

Biochemical and molecular basis of abiotic stress tolerance in barley

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Abstract

The environment has very critical role for the plant growth and development and it is the deciding factor for the growing time and distribution of a crop plant in a particular geographical area. The abiotic stresses are bound to increase in the time to come, because of changing climatic conditions. To sustain the agricultural system, we need to get ready with the crop plants which have durable abiotic stress tolerance. Among the cultivable cereals, barley stands out in terms of abiotic stress tolerance and has the inherent capability to grow in harsh environments with limited resources. Attempt has been made in this article to compile the available information on some of the biochemical and molecular factors contributing to drought, salinity and heat tolerance of barley species. It is expected that this compilation may be useful for the crop improvement programmes in relation to abiotic stress tolerance.

Keywords: Barley, drought, heat, salinity, stress

1. Introduction

Abiotic stresses are one of the major yield-limiting factors of crop plants. Extremes of temperatures, drought and salinity etc are some of the major abiotic stresses having detrimental effects on commercial cultivation of agricultural crops. It is estimated that approximately 90% of total arable lands may be prone to one or more abiotic stresses, and may cause significant losses in the quantity and quality of major food crops (He *et al.*, 2018) The simulation models developed on the basis of integration of climate change and crop yields have predicted considerable loss of productivity in major food crops, thus threatening the food security of the people around the globe. In one metadata analysis, it is predicted that the global average temperatures may show an increase of 2.0 to 4.9°C by 2100 (Raftery *et al.*, 2017). The extant of salinity has increased by 37% during the period of 1990 to 2013 (Qadir *et al.*, 2014). The severity and frequency of drought stress is increasing due to changes in precipitation behaviour and global warming induced increase in avao-

transpiration.. Heavy metal contamination in the arable lands is increasing and this may result into crop yield losses apart from being a human health hazard. (Waqas *et al.*, 2019 and references there in). Different kinds of abiotic stresses limit the geographical distribution of crop plants and yield along with the quality of produce obtained from plants. Over the years, the studies carried out at morphological, physiological, biochemical and molecular levels in relation to abiotic stresses tolerance have shown that multiple processes such as sensing, signalling, transcription, transcript processing, translation and post-translational protein modifications are involved in the mechanisms shielding the plants from these physical stress factors (Figure 1) This information can be used to breed crop varieties through different techniques for enhanced inbuilt stress tolerance in plants to achieve higher yields and better-quality produce (Zhang *et al.*, 2022 and references there in).



The *Hordeum* species has adapted it over the period of time, morphologically, physiologically and in terms of reproductive variability (Figure 2), to grow in varied environments of temperate, tropical, sub-tropical and from the regions of deserts to arctic circles (Bothmer *et al.*, 1995).

Evaluation of biodiversity under abiotic stress conditions to fish out the candidate genotypes with inherent tolerance or resistance which is now supported by molecular biology tools.

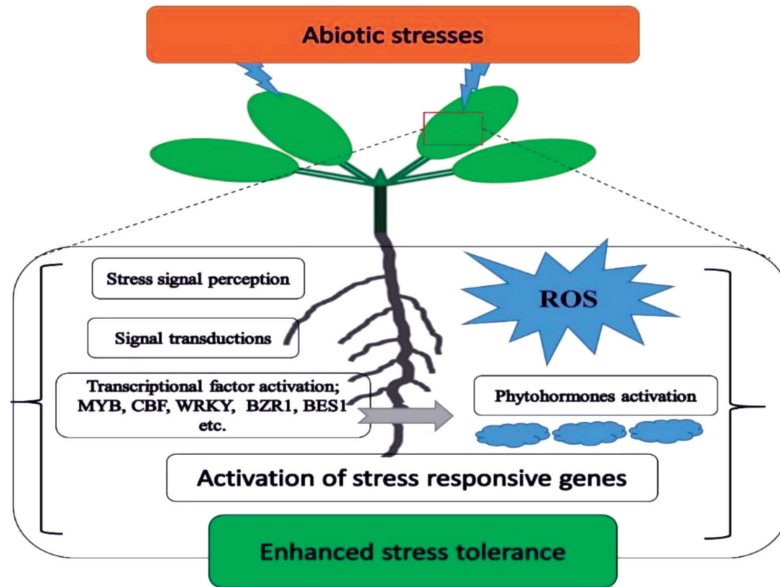


Fig. 1. A simplified mechanism of abiotic stress tolerance in plants (Adapted/Reproduced from Anwar and Kim 2020).

In barley abiotic stresses are known to inflict significant yield losses on a worldwide scale, and yet under severe stress conditions, this wonder cereal is one of the most important sources of energy for human food and animal feed (Newton *et al.*, 2011). Among the cereals “Barley” inherently possesses better abiotic stress tolerance, which provides possibility to extend its cultivation to larger geographical areas prone to abiotic stresses. Besides this, the traits of abiotic stress tolerance can be transferred to other members

of *Triticeae*. Around 10000 years ago wild barley (*Hordeum vulgare* ssp. *spontaneum*) was used for domestication of the modern barley (*Hordeum vulgare* ssp. *vulgare*). Wild barley can be a source to plenish the gene pool in cultivated barley as well as other close knitted species of grass family to cop up with challenges of climate change (Wiegmann, *et al.*, 2019). In this review, an attempt has been made to compile the available information on tolerance to drought, salinity and heat tolerance in barley.

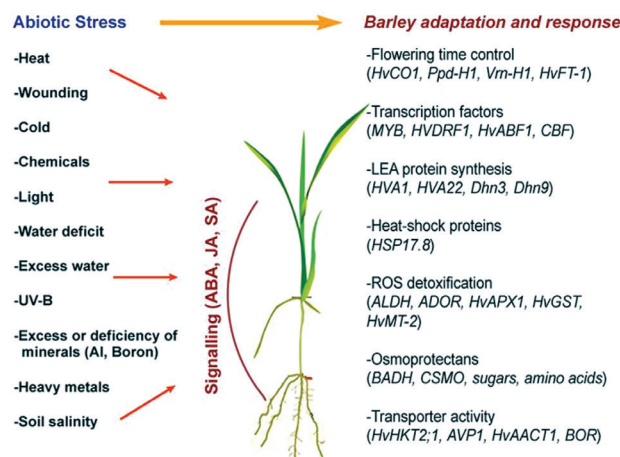


Fig. 2: Some of the possible traits/genes providing abiotic stress tolerance to barley plants (Adapted/Reproduced from: Gürel *et al.*, 2016)



2. Drought Stress tolerance

Drought is a multi-dimensional stress which is outcome of a complex interplay among the genotype, water availability, temperature, and water holding capacity of the soil. Drought severity and incidences may vary from location to location and season to season. For the rainfed barley crop, drought is the most common factor affecting stable barley production.. It occurs either because of insufficient seasonal precipitations received or non-availability of irrigation water. It is estimated that approximately 1/3rd of arable land is arid or semi-arid, due to lack of sufficient quantity of irrigation water. Rain-fed agriculture is the biggest consumer of water as around 70% of the total freshwater is already utilized for irrigation (Foley *et al.*, 2011). The drought stress results in decrease of quantity and quality of plant produce. Barley uses several strategies at physiological, molecular and cellular levels to escape/tolerate the ill effects of drought stress. The drought tolerance in plants can be either through the escape route or by avoiding the stress or tolerance. The early maturity *i.e.* early flowering and grain formation comes under the ambit of escape strategy while the physiological traits such as enhanced root system, stomatal and cuticular resistance *etc.*, provide osmotic stability to the plant and can be considered as avoidance strategy. Drought tolerance is intrinsic to plants and implies the strategies to keep the metabolic machinery functional and attain reproductive stage (Kishor *et al.*, 2014).

Plant hormones have been shown to play major role in imparting stress tolerance in plants through regulation at molecular and physiological levels; which involve production of protective metabolites, stomatal closure, root growth *etc.* Abscissic Acid (ABA) has been shown to be the major hormone involved in providing drought stress tolerance (Ahmed *et al.*, 2015).

Drought stress leads to decrease or inhibition of photosynthetic efficiency/activity through limited carbon dioxide availability because of stomatal closure and increased photo-damage to photosynthetic machinery and Calvin cycle enzymes. Another important implication of drought stress is excess production of reactive oxygen species (ROS) resulting from an imbalance between ROS production and anti-oxidative defence machinery. The reactive oxygen species disturb the structural and functional aspects of cellular organelles/metabolites

resulting in reduced photosynthesis and other growth related activities. A comparison of contrasting genotypes under drought stress conditions has shown that the membranes of thylakoid and chloroplast had more aberrant conformational changes in susceptible genotype (Ji *et al.*, 2012). In the anti-oxidant machinery, the activities of the enzymes catalase and superoxide dismutase play important role in imparting protective coverage during drought stress in barley (Marok *et al.*, 2013).

One of the important physiological parameters related to drought tolerance in barley is stomatal conductance; the lowered conductance is better related to increase drought tolerance. Barley gene *eibi1* shows a strong association between stomatal conductance and drought tolerance ability (Chen *et al.*, 2011). Besides this the PSII has also been shown to provide better protective capacity in tolerant genotypes (Tibetan wild barley XZ 5 and XZ 16) relative to the substantial reduction in maximal quantum yield of PSII (Fv/Fm) in cultivated barley CM 72 (Ahmed *et al.*, 2015). Chlorophyll content is also related to drought tolerant potential, in a study by Guo *et al.*, (2009), brought tolerant genotypes (Martin and HS 41-1) had relatively higher content of chlorophyll than the drought sensitive Moroc 9-75. Drought tolerant genotypes have better cell membrane stability as compared to the susceptible ones (Ahmed *et al.*, 2015).

To keep the metabolic functions and photosynthesis in active mode, it is important that plant maintains cell turgor and water absorption to the extent possible under drought stress. The osmotic adjustment (OA) is the key mechanism to achieve this state. For this plant accumulates large amounts of osmolytes like organic solutes and inorganic ions. A gene *Hsdr4*, situated on long arm 3H chromosome has been shown to be involved in osmotic adjustment and drought stress tolerance in barley (Suprunova *et al.*, 2004). During drought stress, plants, especially the tolerant types, start over-producing the different types of compatible organic solutes or osmo-protectants. Compatibility implies that these compounds are non-toxic to the cell at higher concentrations and are usually low molecular weight and highly soluble. The common osmo-protectants during drought stress are proline and glycine-betaine (GB), besides several others. These compounds facilitate in water uptake and proline (an amino acid) plays important role



in cell membrane stabilization also besides also acting as an antioxidant.

Proline is one of the most important osmo-protectants in barley and its higher accumulation during drought conditions help the plant to sustain metabolic functions, photosynthetic machinery and indirectly the yield. Proline biosynthesis during osmotic stress usually take place from glutamate pathway through the activities of two major enzymes pyrroline-5-carboxylate synthetase (*P5CS*) and pyrroline-5- carboxylate reductase (*P5CR*) and most rate limiting enzyme being pyrroline-5-carboxylate synthase. Drought or water stress results in the increased expression of *P5cs1* and *P5CR* in the leaves especially in chloroplasts, whereas *P5CS2* is primarily linked to the biosynthesis of proline in cytosol. An allele of *pyrroline-5-carboxylate synthase1* is shown to provide drought adaptation and proline accumulation in cultivated Scarlett barley (Frimpong *et al.*, 2021 and references therein). A relation between changes in *P5CS* activity, *P5CS* expression and Abscisic Acid Content on application of drought stress spells out possible role of ABA in inducing the increase in proline content (Bandurska *et al.*, 2017). Role of proline in providing protection against reactive oxygen species induced damage to membranes during drought stress has been shown cultivated barley (Ahmed *et al.*, 2015). Protection of photochemical efficiency of PSII mainly through lipid peroxidation reduction during drought has also been related to increased proline content (Molinari *et al.*, 2007).

Besides the proline content, increase in phenolic contents during combined drought and saline stress also helps in prevention in the formation of ROS in Tibetan wild and cultivated barley (Ahmed *et al.*, 2015 and references therein). Accumulation of Polyamines (PAs) is another strategy

for barley to provide protection to photosynthetic and metabolic machinery during drought stress. Polyamines act at multiple levels by providing stability at structural, osmotic and ionic levels besides acting as anti-oxidants and interacting with other signal molecules (Calzadilla *et al.*, 2014).

Ahmed *et al.*, (2020) have shown that in wild barley, reduced tolerance to the combined stress of drought and salinity was associated with the inhibition of biosynthesis of polyamines such as spermidine and spermine, polyamine oxidase, ethylene, biotin, and antioxidant enzyme activities. In addition to OAs, these osmolytes were suggested to be important for protecting cells against increased levels of reactive oxygen species accumulation under stress conditions.

In nutshell, barley (especially the wild one) possesses better stress signalling pathways (NCED, *PYL2*, *ATM*, *SAPK9*, *SNFRK*, *CPL1*, *HDSR4*); regulation of gene expression (*ABI5*, *HSFA*, *NAC*, *DREB*, *SPL*); antioxidant mechanisms (*HPT*, *GS*, *APX*, *CAT*, *DHAR*, *TRXm*); osmotic adjustment (*SUS*, *P5CS1*, *BAM*, *AQP* and protective proteins *sHSP*, *HSP70*, *HVA1*, *DHN*) for drought tolerance (Marok *et al.*, 2021) and these can potentially be harnessed for improvement of cultivated barley and other related species.

Using genome-wide association scan (GWAS) a panel of 218 spring barley accessions was studied for drought stress related SNPs and a total of 338 SNPs were found to be associated with several traits distributed across 7 chromosomes (Thabet *et al.*, 2018). The information generated at molecular levels is further used for studies and development of drought tolerance genotypes (Sallam *et al.*, 2019).

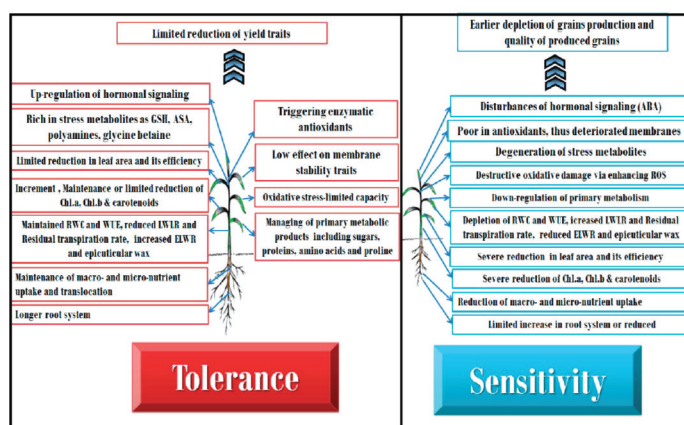


Fig. 3: The differences in physiological traits between tolerant and sensitive plants (Adapted/Reproduced from: Sallam, *et al.*, 2019).



3. Salinity Stress

It is estimated that around 20% of the total cultivated land and approximately half of the irrigated land is affected by salinity (Zhu, 2001). Salinity affects the plant productivity and the response of plants to salinity stress is an outcome of interactions among several quantitative traits which are affected by various environmental factors, encompassing complex physiological and molecular mechanisms. Due to depletion of water table especially in the irrigated rice-growing regions, the area under salinity is increasing exponentially. Salinity affected soils are characterized by excessive soluble salts and exchangeable sodium on its surface and sub-surface layers. The excessive salt content affects plant root systems. As per the Food and Agriculture Organization report, approximately 800 million hectares of land around the world is affected by salinity and around 10 million ha of agricultural land is getting added to it annually due to intensive cultivation, use of contaminated water and climate change (WHO, 2008). If proper measures are not taken, the total saline soils may constitute more than 50% of the arable land by 2050 (Jamil *et al.*, 2011).

Higher concentrations of salts affect the structural and functional metabolic machinery of the plant and even cause the oxidative stress through overproduction of superoxide radicals. Mainly uptake and subsequent accumulation of excess amounts of Sodium and Chloride ions leads to cellular injury. Plants respond to salinity stress deploying several mechanisms, the Na^+/K^+ homeostasis and Na^+ exclusion are the major ones (Kumar *et al.*, 2015

and references there in). Barley is one of the most salt tolerant among cereals and acts as a model crop for studying the biochemical, physiological and molecular mechanisms of tolerance and use of this information for imparting salt tolerant trait in other cereal species (Zhu *et al.*, 2020 and references therein). Barley (*Hordeum vulgare*) has the ability to tolerate the NaCl concentration upto 250mM (Hazzouri *et al.*, 2018) and salinity tolerant barley genotypes have characteristics matching halophytes like excluding Na^+ from uptake and accumulating Na^+ in tissues. Tolerant barley genotypes have the ability to sequester Na^+ in the vacuoles, in turn maintaining high K^+/Na^+ levels in the cytosol and thus decreasing the damage from Na^+ toxicity. Tolerant genotypes accumulate compatible solutes in the cytoplasm to maintain the osmotic balance in view of the vacuolar sodium ion concentration Salinity tolerance is a multi-genic trait and specific traits express depending upon the growth phase of the plant (Colmer *et al.*, 2005).

The wild barley has relatively better salinity tolerance and in certain cases able to tolerate short term exposure upto 300 mM NaCl (Ebrahim *et al.*, 2020). Wild barley in such cases were able to maintain higher K/Na ratio and lower Na concentration in the roots and shoots. Due to homologous nature, *Hordeum spontaneum* germplasm can be a better source of salinity tolerance for breeding better genotypes rather than other wild *Hordeum* species like halophyte *H. Marinum*. The role of structural sterols or sterol-derived hormones has also been shown in imparting the salinity tolerance in barley (Witzel *et al.*, 2014)

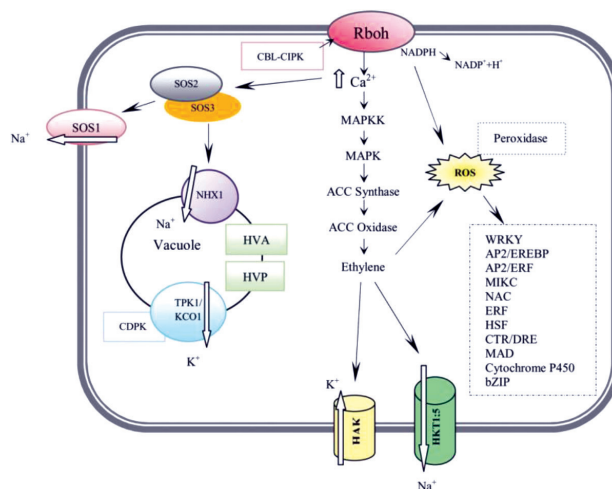


Fig 4. Genes involved in salinity-stress signalling pathways and tolerant mechanisms in the salt-tolerant mutant genotype (Adapted/Reproduced from Yousefirad *et al.*, 2020)



Barley possesses several genes which impart salinity tolerance to plant and these genes have been are grouped for convenience in following groups (Walia *et al.*, 2006; Wu *et al.*, 2011; Yin *et al.*, 2018) (Figure 4 and Table 1).

Table 1: Discovered genes involved in salinity/drought tolerance in barley

Functionality	Genes	References
Osmotic protection	<i>HvPIP2;5</i> , <i>HVA1</i> , <i>HvDREB1</i> , <i>HvCBF4</i> , <i>HvWRKY38</i>	Alavilli <i>et al.</i> , 2016; Lal <i>et al.</i> , 2008, Gürel <i>et al.</i> , 2016
Na ⁺ and K ⁺ transport; Na ⁺ /H ⁺ antiport	High-affinity potassium transporter (<i>HKT</i>) family (<i>e.g.</i> <i>HvHKT1;5</i> , <i>HvHKT1</i> , <i>HvHKT2;1</i> , <i>HvHAK1</i> , <i>HvHKT1</i> , <i>HvHKT2</i>) Na ⁺ /H ⁺ exchanger (<i>NHX</i>) family <i>HvNax4</i> , <i>HvSOS1</i> (<i>HvNHX7</i>), <i>HvSOS2</i> (<i>HvCIPK24</i>), <i>HvSOS3</i> (<i>HvCBL4</i>), <i>HvNHX1</i> , <i>HVA</i>) Na ⁺ /H ⁺ exchanger (<i>NHX</i>) family <i>HvNax4</i> , <i>HvSOS1</i> (<i>HvNHX7</i>), <i>HvSOS2</i> (<i>HvCIPK24</i>), <i>HvSOS3</i> (<i>HvCBL4</i>), <i>HvNHX1</i> , <i>HVA</i>)	Hazzouri <i>et al.</i> , 2018; Huang <i>et al.</i> , 2019, Mian <i>et al.</i> , 2011; Assaha <i>et al.</i> , 2017; Mangano <i>et al.</i> , 2008; Qiu <i>et al.</i> , 2011; Rivandi <i>et al.</i> , 2011; Yousefirad <i>et al.</i> , 2018; Wu <i>et al.</i> , 2019
Regulatory proteins/elements/factors	<i>CBF/DREB</i> (C-repeat-binding protein/dehydration-responsive element-binding protein) family (<i>HvRAF</i>); ethylene response factor (<i>HvAP2/ERF</i>) <i>HvDREB1</i> , <i>HvCBF4</i> , <i>HvWRKY38</i> ; <i>HvDRF1</i>	Jung <i>et al.</i> , 2007; Guo <i>et al.</i> , 2016; Xu <i>et al.</i> , 2009; Gürel <i>et al.</i> , 2016; Xue and Loveridge, 2004
Jasmonate (JA) biosynthesis	Late embryogenesis abundant (LEA) protein genes (<i>e.g.</i> <i>HVA1</i> ; <i>HVA22</i>).	al-Yassin and Khademian, 2015

Based upon the information accessed from the literature, the possible biochemical and molecular factors affecting salinity tolerance can be (also see Figure 5 and Figure 6):

- Reduction in uptake and increase exclusion of Na⁺ and the QTL QSL.TxNn.2H is most probably involved in regulating xylem Na⁺ loading (Zhu *et al.*, 2020)
- Efficient compartmentalization of Na⁺ mainly into vacuoles
- Upregulation of ROS Scavenging, stabilization of Photosynthesis and ATP Synthase related proteins
- Increase in the levels of metabolites involved in cellular protection besides the hexose phosphates and TCA cycle intermediates (Widodo *et al.*, 2009)
- Higher concentration of flavanoids in salt stressed plants (Ahmed *et al.*, 2015).
- The roles of anti-oxidant enzymes and proline in salinity tolerance are yet inconclusive
- For osmotic adjustments in the plant, soluble carbohydrates may also be playing important role

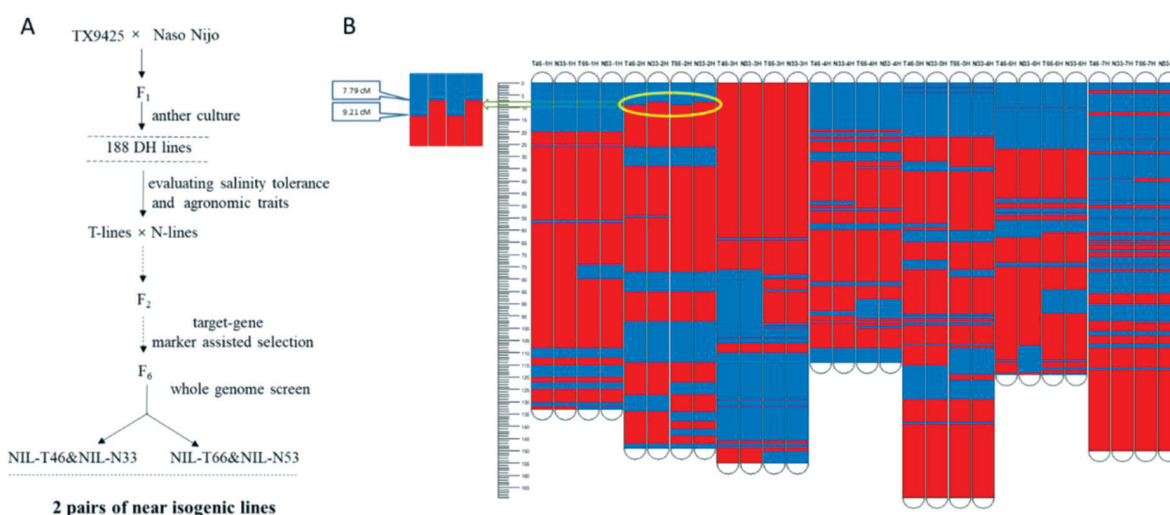


Fig 5. Construction of two pairs of NILs. (A): Strategy for developing NILs. (B): Comparison between genotypes of near isogenic (Pair 1: T46/N33; Pair2: T66/N53). Red: NasoNijo backgrounds; blue: TX9425 backgrounds. Yellow circle: the major difference on 2H at the position of 6.6-9.4 cM for two pair of NILs (Adapted/Reproduced from Zhu *et al.*, 2020)



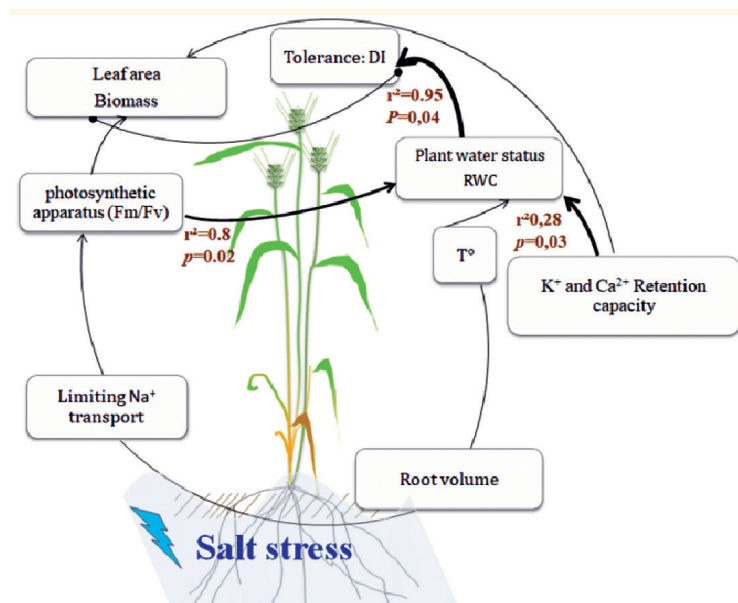


Fig. 6: Physiological schematization of salt stress in barley (Reproduced/Adapted from: Hammami *et al.*, 2020)

Salicylic acid and potassium nitrate application has been shown to provide salinity tolerance (Fayez and Bazaid, 2014) through reduced Na^+ uptake improved photosynthetic pigment content and plant growth. Salicylic acid and KNO_3 treatment also lead to tone down the oxidative stress during salt and drought stress.

4. High Temperature Stress

Temperature is one the most important environmental factors, responsible for pattern in the geographical distribution of plant species and its productivity and/or end product quality. Among the different growth stages of barley from germination to maturity, temperature plays a vital role, however this becomes a critical factor determining grain yield and quality during the flowering and grain filling stage. In sub-tropical climates, like in northern Indian plains, barley crop has to face higher temperature especially during the post anthesis and maturity stages. As per a report by the Intergovernmental Panel on Climate Change (IPCC), the crop production will be seriously challenged by the increasing temperatures, which may rise by 2.0–4.5 °C till the end of this century (Liu *et al.*, 2017). It is speculated that even a change by 1°C will have detrimental effects on biochemical and physiological activities of plants (Anwar *et al.*, 2018). To cope up with the looming threat of high temperature stress, its important to understand and decipher the molecular/genetic basis of high temperature stress tolerance to develop improved crop plants through conventional or

molecular plant improvement techniques (Anwar and Kim, 2020). In one study carried out using wild barley, cultivars and breeding material, it has been reported that the reduction in period of reproduction (grain development and growth) was much lesser in wild types as compared to the cultivated ones (Bahrami *et al.*, 2021), indicating greater utilization of wild type resources for introgression of this abiotic stress tolerance trait

Savin and Nicolas (1996) studied the effect of heat treatment (maximum 40°C for 6 h/ day), with or without drought stress on barley, during the anthesis period. The reduction in grain weight and grain growth filling duration took place under these conditions and combined effect of both the stresses was more detrimental. The reduction in grain weight and growth duration was cultivar dependent. The heat stress resulted in reduction of starch accumulation and increase in the nitrogen content of the grains. Since starch is the major raw material for malt and further fermentation in preparation of malt based end products, the heat stress during the grain filling period may have major impact on grain quality. The heat stress ($\geq 35^\circ\text{C}$) results in starch degradation, starch granule size aberrations and increase in embryo tissue. Even beta glucans degradation has been observed during heat stress resulting in more friable malt (Wallwork *et al.*, 1998). Since starch contributes as the largest component of grain weight, heat stress leads to formation of shrivelled grains. Reduction in starch content takes place mainly because



of rapid decline in photosynthesis and heat sensitivity of starch synthesizing enzymes especially soluble starch synthase (Sallam *et al.*, 2019). The heat stress during early stages of grain development is more serious as compared to the later ones (Savin and Nicolas, 1999). Under Indian sub-tropical climates the cessation of starch biosynthesis in susceptible cultivars occurs more due to utilization of assimilates rather than the supply (Figure 7). During heat stress the activities of acid- and neutral invertase,

sucrose synthase and total amylase attain may attain an early peak (Singh *et al.*, 2008) leading to deterioration of grain quality. The pre-anthesis reserve in taller genotypes could be advantageous as compared to the dwarf ones (Schnyder, 1993). However, the tall genotypes lodge more under climatic fluctuations and thus may have compromised yield and quality. But the pre-anthesis reserves contribute significantly during grain filling under stressful environments (Bidinger *et al.*, 1977).

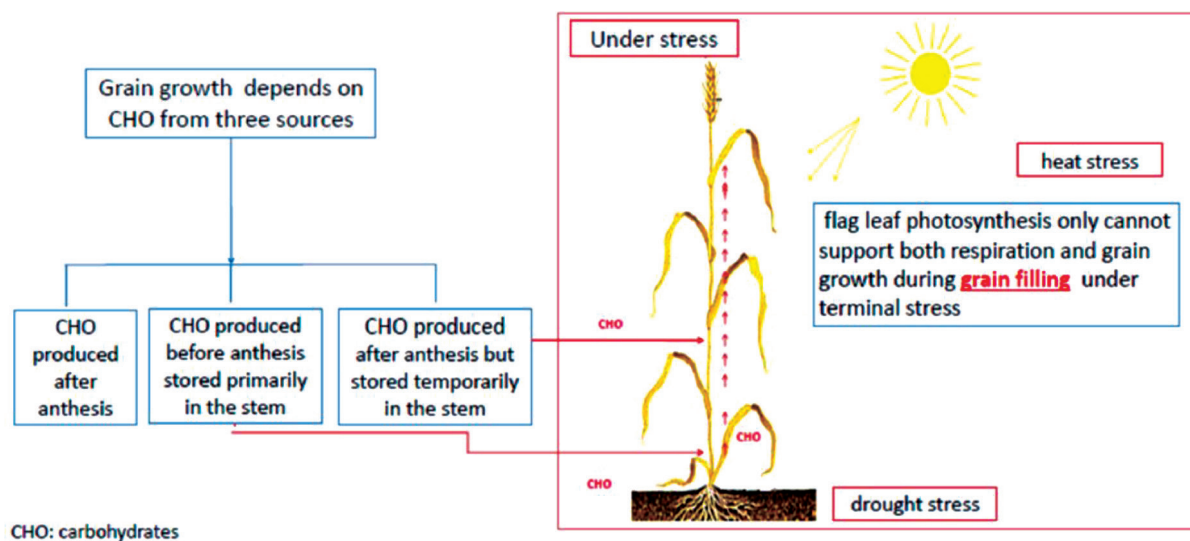


Fig. 7: The three sources of carbohydrates that are transferred into grains during grain filling under drought and heat stresses (Reproduced/Adapted from Sallam *et al.*, 2019)

Gous *et al.*, (2016) have studied the heat tolerance in barley at genetic level and suggested that the most effective markers and genes could be located on chromosomes 1H and 4H (Figure 8). A marker S4_250499621 has been shown to associated with increased proline and chlorophyll content and lesser reduction in thousand kernel weight and grain yield per spike (Gous *et al.*, 2016).. Transcriptomics studies have shown stress induced expression of 958 genes and down regulation of 1122 genes in the developing barley grain (Mangelsen *et al.*, 2011). Down regulation of the genes mainly impacted the biosynthesis of storage compounds and cell growth thus leading to impairment of grain development. This was corroborated by another study by Templer *et al.*, (2017), where the heat/drought stress indicated to QTLs affecting the major genes involved in starch biosynthesis. Some of the traits associated with heat stress tolerance are grain yield per spike (GYPS), starch content (Str), protein content (PC), proline content (Pro), maintenance of leaf water content, chlorophyll stability and starch content.

As indicated earlier also chromosomes 1H and 4H may harbour many alleles/traits for some of these important traits. (Dawood *et al.*, 2020). Hübner *et al.*, (2009) found that temperature and aridity gradients served as major selective pressures in the adaptation of wild barley (*H. vulgare ssp. spontaneum*). Photosynthesis is the most sensitive physiological process which is significantly affected by heat stress (Wang *et al.*, 2015). Under high temperatures, the ability to sustain leaf gas exchange is directly associated with heat tolerance in all plant species (Bita and Gerats, 2013). The wild genotypes maintain the gas exchange values under heat stress better compared to cultivated ones, indicating that the H₂O/CO₂ exchange in the leaves of *Hordeum vulgare ssp. spontaneum* is relatively less affected by high temperatures. It is interesting to note that although both the cultivated and wild barley genotypes exhibited close average values of the total Chlorophyll content under normal conditions, heat stress leads to significantly lower Chlorophyll degradation in the wild barley than that in the cultivated ones. The strong inverse



relationship observed between the total Chlorophyll and grain yield loss under heat stress provides further evidence that leaf Chlorophyll content can be exploited as an indicator of either plant photosynthetic capacity or its yield potential under thermal-stress conditions. The impact of heat stress on the composition of membranes is more destructive than other abiotic stresses because the fluidity of membranes composed of straight chain fatty acids can be easily disrupted by heat. Under field conditions, thermal-tolerant genotypes of *Hordeum vulgare*

ssp. spontaneum were found to employ various strategies to alleviate damages to their chlorophyll, cell membrane integrity, PSII, and photosynthetic rate. Considering the drastic effect of the global warming on the photosynthetic apparatus, the study of thermal-tolerant genotypes of wild barley can contribute tremendously to our understanding and improvement of carbon sequestration in cultivated barley by employing genetics and breeding tools (Bahrami *et al.*, 2019 and references there in)

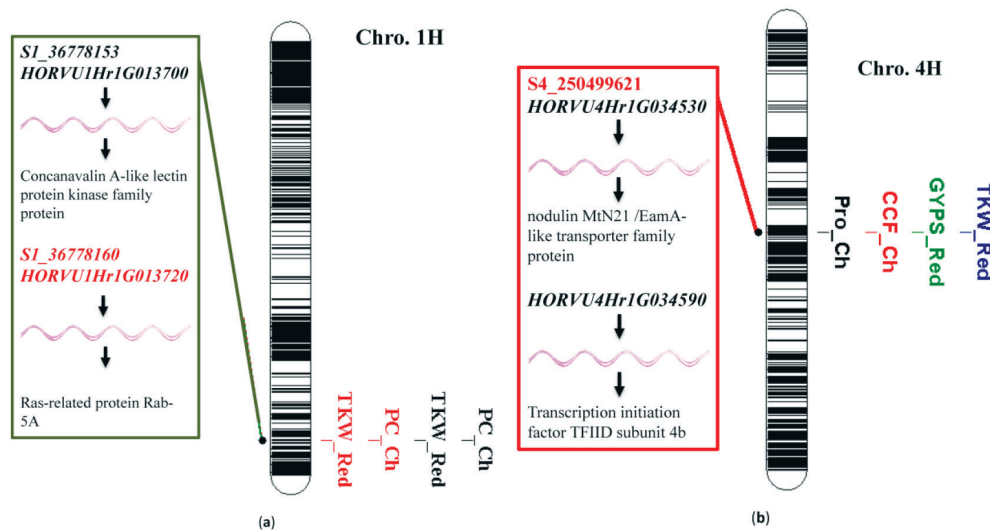


Fig. 8. Significant single nucleotide polymorphisms (SNPs) associated with changes in protein content (PC) and TKW and their candidate genes; (b) significant SNPs associated with the changes in chlorophyll content (CCF) and proline content (Pro), TKW, and GYPS and its candidate genes. Black bands refer to the physical position of the SNP on the respective chromosome. (Reproduced/Adapted from Dawood *et al.*, 2020)

Conclusion

Barley, especially the wild species, deploys several biochemical, molecular and physiological strategies to tolerate or escape various abiotic stresses. Still, the cultivated barley suffers significant yield and grain quality losses owing to drought, heat and salinity. The popular cultivars lacking tolerance to these abiotic stresses are the targets of introgressive breeding which in turn requires the identification and localization of the relevant genes on barley chromosomes. The physiological aspects of tolerance to abiotic stresses in barley need to be dissected at the genetic level in comprehensive details before they can be utilized in the introgressive breeding. The identification of donors for tolerance should ideally encompass different gene pools of barley to have a diversity of sources for broader genetic base of the cultivated varieties. In this context, exploitation of germplasm resources can be

done to develop barley genotypes having desired levels of yield and quality for the regions having shorter grain filling period. Moreover, the study of these parameters at genetic level can be used to transfer these traits in cultivated barley and even in other related crop species to evade the challenges of climate change.

Compliance with ethical standards

NA

Conflict of interest

No

Author contributions

DK: Conceptualization, Data curation, CL, SKB: Writing & updating the manuscript for publication, RPSV and GPS: Supervision, and Validation. All the listed authors read and approved the manuscript.



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