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Barley with improved drought tolerance: Challenges and perspectives

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ABSTRACT

There is a pressing need to improve climate-resilient crops as a consequence of increasingly erratic climatic behavior that threatens global food security. Current scientific efforts aim to elucidate the complex mechanisms behind drought resistance in cultivated barley (*Hordeum vulgare* L ssp. *vulgare*). To develop new cultivars with enhanced tolerance to drought and ensure the well-being of the crop under adverse conditions. Understanding the impact of water stress on barley plants is a complex challenge due to the involvement of redundant regulatory pathways governed by multiple genes. Many of these pathways and associated major or genes controlling various morphological and physiological responses to drought at various stages of plant growth. Hence, a broad understanding of such molecular regulation is a key to developing barley cultivars with superior drought tolerance. In addition, changing breeding procedures to accommodate screening for drought responses is a major step. Justification of such changes should be based on expected outcomes. Our current understanding of drought

Abbreviations: ROS, reactive oxygen species; QTL, quantitative trait locus; N, nitrogen; P, phosphorus; K^+, potassium; Cl^-, chloride; WD, water deficit; ABA, abscisic acid; RWC, relative water content; OA, osmotic adjustment; RuBP, ribulose-1,5-bisphosphate; ATP, adenosine triphosphate; PEPcase, phosphoenolpyruvate carboxylase; FBPase, fructose-1,6-bisphosphatase; Pi, inorganic phosphate; PSII, subunit of photosystem II; H_2O_2, peroxide; O_2, superoxide; OH^{-1}, hydroxyl; O_2^-, singlet oxygen; MDA, malondialdehyde; POD, peroxidase; SOD, superoxide dismutase; CAT, catalase; APX, ascorbate peroxidase; MDHAR, monodehydroascorbate reductase; DHAR, dehydroascorbate reductase; GSH, glutathione; GSSG, oxidized glutathione; ASA, ascorbate; GA, gibberellin; RILs, Recombinant inbred lines; KW, kernel weight; CKs, cytokinins; NADPH, nicotinamide adenine dinucleotide phosphate; CO_2, carbon dioxide; P5CR, pyrroline-5-carboxylate reductase; P5CS, pyrroline-5-carboxylate synthetase; TFs, transcription factors; DREB/CBF, dehydration-responsive element-binding protein/C-repeat binding factor; SPL3, SQUAMOSA Promoter-Binding Protein-like 3; *pp2A*, *PROTEIN PHOSPHATASE 2A*; miRNA, MicroRNAs; *HD-Zip III*, class-III homeodomain-leucine zipper; TILLING, targeting Induced Local Lesions in Genomes; FBL21, F-box protein; *ACO1*, *1-aminocyclopropane-1-carboxylate oxidase*; PYL5, abscisic acid receptor; DHN, dehydrin; LEA, late embryogenesis abundant; ERF062, ethylene-responsive transcription factor; ETR, electron transport at photosystem II; *pmr1*, *premature ripe mutant*; *Eam1*, *early maturity 1 or photoperiod response gene H1 (Ppd-H1)*; *Eam6*, *early maturity 6 gene*; *eps2S*, *earliness per se 2S*; *mat-c*, *praematurum-c*; *HvCEN*, *Hordeum vulgare CENTRORADIALIS*; *Sgh2*, *Spring growth habit 2 or vernalization H1 (Vrn-H1) locus*; *HvPhyC-e*, *Hordeum vulgare phytochrome C with an early allele*; *sls1*, *small lateral spikelets 1 gene*; *flo-a*, *floret-a gene*; *trp1*, *triple awn 1 gene*; GWAS, genome-wide association study; *sdw1*, *Semidwarf 1*; CID, carbon isotope discrimination; CDPKs, calcium-dependent protein kinases; mQTL, metabolic QTL; BOPA, barley Oligonucleotide Pool Assays; NGS, next-generation sequencing technologies; GBS, genotyping-by-sequencing; MAS, marker-assisted selection; GxE, genotype x environment; GS, genomic selection; GM, genomic mating; RNAi, RNA interference; VIGS, viral-induced gene silencing; TALENs, Activator-Like Effector Nucleases; CRISPR/Cas, clustered regularly interspaced short palindromic repeats; PGPM, promoting microorganisms; IAA, indole-3-acetic acid; ACC, aminocyclopropane-1-carboxylic acid; EPS, exopolysaccharides.

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regulatory pathways points out that improvement at both water extraction and its utilization are needed to elevate final yields under water deficit conditions. The current review is an in-depth review, that aims to develop a complete picture of the drought tolerance mechanisms in barley and to provide insights into the manipulation of drought stress responses in barley.

1. Introduction

Drought is a prolonged dry phase in the natural climate cycle that can happen anywhere in the world (Kishor et al., 2014). It is a slow-onset disaster characterized by the lack of precipitation, resulting in a water deficit for plant growth. Drought can have a serious impact on human health and agriculture. Droughts are estimated to affect 55 million people worldwide every year, which are the biggest threats to livestock and crops globally (C2ES, 2021). Water scarcity affects about 40% of the world's population. By 2030, around 700 million people may be displaced from their homes due to droughts (C2ES, 2021). Increasing temperatures make already dry areas drier and wet areas wetter (https://www.who.int). In 2012, droughts struck several major breadbasket regions concurrently, thereby causing food prices to rise (NWS, 2021). The spike in food prices can cause social unrest, famine, or migration in countries already facing a food insecurity (C2ES, 2021; NWS, 2021). Many parts of the world suffer from low levels of soil moisture, which limits plant growth and development (Fig. 1). Despite drought being difficult to predict, proactive measures can mitigate its effects. Drought tolerance can be defined as a plant's ability to extract water from the environment, retain that water, and utilize in processes to convert light energy into chemical energy. Drought tolerance also enhances a plant's ability to capture and convert light energy into chemical energy, utilize chemical energy to sythesize plant tissues, in developing reproductive organs. Genetic improvement of drought tolerance in crop plants is one of the most cost-effective and sustainable solutions to increase crop productivity and yield stability. Unfortunately, tolerance to drought stress is a complex phenomenon regulated by many genes, making it one of the most difficult traits to study, characterize, and improvement.

Barley (*Hordeum vulgare* L.) is an ancient domesticated, annual plant (Badr et al., 2000; Purugganan and Fuller, 2009). Genetic and archaeological evidence indicate that domesticated barley is a mosaic crop, formed from different populations, and possibly there was no single origin for domesticated barley (Dai et al., 2012; Morrell and Clegg, 2007; Poets et al., 2015). Pourkheirandish demonstrated that domesticated barley has two independent origins (Pourkheirandish et al., 2015). The non-brittle rachis genes (*btr1* and *btr2*) must have originated as independent mutants in wild barley. Currently, barley is the fourth most common cereal crop in terms of both yield and in-field production (http://faostat.fao.org). About 75% of global production is used for animal feed, and 25% is malted or consumed as human food (Blake et al., 2011). In poorer countries, barley is therefore an important food source (Grando and Macpherson, 2005), providing harvestable yields in environments, that are marginal and harsh for crop production. Recent research has classified barley as a true functional food in more developed societies. The barley grain is especially high in soluble dietary fiber, which significantly decreases the risk of serious diseases such as type II diabetes. The USA Food and Drug Administration (FDA) has approved cell-wall polysaccharides from barley grain to be used as a human health claim (Collins et al., 2010).

Among annual crop plants, barley has a high tolerance to abiotic stresses (Blake et al., 2011; Munns and Tester, 2008; Wiegmann et al., 2019), providing potential to expand its production to areas affected by climate change. Moreover, the relatively simple diploid genetics of barley and its relatively close relationship to other crops in the *Triticeae*, the grass family of Poaceae facilitate the transfer of barley research knowledge to other cereal crops, for example, wheat and rye

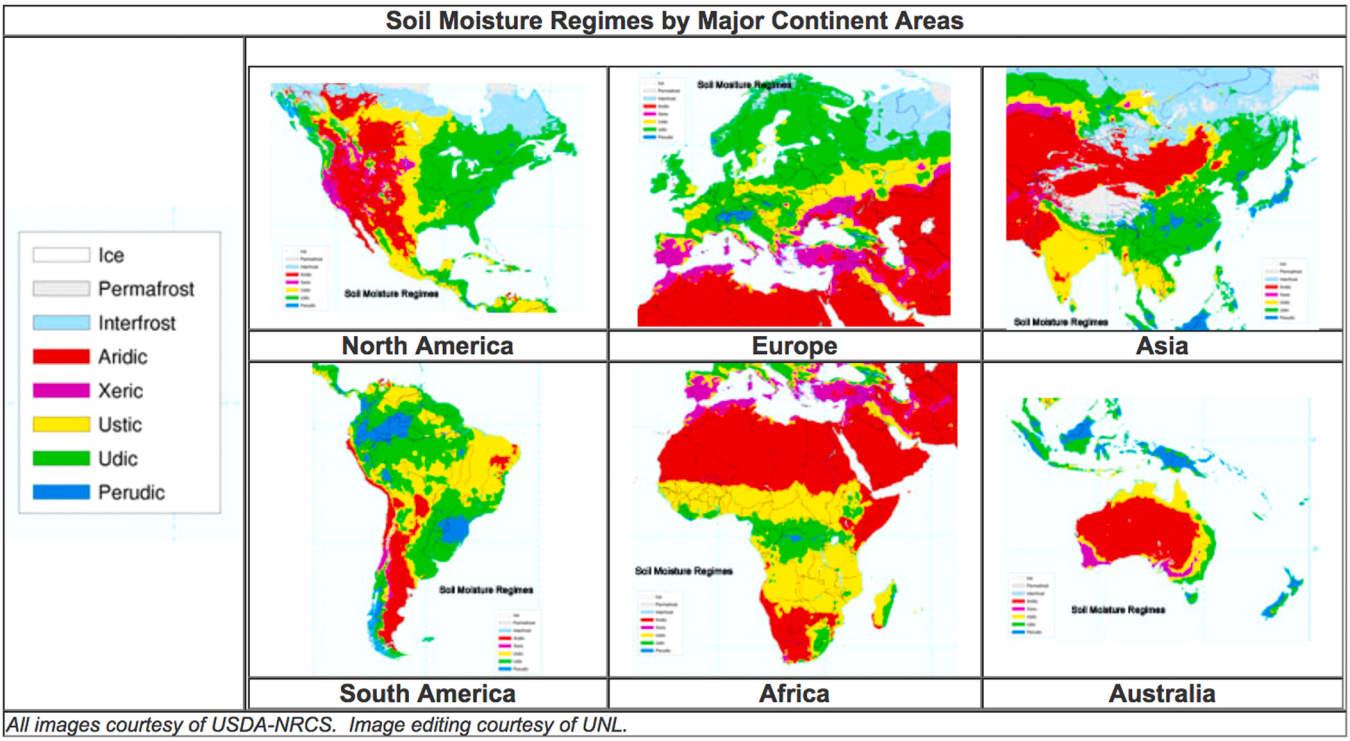

Fig. 1. The Earth soil moisture regime map. (
Source: United States Department of Agriculture, Natural Resources Conservation Service).

(Sreenivasulu et al., 2008). During recent decades, barley has been modified through plant height reduction to release greater yields under irrigated conditions. However, in semiarid and drought-prone locations, achieving yield stability has remained an elusive goal. Frequently, cultivars with good yield and quality potential do not exhibit tolerance to water deficits. It is therefore imperative that genetic gains be made to produce climate-resilient cultivars (Bornare et al., 2012). Drought stress can reduce yields by 50% or more (Pennisi, 2008). Barley is a promising source of genes for drought-related research (Bornare et al., 2012; Mosaddek Ahmed et al., 2016). Barley plant exhibits high genetic variability for stress tolerance responses, which makes it an excellent model plant for studying genetic regulation of water deficiency adaptation.

Several stress-related genes in barley have been characterized using conventional gene cloning methods and extended to large-scale genes expression studies such as transcriptome, metabolomics, and proteomics, which accelerate the understanding of drought stress responses (Asefpour Vakilian, 2020; Harb et al., 2020; Javadi et al., 2021; Talame et al., 2007). High-throughput genomic platforms have been used to characterize stress responses. These approaches have facilitated the identification of major stress factors regulatory networks and pathways (Friedel et al., 2012; Qiu et al., 2020). The ability to identify drought-related genes has significantly improved with the accessibility of a fully annotated and complete genome sequence of the reference cultivar Morex (IBSC, 2012; Luo et al., 2003; Schulte et al., 2009). Further, the current effort toward establishing the pangenome of multiple barley cultivars and landraces provides an excellent gene pool resource. The improvement of drought tolerance in barley requires an elucidating of both the physiologic mechanisms and their genetic regulation that are evolved as drought-related traits at various stages of plant development. In the past several years, technological advances in molecular biology, genomics, and transgenics have enabled drought-related studies, resulting in significant progress in identifying genes involved in drought resistance (Mosaddek Ahmed et al., 2016).

This review presents an overview of the morphological, physiological, genetic, and genomic components of drought tolerance in barley. We consider recent studies that evaluate genes well-characterized as drought tolerance related. Relatively easy to apply and low-cost screening procedures designed to identify more drought-tolerant segregates are suggested. In addition, this review provides an overview of future efforts to combine genetic engineering approaches with traditional breeding methods to develop drought-tolerant barley.

2. Assessment of barley drought tolerance

Drought effects on plant health are caused by accumulative responses to periods of water deficiency. Partial recovery from moisture stress occurs daily during the night. The accumulative effects of these stresses cause morphological, physiological, and biochemical modifications. In environments where drought occurs frequently, morphological responses have been observed in wild barleys and landraces. Plants respond to water deficiency through complicated mechanisms of gene expression and metabolism in individual cells through individual physological levels to ecosystem processes (Colmenero-Flores et al., 2019). At least six main aspects mitigation of drought effects occurs in diffrent ways: (a) *Escape* of drought; when plants complete their life-cycles before severe droughts occur (e.g. earlier flowering). (b) *Avoidance*: Plant enhance their capacity for water uptake through strong root systems (e.g. stomata and leaf area reduction) (Blum, 2017). (c) *Osmotic adjustment*: Plants increase the elasticity of their cell walls to maintain a turgidity (Blum, 2017; Colmenero-Flores et al., 2019; Osakabe et al., 2013; Subbarao et al., 2000). (d) *Metabolic resistance*: Increasing antioxidant metabolism in the plants, for example, to adapt to severe stress (Anjum et al., 2017; Mittler, 2002; Ramachandra Reddy et al., 2004); (e) *Abandoment*: leaf shedding under water stress (Chaves et al., 2003) and (f) *Genetic mutations* and gene modification: Plants can evolve biochemical and physiological traits under long-term drought conditions (Xu et al., 2010). These processes likely involve multiple and simultaneous in barley responses to water deficiency and subsequent re-watering in barley.

The most visible symptoms of water deficiency at the vegetative stage are wilting and rolling of leaves, decreased plant height, leaves area, and the number of leaves. Plant height and shoot and root biomass were significantly reduced in barley plants exposed to drought stress (Askarnejad et al., 2021; Bhattacharya, 2021; Zhao et al., 2009). In addition to plant height reduction, the morphology of plant growth is dramatically affected. Plant leaves are the principal organs for absorption and transpiration and are most affected by water shortage. Under drought stress barley leaf blades have reduced area, thickness, and photosynthesis (Munns et al., 2010). Canopy temperature, leaf blade turgor pressure, and availability of photo-assimilates are the major factors in leaf area modification (Hasanuzzaman et al., 2018; Hein et al., 2016; Hsiao and Xu, 2000; Koroleva et al., 2002; Nieves-Cordones et al., 2019). Under the conditions of drought, photosynthesis and turgor pressure decrease, leading to a reduction in leaf area (Samarah et al., 2009). With continued drought stress the severity of the following morphophysiological traits were adversely affected; plant height, water potential, gross photosynthetic rate, grain filling period, number of spikes, number of kernels per spike, kernel weight, grain and straw yields, and harvest index (Samarah et al., 2009).

Drought survival is an important trait under strong selection pressure. Consequently, many loci contribute to drought survival in plants (Qiu et al., 2020), each of which often makes small contributions to the phenotypic variation (Ravi et al., 2011; Sandhu et al., 2014). Strong genotype × environment plasticity reduces the contributions of individual loci (Makumburage et al., 2013; Swamy et al., 2013). Nevertheless, identifying loci that positively impact drought tolerance in multiple environments and populations might decrease the number of target loci needing characterization (Semagn et al., 2013).

3. Morpho-physiological mechanisms of barley drought tolerance

The utilization of diverse genetic resources, precise phenotyping techniques, reliable traits, assessed at the appropriate growth stage are crucial to identifying drought-tolerant barley. In drought-stressed conditions, physiological and morphological variations are indications of genetic variation. Genotypes with high adaptability to drought stress may serve as genetic resources to enhance drought stress tolerance (Liaqat et al., 2021). Selection for drought tolerance has focused extensively on agronomic and physiological traits, such as grain yield (Mora et al., 2016), biomass yield (Szira et al., 2008), root morphology (Hargreaves et al., 2008), relative water content (Szira et al., 2008), stomatal conductance (Munns et al., 2010), photosynthetic parameters (Gudys et al., 2018; Rapacz et al., 2019), chlorophyll fluorescence (Guo et al., 2007; Jabbari et al., 2019; Rapacz et al., 2019), osmotic adjustment (Teulat et al., 2001a), and hormone content (Gudys et al., 2018).

3.1. Root-related traits

Roots and shoots are the axes of plant development. Interactions among these organs influence specific plant architecture (Fig. 2). Hormonal circuits governed by chemical signaling pathways, such those resulting in auxin and cytokinin, are essential for coordinated development (Naz et al., 2013; Puig et al., 2012; Siddiqui et al., 2021). Root system development can be altered by periods of water deficit and excess, which can occur during the same growing season.

Fibrous roots of cereals consist of two types; seminal roots that develop from the embryonic primordium and nodal roots that develop from the crown or tillering producing region of the culm (Hochholdinger et al., 2004). Seminal roots develop first, then nodal roots emerge at the tillering growth stage. Seminal roots play an important role in drought

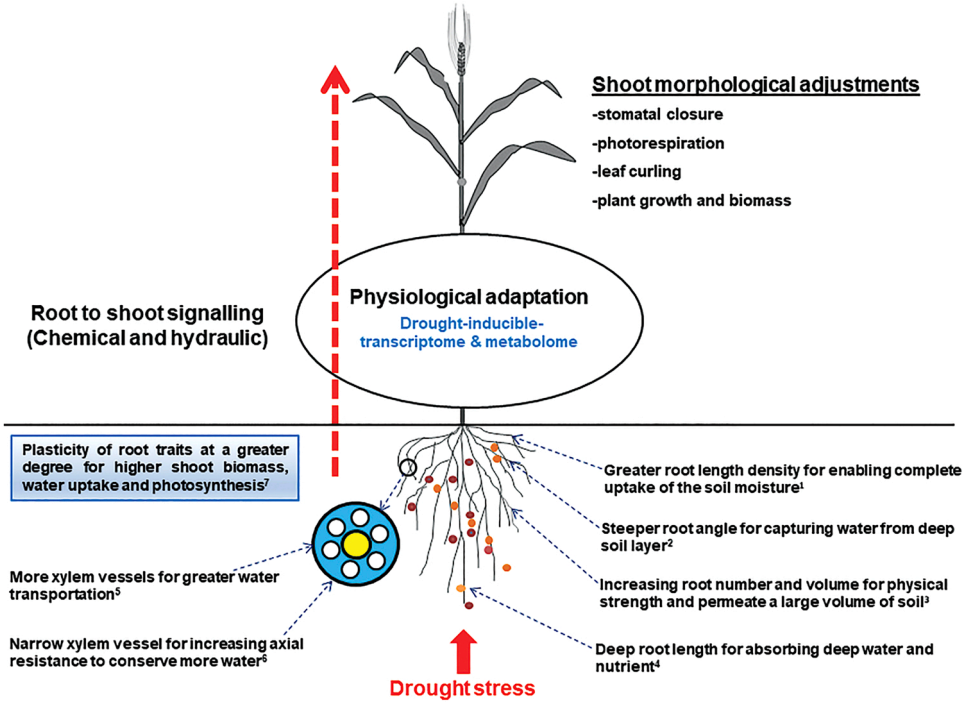

Fig. 2. Schematic of plant roots and shoots under drought stress conditions. The root-shoot signaling system regulates plants response to drought stress (from (Lynch, 2013; Siddiqui et al., 2021)).

adaptation due to different early root growth angles and correlation with grain yields (Richard et al., 2015; Robinson et al., 2018). The few roots 1 (*fer1*) mutant in barley does not develop a secondary root system, yet plant growth is normal (Linde-Laursen, 1977). Plants with deep and thinner root systems may be better-suited to soils suffering from water shortages than those with shallow root systems and thick roots (Lynch, 2015; Oyiga et al., 2020). Under stress, changes occur in root suberization/lignification and large cortical aerenchyma develop (Oyiga et al., 2020). Root adaptations to water stress include elongation of the primary roots, deep root systems, suppression of lateral root branching, rearrangement of the density of branch roots from surface to depth, and elongation of the root hairs (Jovanovic et al., 2007; Lynch et al., 2014; Smith and De Smet, 2012; Uga et al., 2013; Wasson et al., 2012). These related traits may be influenced by molecular networks or pathways that control gene expression and modulate plant-water balance by accumulating stress proteins (Hrmova and Hussain, 2021; Kulkarni et al., 2017; Mia et al., 2020). Under water-deficit stress, root growth may be arrested or stunted (arrested roots) (Sebastian et al., 2016; Xiong et al., 2006; Zhan et al., 2015). While roots are essential organs for adaptation against stress due to water deficiency (Lynch, 2007; Siddiqui et al., 2021), our knowledge of the genetic basis of root adaptation to water deficiency remains poor, partly due to the difficulty of root phenotyping in the field and the doubts about which traits to target (Khan et al., 2016; Wasson et al., 2012). Genetic and environmental factors determine the characteristics of root systems, including length, branching pattern and density, and growth angle (Lynch and Beebe, 1995). A better understanding of desirable root systems would help dissect their adaptation responses to water shortage stress. This would enable the development of stress-resilient cultivars with high potential, to access water from deeper soil layers. Screening genotypes with suitable root architecture might increase grain yield stability if they combine some biological properties of roots that consider morpho-anatomical changes (Lynch and Beebe, 1995). Water capture and extraction efficiency of a crop can be affected by its root architecture (Pennisi, 2008). Despite differences in root architecture between cultivated and wild barley (*H. vulgare* ssp. *spontaneum*), the primary roots of both develop types of primary, lateral, and secondary roots. Compared with modern cultivars, wild barley shows greater variation in the maximum seminal root length (Grando and Ceccarelli, 1995). However, the variation in wild barley is higher because of its diverse ecological adaptations from the deserts of Jordan to the subarctic climates of Tibet (Choo, 2002; Grando and Ceccarelli, 1995; Liu et al., 2020; Nevo and Chen, 2010). Under both irrigated and rainfed conditions, root density and depth directly affect root performance. A significant association between root system size (RSS) and grain yield was observed under drought (Chloupek et al., 2010).

In many agroecosystems, soil and water conditions limit plant growth and grain yield due to inadequate root systems. The size and architecture of the root systems determine whether they carry out these diverse functions efficiently (Lynch, 1995). Root architecture influences mineral nutrition under drought tolerance, particularly phosphorus uptake (Lopez-Arredondo et al., 2014). Breeding for improved nutrient use efficiency, as well as drought tolerance, is one way of addressing this problem. To increase nutrient and water efficiency and plant productivity under non-optimal conditions, it may be necessary to improve the root systems of barley (Comas et al., 2013; Koevoets et al., 2016).

A meta-analysis showed that drought stress decreases nitrogen (N) and phosphorus (P) concentrations in plant tissues (He and Dijkstra, 2014), and can reduce soil nutrient uptake (Ramireddy et al., 2018). During drought, the reductions in nutrient uptake may occur due to the reduction of nutrient supply through the mineralization (Fierer and Schimel, 2002; Sanaullah et al., 2011), and reductions of nutrient diffusion and mass flow in the soil (Chapin, 1991). Drought may also affect the kinetics of nutrient uptake by roots (Bassirirad, 2000).

In general, root length and root density are positively correlated with the uptake of mineral elements, particularly those with limited solubility (Marschner, 2012). Root architecture also determines access to water, and under certain conditions, a correlation was found between root system size and tolerance to drought stress (Comas et al., 2013). Studies have revealed a positive correlation between root system architecture and crop performance and grain yield under drought (de Dorlodot et al.,

2007; Kell, 2011; Meister et al., 2014). Consequently, root architectural traits that optimize soil exploration in time and space are among those considered relevant in crop breeding programs (Comas et al., 2013; Koevoets et al., 2016; Ramireddy et al., 2018). Optimizing the root system by classical breeding strategies requires detailed measurements of roots. In addition, the root system architecture, governed by many intrinsic and extrinsic factors and involving numerous genes (White et al., 2013). These difficulties make it challenging to breed specifically for improved root systems. Yet, a targeted approach to improvement of root systems is desirable, not only for breeding purposes but also to study the functional relevance of the size and complexity of root system.

The homeostasis of ions is a dynamic process required for all organisms. A variety of minerals are essential for biological processes, but over-accumulating them can be toxic. Hence, organisms have evolved effectual systems for acquiring and storing these elements and controlling their organellar and cytosolic concentrations to develop normally (Mulet et al., 2020). Among cationic inorganic nutrients, potassium (K^+) is the most important nutrient responsible for regulating osmotic pressure, cellular growth, and enzyme activation in plants. In response to water deficit, plants accumulate water and K^+. Potassium and chloride (Cl^-) are vital elements of water deficit resistance in plants (Mahajan and Tuteja, 2005; Mulet et al., 2020; Nieves-Cordones et al., 2019). A large root system is desirable, as high K^+ and Cl^- uptake systems also allow the leaf cells to adjust their osmotic potential, which is critical to retaining water within the cell (Nieves-Cordones et al., 2019). During stomatal closure, K^+ and Cl^- are released from guard cells to prevent excessive loss of water. Key mechanisms related to water deficit (WD) resistance retain water as a drought avoidance response such as the closure of the stomata and reduced root water uptake while reducing intracellular water as a drought tolerance response for example osmotic adjustment OA (Fig. 3).

It has been suggested that biotechnological approaches against drought might target proteins that regulate potassium uptake in guard cells (Locascio et al., 2019). Physiological responses to drought include elevations in K^+ uptake and reductions in K^+ loss in drought-stressed plants (Chen et al., 2007, 2016), which prevent cell dehydration through water molecules binding (Wang et al., 2013). Under drought stress in barley, potassium was involved in abscisic acid (ABA) homeostasis and metabolism of carbohydrates as well as in leaf water status, starch concentration, and other primary carbon metabolites (Hosseini et al., 2016). Also, greater drought tolerance was associated with a higher K^+ contents (Feng et al., 2016). Likewise, more stability in levels of major flag leaf carbon metabolites was recorded in drought-adapted barley genotypes (Templer et al., 2017).

3.2. Shoot-related traits

3.2.1. Relative water content

As an indication of drought tolerance and plant water status, relative water content (RWC) is an important screening tool for cereals. RWC is an estimation of plant water status based on the ratio of fresh weight with dry weight and turgid weight measured on sampled leaves (Smart, 1974). As a measure of plant leaf water deficits compared to full turgid pressure, the RWC has been widely used to evaluate plants under varying levels of drought stress, which focus on drought-resistant crops to identify drought-tolerant individuals (Hu and Xiong, 2014). Reassessment of RWC could provide better drought resistance screening parameters for the development of drought-resistant barley cultivars (Matin et al., 1989). Since flag leaf cell volume is related to RWC, it can reveal the relationship between leaf water supply and transpiration rate (Sinclair and Ludlow, 1985). RWC is quantitatively inherited and regulated by genes with additive effects (Teulat et al., 1998, 2003). Water use efficiency is an important factor that regulates transpiration and photosynthetic carbon assimilation balance (Farquhar et al., 1982). A negative relationship between water use efficiency and RWC was mapped in the barley genome along with several common relationships between RWC and chlorophyll fluorescence parameters (Rapacz et al., 2019). That is, plants losing less water under drought had defected with providing high phosphorus and nitrogen, which is a common phenomenon in breeding for drought tolerance. (Lawson and Blatt, 2014; Ruggiero et al., 2017). Finally, a positive correlation was observed in barley between RWC and grain yield (Matin et al., 1989).

3.2.2. Osmotic adjustment

Osmotic adjustment (OA) is a physiological adaptation mechanism that associates osmotic stress and drought responses Efficient OA is essential for maintaining positive turgor pressure in arid and semi-arid environments as they need to attract water into the cells, plant cells must maintain a higher solute concentration than in the external

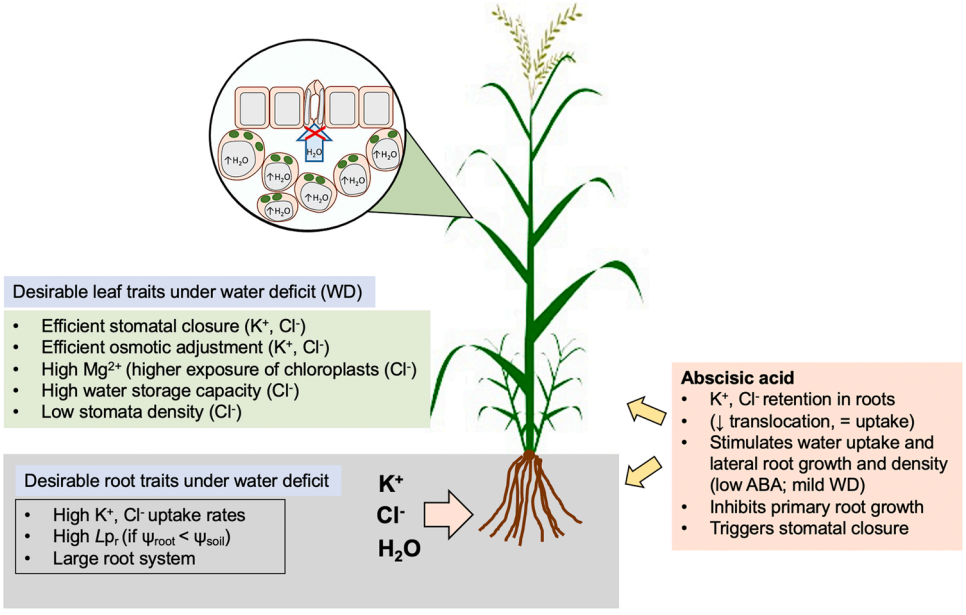

Fig. 3. Overview of the most important factors contributing to water deficit (WD) resistance.

solution (Munns, 1988; Turner, 2018). Under water shortage conditions, plants accumulate several solutes, including sugars, proline, glycine betaine, and phenols. (Ferchichi et al., 2018; Martinez et al., 2004; Turner, 2018). Under drought conditions, osmolytes maintain and stabilize cellular structure and function, save water balance by accelerating water uptake and retention and reduce the dehydration effects by preserving cell turgor and supplementary physiological processes (Anjum et al., 2017). At the reproductive stages, osmolytes further improve carbohydrate partitioning and the yield (Subbarao et al., 2000).

Several mechanisms in barley cell walls contribute to the adaptation of cells, tissues, and organs to water deficits and osmotic stress (Lu and Neumann, 1998). OA studies of barley genotypes under drought stress revealed that genotypes with high OA capacities retain cell turgor pressure (González et al., 2008), while low OA capacity genotypes had lower yields, grain size, and grain protein content (Vahamidis et al., 2017). Photosynthetic activity, water status, and osmotic adjustment varied significantly among contrasting barley genotypes growing under water deficient conditions. These traits were correlated to seedling growth under terminal drought stress, revealing seedling growth rate as an important criterion for selection drought tolerance (Cai et al., 2020). Suggesting that relative water content and osmolality of the youngest fully expanded leaf blade are appropriate selection criteria to screen seedlings for drought tolerance (Cai et al., 2020). In addition to facilitating cell volume and turgor maintenance, OA can also improve growth, plant yield, or survival of plants in saline or dry soils. However, this concept lacks physiological support. It is not possible for OA itself to promote growth; the solutes collected must be transferred from metabolic processes, such as protein formation and cell wall synthesis. Cells of adult plants adjust their osmotic potential by accumulating water-soluble carbohydrates, which reduce proline content and increase the concentration of osmotically active compounds that lower photosynthesis rates, stomatal conductance, and transpiration (Azhand et al., 2015; Teulat et al., 2001a). Genomic regions controlling traits related to plant water status and osmotic adjustment were mapped in a biparental population (Teulat et al., 2001a). It appears now that cell expansion and stomatal conductance are unrelated to turgor. However, osmotic adjustment influences of yields only through other processes whose controls are nearly unexplored (Munns, 1988).

3.2.3. Photosynthesis under drought

In higher plants, the photosynthetic rate decreases with declining RWC and leaf water potential (Lawlor and Cornic, 2002). Under drought conditions, reduction in photosynthesis is generally attributed to stomatal restriction (Cornic, 2000). Reductions in internal CO_2 concentration are believed to be the cause of a decrease in total photosynthetic metabolism. Stomatal closure during drought is also associated with non-stomatal effects, including photophosphorylation (Meyer and Genty, 1999), rubisco activity (Medrano et al., 1997), ribulose-1, 5-bisphosphate (RuBP) renewal (Lawlor, 2002) and adenosine tiphosphate (ATP) synthesis (Tezara et al., 1999). The responses of drought-induced photosynthetic reveal that as drought stress increases, stomata close progressively, eventually resulting in reduced net photosynthetic rates. Leaf water status and stomatal conductance have a high correlation exist between leaf water potential and stomatal conductance. Water deficiency induces root-to-leaf signaling, which triggers stomatal closure and reduces transpiration. There is a direct relationship between xylem ABA level and stomatal conductance, which has been demonstrated by the discovery of that ABA is a chemical signaling agent (Socias et al., 1997). However, there is a high level of co-regulation between stomatal opening and photosynthesis (Farquhar et al., 2001; Hubbard et al., 2001). As a consequence, stomatal movements are dynamic, regulated by several environmental elements, and stomatal conductance could be an integral measurement for assessing photosynthetic response to drought. Stomatal opening is likely a less complex trait than metabolic changes limiting photosynthesis under drought. There is a possibility that changes occur in cellular carbon metabolism early in the process of dehydration. In general, drought reduces the ability to assimilate and utilize carbon.

In higher plants, the rate of photosynthesis depends on the activity of rubisco as well as the synthesis of RuBP (Parry et al., 2002; Tezara et al., 1999). Photosynthesis is a primary cellular process that is directly affected by cellular water status (Chaves, 1991). Drought stress and the consequent reduction in cellular water status significantly reduce photosynthetic rate by limiting CO_2 diffusion through the stomata, and by potentially inducing secondary effects such as oxidative stress, which can damage the photosynthetic machinery (Chaves et al., 2009). Ultimately, this leads to substantial grain yield losses. Under water-deficient conditions, a decrease in chloroplast size could lead to dehydration in the chloroplast. Dehydration can also acidify the chloroplast stroma, resulting in repressed rubisco activity (Meyer and Genty, 1999). Despite this, C_4 plants utilize water more efficiently than C_3 plants, and they require rubisco to attain a given photosynthesis rate. Under drought conditions, phosphoenolpyruvate carboxylase (PEPcase) is suppressed in C_4 plants (Boyer et al., 2021). The activities of phosphoribulokinase and fructose-1,6-bisphosphatase (FBPase) were impacted by decreases in RWC. As a result of drought, the content of starch, sucrose, and the end products of photosynthesis changes (Haupt-Herting and Fock, 2002). It appears that drought stresses will alter starch/sucrose ratios across chloroplast membranes, leading to altered inorganic phosphate (Pi) flux. Because Pi levels in the chloroplasts are reduced, ATP synthesis is inhibited and photophosphorylation results in a greater impact (Tezara et al., 1999). When environmental conditions restrict plant growth, responses to avoid drought-induced damage to photosynthetic apparatus include photo-destruction of the D1 protein of PSII, thermal dissipation of light energy, water-water cycle, the xanthophyll cycle, and detachment of the light-harvesting complexes from photosynthetic reaction centers (Bhargava et al., 2013; Demmig-Adams and Adams, 2006; Niyogi, 1999). Drought-tolerant C3 plants evolved efficient strategies to avoid or respond to drought stress, for example, acclimation mechanisms allow plants to minimize water loss from transpiration. This can occur as a result of stomatal closure, adjusted leaf architecture, reduced leaf growth, and shedding of older leaves (Chaves et al., 2009). Plants can also avoid dehydration by maximizing water uptake as a result of favored root growth relative to shoot growth. Plants exhibiting developmental plasticity can also escape drought by completing their life cycle before the drought stress becomes lethal. Increased levels of osmoprotectants such as proline, glycine, betaine, and polyols, allow plants to maintain turgor and protect cells from plasmolysis (Chaves et al., 2009).

Drought stress in barley decreased plant growth, yield, water relations chlorophyll contents, and grain nutrient contents, but lipid peroxidation and osmolyte accumulation were increased. under drought stress, yield and related traits such as seed priming, biopriming, in particular, grain yield, improved leaf area, chlorophyll contents, accumulation of proline, phenolics, total soluble proteins, glycine betaine, relative water contents, cell membrane stability, pressure potentials, and grain Mn, Zn and B contents were improved, while decreased malondialdehyde contents (Tahira et al., 2018).

3.2.4. Reactive oxygen species and peroxidation

Increasing ROS production in chloroplasts, peroxisomes, and mitochondria is one of the consequences of water deficiency. With increased ROS level, the cellular redox-state is adjusted via a multilateral and cooperative antioxidant system that influences intracellular ROS levels. ROS changes are a primary alarm signal that triggers acclamatory defense response through transduction pathways signals that include H_2O_2 as a secondary messengers (Cruz de Carvalho, 2008). ABA, Ca^{2+} fluxes, and sugar metabolism are all involved in ROS signaling, which could play a role in both upstream and downstream ABA-dependent pathways during water deficiency. Nonetheless, when drought stress occurs over a long period, high ROS levels will overwhelm the anti-oxidant system causing wide cellular damage and death. ROS can have a dual effect

depending on the cellular level of ROS. Keeping ROS levels low may make them part of stress signaling pathways, triggering stress defense and acclimation responses (Dat et al., 2000; Vranova et al., 2002). Overproduction of ROS levels containing hydrogen peroxide (H_2O_2), superoxide (O_2), hydroxyl (OH^{-1}), and singlet oxygen (O_2^-) can lead to oxidative damage as lipid peroxidation of cell membranes (Imlay, 2003). Malondialdehyde (MDA) is regarded as a biomarker of lipid peroxidation that initiates uncontrolled oxidative cascades leading to oxidative stress and finally cell death due to cell membranes damage and other cellular components (Dat et al., 2000; Jones, 2000; Mittler, 2002). Plants possess both enzymatic and nonenzymatic metabolites to control ROS levels and protect their cells. These metabolites may have a significant role in signaling ROS in the plant's (Vranova, 2002). Both enzymatic including, peroxidase (POD), superoxide dismutase (SOD) catalase (CAT), ascorbate peroxidase (APX), monodehydroascorbate reductase (MDHAR), and dehydroascorbate reductase (DHAR) as well as nonenzymatic, glutathione (GSH), oxidized glutathione (GSSG), ascorbate (ASA), and DHA antioxidants decrease the oxidative damage under stressful conditions. Drought stress could be summarized in three successive phases; (i) ROS steady-state levels are disrupted, (ii) ROS production is increased due to stomatal closure, causing the equilibrium to shift upward and triggering defense signal transduction, and (iii) as a consequence of prolonged drought stress, ROS production will increase, which cannot be balanced via the antioxidant system, resulting in toxic oxidative events and eventually cell death (Fig. 4).

The first defiance mechanism against ROS accumulation is the SOD dismutase to O_2- radicals H_2O_2 (Cruz de Carvalho, 2008). APX and CAT enzymes also are scavenging H_2O_2 and inhibit its accumulation to toxic levels by converting it to H_2O and O_2. It has been shown that these enzymes have different affinities for H_2O_2 scavenging; CAT is responsible for most of the H_2O_2 scavenging, because of its low affinity; APX has an elevated affinity toward H_2O_2, which could exploit the regulation of ROS (Cruz de Carvalho, 2008). Furthermore, APX is an ascorbate-glutathione element, which needs ascorbate to H_2O_2 scavenge (Cruz de Carvalho, 2008; Ramachandra Reddy et al., 2004). In plants subjected to long-term drought stress, both enzyme and non-enzyme antioxidants may contribute to stress tolerance (Vranova, 2002; Vranova et al., 2002). These antioxidants are directly or indirectly responsible for the drought resistance of barley Fields(Ahmed et al., 2013; Harb et al., 2015; Feng et al., 2016).

3.3. The main drought stress signals in barley

The physica and chemical nature of the drought-sensing signals includes ABA, a stress hormone that is a key indicator of drought sensing from roots to shoots, even though it is not required in all species (Chaves et al., 2003; Jia and Zhang, 2008). ABA likely exists in stem xylem as an apoplastic component that comes from roots via the apoplastic route and may serve as a linkage signal between shoots and roots (Steudle, 2000). According to phytohormone profiling of barley, ABA concentration increased under osmotic stress despite the presence of K^+ in the medium and even more so under the K^+ deficiency (Hosseini et al., 2017). ABA turnover was higher in drought-tolerant genotypes with higher K^+ concentrations in leaves that were drought-tolerant (Hosseini et al., 2016). When leaf turgor changed significantly before stomatal conductance decreased, ABA appeared to increase in the xylem, implying that root-derived ABA regulated stomatal behavior during moderate drought (Liu et al., 2003). Several morpho-physiological responses associated with drought tolerance in barley are presented in Table 1. Likewise, gibberellin (GA) mediates many responses to drought. GA concentration is reduced, and the DELLA proteins regulators accumulate, which could be attributed to retarded growth under drought (Colebrook et al., 2014). Cytokinins (CKs) and their metabolism are important in plants adaptation to different abiotic stresses including drought (Ha et al., 2012). Both positive and negative effects of CKs on drought tolerance were reported (Zwack and Rashotte, 2015). These observations suggest that the fine-tuned hormonal homeostasis during stress conditions plays an important role in plant response to abiotic stresses. Therefore, plants upregulate their endogenous hormones as a means of self-protection from harsh conditions, notably presence of cytokinins, ABA, and other hormones, which accelerate the negative effects of drought stress.

Assessing hormone accumulation, response and hormonal content provides an effective tool for selecting promissing drought tolerant barley genotypes. Genes related to ABA biosynthesis were found to be differentially regulated under drought stress in both barley flag leaves and developing seeds during seed-filling (Seiler et al., 2011). Thus, genes regulating hormone accumulation under water deficit can be used to improve drought tolerance in barley.

In barley, xylem-borne ABA has an essential function in the stomatal apertures serving to regulate as a line of defense against drought; while elevated CO_2 may interrupt this central mechanism of drought adaptation via stomatal delaying response to soil dehydration (Li et al., 2020a).

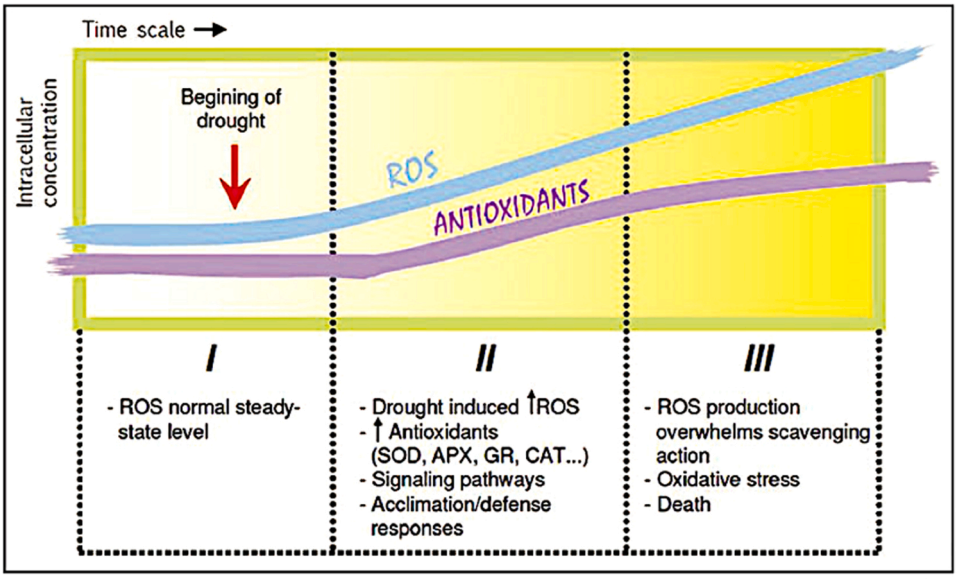

Fig. 4. Reactive oxygen species-based model of the drought stress response: Response of plants to drought in three successive phases (from (Cruz de Carvalho, 2008)).

Table 1
Drought tolerance and physiological responses in barley.

Response	Signaling pathway	Reference
Stomatal closure, reduced hydraulic Stress conductance delays stomatal closure	Transpiration prevention Maintaining photosynthetic activity under stress	(González et al., 1999; Guo et al., 2009; Li et al., 2021; Thameur et al., 2012)
Alterations in carbon sinks and sources	Root growth is induced, while shoot growth is inhibited	(Chen et al., 2011b, 2013; Hubick and Farquhar, 1989; Schnyder, 1993)
Antenna size change in chlorophyll Photodestructio destruction of PSII protein D1	Reduction in photosynthetic electron transport	(Bagues et al., 2018; de Mezer et al., 2014; Harb et al., 2020; Haupt-Herting and Fock, 2002)
Light energy dissipates thermally	Electron transport and photophosphorylation are uncoupled	(Flexas and Medrano, 2002; Kocheva et al., 2004; Saito et al., 2010)
Cycles of water and xanthophyll	Chloroplast ROS protection	(Filella et al., 1996; Lee and Thornber, 1995)
NADPH dehydrogenases, alternative oxidase pathway, uncoupling proteins	Oxidative phosphorylation and electron transport	(He et al., 2021; Ishibashi et al., 2015; Wanniarachchi et al., 2018)
Inhibitors	Maintenance of protein structure in mitochondrial membranes	(Nie and Hill, 1997)
GABA shunt pathway	Prevents reductants from being formed in the TCA cycle	(Abebe et al., 2010; Martin and Iowa, 2015)
Enzymes and substrates of antioxidants	Scavenging ROS	(Gurel et al., 2016; Harb et al., 2015)
Osmotically active solute synthesis	Osmotic adjustment	(Blum, 1989; González et al., 2008; Zhu et al., 2015)
ABA biosynthesis	Stomatal closure, ethylene accumulation, aquaporin activity regulation	(Collin et al., 2020; Daszkowska-Golec et al., 2018; Sreenivasulu et al., 2006)

GABA, gamma-aminobutyric acid

Evidence suggests when the plant is re-watered, high ABA levels can be eliminated, possibly leading to the reopening of stomata (Wan et al., 2009). Under drought conditions, barley plants reduce their water content then, increasing ABA and proline contents in their leaves and roots (Bandurska et al., 2017). As a consequence of drought stress, leaf and root hydration levels gradually decreased while a steady rise in ABA and free proline levels occurred in leaves and roots (Bandurska et al., 2017). Proline and ABA concentrations in the two organs were influenced by levels of tissue dehydration, with highest concentrations of these compounds were highest at the end of drought stress. There was a positive association between tissue dehydration and proline accumulation (de Mezer et al., 2014).

During leaf dehydration, turgor pressure drops, elongation of cells is inhibited, stomata close, photosynthetic activity declines, and productivity of plant dry matter decreases (Chaves et al., 2003). ABA-dependent stomatal closure in drought-stressed barley plants may cause the failure of CO_2 assimilation and consumption of NADPH, and ATP resulting in an imbalance between the PSII photochemical activity and electron transport activity needed for CO_2 fixation (Hsu et al., 2021; Kim et al., 2010; Pei and Kuchitsu, 2005) (Fig. 5).

Proline accumulation is considered a physiological and/or biochemical response that enables drought tolerance (Hayat et al., 2012). Proline is an amino acid that plays an extremely valuable role in plants undergoing various stressful conditions, including drought stress (Hayat et al., 2012). Besides acting as an excellent osmolyte that protects plants against various stress conditions (Bohnert et al., 1995), proline shows three main roles during stress, an antioxidative defense molecule, a metal chelator, and a signaling molecule. Generally, proline is produced from glutamate through pyrroline-5-carboxylate reductase (P5CR) and pyrroline-5-carboxylate synthetase (P5CS) (Colmer et al., 2006). Proline is not only an osmolyte that helps keep cells' osmotic pressure balanced, but it also shows a vital role in controlling the level of ROS (Furbank and Tester, 2011; Yamaguchi and Blumwald, 2005), cell signaling, and plant development (Lehmann et al., 2010). Besides affecting intracellular ionic homeostasis, proline regulates the transport of ions through cellular membranes (Cuin and Shabala, 2007). Since proline concentrations increase significantly in plants under drought conditions, it has been proposed that proline levels can be a suitable biochemical marker for breeding to stress (Ashraf et al., 2008; Yoshiba et al., 1995). Nevertheless, proline concentrations were higher in drought-sensitive plants (Hanson et al., 1979; Singh et al., 1972).

4. Genetic approaches for drought tolerance improvement of barley

4.1. Transcriptional regulation of gene expression

Gene expression or transcriptome analyses determine whether genes are upregulated or downregulated by examining changes in the amount of RNA transcripts under different conditions. Different phenotypic responses can be caused by changes in gene expression levels, despite the same gene sequence in all individuals. A change in epigenetic status can be temporary or hereditary and this can contribute to phenotypic plasticity (Brautigam et al., 2013; Moran et al., 2017).

The study of gene expression in barley involves a range of techniques, most recent studies have used cDNA libraries, cDNA-based microarray (Sreenivasulu et al., 2004, 2006), microarrays (Oztur et al., 2002), oligonucleotide-based Affymetrix arrays (Close et al., 2004; Druka et al., 2006), RNA-seq for expression (Mascher et al., 2013), and BSR-seq profiling Platforms (Qi et al., 2019). Utilization of these techniques depends on the type of tissue being sampled and when in the plant life cycle it is sampled (Fossdal et al., 2007). Barley transcriptome data have been collected for covering different growth-related traits including drought tolerance related-traits (Chen et al., 2018; Harb et al., 2020; Hong et al., 2020; Janiak et al., 2017; Oztur et al., 2002; Zhou et al., 2018). As a consequence of signaling paths modulating gene expression, transcription factors (TFs) are engaged in cellular reprogramming by interacting with *cis*-elements of gene promoters and subsequently modifying cellular transcription (Fig. 6). Plants respond to drought in both leaves and roots by producing many types of TFs. TFs have been identified including; ABF, DREB-CBF, AP2/ERF, MYB/MYC, bZIP, bHLH, NAC, HD-ZIP, MADS-box, WRKY, CAMTA, and Alfin-like, or homeodomain TFs (Bedada et al., 2014; García-Morales et al., 2018; Gurel et al., 2016; Janiak et al., 2019; Zeng et al., 2016).

Most of the genes that regulate abiotic stress responses are in the abscisic acid-dependent signaling pathway, including NCED, SnRK2, MYB/MYC, ABF, LEA, AP2/ERF, and DHN (Zeng et al., 2016), and are both negative and positive regulators of drought response (Mun et al., 2017; Tripathi et al., 2014; Wu et al., 2016). In wild barley populations, several members of the TFs, MYB, and NAC families were detected and their expression is often exacerbated by water stress (Wang et al., 2018). Multi-omics analysis indicated that sugar metabolism facilitates adaptation of wild barley to dry soils while enhanced phenylpropanoid/phenolamide biosynthesis occurs in wild barleys from moist soils, which are rich in fungal pathogens (Cai et al., 2021).

Several NAC genes were reported in different development processes and responses to stress in barley, with some controlled by ABA-dependent signaling pathways (Christiansen et al., 2011). Genetic improvement of cereal crops could rely heavily on the NAC genes (ATA, CUC, and NAM) (Feng et al., 2014; García-Morales et al., 2018; Guerin et al., 2019; Podzimska-Sroka et al., 2015; Saidi et al., 2017). Phylogenetic analyses of the *Arabidopsis* TtNACs with rice, barley, and grape homologues distributed these proteins into eight subgroups (Saidi et al., 2017). *HvSNAC1* overexpression increased drought tolerance in barley,

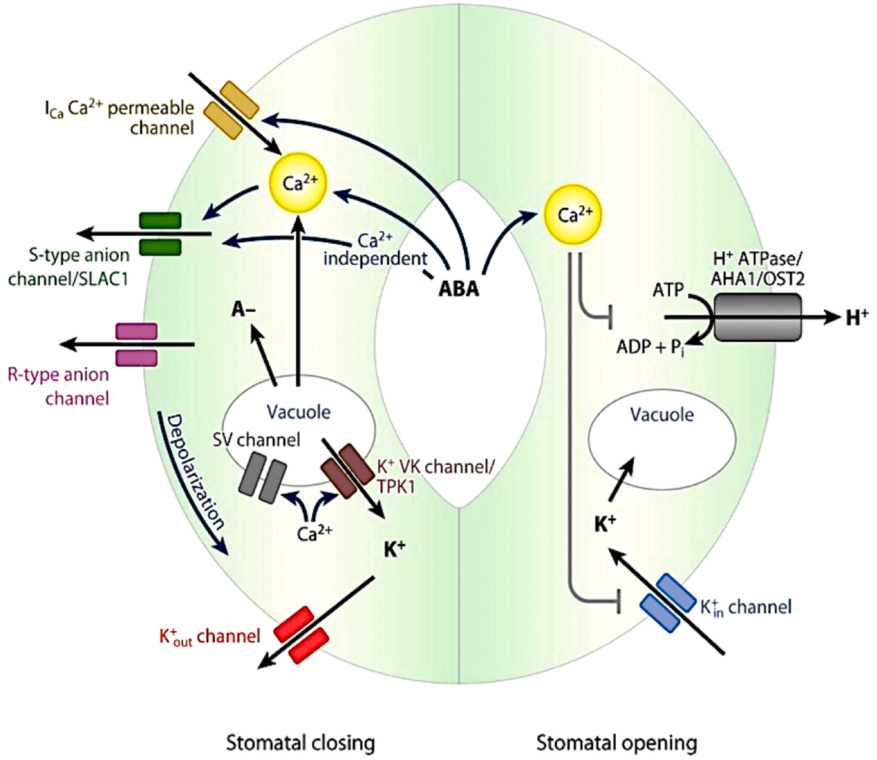

Fig. 5. Diagram showing ion channel regulation and guard cell signaling. Guard cells, plasma membranes, and vacuolar membranes are shown in this model to understand the function of guard cells ion channels and ABA-induced signal transduction (from (Kim et al., 2010)).

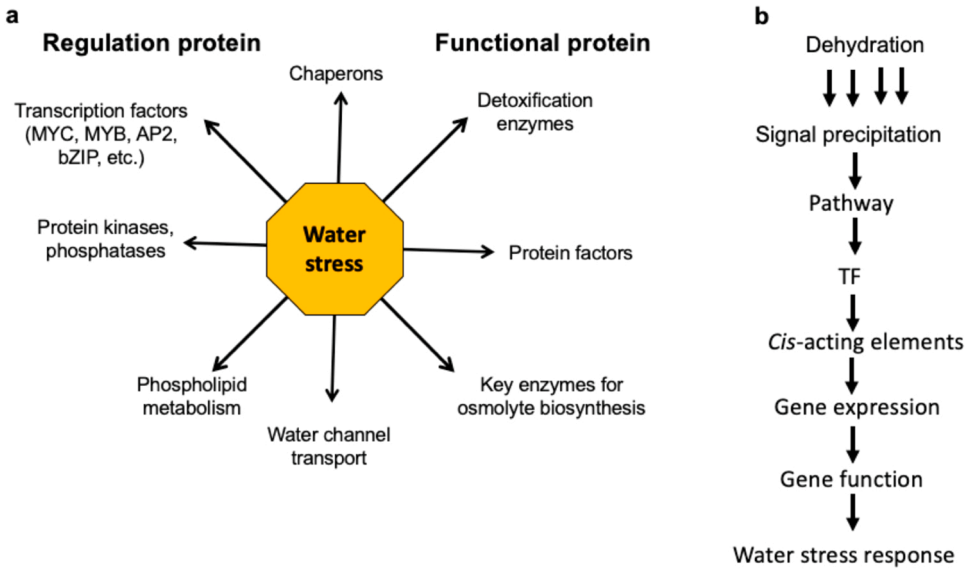

Fig. 6. Molecular mechanisms of the water stress response; Gene products of signal transduction include (a) functional and (b) regulatory proteins.

suggesting that this gene might be used to increase production, as reflected by the improvement in biological yield over the wild-type plants under severe field drought conditions (Al Abdallat et al., 2013).

The transcription factors of dehydration-responsive element-binding protein/C-repeat binding factor (DREB/CBF) in plants are induced by low temperature and are responsible for regulating many genes involved in adaptation to the abiotic stress (Agarwal et al., 2006; Francia et al., 2007; Wojcik-Jagla et al., 2020). These transcription factors are among the first families discovered to regulate gene expression, and they are controlled by a single AP2 DNA-binding domain under water deficit (Guo et al., 2016; Sakuma et al., 2002). Transgenic barley lines expressing a wheat *DREB* isoform and exhibiting increased drought tolerance provide conclusive evidence of the *DREB* factor's beneficial role in the improvement of the abiotic stress tolerance (Yang et al., 2020). However, expression of the DREB TFs is tightly regulated and not eternally related to tolerance. The expression may vary with developmental stage or level of stress.

When studying some barley genotypes that differed for their behaviors towards water stress. (de Mezer et al., 2014), observed no positive correlations between adaptability and *HvDREB1* expression level. Other studies, such as RNA-seq, were conducted to distinguish genes that influence the drought tolerance (Hubner et al., 2015). Researchers

found that *bZIP, WRKY*, and *MADS-box* members were preferentially expressed in drought-tolerant genotypes, but one TF called *AP2*, belonging to the DREB family showed high expression levels in sensitive genotypes. *AP2* and other TFs including *HvMYB1, bHLH*, and *ABI5* were isolated as candidate genes as drought tolerance related-traits at germination, seedling, and reproduction stages (Alexander et al., 2019; Wojcik-Jagla et al., 2018; Zhang et al., 2017; Zhao et al., 2009). The genetic basis of coleoptile length, which correlates with drought tolerance, using genome-wide association mapping was examined (Luo et al., 2020). A plant-specific transcription factor for SPL3, (SQUAMOSA Promoter-Binding Protein-like 3) was strongly associated with coleoptile length. *SPL3* is expressed during coleoptile growth and shows a significant role in seedling establishment under water-shortage conditions. Correlations between alterations in proline, ABA, and water content and the expression of *P5C* and *P5CS* gene enzymes were reported (Bandurska et al., 2017). In leaves and roots of barley under drought stress, accumulated proline is regulated at the transcriptional level by post-translational regulations of *P5CS*.

4.2. Post-transcriptional regulation of gene expression

Stress conditions cause epigenetic regulation of gene expression in addition to regulating transcription. Stress-induced modifications in histones, histone modifications, and DNA methylation influence stress-responsive gene expression in plants under different stresses (Scippa et al., 2004). Under drought conditions, the *HSP17* gene is significantly upregulated in drought-tolerant barley cultivars (Temel et al., 2017). Histone H3 is modified by drought to induce drought-responsive genes. An increase in the histone modification H3 and decreases in H3K9me2 and constitutively transcribed reference genes *PROTEIN PHOSPHATASE 2 A* (*pp2A*) and *ACTIN* were due to drought stress. Contrary, H3K4me3 exhibited a specific increase at the beginning and middle of the coding region of the *HSP17* gene, showing that this gene is essential for drought-responsive transcription (Temel et al., 2017). Seedlings originating from plants under drought stress revealed a faster growth rate due to an elevated level of DNA methylation at the promoter region of *HvCKX2.1*. Likewise, the fast emergence of shoots from these plants may be explained by the cytokinin ribosides accumulation, the known cytokinin-oxidase substrates. *ProHvCKX2.1* methylation and rapid shoot emergence have been confirmed in transgenic plants with modified grain ABA (Surdonja et al., 2017). In barley leaves, *HvCBF2* was a transcriptional activator that promotes the expression of a reporter gene under the control of the *HVA1*s (Xue, 2003). Under drought, salt, and ABA treatments, the *HvDRF1* gene was upregulated in barley leaves, roots, and embryos during seed development. The *HvDRF1* transcripts encode three different forms of AP2 genes, two of which are encoded by AP2 (Xue and Loveridge, 2004).

MicroRNAs (miRNA) regulate stress response genes (Shukla et al., 2008). In barley several miRNA families have already been recognized that participate in response to drought stress including; ABA, cell growth, auxin signaling, antioxidant, osmotic regulation, photosynthesis, and respiration (Fard et al., 2017; Yang et al., 2019). A genome-wide analysis detected 12 novel miRNAs as drought-responsive in Tibetan wild barley (Qiu et al., 2020). Deep sequencing indicated a difference in miRNA expression profiles between Golden Promise cultivated barley and water-stressed barley (Hackenberg et al., 2015). Hv-miR827, miRNA could enhance drought tolerance in four barley cultivars and identified four miRNAs that were differentially accumulated in vegetative cells (Ferdous et al., 2017). Similar analyses were conducted by (Fard et al., 2017) comparing the expression patterns of miRNA between two barley cultivars under drought stress. The *Triticeae* specific hvu-miRX miRNA targeted a range of genes in barley that conferred drought tolerance (Zhou et al., 2018). Several miRNAs were differentially expressed after dehydration, including miR171, miR156, miR408, and miR166 (Kantar et al., 2011). Among the drought-responsive miRNAs, the miR166 transcription factor for the class-III homeodomain-leucine zipper (*HD-Zip III*) is essential for axillary meristem initiation, lateral root development, and leaf polarity (Bouaalem et al., 2008). For plants to adapt to stress, miRNA levels are regulated differently in different tissues. As an example, miR166 is upregulated in leaves, while miR156a, miR171, and miR408 are reduced in barley roots during dehydration. MiR166 was induced in barley leaves but downregulated in roots during dehydration (Kantar et al., 2011). MiR393 has several functions in stomatal density, seedling growth regulation, and auxin signaling level in root in response to aluminum levels and drought stress tolerance (Yuan et al., 2019). It might also be responsible for ABA biosynthesis under drought stress (Yuan et al., 2019). So far, there is limited knowledge of miRNAs expression profiles and their target genes in the wild barley roots. It should be possible to identify miRNA target pathways that have cell or tissue-specific functions under water deficiency by elucidating genes related to drought-responsive miRNAs in individual cells. Increasing our knowledge of miRNA's role in drought tolerance can lead to the utilization of miRNA-mediated gene regulation to increase plant drought tolerance. Hence, a breeding program designed to increase the miRNA copy numbers may produce germplasm more tolerant to abiotic stresses.

The post-translational modification of proteins is also crucial for drought-stress responses. It has already been emphasized that phosphorylation cascades are important to signal transduction. Transcriptional factors are also affected by modifications to their proteins in terms of conformation, activity, and localization (Kline et al., 2010). An important role for post-translational protein modification in hormonal signaling is ubiquitin-dependent protein degradation (Santner and Estelle, 2009). In the Lubuski × CamB barley population, about 90% of the annotated genes involved encoding of the E3 ubiquitin ligases, which allow specificity toward the water-deficit pathway (Ogrodowicz et al., 2017). A study of barley TILLING mutants with different alleles of *HvABI5* revealed that *HvABI5* can regulate drought responses and might also play a role in ABA signaling regulation. HvABI5 also acts differently in drought response and regulating seed germination (Collin et al., 2020). Additionally, an F-box protein (FBL21) associated with OA was detected (Wehner et al., 2015). ABA mediates drought stress responses in *Arabidopsis thaliana* through these proteins, which are ubiquitin-related (Lyzenga and Stone, 2012). Likewise, an association between *1-aminocyclopropane-1-carboxylate oxidase* (*ACO1*) and OA was observed to inhibit ethylene biosynthesis and thus limit leaf growth, which leads to drought tolerance (Wehner et al., 2015). Additionally, ABA receptor (*PYL5*) activates ABA signaling and the drought stress-related protein, dehydrin (DHN), and was related to BY and stomatal closure and germination inhibition (Choi et al., 1999; Rizhsky et al., 2002). This protein belongs to the late embryogenesis abundant (LEA) family, which upregulates response to drought stress in wheat (Rampino et al., 2006). Under drought stress, an ethylene responsive protein was correlated with BY (Wehner et al., 2015). Transcriptional factor *ERF062* displays gene expression regulation by stress factors and by senescence of leaves in *Arabidopsis thaliana* (Koyama et al., 2013). The cation/H $^{(+)}$ antiporter 2 (CHX) was identified as linked with the rate of electron transport at photosystem II (ETR) (Wehner et al., 2015), that is essential for maintaining pH gradients in the cell. This protein is essential to conserve ionic balances in cellular and intercellular in *Arabidopsis thaliana* under drought stress (Song et al., 2008).

4.3. Complexly inherited responses to drought

Quantitative trait loci (QTL) mapping is a technique for associating variation in genetic expression of traits with particular regions of the genome to isolate as selected genes or genomic regions (Abiola et al., 2003). Genetic maps of QTL for drought-associated traits have been generated for many barley mapping populations (Abou-Elwafa, 2016; Jabbari et al., 2018; Pham et al., 2019; Swamy et al., 2013; Varshney et al., 2012; Wojcik-Jagla et al., 2018; Zhang et al., 2017). The main goal of these studies was to detect genomic regions that contain genes

involved in morphological and physiological responses to abiotic stresses. Although biparental population and genome-wide association studies have identified a large number of traits associated with genomic regions involving drought stress responses, identifying specific genes controlling these responses has been difficult.

4.3.1. Yield and yield components

The results of (Cai et al., 2020) suggest that responses to various biochemical measures of seedling tolerance to terminal drought are optimal in some wild barley accessions, but most farmers would not consider planting wild barley. Our concept of cultivated barley has changed considerably since the crop was first domesticated. Cultivated barley needs many desirable attributes to produce high-quality forage and/or grain in water stressed environments. The yields of barley crop are the product of severals yield components. Yield components measure the number of fertile tillers per unit area, number of kernels spike, and kernel weight. Some traits such as premature senescence of leaves affects all yield components and can cause rapid ripening of older plants, and post-ripening collapse of stems. It was observed in older leaf blades of drought susceptible seedlings (Cai et al., 2020). An extreme example of a short grain-fill period is the premature ripe (*pmr1*) mutant, which causes plant senescence soon after anthesis and leads to straw collapses and very thin kernels (Franckowiak et al., 2016a). The opposite extreme is observed in seedlings and adult plants having the stay-green trait (Gous et al., 2013). Spikes mature before stems and leaf sheathes have completely lost their chlorophyll.

Other morphological traits of barley affect consumer acceptance and pricing of barley fodder or grain. For example, long rachilla hairs, controlled by alleles at the *Srh1* locus, increase the amount of grain dust produced during harvest and grain handling. The presence of barbs on the awns (*Raw1*, *Raw2*, and *Raw3*) and lemma veins (*Gth1*) can change the relative value of barley hay or straw. The study of progeny from crosses between wild and cultivated barley and multi-parental population under several environmental conditions have identified many QTL associated with barley grain yield (Table 2). These studies have identified many critical chromosomal regions containing genes for growth-related traits such as early heading, which is a drought escape mechanism that interacts with environments and plays a major role in the expression of yield components.

Table 2
Studied populations for drought associated traits in barley.

Population	Source	Reference
Germplasm	Wild species; *H. spontaneum*	(Baum et al., 2003; Forster et al., 1997)
	Breeding lines and cultivars	(González and Ayerbe, 2009)
	Accessions	(Knüpffer, 2009)
S42IL	Accession ISR42–8 in the cultivar Scarlett background	(Naz et al., 2014)
RILs	Lubuski × CamB	(Mikolajczak et al., 2017; Ogrodowicz et al., 2017)
	Tadmor x Er/Apm	(Teulat et al., 2001)
	"Arta" x *H. spontaneum 41–1*	(Baum et al., 2003)
DH	'Scarlett' x 'ISR42–8'	(Honsdorf et al., 2017; Liu et al., 2015; Obsa et al., 2016; Wang et al., 2016)
	Huaai 11 x Huadamai	
	Henni x Meltan	
	Igri x Triumph	(Laurie et al., 1994)

S24IL, wild barley introgression lines; RILs, recombinant inbred lines; DH, doubled haploid.

4.3.1.1. Kernels per spike. Spike type is the main trait determining number of fertile spikelets per spike. Six-rowed cultivars (*vrs1.a*) have three fertile spikelets per rachis node while two-rowed cultivars (*Vrs1.b* and *Vrs1.t*) have one. Two-rowed barleys originated before six-rowed barley and have traditionally been considered more drought tolerant than six-rowed barleys (Harlan, 1968), but six-rowed cultivars are grown in production areas where frequent drought occurs. The deficiens allele (*Vrs1.t*) from Ethiopia greatly reduces the size of sterile lateral spikelets and is now present in some two-rowed cultivars. This change in spike morphology apparently improves tolerance to drought by reducing the number of kernels per spike and the amount of vegetative tissue in spikes.

Early heading enhances drought escape by reducing the number of fertile rachis nodes (the 2-rowed types usually have higher tiller than 6-rowe). Information on the effects and interactions of winter growth habits and early maturity genes was reviewed by (Fernandez-Calleja et al., 2021). Combinations of these genes deterimine days to head or spike emergence from the boot. The Early maturity 1 (*Eam1*) or photoperiod response gene H1 (*Ppd-H1*) locus was the first early heading gene described in barley (Griffee, 1925; Laurie et al., 1994). The dominant allele, present in wild barleys and many fall sown spring and winter barleys causes earlier heading. Mansour et al., (2014) identified the *Eam1* locus as a QTL in the 'Steptoe' / 'Morex' population near the SNP 11_21015 molecular marker, which is located in the short arm of chromosome 2 H near BOPA2_12_30871 at 29,127,021 bp (Table 3) based on Barley 50k iSelect SNP Array (Bayer et al., 2017). Woodward, 1957 found a dominant early maturity gene in 2 H linked to the spike type (*vrs1*) locus, which was later identified as Early maturity 6 (*Eam6*) (Robertson et al., 1965), earliness per se 2 S (*eps2S*) (Laurie et al., 1995), praematurum-c (*mat-c*) (Søgaard and von Wettstein-Knowles, 1987), or *Hordeum vulgare* CENTRORADIALIS (*HvCEN*) (Comadran et al., 2012; Matyszczak et al., 2020). (Comadran et al., 2011) identified using autumn-sown Mediterranean barleys, a QTL associated with earlier heading and higher yield in the centromeric region of 2 H near the *Eam6* locus. Over 18 trials in Mediterranean environments, the most frequently identified QTL for yield and early flowering was near the *Eam6* locus with a positive effect associated with the parent 'Nure' of the biparental population (Tondelli et al., 2013). A QTL for grain yield in 2 H near the *Eam6* locus was found in a biparental mapping population sown in the autumn (Mansour et al., 2014), but no association with heading date was observed. In introgression lines from a cross to wild barley, fewer kernels per spike were associated with the *Eam1* locus (Li et al., 2020a) and with both the *Eam1* and *Eam6* loci (Schmalenbach et al., 2009; Zahn et al., 2020). Epistatic interactions involving photoperiod response genes *Eam6*, *Ppd-H2*, and *VRN-H3* (*HvFT1*) contributed to early heading in the North American cultivar 'Logan' (Casas et al., 2021). A highly significant QTL for heading date and grain yield was associated with the spring growth habit 2 (*Sgh2*) or vernalization H1 (*Vrn-H1*) locus in 5 H (Mansour et al., 2014). The first evidence for the existence of this maturity gene was published by (Wexelsen, 1934). The gene was named Early maturity 5 with the assigned gene symbol being *Eam5*. The locus is very close to the *Vrn-H1* locus and was identified as *Hordeum vulgare* phytochrome C with an early allele given the symbol (*HvPhyC-e*) (Nishida et al., 2013; Szucs et al., 2006). Possible, origins of

Table 3
QTL for drought-related trait in barley under drought stress.

Traits	Linkage group	References
Yield releated		
Grain yield	1 H, 2 H, 3 H, 4 H, 5 H, 6 H, 7 H	(Gudys et al., 2018; Mora et al., 2016; Tondelli et al., 2006; Varshney et al., 2012; von Korff et al., 2008)
Kernel weight	2 H, 4 H, 5 H, 6 H	(Honsdorf et al., 2017; Mikolajczak et al., 2017; Varshney et al., 2012)
Grain weight per plant	2 H, 3 H, 4 H, 5 H, 6 H, 7 H	(Mikolajczak et al., 2017)
Grain filling period	4 H	(Honsdorf et al., 2017)
Grain number spike	3 H, 5 H, 6 H	(Jabbari et al., 2018)
Tiller number	3 H, 4 H	(Honsdorf et al., 2014a, 2014b)
Number of productive tillers	2 H, 5 H	(Mikolajczak et al., 2017)
Morphological		
Date of heading	2 H, 4 H, 5 H.3, 7 H	(Borràs-Gelonch et al., 2012; Comadran et al., 2011; Mansour et al., 2014; Muñoz-Amatriaín et al., 2011; Ogrodowicz et al., 2017; Ren et al., 2010)
Plant height	All chromosomes	(Honsdorf et al., 2014a, 2014b) (Mikolajczak et al., 2017)
Lateral spike characteristics	2 H, 3 H, 4 H, 5 H, 7 H	(Mikolajczak et al., 2017)
Grain kernel discoloration	4 H, 7 H	(Jia et al., 2021)
Main spike characteristics	1 H, 2 H, 3 H, 4 H, 5 H, 7 H	(Mikolajczak et al., 2017)
Flag leaf length	2 H, 3 H, 4 H, 5 H	(Jabbari et al., 2019)
Flag leaf width	2 H, 3 H, 4 H, 5 H	(Jabbari et al., 2019)
Physiological		
Osmotic adjustment	1 H, 2 H, 4 H, 5 H, 7 H	(Teulat et al., 2001a, 2001b)
Stomatal and gas exchange	All chromosomes	(Liu et al., 2017)
Water use efficiency	4 H, 6 H	(Honsdorf et al., 2014a, 2014b)
Relative water content	2 H, 5 H, 6 H, 7 H	(Diab et al., 2004; Gudys et al., 2018; Wojcik-Jagla et al., 2018)
Chlorophyll	1 H, 2 H, 4 H, 6 H, 7 H	(Guo et al., 2007; Jabbari et al., 2019; Rapacz et al., 2019)
Biochemical		
Proline	3 H, 4 H, 5 H, 6 H	(Sayed et al., 2012)
Grain carbon isotope discrimination	2 H, 3 H, 6 H, 7 H	(Diab et al., 2004)
Hormone content	2 H, 3 H	(Gudys et al., 2018)
Antioxidants;		
α-tocopherol	6 H	(Gudys et al., 2018; Templer et al., 2017)
γ-tocotrienol	3 H	(Gudys et al., 2018; Templer et al., 2017)
Photosynthetic	2 H, 4 H, 5 H 7 H	(Gudys et al., 2018; Salter et al., 2020; Wojcik-Jagla et al., 2018)
Rubisco		(Salter et al., 2020)

the *Eam5.x* mutant are winter barley (Pankin et al., 2014; Szucs et al., 2006), Japanese cultivars (Nishida et al., 2013), and ICARDA breeding lines from CIMMYT in Mexico (Pankin et al., 2014). Based on 50k marker haplotypes, the *Eam5.x* mutant is also present in Ethiopian landraces. A strong interaction between the *Eam1* and *Eam5* genes was reported under short-day conditions (Pankin et al., 2014). The photoperiod response H2 (*Ppd-H2*) (Laurie et al., 1995) or *Hordeum vulgare* flowering time 3 (*HvFT3*) (Kikuchi et al., 2009) promotes earlier flowering. The short-day *Early maturity 7* (*eam7*), was observed in ICARDA breeding lines from CIMMYT in Mexico, as another early mature gene (Gallagher, 1991). This earliness gene was first reported by (Ramage and Suneson, 1958) and causes early heading under both short- and long-day conditions (Stracke and Börner, 1998). Based on 50 K marker haplotypes, the *eam7.g* allele is present in Ethiopian landraces and ICARDA breeding lines from CIMMYT in Mexico. A QTL for late heading under short-day conditions was found in the terminal region 1HL of winter barleys (Malosetti et al., 2011; Pillen et al., 2003; Rode et al., 2011; Wang et al., 2014) and tentatively assigned the locus to name Early maturity 11 (*eam11*). Even though many early maturity mutants have been induced (Lundqvist, 1992) and many mapping population-specific QTL for heading have been reported in many mapping populations, data on their drought responses are limited.

A reduced seed set is one of the responses of barley to moisture deficits. Cereals are highly vulnerable to water deficit during reproductive development, which starts with the transformation of a vegetative meristem into inflorescence primordia and ends with the physiological maturity of seeds (Boyer and Westgate, 2004; McLaughlin and Boyer, 2004; Saini and Westgate, 2000). The most venerable stages during meiosis and anthesis (Saini and Westgate, 2000). When water deficit occurs, invertase activity and sugar-responsive genes are like limiting enzymes during reductive development and grain filling (Boyer and Westgate, 2004; McLaughlin and Boyer, 2004). Differential impacts of these water-deficient effects can be observed in barley grown under glasshouse or greenhouse conditions where low light intensities, night temperatures above 20 °C, and watering techniques for pot-grown plants often cause periodic stresses. Anthesis may be delayed until terminal spikelets are emerge from the leaf sheath. Observiations indicated that some breeding lines with the early maturity 5 gene (*Eam5.x*) delay anthesis until the terminal spikelets are starting to emerge from boot. This suggests taht the spikes of stress-tolerant plants are more mature before anthesis occurs. Development of anthers in terminal and basal spikelets is more normal in stress-tolerant plants. Late tillers also exhibit less sterility. And culms do not collapse as plants approach maturity. Using these responses as a guide crosses may be made with more stress-tolerant parents can be saved.

4.3.1.2. Kernel weight. Kernel size and plumpness are often made as measures of response to drought stress (Sallam, et al., 2019b). Kalladan et al., (2013) found 11 QTL associated with the KW, at two positions qTGW3.1 and qTGW3.2, further the HS584 (*H. vulgare ssp. spontaneum*) contributed to the increase in KW under control conditions. Ren et al., (2013) identified two QTLs for grain weight per ear on chromosomes 4 H and 7 H. Both studies may have detected a common QTL for 7 H. In greenhouse experiments, Mikolajczak et al., (2017) examined barley RILs under water-deficient conditions and found QTL for grain weight per ear on 2 H which is similar to QTL QGWE 0.2 H.2 previously detected (Honsdorf et al., 2017). A study by Lakew et al. (2012) described four QTL for KW on chromosome 7 H. Two of them could be at the QTLs found by (Honsdorf et al., 2017). Trait-reducing effects within the same chromosomal area have been reported on 7 H using the S42 population (von Korff et al., 2006). QTL on 2 H, 4 H, and 7 H were also identified by Mora et al., (2016) and Arriagada et al. (2017). Introgression lines derived from the cross between wild barley accession ISR42–8 (*Hsp*) and the German malting cultivar 'Scarlett' were used to identify QTL controlling grain-filling under terminal drought stress applied 10 days after anthesis (Honsdorf et al., 2017). Two QTL for increased KW in 2 H and 4 H from wild barley provide promising

candidates for improving yield under the water deficiency stress. The QTL in 2HS of S42IL-108 decreased heading date by 21 days, plant height, and biological yield and overlapped the *Eam1* (*Ppd-H1*) locus for a strong long-day response. The QTL in S42IL-121 are located in the centromeric region of 4 H and showed drought tolerance during the juvenile development (Honsdorf et al., 2014b). Among the five QTLs identified in the LCam and MCam populations for grain yield, three were found on chromosome 2 H (Mikolajczak et al., 2017). QTL for the heading stage, grain weight, number of grains per spike, grain yield, and KW in the LCam population were located at the same postion at 10.74cM, near markers previously associated with both earliness and grain yield (Li et al., 2005). Most QTL for increased KW found in progeny from crosses to wild barley were contributed by the cultivated parent (Honsdorf et al., 2017, Kalladan et al., 2013, Lakew et al., 2012), but those from wild barley were often associated with early heading dates (Mora et al., 2016).

Grain-filling period has been related to grain protein content (Jukanti et al., 2008), with a low grain protein content locus in 6HL. The *gpc1.c* allele is associated with delayed whole-plant senescence, which presumably extends the grain-filling period and increases grain yield in six-rowed barley. A second low grain protein content variant, *gpc2*, was identified in 5HL (Emebiri, 2015). When the two low protein genes are combined, lines had grain protein levels up to 4% lower than that of the standard check over environments (Emebiri, 2015).

In six-rowed spring barley grown in the Upper Midwest of the USA, several genes for increasing grain size and diameter have accumulated to offset the decrease in grain size caused by the six-rowed spike type. As a result, the six-rowed parent in bi-parental mapping populations frequently contributes QTL for grain weight (Marquez-Cedillo et al., 2000). Drought tolerance responses of six-rowed cultivars were better than those of two-rowed ones (Samarah et al., 2009). Two QTL for reduced kernel length from the Australian cultivar 'Vlamingh' were mapped in 5 H and 2 H (watt et al., 2019). In two-rowed barley bred for the Upper Midwest, morphological expressed genes that might increase kernel width have accumulated. They might include small lateral spikelets 1 (*sls1*), extra floret-a (*flo-a*), and triple awn 1 (*trp1*) (Druka et al., 2011).

4.3.1.3. Biomass yield. To identify genomic segments of wild barley that contribute to biomass production, wild barley accessions were backcrossed in two-rowed malting barley cultivars. A genome-wide association study (GWAS) study of lines from such crosses discovered a large QTL for biomass yield under drought conditions near the Semidwarf 1 (*sdw1*) locus (Varshney et al., 2012). Many QTL for biomass yield and seedling drought tolerance were found in a GWAS study of winter barleys (Wehner et al., 2015). In wild barley introgression lines, seedling drought tolerance was measured as plant biomass and leaf senescence (Honsdorf et al., 2014a, 2014b). Line S42IL-129 with a small introgression in chromosome 6 H was not affected by severe drought stress when compared with 'Scarlett'(Honsdorf et al., 2014b). When wild barley introgression was tested in field experiments for drought tolerance (Lakew et al., 2012), QTL in chromosomes 2 H and 6 H were associated with the biomass yield. Backcross-derived lines from the malting barley cultivar 'Harrington' and the wild barley 'Caeserea 26–24' were evaluated under rainfed conditions (Arriagada et al., 2017; Mora et al., 2016) and QTL associated with biomass were mapped in 2 H, 5 H, and 7 H.

4.3.2. Morphological mechanisms of drought stress tolerance

Plant height reduction genes of 'Green Revolution' in wheat and rice are known as vital players in biosynthesis and signaling of gibberellic acid (GA). A rice *SD1* and wheat *Rht-1* gene mutations, which shortened culms and increased ears weights and grain yields under high fertility levels (Dockter and Hansson, 2015). Studies in barley have identified many genes and mutants for decreased culm length, but few are used or well described. Enhanced lodging resistance and yield can be achieved by barley upright-growth habit, for example, the *uzu1.a* gene in more densely populations (Chono et al., 2003; Janeczko et al., 2016).

The most widely used semidwarf gene in barley is the semidwarf 1 (*sdw1 or denso*) mutant (Vagner Haahr, 1976). Besides reducing plant height, the *sdw1* mutant has pleiotropic effects on many agronomic traits including delayed heading (Yin et al., 1999). The low expression levels of the *Hv20ox2* gene in *sdw1* mutants reduce gibberellin accumulation, limiting apical meristem growth and promoting the formation of more tillers (Jia et al., 2009; Saisho et al., 2004). The *sdw1.d* mutant is located in 3HL at about 113.07 cM and near the 50k marker JHI-Hv50k-2016–205550 based on the phases for 50k markers near the mutant gene (Table 4). Breeding programs in North America, Europe, Japan, and Australia have focused on *sdw1* loss-of-function alleles, which is an ortholog of the rice 'Green Revolution' gene *SD1* encoding a *GA20ox-2* oxidase in the gibberellic acid (GA) hormone biosynthetic pathway (Jia et al., 2011). Other semidwarf genes deployed in barley include the Semidwarf 4 (*sdw4*) mutant in 7HL from China (Franckowiak et al., 2016a) and the induced mutant *Erectoides-k* (*ert-k*) in 6HL from Sweden (Kristensen et al., 2016).

Progeny from biparental crosses of widely related cultivars can facilitate the detection of QTL for plant height genes. RILs from the cross of the European cultivar 'Maresi' to the Syrian line 'CamB' were evaluated for agronomic traits under moisture stress in greenhouse experiments (Mikolajczak et al., 2017). The most significant QTL for the main stem length was located near SNP 1865–396, which is in 2HS near the *Eam1* locus. The second most important QTL for plant height was located in 3HL near SNP 5260–462, which is near the *sdw1* locus. A third plant height QTL was located in 5HL near the *Eam5* and *Vrn-1 H* loci, but no evidence for vernalization response was reported (Mikolajczak et al., 2017). The earliness genes *Eam1* and *Eam6* had a pleiotropic effect on plant height in wild barley introgression lines (Wang et al., 2010). In a GWAS study of agronomic traits in a worldwide collection of most barley cultivars, many QTL were near loci known to alter plant height and heading date (Pasam et al., 2012). Major effect QTL for plant height involved SNP near the Breviaristatum-e (*ari-e*), Dense spike 1 (*dsp1*), *Eam1*, *Eam5*, *Eam6*, *ert-k*, *sdw1*, *sdw4*, and Uzu 1 (*uzu1*) loci (Table 5). In progeny from a winter barley cross grown in Italy and Spain, QTL for plant height was near the Aluminum tolerance 1 (*Alp1*), *dsp1*, *Eam1*, and Salt tolerance 1 (*Slt1*) loci (Mansour et al., 2014). Three major effect of QTL for plant height was identified in the progeny of a three-way cross near the *Eam6*, *sdw1*, and *ari-e* loci in 2HS, 3HL and 5HL, respectively (Malosetti et al., 2011). In a population of RILs from the cross of Tadmor and ER/Apm under Mediterranean conditions, QTL for plant height and heading date were found near the *Eam6*, *sdw1*, and *Eam5* loci (von Korff et al., 2008).

Peduncle length may be an important trait in drought tolerance because the difference in peduncle diameter and elongation is observed in wild barley. Thicker peduncle tissues were associated with reduced lodging (Zahn et al., 2020). Since the peduncle is much longer in wild barley than in cultivated barley (Lakew et al., 2012; Mora et al., 2016), selection for this trait in semidwarf barleys might improve drought tolerance.

Table 4
Genes contributing to expression of drought tolerance or consumer acceptance in barley.

Traits / Locus Names	Locus symbols	Phenotypic expression	Allele	Chr	cM	Nearby mol. marker	Position (Mb) (v1)	BGS No	Reference
Eceriferum-yy (Glossy spike 1)	*Cer-yy*, *Gle1*	Reduced surface waxes on the spike	*Gle1.a*	1 H	1.38	SCRI_RS_142714	1275213	BGS 536	(Lundqvist and Von Wettstein-Knowles, 1982)
Early maturity 1	*Eam1, Ppd-H1*, *HvPRR37*	Early heading under long-day conditions	*Eam1.a*	2 H	38.60	BOPA2_12_30871	29127021	BGS 065	(Laurie et al., 1994)
Early maturity 6	*Eam6*, *HvCEN, mat-c, eps2S*	Constitutive early to very early heading	*Eam6.h*	2 H	69.55	BOPA1_2634–2228	520261753	BGS 098	(Jayakodi et al., 2020)
Reaction to Barley Yellow Dwarf Virus 2	*Ryd2*	Resistance to barley yellow dwarf virus	*Ryd2.b*	3 H	51.68	JHI-Hv50k-2016–164264	45314385	BGS 123	(Collins et al., 1996)
Aluminum tolerance 1	*Alp1*, *HvACCT1*	Acid soil tolerance	*Alp1.a*	4 H	57.62	BOPA1_4276–1082	537437603	BGS 188	(Fujii et al., 2012)
Smooth awn 1	*raw1*	Awn barbs reduced in size and density	*raw1.a*	5 H	106.15	JHI-Hv50k-2016–325667	577088889	BGS 312	(Milner et al., 2019)
Early maturity 5	*Eam5*, *HvPHYC*	Early heading in short-day environments	*Eam5.x*	5 H	125.23	JHI-Hv50k-2016–335111	597573379	BGS 348	(Pankin et al., 2014)
Smooth awn 2	*raw2*	Semi-rough awn, reduced awn barbs	*raw2.b*	5 H	134.12	BOPA1_407–259	612799247	BGS 340	(Franckowiak et al., 2016a)
Grain protein content 1	*gpc1*, *HvMAN-1*	Lower grain protein content (Karl)	*gpc1.c*	6 H	54.10	SCRI_RS_119674	51410691	BGS 276	(Falcon et al., 2019)
Smooth awn 3	*raw3*	Awn barbs reduced in size and density	*eaw3.c*	7 H	19.22	JNI-HV50k-2016–452461	19656334		(Milner et al., 2019)
Reaction to *Puccinia striiformis 4*	*Rps4*, *Yr4*	Resistance to stripe (yellow) rust	*Rps4.d*	1 H	26.32	BOPA1_4226–570	15607329		(Chen et al., 1994)
Small lateral spikelets 1 (from six-rowed)	*sls1*	Small terminal lateral spikelets (two-rowed)	*sls1.a*	1 H	50.30	BOPA2_12_30110	374864786	BGS 227	(Franckowiak and Lundqvist, 2018)
Photoperiod response-H2	*Ppd-H2*, *HvFT3*	Constitutive early heading	*Ppd-H2*	1 H	88.54	JHI-Hv50k-2016–39891	506607541		(Kikuchi et al., 2009)
Reaction to *Puccinia hordei* 15	*Rph15*	Resistance to leaf rust	*Rph15.ad*	2 H	53.26	SCRI_RS_206586	52372976	BGS 096	(Chen et al., 2021)
Reduced kernel length	*qGL2H*	Shorter kernels	*qGL2H*	2 H	72.64	JHI-Hv50k-2016–100468	608070614		(Watt et al., 2020)
Absence of lemma barbs 1	*Gth1*	Barbs on the lateral lemma veins	*gth1.b*	2 H	76.30	JHI-Hv50k-2016–101424	616727336	BGS 069	(Smith, 1951)
Reaction to *Heterodera avenae* 2	*Rha2*	Resistance to cereal cyst nematode	*Rha2*	2 H	103.48	JHI-Hv50k-2016–111588	680461040		(Van Gansbeke et al., 2019)
Reaction to *Pyrenophora graminea* 1	*Rdg1*	Resistance to barley stripe	*Rdg1.a*	2 H	173.53	JHI-Hv50k-2016–141352	754503750		(Biselli et al., 2010)
Reaction to *Rhynchosporium commune*1	*Rrs1*	Resistance to scald	*Rrs1.a*	3 H	53.42	JHI-Hv50k-2016–164528	50399344		(Graner and Tekauz, 1996)
Semidwarf 1 (denso mutant)	*sdw1* (*denso*)	Semidwarf, more tillers, delayed heading	*sdw1.d*	3 H	113.42	JHI-Hv50k-2016–205545	634624230	BGS 518	(Xu et al., 2017)
Triple awn 1	*trp1*	Three lemma awns to slight awn branching	*trp1.a*	4 H	52.67	SCRI_RS_130433	47783030	BGS 061	(Druka et al., 2011)
Reaction to *Puccinia hordei* 20	*Rph20*	Adult plant resistance to leaf rust	*Rph20.ai*	5 H	21.24	JHI-Hv50k-2016–280910	9289018	BGS 717	(Hickey et al., 2012)
Grain protein content 2	*gpc2*	Lower grain protein content (Bowman)	*gpc2.d*	5 H	44.99	BOPA1_7140–595	439204512		(Emebiri, 2015)
Reduced kernel length	*qGL5H*	Shorter kernels	*qGL5H*	5 H	48.43	JHI-Hv50k-2016–307644	482478497		(Watt et al., 2019)
Six-rowed spike 1 (deficiens)	*srh1*	Short branched rachilla and rachis hairs	*srh1.a*	5 H	81.30	SCRI_RS_10386	552724040	BGS 321	(Javaid et al., 2009)
Reaction to *Heterodera avenae* 4	*Rha4*	Resistance to cereal cyst nematode	*Rha4*	5 H	138.44	BOPA2_12_10904	622368515		(Barr et al., 1998)
Early maturity 7	*eam7*, *HvCO7*	Early heading under short-day conditions	*eam7.g*	6 H	20.36	BOPA1_1066–2110	16132372	BGS252	(Stracke and Börner, 1998)
Salt or salinity tolerance 1 (tentative)	*Slt1*	Less biomass reduction under stress	*Slt1.a*	6 H	59.21	JHI-Hv50k-2016–400174	37465259		(Long et al., 2013)
Reaction to *Pyrenophora teres* f. *teres* 5	*rpt5.f*	Resistance to net form net blotch	*rpt5.f*	6 H	59.71	BOPA2_12_30857	384634321	BGS 272	(Clare et al., 2020)
Erectoides-k (Pallas semidwarf)	*ert-k*	Semi compact spike, reduced culm length	*ert-k.32*	6 H	65.28	JHI-Hv50k-2016–405806	431718396	BGS 562	(Skov Kristensen et al., 2016)
Extra floret-a (Bowman)	*flo-a*	Extra spikelet below central spikelet	*flo-a.1*	6 H	74.18	BOPA2_12_10596	504918359	BGS 182	(Lundqvist, 2015)
Reaction to *Puccinia graminearum*1	*Rpg1*	Adult plant resistance to stem rust	*Rpg1.a*	7 H	1.08	SCRI_RS_200895	2351163	BGS 511	(Brueggeman et al., 2006)
	Rpt4		*rpt4.e1*	7 H	130.44	SCRI_RS_93571	625768441		(Williams et al., 2003)

(*continued on next page*)

Table 4 (*continued*)

Traits / Locus Names	Locus symbols	Phenotypic expression	Allele	Chr	cM	Nearby mol. marker	Position (Mb) (v1)	BGS No	Reference
Reaction to *Pyrenophora teres* f. *maculata* 4		Seedling resistance to spot form net blotch							
Semidwarf 4 (China)	*sdw4*, *qCUL*	Semidwarf with shorter low culm internodes	*sdw4.ba*	7 H	143.44	JHI-Hv50k-2016–509519	638051791	BGS 045	(Sameri et al., 2009)
Breviaristatum-e	*ari-e, HvDep1*	Semidwarf, short awn, salt tolerant	*ari-GP*	5 H	52.30	JHI-Hv50k-2016–307744	482690418	BGS 328	(Wendt et al., 2016)
Early maturity 8	*Eam8, mat-a, HvELF3*	Very early heading, photoperiod insensitive	*eam8.k*	1 H	138.95	SCRI_RS_150786	550268409	BGS 214	(Zakhrabekova et al., 2012)
Early maturity 11	*eam11*	Late heading in winter barley	*eam11.o*	1 H	142.74	BOPA1_4057–2114	555618220		(Malosetti et al., 2011)
Reaction to Cochliobolus sativus 5	*Rcs5*	Resistance to spot blotch	*Rcs5.e*	7 H	31.75	SCRI_RS_114639	30199770		(Zhou and Steffenson, 2013)
Uzu 1	*uzu1, HvBRI1, HvDWARF*	Semidwarf, short awn, heat sensitive	*uzu1.a*	3 H	57.10	JHI-Hv50k-2016–166035	104710272	BGS 102	(Dockter et al., 2014)
Vernalization H1	*Vrn-H1, Sgh2*	Cold treatment not required, spring growth habit	*Vrn-H1*	5 H	119.72	JHI-Hv50k-2016–335334	597724697	BGS 309	(Fu et al., 2005)
Vernalization H2	*vrn-H2, sgh1*	Cold treatment not required, spring growth habit	*vrn-H2*	4 H	120.73	JHI-Hv50k-2016–272187	638052199	BGS 163	(Karsai et al., 2005)

"v1" Volume1 of the barley reference genome.

4.3.3. Physiological mechanisms of drought stress tolerance

In barley, QTL analyses for many physiological and biochemical related traits have been conducted under drought stress and/or rainfed conditions (Table 3).

In a study aiming to identify QTL for developmental morphological and physiological traits from wild barley using the high-throughput phenotyping platform ''The Plant Accelerator'', Adelaide, Australia (Honsdorf et al., 2014a), a QTL for decreased flag leaf area was detected in 2 H. Two QTL for tillers were found with the allele from 'Scarlett' in 3 H near the *sdw1* locus increasing tiller number and the allele in 4 H near the *vrn-H2* locus from wild barley. Improved growth was associated with a QTL in 4HL from wild barley (Honsdorf et al., 2014). A QTL for more biomass production, previously named QHei.S42IL-4 H.a height (Schmalenbach et al., 2009), was observed in 4HL (Honsdorf et al., 2014a).

RILs derived from a cross between Er/Apm (a moderately drought-tolerant) and Tadmor (a drought-tolerant) were evaluated in the growth chambers under drought conditions. QTL for RWC under well-watered conditions were located in 2 H and 7 H (Teulat et al., 2001a, 1998), whereas those observed under drought stress conditions were found in 5 H (Teulat et al., 2001a, 1998). Leaf water content and osmotic potential were associated with a QTL on chromosome 7 H (Teulate et al., 2001). The 7 H QTL is near the *Acl3* locus (Hansen and von Wettstein-Knowles, 1991). *Acl3* gene encodes barley acyl carrier protein III, which is regulated by the fatty acyl chain synthesis (Teulat et al., 1998). Under stress conditions, *ACl3* may protect and maintain membrane fluidity, which may improve the drought tolerance (Hansen and von Wettstein-Knowles, 1991). For studying the transpiration efficiency, the association between this QTL and carbon isotope discrimination was demonstrated (Teulat et al., 2002). In Mediterranean field condations, QTL for RWC were also mapped, six QTLs identified were founded in 1 H, 2 H, 4 H, 5 H, 6 H, and 7 H for three of the five environments studied (Teulat et al., 2003). The most consistent QTL was found in the long arm of chromosome 6HL controlling RWC. This region was previously implicated in root water content and leaf osmotic potential under osmotic adjustment and water stress (Teulat et al., 1998). According to Jabbari et al., (2021) chlorophyll content in barley plants under water-deficit conditions was associated with QTL in 1 H, 2 H, 3 H, and 4 H. One QTL was detected in 2 H for catalase activity under well-watered conditions, and two QTL in 3 H and 5 H were identified for catalase activity under drought stress conditions (Gudys et al., 2018).

Based on mature grain grown under Mediterranean conditions, ten QTL for carbon isotope discrimination (CID) were identified (Teulat et al., 2002). A single effect was found across two environments, two were found to interact with the environment, six were found to overlap three environments or two and one produced both effects. Eight genomic regions were associated with QTLs previously found in the same population (Teulat et al., 2001b), either for physiological or agronomic related traits, such as OA or drought resistance (Teulat et al., 2001a). On chromosome 2 H, six regions are associated with agronomic traits co-located with CID QTLs, including QTLs related to KW and plant height. Six regions related to agronomic traits co-located with CID QTLs on chromosome 2 H, including QTLs related to KW and plant height (Teulat et al., 2001b). Four associated CID QTLs co-located with regions where QTLs for water status in plant and OA have been plotted earlier (Teulat et al., 2001a), including a chromosome 7 H for RWC and leaf osmotic potential, chromosome 2 H region for water-soluble carbohydrates and chromosomes 4 H and 7 H for OA (Teulat et al., 2001a, 1998). After the generative stage treatment, five QTLs also were found on chromosomes 2 H, 4 H, 6 H, and 7 H. Some of them were reported previously for this trait on chromosomes 3 H, 6 H, and 7 H (Diab et al., 2004). The results of QTL analyses are sometimes shown without marker positions, which makes comparison difficult (Liu et al., 2015).

QTLs for leaf wilting were identified on 2 H and 5 H along with QTLs for drought tolerance (QDT.TxFr 0.2 H and QDT.TxFr 0.5 H) (Fan et al., 2015). These QTLs were not the same as those described by Sayed et al. (2012) who studied leaf wilting as a drought tolerance criterion. Common genetic control for QDT.TxFr 0.2 H and QTL for relative moisture content (QRMO.TxFr 0.2 H) suggest that drought tolerance could be achieved by maintaining RMO under drought stress. Using drought stress conditions, four QTL in 3 H, 4 H, 5 H, and 6 H associated with proline content in barley were identified (Sayed et al., 2012).

Wojcik-Jagla et al. (2018) found major markers around the QPSII. the-2 H, Qqp.sthf-2 H, and QWC.sthf-2 H regions were associated with chlorophyll fluorescence (Wjcik-Jaga et al., 2013). Chromosome 2 H was inveterate as significant for drought responses (Guo et al., 2007). This region contains two QTLs for drought response and confirms that it contributes to drought responses. 3 H, 4 H, 5 H, 6 H, Guo et al., (2007) and Wjcik-Jaga et al., (2013) found additional QTL regions for these parameters on chromosomes 3 H, 4 H, 5 H and 6 H. In addition, Qqp.

sthf-2 H and QPSII.sthf-2 H are primarily associated with chlorophyll fluorescence parameters.

4.3.4. Biochemical and metabolic-related traits

DH lines from a cross of the Chinese drought-tolerant landrace 'TX9425' and 'Franklin' drought-sensitive cultivar were used to demonstrate the MLOC_18300 encodes the *9-cis-epoxycarotenoid dioxygenase 2* (*HvNCED2*), and is located near bpb-3241 marker on chromosome 5H (Fan et al., 2015). Under drought stress, *HvNCED2* plays an important role in ABA synthesis. The overexpression of *HvNCED2* gene enhacibg drought tolerance and ABA levels (Qin and Zeevaart, 2002). Several transcriptional factor genes such as ARF WRKY were discovered in the same region, which could be involved in the abiotic stress (Fan et al., 2015).

Wild barley from highly moisture stressed sites had less phenylpropanoid/phenolamide biosynthesis and the development of anthocyanin pigments compared to accessions from a more moister site (Cai et al., 2021). The anthocyanin less 1 (*ant1*) or *Hordeum vulgare Myb protein Colorless 1* ortholog H1 (*HvMpc1-H1*) (Shoeva et al., 2015) and anthocyanin less 2 (*ant2*) or basic helix-loop-helix domain / Myelocytomatosis (*HvbHLH1*) (Shoeva et al., 2016) loci are the most common loci that alter the expression of red/purple stem pigments in cultivated barley.

Major effect markers around QPSII.the-2 H, Qqp.sthf-2 H, and QWC. sthf-2 H regions were associated with chlorophyll fluorescence (Wjcik-Jaga et al., 2013). An inveterate gene in 2 H was significant for drought responses (Guo et al., 2007). This region contains two QTL for drought response and confirms that it contributes to drought responses. Additional QTL were found for these parameters in 3 H, 4 H, 5 H, and 6 H (Guo et al., 2007; Wjcik-Jaga et al., 2013).

Under drought stress, roots are also crucial for acquiring water. A smaller root system in spring barley is associated with lower grain yields when grown in arid conditions (Chloupek et al., 2010). Using the barley diversity panel, a QTL in 5 H associated with root dry weight under drought was identified (Reinert et al., 2016). There is strong evidence that the *HvCBF10A* and *HvCBF10B* genes are responsible for this QTL, which harbored a deletion of 37 amino acids compared to cultivated barley genotypes.

Agronomic traits of RILs in the Tadmor - ER/Apm population were evaluated in different Mediterranean environments with variable drought conditions (Teulat et al., 2001b; von Korff et al., 2008). Grain yield was more affected by environmental factors than other traits. The Tadmor alleles of the pHva1 marker gene in 1 H influenced grain yield in locations with greater drought severity (von Korff et al., 2008). The pHva1 marker co-localizes with the *HvHVA1* gene, which affects the low-temperature tolerance (von Korff et al., 2008). This locus also important for the wilting score in a 'Scarlett' BC_2 mapping population. Based on the *HvHVA1* QTL, 12% of the genetic variation was explained, with wild alleles causing a 17% reduction in wilting scores (Sayed et al., 2012). Several studies identified QTL associated with drought tolerance under controlled conditions and in the field (Diab et al., 2004; Honsdorf et al., 2014a; Lakew et al., 2012; Teulat et al., 2001b, 1998; von Korff et al., 2008) (Table 3). These studies, however, simply identify the QTL that determines traits of interest, while the genes that are responsible for drought tolerance in barley remain uncharacterized. With the improved barley genome sequence, it may be possible to reanalyze many of these studies to validate revealed QTL or detect new ones (Mascher et al., 2017). By using higher quality reference genomes and markers, the physical map and markers of barley can be improved substantially. Eventually, drought tolerence QTL and their causal genes will be more accurately identified. In addition to identifying homologs for drought-tolerance genes in barley, the progress of the high-quality barley genome sequence facilitates a genetic-based approach to identifying drought-tolerances genes. For instance, the barley calcium-dependent protein kinases (CDPKs) expression analyses revealed the role of CDPKs signaling pathways in response to drought stress (Fedorowicz-Stronska et al., 2017).

Abiotic stresses are known to have profound effects on plant metabolism. The accumulation of compatible solutes such as proline, sugars, fructans, polyamines, and glycine betaine is associated with improved drought tolerance in plants (Krasensky and Jonak, 2012). QTL for soluble sugar and proline accumulation and leaf osmotic potential have been identified in drought-stressed barley (Teulat et al., 2001a). The development of robust metabolomics protocols and the establishment of metabolomics platforms have enabled the investigation of metabolic QTL (mQTL), which can be explored in a similar fashion to QTL for agronomic and morphological traits. To detect mQTL in barley, a genome-wide association between the quantitative accumulation of a metabolite of interest and alleles of molecular markers calculated from a set of genotypes consisting of German elite breeding lines and Mediterranean landrace genotypes to reveal the genetic basis for metabolic variation (Templer et al., 2017). The potential differences in the metabolic adaptation of barley flag leaves to terminal drought and combined heat and drought stress and to identify mQTL A set of 57 metabolites from the primary C and N as well as antioxidant metabolism in flag leaves under control and stress conditions. The drought-adapted genotypes attenuated leaf carbon metabolism much more strongly than elite lines during drought stress adaptation. Furthermore, mQTL for flag leaf γ-tocopherol, succinate content, and glutathione were identified which co-localize with genes encoding enzymes of the pathways producing these antioxidant metabolites (Templer et al., 2017). In a barley RIL population, the mQTL study detected 98 different stress-responsive metabolites and observed that their abundance modulates through coordinated expression of several genes to function under drought conditions (Piasecka et al., 2017). A mQTL study, was applied in the large barley nested association mapping (NAM) population (Gemmer et al., 2021). Approximately 130 sugars and sugar-like metabolites were detected on ealry and late sampling dates. Sugar-related genes, encoding mainly sugar transporters, have been identified as candidate genes for most of the mQTL. Some of them co-localized with known flowering time genes such as *Ppd-H1*, *Vrn-H1*, *HvELF3*, *Vrn-H3*, and Vrn-H2, possibly related to role of sugars in flowering (Gemmer et al., 2021).

The investigation of metabolites in plant breeding requires a deeper understanding of the genes involved in metabolite accumulation. Therefore, detecting mQTL and candidate genes, which control the accumulation of specific metabolites, is of great interest for breeding barley cultivars torerant of abiotic stresses.

4.4. Genotyping and genome-wide association studies

Developing new cultivars for drought tolerance requires a complicated strategy, and traditional selection criteria have limits. In the previous context we pointed out that to understand drought tolerance, we need to study many related traits. As a result, the number of characterized genes depends on the number and accuracy of traits assessed. Several approaches can identify new genes that control drought tolerance through QTL mapping and genome-wide association studies. In recent years, new genotyping approaches have produced a large number of markers, making association analyses a very attractive and powerful tool. A wide range of SNP genotyping methods has been developed, including Barley Oligonucleotide Pool Assays (BOPA1 and BOPA2), which are efficient and abundant markers for association mapping (Close et al., 2009), the 9 K Illumina iSelect chip (Comadran et al., 2012), and the 50 K Illumina Infinium array (Bayer et al., 2017). Recent advances in next-generation sequencing technologies (NGS) have made it easier to detect a large number of SNPs by reducing the complexity of the barley genome, which is achieved with restriction enzymes such as genotyping-by-sequencing (GBS) (Poland and Rife, 2012). Using this approach, thousands of SNP markers can be identified for all seven barley chromosomes at a low cost for every genotype (Abed et al., 2018; Poland and Rife, 2012). Additionally, very good reference genomes for barley are now available (Mascher et al., 2017), allowing location of

each SNP and the imputation of any missing geneotypes. Indeed, (Abed and Belzile, 2019a), demonstrated that the imputation yielded a high level of accuracy (89%) with an association population. The large number of SNPs and the good distribution across the genome will increase the probability of detecting more genomic regions associated with drought tolerance.

GWAS studies have been conducted at different growth and developmental stages under drought stress (germination, reproductive stage, post-anthesis stage) and have detected highly significant associations and some new genomic regions having QTL that colocalized with genes related to drought tolerance mechanisms (Abou-Elwafa, 2016; Tarawneh et al., 2020; Thabet et al., 2018). More interestingly, Pham et al. (2019) used a population derived from wild barley to detect new regions/alleles using GWAS, found that, the wild allele was responsible for increased biomass and phenotypic values under drought stress. For GWAS, three statistical models are available: single-SNP, multi-SNP, and haplotype-based. In a study comparing these three models. Abed and Belzile, (2019a) demonstrated that the multi-SNP approach and the haplotype-based approaches, which simultaneously test multiple SNPs, were more effective in QTL detection than the single-SNP approach. Moreover, an integrated GWAS procedure, combining single-locus (SNP or haplotype) and multi-locus GWAS methods, develops the capacity and reliability of association analysis to detect more QTL (Abed and Belzile, 2019a; Contreras-Soto et al., 2017; Lorenz et al., 2011). The complex and quantitative feature of a trait such as drought tolerance will require additional information from different GWAS models to establish a more complete genetic profile. All these studies will contribute to a better understanding of the underlying architecture of drought tolerance and which drought-related traits are more informative. It provides a pool of target alleles for pre-breeding to enlarge the genetic diversity of cultivated barley tolerant to drought stress. Marker-assisted selection (MAS) is an efficient selection strategy for some disease resistances determined by major effect genes (Steffenson and Smith, 2006). However, this is not the case for drought tolerance where the complexity of the genetic architecture has made it difficult to practice MAS became the contribution of each QTL/gene is small and combining several genomic regions related to drought tolerance via a pyramiding approach is very challenging.

4.5. Genomic prediction approaches

Developing drought-tolerant cultivars is challenging mostly because it is difficult to assess accurate phenotypes accurately due to both the complex qualitative nature of the trait as well as the impact of genotype x environment (GxE) interactions (Elakhdar et al., 2017; Sallam et al., 2019a). Genomics predictions have been proposed as promising strategies for selection of complex traits. These strategies have the advantage of providing a prediction of the phenotypic performance of progeny with genomic selection (GS) based on a previously identified statistical relationship between the genotype and the phenotype within a population (Crossa et al., 2017; Meuwissen et al., 2001), and crosses with genomic mating (GM) (Abed and Belzile, 2019b; Adeyemo and Bernardo, 2019; Endelman, 2011; Mohammadi et al., 2015) based only their genotypes. Studies have revealed the potential of GS to increase genetic gain for complex traits (Lorenz et al., 2011; Sallam et al., 2015). Based on the genetic architecture and the complexity of the trait, statistical models are available (Crossa et al., 2017; Gianola and van Kaam, 2008; Gonzalez-Camacho et al., 2018) that account for GxE. Several studies have demonstrated that phenotypic variance can be attributed to GxE, and modeling can lead to phenotypic improvements in selection efficiency (Crossa et al., 2017; González-Barrios et al., 2019; Monteverde et al., 2018). These models allow the effective prediction of lines performance by incorporating information across environments. Breeding methods vary depending on the choice of parents to cross. Traditional breeding programs are based on limited data, especially when it comes to complex traits where yield and drought tolerance must be improved simultaneously. By using GM, a breeder can select the best crosses based on these predictions. Breeders can have a chance of identifying transgressive segregants from these crosses. To develop breeding methodologies, the GM could be used as an initial step to identify the most promising parents, followed by the GS to ensure an efficient selection of lines within a cross. Using the genotypes of lines, better decisions might be made than by evaluating the performance of lines in the field.

Genomic prediction techniques assume that one set of agronomic data can identify superior individuals, that elite breeding populations contain a high portion of the desirable genes, and that the frequencies of desirable genes are high. None of these assumptions are true for the drought tolerance breeding problem. Droughts are a problem in most barley production areas, but drought patterns range from terminal droughts to periodic water shortages that can occur at any growth stage (Chenu et al., 2013). Hence, selection cultivars with a high level of drought tolerance requires testing at many growth stages and over a wide range of environments. Papers on drought tolerance identified many different responses to moisture stress in a wide array of barley germplasm. As expected, the results are likely applicable to specific stresses and specific genetic resources. Because of the diversity of environments in which barley cultivars are developed, no one germplasm resource has a high frequency of genes involved in drought tolerance.

4.6. Genes regulating drought tolerance in barley

Several corresponding droughts genes and their functions have been elucidated (Table 5). Researchers have developed a transgenic barley plant that carries both constitutive and drought stress-inducible *TaDREB3* and *TaDREB2* transcription factors which were resistant to drought stress. Stress-responsive promoters *HDZI-3* and *HDZI-4* have been found useful in modulating the expression of both *DREB/CBF* genes, *TaDREB3* and *TaCBF5L* on transgenic wheeat and barley (Yang et al., 2020). Transgenic plants can be enhanced with *HDZI* promoters combined with *DREB/CBF* factors for the reduction of transgene-induced negative effects on plant growth and grain yields and improved abiotic stress tolerance.

In wild barley Suprunova et al. (2007), isolated *H. spontaneum dehydration-responsive 4* (*Hsdr4)* that codes for a Rho-GTPase-activating-like protein that participates in drought tolerance. It is known that the *Arabidopsis* Rho GTPase (*AtRac1*) is crucial for ABA-mediated stomatal closure (Lemichez et al., 2001). In addition to controlling water loss through the stomata, the cuticle is also essential for plant drought adaptation. A mutagenesis investigation detected 79 Eceriferum (*cer*) loci involved in the deposition of epicuticular waxes in barley (Lundqvist and Lundqvist, 2008). The *Cer-yy* gene, carrying a spike-specific reduction of cuticle wax, is the only surface wax variant common in wild barley (Lundqvist, 1982). According to Chen et al., (2004) the *eibi1* spontaneous mutant in wild barley is extremely sensitive to drought conditions and has a low water retention capacity. This genotype is hypersensitive because of low cutin deposition in the cuticle. The *eibi1* was discovered in 3 H (Chen et al., 2008). Proteomic and metabolomic analysis for root and leaf tissues under drought showed several proteins have been accumulated including, proline, HSP70, and ascorbic acid and carbohydrates, nevertheless protein or metabolite signals were elevated in drought-tolerant genotypes, but not correlated with drought tolerance. Therefore, a predisposition to drought may be conferred by some biochemical signals (Chmielewska et al., 2016). Barley genes have been used successfully to develop drought resistance not only in barley but also in other crops, including the overexpression of *HvSNAC1* in barley (Al Abdallat et al., 2013) and *HvCBF4* in rice (Oh et al., 2007).

The *cis*-acting and trans-activated elements including *AREBs/ABFs,* could be used to enhance drought tolerance. ABA-responsive (ABRE) can bind to AREBs/ABFs *cis*-acting element downstream gene expression. Overexpress of *AREB/ABF* in barley plants displays ABA sensitivity and

Table 5
Genes that regulate drought tolerance related traits.

Gene	Functional	Reference
HvMYB1	Mediates the action of abscisic acid in the vegetative plant to protect the plant from drought	(Alexander et al., 2019)
HvSNAC1	Improve water status, photosynthetic activity	(Furihata et al., 2006)
HvAKT2 and *HAK1*	Enhancing K^+ uptake and H^+	(Feng et al., 2020)
DHNs	Dehydration tolerance of plant membranes	(Karami et al., 2013)
HvEXPB7	Improves root hair growth of Tibetan wild barley under drought conditions	(He et al., 2015)
Dhn3, Dhn9	Enhancement of chlorophyll a, b, OA, stomatal conductance, and grain yields	(Karami et al., 2013)
HvSAMS3	Regulates drought and salinity tolerance	(Ahmed et al., 2020)
Hsdr4	Osmotic adaptation	(Suprunova et al., 2007)
Hv-WRKY38	Regulatory role in cold- and drought-response	(Mare et al., 2004)
LEA (*HvHVA1*)	LEA overaccumulation, increases drought tolerance	(Liang et al., 2011)
ERA1	Photosynthesis efficiency	(Daszkowska Golec et al., 2018)
HvNACs	Leaf senescence, root development	(Christiansen et al., 2011)
MYB	Growth and development	(Tombuloglu et al., 2013)
CBF/DREB	Damage and desiccation protection for cells	(Morran et al., 2011)
Vrn-H1 and *Vrn-H2*	Improved yield stability	(Rollins et al., 2013)
HvTX1	Seed development	(Papaefthimiou and Tsaftaris, 2012)
HvDME	Seed development under drought	(Kapazoglou et al., 2013)
HVSRG6	Improves cellular water absorption and retention	(Romanek et al., 2011)
HvWRKY38	Enhance survival and biomass accumulation after drought stress	(Xiong et al., 2009)
Hsdr4	Osmotic adaptation in barley	(Suprunova et al., 2007)
eibi1	Leaf water conservation	(Chen et al., 2011a)
HvDWARF (*uzu1*)	Involved in brassinosteroid biosynthesis; increase the activity of antioxidant enzymes, increase proline levels and photosynthetic pigment content	(Janeczko et al., 2016)
HvCPI-2 and *HvCPI-4*	Enhancing tolerance to drought	(Velasco-Arroyo et al., 2018)

improved freezing, drought, and salt stress tolerance (Furihata et al., 2006). Under dehydration stress, rice overexpressing the barley *HvHVA1* gene had greater stress tolerance than control plants (Rohila et al., 2002). Moreover, the barley *HVA1* gene derived by *rd29A* promoter decreased negate growth retardation in non-stressed plants, in addition to enhancing the drought tolerance for the transgenic mulberries (Checker et al., 2012). The transcription factor HsDREB1A was isolated from wild barley and inserted into *Paspalum notatum* utilizing the *HvHVA1* barley promoter (James et al., 2008).

Among the most likely candidate genes for chlorophyll fluorescence and RWC under drought are the protein kinases F2DHHH6 and M0W3T9. These signal proteins may contribute to both the control of stomatal water loss and the response to drought stress events in general (Ruggiero et al., 2017). Especially important is to examine kinases that may influence cell surface signal perception as well as those associated with cell walls. The interaction between the cell wall-plasma membrane interactions after RWC decline causes an actin microfilament reorganization, which regulates the ABA-independent drought signal besides the expression of *HvHVA1* dehydrine (Sniegowska-Swierk et al., 2016). Interestingly, another gene, *CCR3*, encodes a zinc finger transcription factor that is also required for the biosynthesis of the lignin (Bi et al., 2010). During droughts, lignin composition and contents change to regulate the water loss (Moura et al., 2010). There were also three disease resistance gene homologs including *RGA2, RGA3*, and *RGA4* among the candidates for drought response. Pathogen recognition and restriction of their growth are generally attributed to these proteins that are found in many plants (Liang et al., 2015). Candidate *F2CYU9* gene for hydrolase activity with Gene Ontology molecular function hydrolase activity has the potential to hydrolyze ester bonds between sugars and ferulic acid in cell walls. A previous study identified this process as being important for drought resistance in cereals (Hura et al., 2012). There is also evidence that the cell wall-bound phenolics have a relationship with OJIP parameters (F_v/F_m and ABS/CS) in triticale under drought conditions (QCWPh. 4B).

5. Genome editing and functional validation of isolated genes

Genetic analyses using mutants are essential for understanding gene function in both basic and applied research. A targeted gene-editing technology can generate mutants of a target gene with greater efficiency and ease than traditional random mutagenesis and screening. Genetic crosses could be made with translocation lines to produce mutants with distinct phenotypic characteristics. Through the link between mutations and translocation breakpoints, specific genes could be assigned to particular chromosomes. For example, the *eibi1* mutant was isolated from the wild barley and is hypersensitive to drought (Chen et al., 2004). Consequently, the translocation lines linked mutated genes to specific chromosomes. Isolated barley mutants usually contain one or more alleles that can validate the underlying gene function. In the case of genes identified by conventional biparental analyses, genetic association studies, genome-wide association studies, or mutants with a low number of mutant alleles, reverse genetic approaches such as TILLING are required to validate the isolated genes. Now, several barley TILLING populations are available including, TILLMore population derived from Morex (Talame et al., 2008), TILLING population induced from Barke (Gottwald et al., 2009), and Optic TILLING in two rows induced by EMS (Caldwell et al., 2004). By using these reverse genetic tools, genes in mutants of interest can be functionally assessed. Using transgenics as a tool for functional genetics is common method (Hensel et al., 2011). In barley, several transgenic approaches were developed to enhance, downregulate, knockout or overexpress a gene of interest. The complementation method is a straightforward process by which a mutant gene is replaced with its wild-type to restore its function. RNA interference (RNAi) and viral-induced gene silencing (VIGS) measure the quantitative effect of a gene using homology-dependent post-transcriptional gene silencing methods (Hein et al., 2005). But these approaches are prone to off-target effects (family members). Transcriptional Activator-Like Effector Nucleases (TALENs) provide a solution to this problem by targeting genes in plants at specific sequences with no off-target effects in the host genome (Boch et al., 2009). Successful applications of this technology have been demonstrated in barley (Gurushidze et al., 2014). The RNA-guided Cas9 technique was shown effective in knocking out genes in barley (Lawrenson et al., 2015). Different genome-editing analyses have been achieved in barley with CRISPR/Cas9, for example, the increase in vitamin E biosynthesis by knockout mutations of *HGGT* and *HPT* genes (Zeng et al., 2020), reduce lignin content *HvCOMT1* (Lee et al., 2021), and enhancing the abiotic stress by creating the *HvITPK1* mutant. In addition to, low *D hordein* content mutants that could provide a new germplasm resource for studying the function of D hordein and may allow the breeding of new cultivars with better seed quality (Li et al., 2020b). However, CRISPR/Cas9 genome editing technology is until now limited to the Golden Promise barley variety because of the transformation complications in other barley variates.

6. Plant-microbe interactions and drought stress tolerance

The plant-microbe interactions are an essential controlling factor in ecosystem processes (Cheng et al., 2019). Microbial communities in root systems are intimately related to plant (Friesen et al., 2011). Overall, the roots profile the environment or niche where the microbial communities thrive and survive, while the plant-correlated microbes, particularly plant growth-promoting microorganisms (PGPM) may influence the host plants growth, nutritional condition, growth, and fitness (Ma et al., 2020; Pascale et al., 2019). Several direct and indirect mechanisms are used by microbes to improve the growth and the development of plant inducing. There are several potential mechanisms including (a) accumulation of phytohormones for example cytokinins, indole-3-acetic acid (IAA), and abscisic acid (ABA); (b) 1-aminocyclopropane-1-carboxylic acid (ACC) deaminase; (c) bacterial exopolysaccharides; and (d) induced systemic tolerance. These phytohormones produced in plants are essential for development and growth (Porcel et al., 2014). Furthermore, PGPR has capability of synthesizing plant hormones which encourages cell division and growth under stress conditions. During drought stress, IAA is a regulator of vascular-tissue differentiation, including cell division, shoot development, and differentiation of adventitious and lateral roots (Goswami et al., 2015). ABA plays a key role in growth regulation under drought stress condations. Plants and seeds inoculated with PGPR produce more ABA, which reduces the effects of drought stress. Drought stress is ameliorated by ABA through transcription regulation of drought-related genes and the hydraulic conductivity of the root (Jiang et al., 2013). Despite variances among microbes, the PGPM lines may colonize the plant's endo-rhizosphere and may defend plants from the abiotic stresses including drought and salinity (Ma et al., 2019). Direct mechanisms include nitrogen fixation, sequestration of siderophores, solubilization of potassium and phosphate, are nutrient acquisition (Kohler et al., 2009), phytohormone biosynthesis such as cytokinin, auxin, ABA, and gibberellic acid (GA) (Ma et al., 2019), exopolysaccharides (EPS) (Naseem et al., 2018), are ACC deaminase (Forni et al., 2016). PGPMs may contribute to improved plant performance according to their potential roles in responding to changes in the environment. Hence, understanding plant-associated microbes' responses to environmental changes can assist in improving plant performance (Compant et al., 2010). Inoculating plant seeds by probiotic microbiota enhanced germination rates, altered the architecture of roots, improved ROS response, and elevated proteins and sugars accumulation and increased proline accumulation in the plant leaves (Naseem et al., 2018; Naveed et al., 2013).

Abiotic stresses are alleviated by microbes with their intrinsic metabolic and genetic capacities (Gopalakrishnan et al., 2015). Increasing the production of IAA and ACC-deaminase in salinity-affected soils was observed with *Acinetobacter sp.* and *Pseudomonas ssp*. in barley and oat (Chang et al., 2014). Root endophytic basidiomycete *Piriformospora indica* was exhibited to improve barley's tolerance to salt stress using *Pseudomonas ssp*. CMH3 strain in greenhouse trials by increasing shoot growth by 100% and root biomass by 200% (Baltruschat et al., 2008). The application of unsaturated fatty acids exogenously to barley has been shown to protect the plant against NaCl-induced stress in the past (Zhao and Qin, 2005). It was observed previously that salt-treated barley roots had lower levels of oleic acid leaves under *P. indica* colonization. (Liang et al., 2005). *P. indica* somewhat improved the C18:3 fatty acid accumulation in the isolated phospholipid fraction. The changes in fatty acid composition caused by *P. indica* generally resembled those caused by salinity (with one exception: C16:1). In hostile environments, such changes in the fatty acid composition of host plants can be evidence of a symbiotic adaptation to cope with salt stress mediated by the endophyte (Baltruschat et al., 2008; Rodriguez et al., 2008).

Barley plant leaves inoculated with *P. indica* were characterized for proteomic and metabolomic responses to moisture stress (Ghaffari et al., 2019). Drought stress upregulated several proteins related to photosynthesis, including ferredoxin, the photosystem complex proteins (PSBO, PSAG, and PSAK), phosphoglycollate phosphatase (a main photorespiration enzyme), and photosystem components LHC-I and II. Drought stress reduced Calvin cycle enzyme activity, that maintained by *P. indica* inoculation. Under stress, the NADPH producing enzymes active within the pentose phosphate pathway (6-phosphgluconate dehydrogenase and ribose 5-phosphate isomerase) were downregulated. Nevertheless, the inoculation treatment restored their levels, perhaps indicating more activity of NADPH synthesis, which is required during periods of stress for antioxidant production (Ghaffari et al., 2019). Barley roots colonized by *P. indica* display an induction of light-sensing mechanisms and metabolite readjustment in photorespiration, which enhances the plant adaptation to drought stress conditions (Couee et al., 2006).

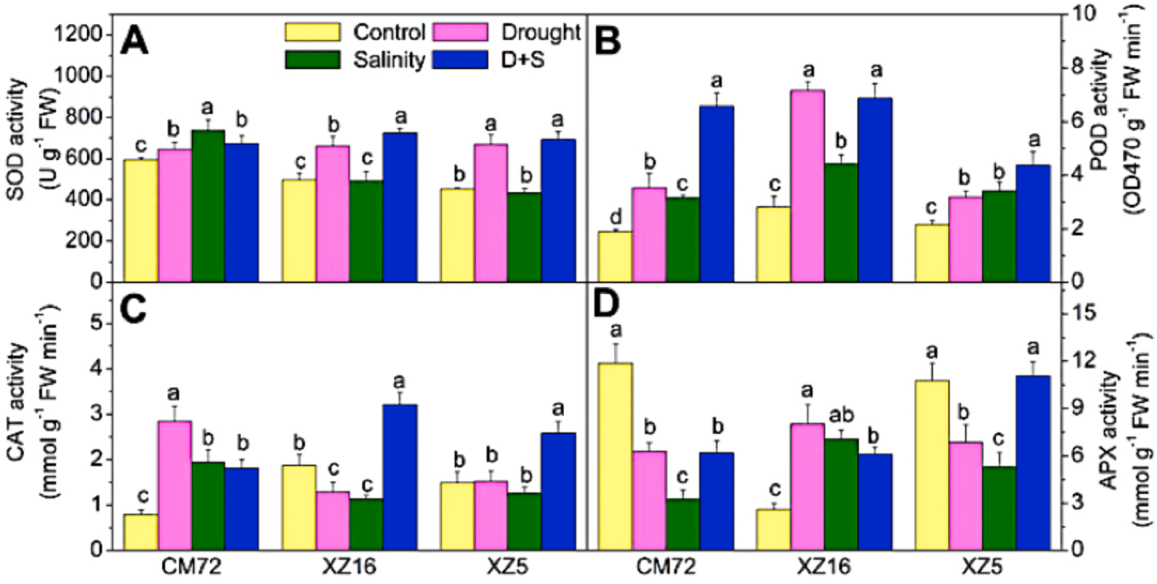

Fig. 7. The antioxidant enzyme (A: CAT, B: SOD, C: POD and D: APX) activities in cultivated and Tibetan wild barley genotypes (CM72; salinity tolerant, XZ5; drought tolerant, XZ16; salinity/aluminum tolerant) (from: Ahmed et al., 2013).

7. Drought and salinity stress strategies for enhancing plant survival

Elucidating mechanisms underlying abiotic tolerance in plants has made tremendous progress. In addition, comprehensive studies have been done on how plants respond to various stresses and how they affect plant growth (Abuqamar et al., 2009; Elakhdar et al., 2016). Based on the nature of the stress or the stress signal, these responses require a complex network of molecular mechanisms. Plants present in nature must simultaneously cope with different and interacting stresses that occur simultaneously or in sequence. Salinity stress is the foremost abiotic stress affecting major crops productivity worldwide (Kaushal and Wani, 2016). Both salinity and drought stresses have similar physiological, biochemical, molecular, and genetic effects on plants (Sairamaf and Tyagi, 2004). In most plants, drought and salinity stresses have common physiological mechanisms: both stresses decrease soil water potential, thus causing water deficits or osmotic effects which reduce growth. As a result of the decreased osmotic potential of soil due to salinity, plants are affected by the toxic effects of Na^+ and Cl^- ions and the disrupted water processes (Munns and Tester, 2008). Drought and salinity stress adversely affect plant development and productivity by reducing transpiration, photosynthesis, and enzyme activity (Ma et al., 2020). When plants are exposed to these stresses, they are subjected to oxidative stress, which results in increased electron leakage toward O_2 during photosynthetic and respiratory processes, resulting in an increased ROS formation (Asada, 2006).

Ahmed et al., (2013) studied the physiological antioxidant responses underlying salinity and drought tolerance in three Tibetan barley genotypes to comprehend the tradeoffs among salinity and drought tolerance, and to identify characteristics that are correlated with a high tolerance to both stress factors. The SOD activity in flag leaves significantly ($P < 0.05$) increased in all genotypes under drought and D+S and CM72 under salinity stress alone. POD activity increased under drought, salinity alone and D+S treatments in all genotypes. in D+S treatment, CAT activities during anthesis at a soil moisture level of 4% were higher in Tibetan wild type genotypes than in CM72. Compared to controls, APX activity decreased in CM72 and increased in XZ16 under the three stress treatments (Fig. 7). In addition, several physiological traits were impacted under both stress treatments. A significant decrease was observed in the cell membrane stability index, total biomass, glutathione contents (GSH), 1000-grain weight, and grain yield (Ahmed et al., 2013). High levels of malondialdehyde (MDA), glycine-betaine and soluble sugars, protease activity, and soluble protein contents were demonstrated. The results indicated that high tolerance to drought and salinity stresses was related to the low Na^+/K^+ ratio, as well as improved sugar contents, soluble protein, and glycine-betaine enhanced protease, antioxidative capability, and ATPase activities for scavenging ROS at anthesis stage (Ahmed et al., 2013). Based on these results, the question becomes whether the same change in water status, whether precipitated by salinity or drought, results in the same reduction in yield.

Since the tolerance to drought and salinity stress are regulated by complex mechanisms combined to escape, avoid or tolerate water deficiency. The drought and salinity stress strategies for enhancing the plant survival are correlated with plant adaptability to different abiotic-prone environments (Farooq et al., 2009). There are significant gap in our understanding of the combined impacts of these commonly co-occurring stresses during the vegetative period of plants, despite the latest advances in the clarification of their effects. There is potential for crop improvement with the identified traits, QTL, and genes associated with salt and drought tolerance. However, it is essential to validate their effects on yield enhancement under targeted environments. Hence, their application in breeding programs could be considered, as there is a big gap between genes (traits) and a realistic cultivar released to the farmers (Nevo and Chen, 2010).

As a molecular basis of drought and salinity tolerance; a combination of QTL advanced backcross analysis, introgression libraries from the wild barley donors, and cloning and validation of the QTL will show principal roles in elucidating the molecular control underlying drought and salinity tolerance in barley, which could be review in an independent study.

8. Growth limiting factors and drought tolerance

Drought-tolerant barley cultivars respond to the many abiotic and biotic agents that occur locally in various production areas. The responses to these agents can be mitigated by both production practices and genetic resistance. Drought escape might be the most important drought tolerance mechanism and the easiest to manipulate. Many moisture stresses faced by barley involve gradually increasing moisture shortages typified by terminal drought and heat stress. Hence, rapid completion of the lifecycle is often critical for both wild and cultivated barley. Wild barley, which is a winter annual, has the *Eam1* gene for a strong long-day response when germination is delayed by dry soils. This gene is retained in many landraces and cultivars planted during the autumn or winter. The *Eam5* and *Eam6* genes can confer desirable photoperiod responses in winter and spring-planted barley, respectively. Although many modifiers of heading date exist, alleles at the *Ppd-H2*, *HvFT1*, *eam7*, and *eam11* loci are more frequently involved based (Casas et al., 2021).

The ability of root systems to extract moisture from soils is related to their size, depth, and health. A more vertical growth angle of seminal roots can help roots penetrate deeper into relatively dry soils (Robinson et al., 2018), while width root angles are favorable in soils that are frequently waterlogged. The health of the root system can be diminished by aluminum and boron toxicity, saline soils, nematodes, root rots, and viral diseases. Some genetic factors conferring tolerance and/or resistance to these agents have been identified and mapped (Table 5). More important control genes include aluminum tolerance or acid soil tolerance (*Alp1* in 4HL), Reaction to *Heterodera avenae* (cereal cyst nematode) (*Rha2* in 2HL and *Rha4* in 5HL), Reaction to barley yellow dwarf virus (BYDV) (*Ryd2* in 3HS and *Ryd3* in 6HL), and salt or salinity tolerance.

Foliar diseases alter protein patterns and the utilization of metabolic energy as plants respond to pathogen attacks. These responses and subsequent disease development cause adverse responses to moisture stress. For example, changes are defense protein concentrations were observed in Bowman four days after inoculation with the leaf rust pathogen, *Puccinia hordei*, but not in the resistance near the isogenic line with the *Rph15.ad* allele (Bernardo et al., 2012). Presumably, these changes in plant proteomics alter the plant's responses to moisture deficiencies. Although many foliar pathogens attack barley, only a few occur in many production areas. Some genes conferring resistance to the frequently occurring pathogens have been mapped and are associated with 50k molecular marker haplotypes (Table 5). These include reaction to *Pyrenophora teres* f *maculata* (spot form net blotch) (*Rpt4* in 7HL), reaction to *P. teres* f. *teres* (net form net blotch) (*Rpt5* in 6HL), reaction to *P. graminea* (barley stripe) (*Rdg1* in 2HL), reaction to *Rhynchosporium commune* (scald) (*rrs1* in 3HS), Reaction to *Puccinia hordei* (leaf rust) (*Rph15* in 2HS and *Rph20* in 6HS), reaction to *P. graminearum* (stem rust) (*Rpg1* in 7HS), reaction to *P. striiformis* (stripe or yellow rust) (*Rps4* in 1HS), and reaction to *Cochliobolus sativus* (spot blotch) (*Rcs5* in 7HS).

Lodging and preharvest straw breakage can severely limit the benefits of drought tolerance. Reduced lodging and post-ripe straw collapse are important agronomic traits that help farmers obtain more in well-wated crops.

9. Challenges and future perspectives (Breeding for drought tolerance)

There are many metabolic and genetic pathways in barley regulate their response to water deficit stress, making the development of

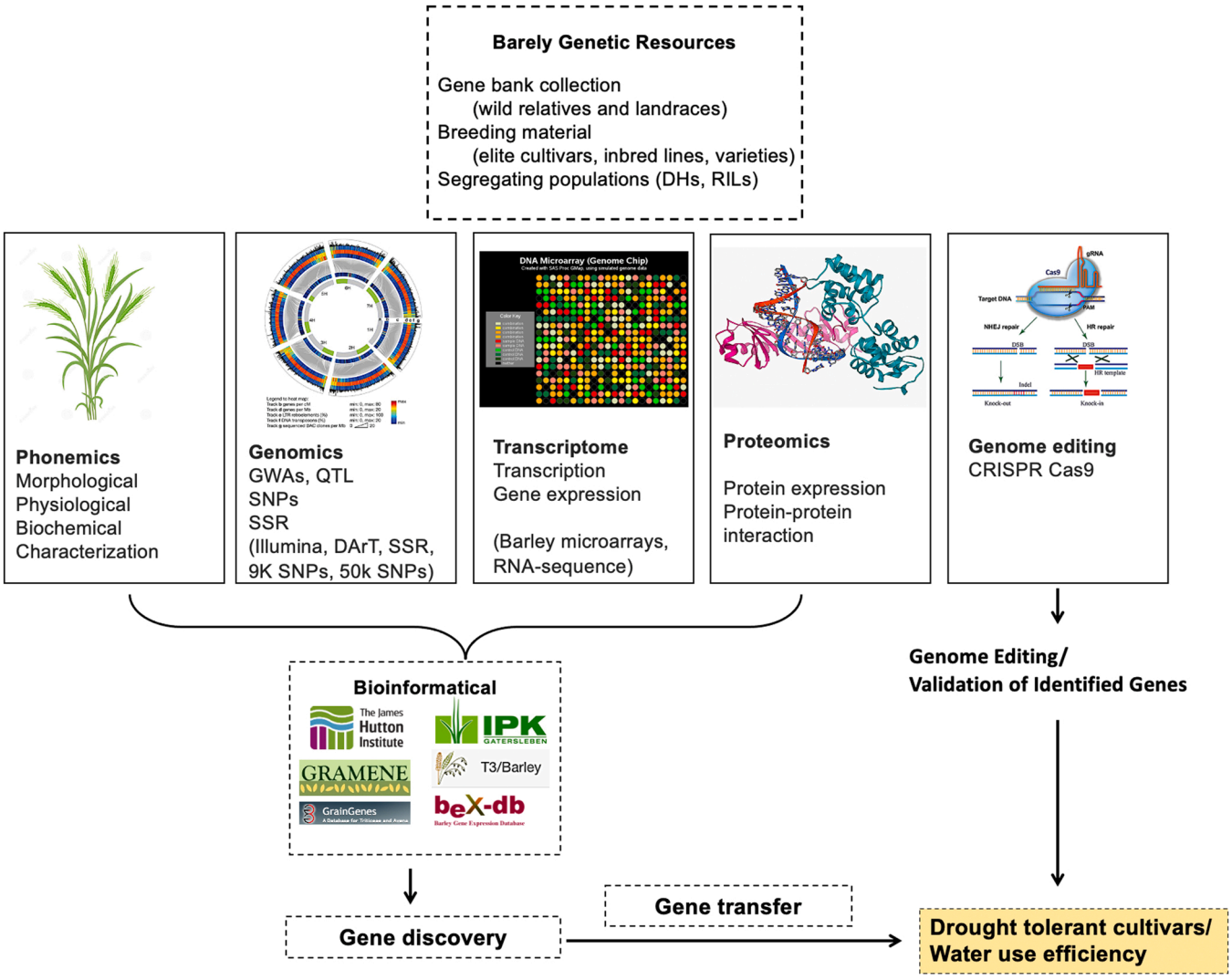

Fig. 8. Schematic framework for the integrating of physiology, genomics, and breeding approaches of genome-based molecular breeding for drought tolerance in barley.

drought tolerance barley cultivars a daunting challenge. Periodic moisture stress has been encountered worldwide during the domestication of barley. Wild barley in the large drought-prone area of Southwestern Asia and North Africa, likely accumulated traits and genes favoring drought escape and tolerance. Farmers for ions have selected the largest spikes and plumpest kernels to plant next season's barley crop. Thus, the genetic resources needed to improve drought tolerance may already exist in barley germplasm collections. Even though many desirable genes have small effects with complex interactions, targeting them in breeding programs should be feasible. However, local adaptations developing abiotic and biotic constraints are critical in cultivar development.

Two concepts essential to making progress toward better drought tolerance. First, barley breeders must have access to genetic resources that can contribute to improving drought tolerance. Many of the desirable seedling responses to moisture deficiency can be summarized by analysis of moisture content of seedling leaves under terminal water stress (Cai et al., 2020). They found that the accessions with the best responses are present in the collection of both cultivated and wild barleys. Hence, the cultivars should have many genes for tolerance to terminal and seedling drought. One of the best cultivars is Morex (Cai et al., 2020), a six-rowed spring barley bread for the Upper Midwest of the USA (Rasmusson and Wilcoxson, 1979). The stay-green trait (Gous et al., 2015) and multiple genes for early heading (Casas et al., 2021) are present in cultivars developed in the same production area.

Second, breeders must determine if desirable traits and genes are present and expressed in locally adapted breeding materials. Since drought tolerance is associated with the expression of many genes, they must be identified using visual observations, yield trials, quality tests, and molecular markers. Molecular markers may be gene-specific or based on haplotypes phases of closely linked markers to critical genes (Abed and Belzile, 2019a). These markers will aid breeders in identifying genes controlling resistance to abiotic and biotic agents already present in locally adapted breeding materials.

Genes and traits involved in drought tolerance can be selected visually in segregating material in early generations. Examples include spike type, early heading, awn barbs, plant height, peduncle length, glossy spike, stem pigmentation, and kernel size and shape. These traits may be selected for in the F_2 or F_3 generation under, only 'good' selections should be included in field plots, disease tests, and/or MAS evaluations. Visual selection and offseason nurseries could be employed to complete one cycle of crossing and selection in one year (Hickey et al., 2017). Thus, the accumulation of the many genes involved in moisture stress responses should be rapid.

To develop climate-resilient and high-yielding barley cultivars over a short period of time, advanced genetics and genomics techniques may be

applied (Fig. 8). Consequently, more genes and QTL are identified as candidates with a potential role in stress tolerance. There are currently only a small number of functional markers for MAS that have been validated. However, MAS has had only a limited effect on breeding for multi-genic traits that are strongly influenced by the environment. MAS has been inadequate in its impact on barley breeding in past years, largely because of an inadequate molecular markers, and ineffective method of utilizing these markers. Recent advances in bioinformatics with high-throughput phenotyping approaches based on the next-generation sequencing technologies will support our capability to associate with specific genomic regions and to isolate drought-related loci.

Since barley has only seven chromosomes closely linked genes can influence the germplasm chosen to may crosses. For example, the early heading 5 (*Eam5.x*) gene at about 125.23 cM is 5HL is between the smooth awn genes (*raw1* and *raw2*) at 106.15 cM and 134.12 cM, respectively. Recombinants will make the selection for the *Eam5.x* gene in elite breeding materials easier. The low grain protein content 1 (*gpc1.c*) gene at about 54.10 cM in 6HL is very close to the reaction to *Pyrenophora teres* f. *teres* 5 (*rpt5.f*) locus at 59.71 cM. A line with the two 2 H QTL for short kernels, qGL2H, at about 72.64 cM and the 2 H gene for the absence of barbs on the lemma veins (*gth1.a*) at 76.30 cM in coupling might be useful. These are a few of the non-random gene assortments that might influence the selection of parents and breeding procedures.

Choosing drought-responsive traits to focus on, is difficult because the priorities across production areas are different. The deficient spike type (*Vrs1.t*) is not a morphologically by acceptable trait in all production areas. Smooth awns in spite of the potential yeild adaptive not acceptable by the farmers. Accumulating early maturity genes may depress yield. The rapid post-ripe straw collapse might not improve the value of barley straw. Since lodging is a major production problem in some seasons and locations, height reduction may effective.

In conclusion, breeding drought-tolerant barley involves the utilization of germplasm having a number of genes for desirable moisture stress responses. Visual selection, appropriate assay for drought tolerance traits, and rapid breeding techniques will reduce the time required to develop drought-tolerant cultivars, accepted by farmers and consumers. It is necessary to combine the modern techniques of plant breeding, physiology, genomics, and gene-editing approaches to study complex drought tolerance traits to develop next-generation crops adapted to changing climates by elucidating the molecular basis of drought tolerance (Fig. 8). In the future, the more effort to evaluate the validating and the discoverd candidate genes related to drought tolerance. Through increasing the frequency of promising alleles of the validated genes, strong germplasm can be available for releasing next-generation climate climate-resilient varieties.

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Author contributions

Ammar Elakhdar: Conceptualization, Investigation, Mthodology, Supervision, Visualization, Writing – original draft, Writing – review & editing. **Jerome D. Franckowiak:** Supervision, Visualization, Methodology. **Calvin O. Qualset:** Supervision, Visualization, Writing – review & editing. **Shyam Solanki:** Writing – review & editing. **Takahiko Kubo:** Review & editing. **Amina Abed:** Writing – review & editing. **Ibrahim Elakhdar:** Review & editing. **Rania Khedr:** Review & editing. **Aladdin Hamwieh:** Writing – review & editing. **Ludovic J.A. Capo-chichi:** Review & editing. **Mohamed Abdelsattar:** Review & editing. All authors have read and agreed to the published version of the manuscript.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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