \approx 550 up-regulated and about 350 down-regulated different abundant proteins (DAP) after both 4 and 8 h. In the cultivar Himalaya 10 the gene expression pattern of 853 potential drought-resistant-related genes clustered into nine clusters. Furthermore, Z772 was compared with the drought sensitive genotype Z013 [49]. Both showed among the best-expressed genes several LEA proteins (Late Embryogenesis Abundant) such as HVU0335383.1, HVU037049, HVU005858.3, HVU032486.1, and HVU037051. Moreover, common mechanisms in both drought-sensible and -tolerant genotypes were identified in phosphatidylinositol signaling and in the regulation of chlorophyll synthesis and photosynthetic antenna proteins; other up-regulated factors of drought stress response are trehalose 6-phosphate synthase/phosphatase, delta-1-pyrroline-5-carboxylate synthase (P5CS), heat shock protein 70 kDa (HSP70), and protein phosphatase 2C (PP2C) [49].

Regulations of enzymes involved in the avoiding of water loss were also reported for Tibetan genotypes subjected to salinity and nitrogen starvation [58,59]. Particularly, wax biosynthesis was a major process regulated in Z772 after a short-term drought.

Cuticle wax and cell wall play an important role in the survival of plants, creating an interface between plants and biotic/abiotic environmental stress response [60,61]. CER1 (Very -long-chain aldehyde decarbonylase) and FAR (fatty acyl-CoA reductase) were quickly up regulated, thus highlighting the importance of an increased wax biosynthesis, in order to protect plant from an excessive water loss, particularly through non-stomatal processes. CER1 encodes for the major enzyme synthesizing long-chain alkanes; it plays a crucial role in wheat wax alkane biosynthesis under drought and other stresses [62]. *Arabidopsis* plants overexpressing CER1 showed a reduced cuticle permeability together with a minor water deficit susceptibility and an increased tolerance to osmotic stress [63]. Similarly, the expression of FAR genes is induced by drought, cold, and ABA treatments, increasing the cuticular wax accumulation in *Brachypodium distachyon* and wheat [61,64].

Different results have been obtained in XL genotypes where drought induced changes in the regulation of ethylene, salicylic acid, and abscisic acid [57]. Conversely, similar analysis in the drought-sensitive cultivar DQ showed an increase of osmotic stress sensors and leaf senescence-related genes. These differences could be caused by the different response of hormone-related genes, particularly for ethylene [57]. In addition, XL genotypes showed an efficient regulation of genes involved in ROS response. The expression of ascorbate peroxidase, glutathione peroxidase, and peroxyredoxins increased during the short-term drought response, suggesting an efficient detoxification mechanism in XL genotype [57].

Comparison between drought-tolerant and -sensitive genotypes were reported using the XZ5 and XZ54 genotypes [57]. This analysis identified 36 genes that were differentially up-regulated or unchanged in XZ5 and showing a decreased expression in XZ54 upon drought. These genes were related to cell wall modification, antioxidant process, and root hair development. In this regard, the authors identified a novel β -expansin gene (*HvEXPB7*), showing a critical role in root hair growth, conferring an increased drought stress tolerance [57].

Phenotyping and genotyping approaches on a collection of Mediterranean barley landraces identified QTLs able to contribute drought and heat stresses tolerance in these genotypes [65,66]. These landraces showed an efficient attenuation of leaf carbon metabolism under drought when compared with German genotypes [41,67]. Similarly, a sequencing approach on 135 barley landraces from Spain identified 9920 bi-allelic markers. These SNPs can be associated with agro-climatic parameters, thus identifying candidate genotypes adapted to cold-stress and water availability [67].

Furthermore, a comparison between Spanish barley landrace SBCC07 and German selected cultivar Scarlett (sensitive to water stress) identified genotypic and transcriptomic differences in different metabolic pathways in plants subjected to severe and prolonged water deficit, thus suggesting the evolution of different strategies to counteract environmental stresses in elite cultivar and landraces [41]. Particularly, SBCC07 showed the peculiar regulation of phenylalanine metabolism, glycine-betaine biosynthesis, ferulate, and sinapate biosynthetic pathways, while common drought-regulated mechanisms were observed, including starch phosphorylation, chorismate biosynthesis, ascorbate biosynthesis, and metabolism of spermidine [41].

Barley resistance to abiotic stress in different varieties, landraces, and wild relatives have important fallout on yields and quality of seed grains.

The most important utilization of barley harvested in Europe and North America is the utilization as substrate for malting process [68–70] and brewing, a thousand-years-old practice which has played a crucial role in human societies [71]. A metabolomic approach was made on cultivated genotypes and Tibetan barley accessions, in order to examine how the genomic differences and the drought response can affect malting quality [72]. Intriguingly, Tibetan accessions showed higher levels of sugars (e.g., fructose) and organic acids (e.g., malic acid) compared to cultivated genotypes, upon both control conditions and drought stress. Under water deprivation, the wild Tibetan barley showed an increased β -amylase expression and enzymatic activity.

Definitely, these results demonstrate the potential of barley landraces to improve malting quality in adverse environments.

4. Physiological Adaptation of Barleys upon Abiotic Stresses

Wild barley (*Hordeum vulgare* ssp. *spontaneum* L.) has a large geographical distribution, ranging from deserts to highlands [19]. This results in a wide environmental stress exposition, such as drought, high temperature, and soil salinity. The correlation between genetic and environmental variation vs. distribution suggests a local adaptation along micro- and macro-environmental gradients [39,73]. Among the traits characterizing the tolerance of barley to drought, leaf water content [74], osmotic potential, and full turgor [74,75], concentration of water-soluble carbohydrates [75] and chlorophyll parameters (e.g., fluorescence) [76] are the most evident. These characteristics are correlated with morphological characteristics such as germination, flowering time, plant height and tillering, root growth, and grain yield. Furthermore, differences between the ecotypes of desert and Mediterranean wild barleys were observed, suggesting the adaptation to specific environmental conditions [40,55,77].

High genomic variations were observed in five cultivated and wild barley cultivars from Barley1K collection, almost twice as much genetic variation in nature as cultivated barley [78]. This suggests that many untapped, and potentially useful, genetic variations are separated in wild barley [41,79]. Bedada et al. [39] have selected B1K2 and B1K30 from the B1K4 collection based on their response to drought. They observed perspiration, weight gain and weight loss, water efficiency (WUE), and relative leaf content (RWC) in greenhouse-grown plants, under natural light and semi-controlled humidity. Unexpectedly, the desert ecotype lost more water than the Mediterranean cultivar upon both well-watered conditions and drought (reduced volumetric water content to 30%). Despite its higher transpiration, the desert cultivar maintained a higher RWC than the Mediterranean ecotype in dry conditions. In addition, the ratio of cumulative weight gain on plant transpiration revealed that the desert ecotype has a higher WUE than the Mediterranean ecotype, with the WUE calculated as the ratio between RWC and transpiration rate [39].

Cantalapiedra et al. [41] determined—on two Scarlett cultivars and a Spanish landrace (SBCC073)—changes in physiological properties in both greenhouse and growth chamber, by imposing water stress after the beginning of stem lengthening. The authors analyzed parameters such as leaf water potential (LWP), stomatal conductance, and relative water content (RWC). LWP was proportional to different water regimes with drought-prone plants showing a higher LWP than those that were well irrigated. The highest absolute value corresponded to Scarlett's plants upon drought, while SBCC073 plants were comparable to Scarlett exposed to heat and drought stress. RWC was lower in drought-stressed plants of both genotypes, but mild heat conditions showed similar values for SBCC073 control and treated plants, and drought-exposed Scarlett variety [41].

Rollins et al. [38] reported a case study for the Syrian landrace Arta and the Australian variety Keel upon drought, heat, and combined stresses. These treatments caused significantly stronger senescence of lower leaves in Arta than in Keel. Moreover, drought had a stronger effect on morphology than physiological traits. Water regime induced a 26% grain yield (GY) change, a 57% biomass increase, and 79% of the peak number variation (SN), while it caused only 18% of the relative water content (RWC) and less than 1% of the photosynthetic performance index (PI). In contrast, heat treatment had stronger effects than drought, thus explaining a 54% variation in water use effectiveness (WUE), 34% in RWC, and 74% in PI. In contrast, heat treatment had minor effects on plant growth, causing a slight 8% change in biomass and 2% in plant height [79].

More evident changes were observed under combined treatments, particularly a strong reduction in GY. GY was significantly lower in Keel than Arta under separate stress, while significant decreases in GY were not significantly different under either drought or heat [38].

5. Mycorrhizal Symbiosis in Cereals: Perspectives for Improving Barley Yields

Arbuscular mycorrhizal fungi (AMF) represent the most widespread form of symbiosis present in terrestrial environments, associated to the majority of land plants [80]. AMF strongly influence diversity and productivity of both forests and agricultural fields, playing a central role in nutrient cycles (e.g., phosphorus, K), and showing evident impacts on microbial populations, also protecting plants from pathogens' attack, even affecting soil texture and composition [81,82]. Roughly 90% of plant species spontaneously associate with mycorrhizal fungi, and these symbioses are present in 79% of monocotyledons, including most cereal crops [80,83].

Endosymbiosis with mycorrhizal fungi requires hundreds of plant genes, involved in many signaling pathways, including stress response [84]. It has been suggested that land plant ancestors were pre-adapted to mycorrhizal symbioses: several components of signaling involved in symbiosis have been identified in the genome of green algae [85]. On the other hand, it has been recently proposed that fungal symbioses originated from the selective loss/shift of genes involved in the secretion of cell wall hydrolytic enzymes, in order to allow the access of microorganisms in the plant tissues [86].

In cereals, a genotype-dependent variation of mycorrhization levels has been reported, indicating that older wheat varieties (before 1950) show a higher root colonization degree when compared to varieties selected after 1950. Similarly, the oldest barley varieties (i.e., Nürnberg, 1831) present a deeper AM colonization with respect to more recent genotypes (i.e., Xanadu, 2003) [87].

Mycorrhizal symbioses in the roots of cereals have been thoroughly investigated and reviewed [88]. Furthermore, modern selected varieties lost part of those genes involved in symbioses with opportunistic AM strains, due to standard cultivation practices. This results in a loss of benefits deriving by mutualistic symbioses under not-controlled growth conditions, such as stress [89].

Many points are still obscure, e.g., the effects of phytohormones on the establishment of AM symbioses. It should be underlined that if the involvement of strigolactones/karrikins signaling during the establishment of AM is predictable [88], the effects of auxins [90] and gibberellins signaling and transduction on the type and degree of AM symbiosis requires further investigations [91]. These studies clearly connect the establishing of these symbioses with stress conditions, which could severely affect the colonization by specific mycorrhizal strains. Recently, wheat (*Triticum aestivum* ssp. *vulgare*) and spelt (*Triticum aestivum* var. *spelta*) have been studied under drought to establish changes in roots–fungi association [92]. It has been shown that changes occur in the composition of fungal communities in both endosphere and rhizosphere. Interestingly, it has been proven that over 117 fungal strains, representing 22 genera, are able to colonize *T. aestivum* ssp. *spelta* L. and *T. aestivum* ssp. *vulgare* L. [92].

Intriguingly, in wheat the composition of the mycobiome depends on root tissue and soil preparation, but it looks barely dependent on irrigation and/or drought [92]. In contrast, a recent study in *Oryza sativa* varieties demonstrates that drought tolerance is determinant for fungal colonization and endophytic mycobiota in rice [93]. Therefore, different parameters can influence the association and determine modifications in the growth and productivity of cereals.

The majority of fungal strains were detected in the rhizosphere (63 strains), while in the endosphere 54 strains were observed. It should be underlined an almost identical diversity among endophytic fungi; (25 vs. 27 strains). At the same time, one third of fungal species were detected in both endosphere and rhizosphere. Another point is that AM colonizing spelt are substantially identical to those known for wheat. This would suggest that the variability of fungal communities in different cereals would depend on soil composition more than specie-specific parameters. Particularly, *Trichoderma* strains exerted positive effects by ameliorating a number of physiologic and biochemical parameters and increasing the resistance vs. fungal pathogens, such as *Botrytis cinerea*, *Fusarium* spp., *Pythium*, and many others [93].

Thus, it could be argued that the age of the variety could affect AM protection against pathogens, and thus AMF colonization in plant roots causes bioprotective effects against soil fungal pathogens [94,95]. It has been reported that root colonization by AMF reduced root lesions caused by *Gaeumannomyces graminis* var. *tritici* in both wheat and barley [96].

Particularly, the protection in AM-colonized roots is more evident in some barley genotypes, but not in others. This protection against pathogens can be observed only over a critical level of AM root colonization. Furthermore, it looks like this protective effect varies between oldest and modern barley varieties [87].

Therefore, the use of mycorrhizal fungi in agricultural fields, and particularly in cereal crops, can reduce the use of agrochemicals, because AMF symbioses protect the roots against pathogens. In the long term, their use can reduce the cultivation charges both in developing and industrialized countries. In addition, mycorrhized plants are often more competitive and tolerant to environmental stress than not-mycorrhized plants [85].

A further important point is that the colonization of cereal roots by specific fungi is able to protect, or avoid, the infection from specific fungal pathogens, such as *Gaeumannomyces graminis* and different *Fusarium* species (*F. avenaceum*, *F. culmorum*, *F. graminearum*, *F. oxysporum*, and *F. poae*) [93].

As confirmed, the ancient barley landrace Nürnberg after AM root colonization showed a protective effect in lesioned roots, and an ameliorated fresh weight (FW), suggesting an enhanced bioprotection caused by AMF; in the modern variety Xanadu, only the root FW was positively affected by AM colonization [87].

Investigations of wild barley for reaction to different pests revealed extensive genetic variation as well in specie-specific as partial resistance. One exception is the *mlo* genes (Mildew Resistance Locus) in barley [97]. The Mlo resistance to powdery mildew (caused by the fungal pathogen *Erysiphe graminis* f. sp. *hordei*) derived from a spontaneously occurring *mlo* gene present in Ethiopian landrace barleys. MLO proteins have been identified as general mechanical-response proteins in plants [98,99]. Extensive studies on mutagen-induced Mlo resistance have paved the way for the present extensive use of Mlo resistance in barley breeding and production in Europe. It has been suggested that MLO1 gene was required for colonization by arbuscular mycorrhiza in cereals and other plants [100]. This hypothesis has been recently confirmed by demonstrating that orthologous of MLO1 are present only in those plants able to host vesicular arbuscular mycorrhiza (VAM) [84,99]. Correspondingly, MLO increase was observed during powdery mildew penetration [100] and the specificity of MLO1 in barley and wheat during plant–fungal interaction has been demonstrated [101].

In barley, the role of MLO1 gene was investigated using a polyphasic approach [101]; this study was based on phylogenetic analysis, mutant phenotypes, and gene expression revealing that MLO1 is required for well-timed and/or full-activation of early colonization by mycorrhiza, thus suggesting a conserved role for MLO1 in cereals, and particularly in barley. Moreover, MLOs act redundantly, with multiple MLOs playing different roles based on cell type and developmental stage. These results require further investigation about the role of MLO in mycorrhizal symbiotic interactions of land plants, in order to gain important information for sustainable agriculture [73,102].

These results underline the requirement of further studies on barley–fungi relationships, due to the evident influence that these associations can exert on growth, productivity and pathogen resistance.

6. Conclusions

The identification and integration of those traits responsible for significant improvements in abiotic stress tolerance, biotic association, and commercial application (e.g., malting) represent a significant challenge for barley. The results here reviewed suggest that valuable resources are yet to be explored to identify stress-responsive genes and proteins, highlighting the regulatory mechanisms of barley wild relatives and landraces from different regions of the world. A precious number of genes, physiological aspects, genotypes, and

genomic traits has been released, thus providing new chances to understand the molecular basis of abiotic stress tolerance in barley, and possibly translate this knowledge to other cereal species as well. A further step of this research is the investigation of the interaction of landraces and varieties with specific strains of fungi able to establish AMF symbioses to reduce pathogen susceptibility of barley crops, decreasing the use of pesticides and increasing yields.

The data reviewed support the idea of landraces as a central—and still unexploited—resource to improve currently cultivated varieties through both conventional and unconventional approaches; at the same time, geographical and historical origin dissection of wild relatives and landraces could show the intrinsic and ancient ability of barley to tolerate adverse environments and complex stress conditions.

Finally, climatic change, and the possibility of more stressful environments, highlights the importance of further investigation about wild relatives, old genotypes, and local varieties, in order to improve barley quality and yields worldwide.

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