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Review:

Salinity tolerance in barley during germination—homologs and potential genes[#]

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Abstract: Salinity affects more than 6% of the world's total land area, causing massive losses in crop yield. Salinity inhibits plant growth and development through osmotic and ionic stresses; however, some plants exhibit adaptations through osmotic regulation, exclusion, and translocation of accumulated Na^+ or Cl^-. Currently, there are no practical, economically viable methods for managing salinity, so the best practice is to grow crops with improved tolerance. Germination is the stage in a plant's life cycle most adversely affected by salinity. Barley, the fourth most important cereal crop in the world, has outstanding salinity tolerance, relative to other cereal crops. Here, we review the genetics of salinity tolerance in barley during germination by summarizing reported quantitative trait loci (QTLs) and functional genes. The homologs of candidate genes for salinity tolerance in *Arabidopsis*, soybean, maize, wheat, and rice have been blasted and mapped on the barley reference genome. The genetic diversity of three reported functional gene families for salt tolerance during barley germination, namely dehydration-responsive element-binding (DREB) protein, somatic embryogenesis receptor-like kinase and aquaporin genes, is discussed. While all three gene families show great diversity in most plant species, the *DREB* gene family is more diverse in barley than in wheat and rice. Further to this review, a convenient method for screening for salinity tolerance at germination is needed, and the mechanisms of action of the genes involved in salt tolerance need to be identified, validated, and transferred to commercial cultivars for field production in saline soil.

Key words: Genetics; Barley; Quantitative trait locus (QTL); Germination; Salinity tolerance; Homologous gene; Diversity
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1 Introduction

Salinity affects about 6% of the world's total land area, including 20% of arable land and 33% of irrigated land (Shrivastava and Kumar, 2015; Machado and Serralheiro, 2017; Kuang et al., 2019; Safdar et al., 2019), causing estimated yield losses of 20% (Ashraf and Harris, 2005; Pirasteh-Anosheh et al., 2016). Furthermore, land salinisation is increasing, with 10 million ha of agricultural land destroyed annually by salt accumulation (Pimentel et al., 2004) due to several factors including the use of contaminated irrigation water, intensive farming and poor drainage, and climate change (Machado and Serralheiro, 2017; Isayenkov, 2019). Without proper and sustainable control, salinity-affected areas will increase to more than 50% of the world's total arable land by 2050 (Ashraf, 2009; Anosheh et al., 2011; Jamil et al., 2011; Emam et al., 2013).

According to Pirasteh-Anosheh et al. (2016), plants experience four types of stress under saline conditions: (1) salinity reduces water uptake due to

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ORCID: Chengdao LI, https://orcid.org0000-0002-9653-2700 the low water potential of the soil which interferes with the osmotic gradient (Munns and Tester, 2008); (2) the absorbed salt reaches a level that causes severe cellular toxicity due to low sequestration of Na^+ into vacuoles (Nawaz, 2007); (3) the salt interacts with minerals causing nutrient imbalance and deficiency (Nawaz, 2007); and (4) salinity accelerates the production of active oxygen radicles, such as H_2O_2 (hydrogen peroxide), $\bullet O_2^-$ (superoxide), $^1O_2$ (singlet oxygen), and $\bullet OH^-$ (hydroxyl radicle), which can damage or even kill plants (Hernández et al., 2001). Greenway and Munns (1980) classified plants into two major categories based on their salinity tolerance, namely (1) halophytes and (2) glycophytes. Halophytes have an exceptional ability to produce heteromorphic seeds that have diverse dormancy and germination capacity under saline conditions (Liu RR et al., 2018). Seed germination in glycophytes is severely inhibited under salinity due to both osmotic stress and ionic toxicity stress, unlike in halophytes that are less affected by osmotic pressure (Romo and Haferkamp, 1987; Dodd and Donovan, 1999; Zhang et al., 2010). Halophytes can better regulate the ion-gate-controlled NaCl influx into seed cells (Glenn et al., 1999; Huang et al., 2018). However, salinity-tolerant glycophytes have a lower osmotic potential than sensitive glycophytes, enabling them to absorb more water from the soil during germination (Zhang et al., 2010).

Barley, the fourth most important cereal in the world (Schulte et al., 2009; Visioni et al., 2019), is a glycophyte, but its salinity tolerance varies among genotypes (Mano and Takeda, 1997; Flowers and Hajibagheri, 2001; Xue et al., 2009; Debez et al., 2019). Some barley genotypes are able to thrive in saline conditions (Harlan, 1995; Shen et al., 2018). Salinity-tolerant barley genotypes exhibit halophytic features such as excluding Na^+ from uptake (Chen ZH et al., 2007) and accumulating Na^+ in tissues (Munns et al., 1988; Munns and Tester, 2008). Tolerant genotypes sequester Na^+ in their intracellular vacuoles, thereby maintaining high K^+/Na^+ levels in the cytosol while reducing damage from Na^+ toxicity (Shabala et al., 2010; Mian et al., 2011; Fu et al., 2018; Han et al., 2018; Ishikawa and Shabala, 2019). They can also synthesize compatible solutes in the cytoplasm to balance the osmotic potential of vacuolar Na^+ (Widodo et al., 2009). Salinity tolerance is controlled by multiple genes that are expressed differently during different growth phases (Qiu et al., 2011; Ahmed et al., 2013a). Germination, which determines seedling vigour and the plant population, is the most important growth stage, but is sensitive to salinity stress (Zhang et al., 2010; Bewley et al., 2013).

Several genes have association with enhanced salinity tolerance in barley (Wu et al., 2011) and are grouped into four classes based on their function (Walia et al., 2006; Wu et al., 2011; Yin et al., 2018). (1) Genes that enhance osmotic protection, such as *HvPIP2;5* (Alavilli et al., 2016), *HVA1* (Lal et al., 2008), *HvDREB1*, *HvCBF4*, *HvWRKY38* (Gürel et al., 2016), and reactive oxygen species (ROS)-scavenging genes that include osmoregulatory trehalose synthesis, mannitol-1-phosphate dehydrogenase (M1PD), and pyrroline-5-carboxylase synthetase (P5CS). (2) Genes controlling Na^+ and K^+ transport, such as the high-affinity potassium transporter (*HKT*) family (e.g. *HvHKT1;5* (Hazzouri et al., 2018; Huang et al., 2019), *HvHKT1;1* (Han et al., 2018), *HvHKT2;1* (Mian et al., 2011; Assaha et al., 2017), *HvHAK1* (Mangano et al., 2008), *HvHKT1*, *HvHKT2* (Qiu et al., 2011)), the Na^+/H^+ exchanger (*NHX*) family (*HvNax4* (Rivandi et al., 2011), and salt overly sensitive (SOS) engaged Na^+/H^+ antiporters (*HvSOS1* (*HvNHX7*), *HvSOS2* (*HvCIPK24*), *HvSOS3* (*HvCBL4*), *HvNHX1*, *HVA*) (Yousefirad et al., 2018; Wu et al., 2019). (3) Genes that produce regulatory proteins, such as the *CBF*/*DREB* (C-repeat-binding protein/dehydration-responsive element-binding protein) family (e.g. *HvRAF* (Jung et al., 2007), *HvAP2*/*ERF* (ethylene response factor) (Guo et al., 2016), *HvDREB1* (Xu et al., 2009), *HvCBF4*, *HvWRKY38* (Gürel et al., 2016), *HvDRF1* (Xue and Loveridge, 2004)) in the signalling pathways of long distance and downstream gene expression. Salinity and drought stresses induce the expression of root abundant factor (*RAF*), *CBF3*, and *CBF4* from the *CBF*/*DREB* gene family in most plants. Twenty *CBF* genes have been identified in barley, which enhance tolerance to drought, salinity, and low temperature (Wu et al., 2011). (4) Genes that induce jasmonate (JA) biosynthesis, such as late embryogenesis abundant (LEA) protein genes (e.g. *HVA1* expressed in response to water and salinity stresses, *HVA22* expressed in response to dehydration, extreme temperatures, abscisic acid (ABA) secretion, and salinity stress (al-Yassin and Khademian, 2015)).

2 Seed germination process and roles of hormones

Seed germination requires optimum environmental factors, including water, oxygen, and temperature. Other environmental factors, such as light and nitrates, can also affect seed germination (Finch-Savage and Leubner-Metzger, 2006; Rajjou et al., 2012). The process of germination occurs in three main phases regulated by hormones, reactive nitrogen species, and ROS (Ma et al., 2017). The first phase involves the expression of genes that play a major role in cell wall metabolism. The second phase encompasses significant stimulation of hormonal and enzyme activity by genes involved in amino acid synthesis, starch metabolism, nucleic acid synthesis, protein synthesis and transport (Weitbrecht et al., 2011). The third phase involves the induction of genes for photosynthetic metabolism after radicle protrusion (Ma et al., 2017). Hormonal imbalance, caused by factors such as low temperature, drought, and salts (saline and sodic) that increase ground osmotic pressure (Bartels and Nelson, 1994), can affect the seed germination process (Lopez-Molina et al., 2001; Belin and Lopez-Molina, 2008).

Several hormones produced by plant and soil microorganisms such as bacteria play a role in inducing or breaking seed dormancy and thus contribute to the germination process (Bewley, 1997; Baskin and Baskin, 2001; Koornneef et al., 2002; Hoyle et al., 2015). Interestingly, as much as gene expression controls plant hormone activity, the reverse can be true with some hormones regulating gene expression (Miransari and Smith, 2014). For example, ABA usually induces dormancy at seed maturation and gibberellins (GAs) break dormancy during germination (Fig. 1) (Bentsink and Koornneef, 2008; Hauvermale et al., 2012). When an environmental stress such as salinity occurs during germination, ABA is produced in the seeds (Weyers and Paterson, 2001) to upregulate transcription factors (TFs) such as *AB13* and *AB15* that stimulate genes encoding the osmotolerance protein and block the germination process (Fedoroff, 2002; Lopez-Molina et al., 2002; Graeber et al., 2010; Miransari and Smith, 2014). However, ABA is negatively regulated by ABA-INSENSITIVE1 (*ABI1*) and *ABI2* and the expression of the *HvABA8'OH-1* gene (Ma et al., 2017). GAs release seeds from dormancy by stimulating the production of hydrolases for the germination process (Miransari and Smith, 2014; Abido et al., 2019). The embryo synthesizes GA after imbibing water (Diaz-Mendoza et al., 2019). The GA binds to receptors to promote the breakdown of repressor of GA-like2 (RGL2), a DELL factor suppressing germination, the expression of several genes (*GAMYB*, *HvPTR*, *WRKY*, *PP2C*, *GATA*, and *HvKAO1*), and the production of essential proteins during germination in stress environments (Marrs, 1996; Sun and Gubler, 2004; Ma et al., 2017). The effect of GA is terminated by the expression of GA 2-oxidase 1 (*HvGA2ox*), which is responsible for its inactivation (Fig. 1) (Ma et al., 2017).

During germination, the concentration of ethylene increases (Yang and Hoffman, 1984; Pennazio and Roggero, 1991; Petruzzelli et al., 2000), which reduces plant growth under saline conditions in the presence of ABA (Matilla, 2000; Rinaldi, 2000; Jalili et al., 2009). Auxins (indole-3-acetic acids (IAAs)) are essential for cell elongation, and radicle and embryo growth during germination (Popko et al., 2010; Hauvermale et al., 2012). Brassinosteroids (BRs) and IAA on the other hand stimulate the secretion of ethylene which works in conjunction with GAs to induce germination (Arora, 2005; Miransari and Smith, 2014). Auxins reduce seed sensitivity to ABA by overexpressing microRNAs (Liu et al., 2007) and interacting with GAs to counteract ABA suppression during germination (Chiwocha et al., 2005; Hentrich et al., 2013). Cytokinins interacting with ethylene enhance cell division and alleviate abiotic stresses like salinity during germination (Chiwocha et al., 2005; Subbiah and Reddy, 2010; Peleg and Blumwald, 2011; Miransari and Smith, 2014). BRs, in conjunction with GAs and ethylene, improve seed resistance to abiotic stress, enhance embryo growth out of the seed, and reduce the effects of ABA (Bajguz and Hayat, 2009; Miransari and Smith, 2014; Procházka et al., 2015) and salt stress (Vázquez et al., 2019) during germination. JAs are signalling molecules for plant defence against osmotic stress caused by salt (Kazan and Manners, 2012; Nguyen et al., 2019). They obstruct the production of two primary ABA biosynthesis genes (*TaNCED1* and *TaNCED2*) with acetylsalicylic acid (ASA) in stress germination in wheat (Xu et al., 2016).

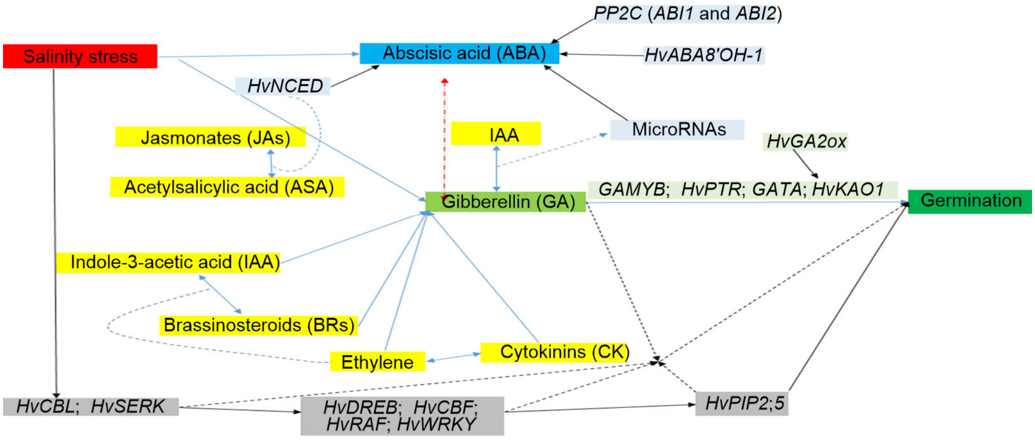

Fig. 1 Interactions among the hormones and gene regulatory pathways in barley during germination under salinity stress
Blue lines indicate hormonal regulation, while black lines are for genes and transcription factor expression. Red double-arrowed dotted line shows the negative interaction between ABA and GA during germination, while blue double-arrowed line shows the positive interaction among the hormones. Blue dotted lines show the stimulation outcome of the hormonal interactions, while black dotted lines show the regulatory interactions of genes. *GAMYB*: GA-induced Myb (myeloblastosis)-like protein; *HvPTR*: barley scutellar peptide transporter; *HvKAO1*: barley kaurenoic acid oxidase 1; *HvGA2ox*: barley GA 2-oxidase 1; *HvNCED*: barley nine-*cis*-epoxycarotenoid dioxygenase; *PP2C*: protein phosphatase type 2C; *ABI1*: ABA-insensitive 1; *HvABA8'OH-1*: barley ABA 8' hydroxylase; *HvCBL*: barley calcineurin B-like protein; *HvSERK*: barley somatic embryogenesis receptor-like kinase; *HvCBF*: barley C-repeat-binding protein; *HvDREB*: barley dehydration-responsive element-binding protein; *HvRAF*: barley root abundant factor; *HvPIP2;5*: barley aquaporin 2;5

3 Salinity versus sodicity

Saline soils predominantly contain sodium (Na^+) cations and chloride (Cl^-) anions and, in some cases, Ca^{2+}, Mg^{2+}, SO_4^{2-}, but not HCO_3^- or CO_3^{2-} (Abrol et al., 1988). Saline soils have good structure, an advantage for proper tillage and crop cultivation, and usually an electric conductivity extract (ECE) higher than 4 dS/m (40 mmol/L), an exchangeable water-soluble sodium of >15%, and a pH of <8.5 but >7. However, when the surface of the ground appears black, hard, and dry, the soil is sodic. In this case, the predominant cation is Na^+, but the primary anions are Cl^-, SO_4^{2-}, HCO_3^- and a small amount of CO_3^{2-}. Sodic soils have an exchangeable Na^+ of >15%, an ECE of >4 dS/m, and a pH of >8.5 (Abrol et al., 1988).

3.1 Causes and types of salinity

Soil salinity is caused by (1) natural or primary, and (2) secondary or human-induced events (Manchanda and Garg, 2008; Parihar et al., 2015) and is either (1) groundwater-associated (dryland salinity), (2) non-groundwater-associated (transient salinity), or (3) irrigation-associated (Ghassemi et al., 1995; Rengasamy, 2006; Majeed and Muhammad, 2019). Transient salinity fluctuates with soil depth and its effect on plant growth is dependent on rainfall. It occurs in semi-arid environments where there is insufficient rain to leach the soil. Clay layers below the topsoil hinder the movement of water and salts, leading to ion accumulation on the soil surface (Rengasamy, 2002, 2006). Most of Western Australia is characterized by a temperate climate. Ion accumulation in the topsoil following dry, hot summers can result in high salinity at sowing, which affects seed germination. These ions can be leached only by rainfall or irrigation. Dry-seeding or seeding with the first rain increases the likelihood that germinating seeds will be affected by salinity stress.

3.2 Effect of salinity on germination

Salinity affects the seed germination process by altering water imbibition, changing enzymatic activities causing ionic toxicity, interfering with protein metabolism, causing hormonal imbalances, and reducing the possibility of seeds using their reserves, all of which delay and reduce the number of sprouting seeds (Läuchli and Grattan, 2007; Bordi, 2010; Munns et al., 2012; Parihar et al., 2015; Debez et al., 2019). Saline conditions create an external osmotic stress that reduces water availability and uptake

(Bernstein, 1963; Bliss et al., 1986; Sayar et al., 2010; Sabagh et al., 2019) and increases the toxic absorption of ions (Hampson and Simpson, 1990), which decreases seed germination (Dodd and Donovan, 1999; Luan et al., 2014; Narsing Rao et al., 2019; Polash et al., 2019).

3.3 Salinity tolerance mechanisms

Plants overcome salinity stress through various mechanisms that involve osmotic adjustment, Na^+ exclusion, and tissue tolerance (Munns and Tester, 2008; Liang et al., 2018; Miransari and Smith, 2019). These encompass biochemical, physiological, and molecular mechanisms of variable complexity (Han et al., 2015; Pirasteh-Anosheh et al., 2016; Kumari et al., 2019). During germination, plants become saline-tolerant by (1) excluding salts from seed cells while maintaining high osmotic potential using organic solutes, or (2) accumulating salt ions in seed cells to increase osmotic potential while putting mechanisms in place to mitigate toxicity (Zhang et al., 2010). Seeds of salt-tolerant barley genotypes take up sodium to increase osmotic potential to absorb water during germination under salinity stress (Zhang et al., 2010), while minimising K^+ losses (al-Karaki, 2001). The vacuole is a vital cell organelle for compound deposition during osmotic stress regulation, and its size is a measure of salinity tolerance (Lauchli and Epstein, 1990; Volkmar et al., 1998; Yarra, 2019; Yarra and Kirti, 2019).

3.3.1 Indicators of salinity tolerance

Salinity tolerance indicators in plants can be divided into three main groups: (1) agronomic/morphological, (2) physiological, and (3) biochemical.

3.3.1.1 Agronomic/morphological indicators

Salinity tolerance is expressed externally through visible morphological/agronomic traits as a result of several physio-chemical processes that take place inside the plant. They are a reflection of genetic and physiological mechanisms influenced by the environmental effect on the plant that confer salinity tolerance (Ashraf and Harris, 2004). They occur at the whole plant or organ level and are mostly physically visible. These indicators are easy to measure and include germination percentage, yield, survival rate/percentage, plant height, leaf area, leaf injury, relative growth rate, and relative growth reduction. Distinguishing between tolerant and non-tolerant plants using agronomic indicators can be subjective.

3.3.1.2 Physiological indicators

Like the other indicator groups, physiological indicators are the result of processes that take place inside plant tissues, organs, cells, and organelles when exposed to salinity stress. They include the transportation of excess ions to the vacuole or sequestering them in older tissues. This group of indicators is measured by traits that include relative growth rate, germination speed, ion homeostasis, photosynthesis, transpiration, and senescence (Negrão et al., 2017). They provide more objective information than morphological indicators when combined with knowledge of the genetic model of salinity tolerance (Ashraf and Harris, 2004). Sodium ions are transported and compartmentalized in the vacuoles using two types of H^+ pumps (V-ATPase and H^+-ATPase) and vacuolar pyrophosphatase (V-PPase). The pumps are facilitated by SOS pathways with three types of proteins (SOS_1, SOS_2, and SOS_3). SOS_1 is essential for regulating Na^+ efflux at the cellular level and enhancing Na^+ transportation in the organelles and tissues. The SOS_2 can not only interact with SOS_3 and subsequently activate SOS1, but also increases transport activity of proteins such as NHX (Gupta and Huang, 2014). Electron transport chains in mitochondria can overflow, deregulate, or become disrupted by salinity stress leading to the accumulation of toxic compounds. Antioxidant enzymes and nonenzymatic compounds are essential for detoxifying ROS, which include helicase proteins, catalase (CAT), peroxidase, polyphenol, flavonoid, ascorbate, and glutathione (Gupta and Huang, 2014).

3.3.1.3 Biochemical indicators

Biochemical indicators are chemical solutes that build up inside plants in response to salt stress (Ashraf and Harris, 2004). The accumulation of low molecular weight organic solutes, inorganic ions, compatible osmolytes, soluble sugars, soluble proteins, amino acids and amides, quaternary ammonium compounds, polyamines (PAs), polyols, antioxidants, and ATPases is associated with tolerance to salinity stress. Secretion of biochemical compounds occurs during healthy growth and germination; hence it is not easy to tell whether a chemical is a reaction or tolerance to salinity stress, or an adaptive plant mechanism (Ashraf and Harris, 2004). Plant compatible osmolytes are organic compounds synthesized by various plant species which accumulate in variable amounts and are soluble in cells and do not disturb cellular activities at high or low concentrations (Hanin et al., 2016). These compounds, including proline, glycine betaine, sugars, and polyols, increase within the cell in response to salinity stress, and are sustained by permanent synthesis and/or degradation. Accumulation of these compounds is proportional to the surrounding osmolarity, and they function to shield the cell structure and maintain osmotic balance through constant water entry (Hasegawa et al., 2000; Mansour and Ali, 2017; Alhasnawi, 2019).

The secretion of PAs has a diverse function in healthy plant growth, including seed germination, and is critical for abiotic stress adaptation, including salinity. Diamine putrescine (PUT), tetra-amine spermine (SPM), and triamine spermidine (SPD) are some typical PAs found in plants (Shu et al., 2012) and whose increase has been associated with salinity stress (Gupta and Huang, 2014). Nitric oxide (NO) regulates several plant growth and developmental activities, stress signalling molecules and stress responses, including salinity and the activation of antioxidant enzymes (superoxide dismutase (SOD), CAT, guaiacol peroxidase (GPX), ascorbate peroxidase (APX), and glutathione reductase (GR)), and triggers the expression of various redox-regulated genes that enhance germination and root growth under salinity stress (Gupta and Huang, 2014). Salinity stress mitigation by NO is due to its antioxidant functions, modulation of the ROS detoxification system (Mishra et al., 2011) associated with an increase in antioxidant enzymes, such as SOD, CAT, GPX, APX, and GR (Zhao et al., 2004; Ali et al., 2018), and suppression of malondialdehyde (MDA) production during lipid peroxidation (Nalousi et al., 2012). NO offers a force for Na^+/H^+ exchange, providing the H^+ gradient to stimulate H^+-ATPase (H^+-PPase) and contributing to K^+ and Na^+ homeostasis (Zhang et al., 2006; Gupta and Huang, 2014).

Other biochemical indicators include the production of several hormones in response to salinity stress, including ABA in roots and shoots, which mitigates the antagonistic effect of salinity stress on physiological processes (Popova et al., 1995; Jaschke et al., 1997). ABA accumulation triggers the expression of salinity stress tolerance enhancing genes in cultivated barley (*HVP1*, *HVP10*, and *HvVHA-A*) and wheat (*MAPK4-like*, *TIP 1*, and *GLP 1*) (Keskin et al., 2010). Salicylic acid (SA) concentration, along with the SA biosynthetic enzyme, increases under salinity stress in rice seedlings (Jayakannan et al., 2013). Application of BR promotes antioxidant enzyme (SOD, POX, APX, and GPX) activity and the accumulation of salinity stress mitigating nonenzymatic antioxidant compounds, such as tocopherol, ascorbate, and reduced glutathione (Ashraf et al., 2010; el-Mashad and Mohamed, 2012; Gupta and Huang, 2014).

3.3.2 Salinity stress signalling pathways and molecules

The response to salinity stress in plants involves three types of signalling pathway: (1) ionic and osmotic stress signalling (homeostasis) essential for the re-establishment of cellular homeostasis, (2) detoxification signalling that regulates and repairs damage, and (3) cell division and expansion signalling (Zhu, 2001). Homeostatic signalling governs detoxification leading to tolerance by reducing the response of growth inhibitors (Zhu, 2002). The signalling information flows in a way that ionic (Na^+), osmotic (turgor pressure change), and detoxification are stress input, while salinity-induced damage, control, and repair are output (response) (Xiong and Zhu, 2001; Zhu, 2002). The outcomes of osmotic signalling include gene expression or activation of osmolyte biosynthesis enzymes and the water and osmolyte transport system (Zhu, 2001). Detoxification signalling changes induced by salt include phospholipid hydrolysis, changes in the expression of LEA/dehydrin-type genes, molecular chaperones, and proteinase to remove denatured proteins, and the activation of enzymes for the generation and removal of ROS and other detoxification proteins (Zhu, 2001, 2002).

Signalling molecules are crucial components for salinity stress tolerance in plants, and they determine downstream actions involving protein phosphorylation, dephosphorylation, phospholipid metabolism, and calcium ion (Ca^{2+}) sensing (Agarwal et al., 2013). Ca^{2+} signalling is one of the first responses to salt stress and is essential for ion homeostasis (Zhu, 2003; Reddy and Reddy, 2004). It is sensed by calcineurin B-like proteins (CBLs) that are involved in the salt stress indication transduction pathway and govern the influx and efflux of Na^+. CBLs increase germination under salinity stress in tobacco (Pardo et al., 1998), *Arabidopsis* (Liu and Zhu, 1998), and maize (Wang MY et al., 2007). Other molecules include mitogen-activated protein kinase (SAPK) (Diédhiou et al., 2008), CBL-interacting protein kinase (CIPK), nucleoside diphosphate kinase (NDPK), and mitogen-activated protein (MAP) kinase (MPK) (Moon et al., 2003), whose overexpression enhances salinity tolerance capacity by increasing seed germination. Initiation of the MPK cascade is the second response to decode external salinity stress into cellular responses (Teige et al., 2004). This includes signalling modules that phosphorylate particular serine/threonine residues on amide protein substrates that regulate several cellular processes (MAPK Group et al., 2002). Overexpression of MAP in rice (Xiong and Yang, 2003; Jeong et al., 2006) and maize MAP in *Arabidopsis* (Kong et al., 2011) enhances salinity tolerance and activates transcriptional factors controlling downstream genes such as *COR47*, *RD29A*, *P5CS2* (Wurzinger et al., 2011), and *CDPK* (Capiati et al., 2006).

3.3.3 Salinity stress tolerance: transcriptional regulation and gene expression

Salt stress prompts the induction of various genes that fall into two broad groups: (1) single function genes that facilitate the production of protective metabolites, and (2) regulatory genes that control the expression of downstream genes (Agarwal et al., 2013). Single function genes promote the release of compounds such as transporters/channel proteins, osmolytes, lipid biosynthesis genes, antioxidative enzymes, and PAs, while *DREB*, *bZIP*, *NAC*, and *MYC/MYB* (myelocytomatosis/myeloblastosis) are regulatory genes (Shinozaki and Yamaguchi-Shinozaki, 2007; Agarwal and Jha, 2010). Many of these genes from both groups play different roles in enhancing the adaptation process, and are further categorized into functional groups that include: (1) senescence-associated genes (SAGs), (2) ion transport or homeostasis genes (*SOS*, *HKT*, *AtNHX1*, and *H^+-ATPase*), (3) molecular chaperones (*HSP* genes), and (4) dehydration-related TFs (*DREB*) (Hasegawa et al., 2000; Liu et al., 2000; Shi et al., 2000; Yen et al., 2000). Under osmotic pressure from salinity stress, plants synthesize novel proteins that increase the expression of genes, such as osmotic regulation (OR) genes, at the cell level to aid their adaptation. The OR genes are categorized into nine groups, namely LEA genes, osmolyte biosynthesis genes, transporter genes, OR genes that encode regulatory proteins, photosynthetic genes, OR genes encoding proteins involved in protein synthesis processes and degradation, heat shock protein genes, osmotins, and other protein genes (Zhu et al., 1997; Turan et al., 2012). Other OR genes include those encoding RNA-binding proteins, putative lipid transfer, *RD29A*, *RD29B*, *Kin1*, and *Kin2*. Considerable variation among factors such as plant tissue type, age, and developmental stage also affects the expression of OR genes (Zhu et al., 1997).

Transcription factors (TFs), including *bZIP*, *WRKY*, *AP2*, *NAC*, C_2H_2 zinc finger gene, and *DREB*, are the most important regulators of gene expression under salinity stress (Gupta and Huang, 2014). They interact with diverse *cis*-elements in the promoter regions of many downstream genes and modify their expression. There are many different types of TFs in the plant kingdom (Shiu et al., 2005) with more than 50 families distinguished by their DNA-binding domains (Riechmann et al., 2000). Several TFs have been identified in *Arabidopsis*, including a basic-leucine zipper, *AP2/ERF* (APETALA2/ethylene-responsive factor), *MYC*, *HD-ZIP* (homeodomain-leucine zipper*)*, *MYB*, and different classes of zinc finger domains (Shinozaki and Yamaguchi-Shinozaki, 2000). The expression of a given number of genes occurs through TF interactions with non-DNA-binding proteins and/or *cis*-regulatory elements (Grotewold, 2008). On the same transduction pathways, ABA, SA, ethylene, BR, and JA regulate TF expression (Agarwal et al., 2006; Seo et al., 2008; Agarwal and Jha, 2010; Gürel et al., 2016). The four classes of TFs are: (1) ABA-dependent (CBF/DREB proteins), (2) ABA-independent (MYC, MYB, ABA-responsive element-binding protein (AREB), ABA-binding factor protein (ABF)) (Agarwal and Jha, 2010; Liu SW et al., 2018), (3) ABA-dependent and -independent (no apical meristem, ATAF1,2 and cup-shaped cotyledon (NAC)) (Agarwal et al., 2013; Joshi et al., 2016), and (4) TFs that do not belong to any of the first three groups, including homeodomain TFs osmotically responsive gene 9 (HOS9) and an R2R3-type MYB protein (HOS10) (Zhu et al., 2004, 2005).

4 Genetics of salinity tolerance at germination in barley

4.1 QTLs for salinity tolerance in barley and the homologous genes from *Arabidopsis*, soybean, maize, wheat, and rice at the germination stage

At the germination stage, salinity tolerance is controlled by various loci (Mano and Takeda, 1997), indicating that it is polygenic. Angessa et al. (2017) reported transgressive phenotypic segregation for germination percentage in a doubled haploid (DH) population developed from salinity-tolerant genotype CM72 and the sensitive commercial Australian barley cultivar Gairdner. Using 150 and 300 mmol/L NaCl, Angessa et al. (2017) mapped two stable quantitative trait loci (QTLs) to chromosome 2H, close to the sodium concentration QTL reported by Xue et al. (2009). A third QTL reported by Angessa et al. (2017) at 300 mmol/L NaCl was mapped to chromosome 5H, but slightly distant from the potassium concentration-linked QTL of Xue et al. (2009). Mano and Takeda (1997) reported QTLs controlling ABA response on chromosomes 2H, 3H, 1H, and 5H in Steptoe/Morex DH lines, and 2H and 5H in Harrington/TR306 DH lines. In both crosses, chromosome 5H was very close to the position of the salinity tolerance QTL. A QTL analysis of the Oregon Wolf Barley mapping population (DOM×REC) by Witzel et al. (2010) at the germination stage identified two chromosomal regions on 5H, one on 7H, and one on 2H associated with the salt stress response. A single chromosomal region on 5H, responsible for 42% of the variation in the phenotype, was constant across all NaCl concentrations (Table 1).

Protein sequences of functional salinity tolerance genes during germination in *Arabidopsis*, soybean, maize, wheat, and rice were extracted from the National Center for Biotechnology Information (NCBI) website (https://www.ncbi.nlm.nih.gov/protein) (Benson et al., 2013). The protein sequences in FAST formats were blasted on BARLEX (https://apex.ipk-gatersleben.de/apex/f?p=284:10) to identify homologous genes from the barley genome with the highest percentage match depending on length and expression levels in tissues at different growth stages (Colmsee et al., 2015). There were 63 functionally characterized genes (*Arabidopsis* (13), maize (4), rice (12), soybean (7), and wheat (27)) for salinity tolerance at the germination stage (Table 2). Overall, 65 homolog genes were identified in barley, with the percentage match ranging from 100% (between wheat gene *TaPLDα* (phospholipase D) and barley homolog gene HORVU1Hr1G048970.4 (phospholipase D P2)) to 30% (between rice gene *OsOPT10* (oligopeptide transporter family homolog) and barley's HORVU6Hr1G067430.2 (oligopeptide transporter 4)) (Table 2). Generally, the

Table 1 Reported quantitative trait loci (QTLs) for salinity tolerance in barley during germination

Trait at germination	Salt level	Mapping population	Analysis type	QTL number and location	Percentage explained	Reference
Germination percentage	150 mmol/L NaCl	103-DH of CM72/Gairdner	Bi-Parent	1 (2H)	21.8	Angessa et al., 2017
	300 mmol/L NaCl	103-DH of CM72/Gairdner	Bi-Parent	1 (2H)	16.1	Angessa et al., 2017
	300 mmol/L NaCl	103-DH of CM72/Gairdner	Bi-Parent	1 (5H)	10.0	Angessa et al., 2017
Germination speed	250 mmol/L NaCl	149-DH of Steptoe/Morex	Bi-Parent	2 (2H), 3 (3H), and 7 (5H)	7.6–20.3	Mano and Takeda, 1997
	300 mmol/L NaCl	146-DH of Harrington/TR306	Bi-Parent	1 (7H), 6 (6H), and 7 (5H)	8.7–15.3	Mano and Takeda, 1997
Salt tolerance	250 mmol/L NaCl	149-DH of Steptoe/Morex	Bi-Parent	4 (4H), 6 (6H), and 7 (5H)	6.8–46.7	Mano and Takeda, 1997
	300 mmol/L NaCl	146-DH of Harrington/TR306	Bi-Parent	5 (1H) and 7 (5H)	17.4–41.1	Mano and Takeda, 1997
	1.5%*	94-DH of DOM/REC	Bi-Parent	1 (5H) and 1 (7H)	42	Witzel et al., 2010
	2.0%	94-DH of DOM/REC	Bi-Parent	1 (5H) and 1 (7H)	42	Witzel et al., 2010
	2.5%	94-DH of DOM/REC	Bi-Parent	1 (5H) and 1 (7H)		Witzel et al., 2010
	1.5%	94-DH of DOM/REC	Bi-Parent	1 (2H)		Witzel et al., 2010
	1.5%–2.5%	94-DH of DOM/REC	Bi-Parent	2 (5H), 1 (7H), and 1 (2H)		Witzel et al., 2010

* 1%=0.01 g/mL

wheat genes had the highest match with barley homologs, averaging 90.93%, followed by maize (83.00%), rice (67.58%), soybean (59.43%), and *Arabidopsis* (57.94%). Apart from homolog connections, gene expression patterns in tissues can suggest the function of particular genes. For instance, the expression levels of the 65 barley homologs for the first three development stages (4-d embryo (EMB), root from seedlings (ROO1; 10 cm shoot stage), and shoot from seedling stage (LEA; 10 cm shoot stage)) were more than zero for all except HORVU1Hr1G080820.6 (CBL protein 8). The aquaporin-like superfamily protein (HORVU2Hr1G096360.13) had the highest expression levels in the EMB, ROO1, and LEA stages at 1305.90, 1094.39, and 1133.08 fragments per million kb, respectively (Table S1) (The International Barley Genome Sequencing Consortium, 2012; Colmsee et al., 2015; Mascher et al., 2017).

4.2 Barley salinity tolerance characterized transcriptional factors and genes during germination

A highly positive correlation has been reported between salinity stress and polyethylene glycol treatments, indicating that salt stress in germinating seed is mostly osmotic (Mano et al., 1996). Therefore, osmoprotection is the likely early response in barley geminating seeds (Walia et al., 2006).

4.2.1 6PGDH and Glc/RibDH

Salinity tolerant lines at germination in a mapping population containing 94 DH lines of DOM/REC expressed a higher level of 6-phosphogluconate dehydrogenase (6PGDH) and glucose/ribitol dehydrogenase (Glc/RibDH) in mature seeds (Witzel et al., 2010). Overexpression of the two enzymes in yeast enhanced the growth of transformed cells in saline media (Witzel et al., 2010). Cytosolic 6PGDH is an enzyme participating in the pentose phosphate pathway, which provides reduced nicotinamide adenine dinucleotide phosphate (NADPH) as an electron donor in the reductive biosynthetic process, and is important for the ascorbate–glutathione synthesis phase in the plant antioxidant protection system (Corpas et al., 1998). This protein concentration is increased under salinity stress in olive (Valderrama et al., 2006) and rice (Huang et al., 2003; Hou et al., 2007). Transcripts and protein Glc/RibDH are short alcohol dehydrogenases (Jornvall et al., 1984) found in developing barley embryos, whose level of transcription reduces with germination (Alexander et al., 1994), and which catalyse the oxidation of D-glucose to synthesize sugars for osmoprotective functions (Witzel et al., 2010).

4.2.2 Dehydrins

Dehydrins (DHNs), a subfamily of LEA proteins from *Hordeum vulgare* (*aba2*), enhanced seed germination in transgenic lines of *Arabidopsis* under salinity stress, relative to the wild type (Calestani et al., 2015). Similar protein-coding genes have been identified in wheat (*Dhn5*) and maize (*Rab17*) with comparable results when overexpressed in transgenic *Arabidopsis* plants (Figueras et al., 2004; Brini et al., 2011). DHNs are thought to be involved in protecting the embryo through seed desiccation and rehydration (Skriver and Mundy, 1990; Blackman et al., 1991; Tunnacliffe and Wise, 2007) by increasing their contents during the last phase of seed development, and in dormant embryos. DHN content decreases when imbibition and germination begin as seeds lose their capacity to withstand desiccation (Blackman et al., 1991; Han et al., 1997). DHNs also facilitate water uptake during seed germination on media with low osmotic potential (Hara, 2010), and may act as a hydration buffer inside cells in the presence of sugars (Walters et al., 1997; Hara, 2010). Moreover, they are likely to play a role in cellular detoxification because they contain lipids and metal-binding capacity that can prevent lipid peroxidation (Cheng et al., 2002; Krüger et al., 2002; Alsheikh et al., 2003; Koag et al., 2003, 2009).

4.2.3 CBLs

Rice transgenic lines with CBL protein 8 (*HsCBL8*) transferred from wild barley homolog to *HvCBL8* of cultivated barley improved seed germination, reduced Na^+ uptake, adjusted K^+ concentration in tissues, provided in vivo water protection of the plasma membrane, and accumulated more proline under salt stress (Guo et al., 2016). The build-up of compatible osmolytes, like proline, is linked to stress tolerance in plants (Ahmed et al., 2013b; Mekawy et al., 2015). Phylogenetic analysis of *HsCBL8* showed that it encodes proteins of the CBL group modified with only N-myristoylation or S-acylation (Batistič et al.,

Table 2 Homologs of candidate functional salinity genes in barley during the germination of *Arabidopsis*, maize, rice, soybean, and wheat

Gene source	Gene ID	Transgenic host	Homolog ID in barley	Similarity (%)	Gene name in barley	Chromosome	Location	Reference
Arabidopsis thaliana L.	*AtRZFP*	*Arabidopsis*	HORVU5Hr1G001400.5	52	RING finger protein 5	5	4181876–4184642	Zang et al., 2016
A. thaliana L.			HORVU4Hr1G003600.1	51	RING finger protein 5	4	7870080–7872190	
A. thaliana L.	*AtNHX1*	Maize/wheat	HORVU2Hr1G021020.4	69	Sodium hydrogen exchanger 2	2	59025629–59030226	Yin et al., 2004; Xue et al., 2004
A. thaliana L.			HORVU4Hr1G033760.1	69	Sodium hydrogen exchanger 2	4	238472323–238482634	
A. thaliana L.			HORVU7Hr1G046030.1	62	Sodium hydrogen exchanger 3	7	148709554–148713307	
A. thaliana L.	*AtSOS1*	*Arabidopsis*	HORVU3Hr1G003150.1	58	Sodium hydrogen exchanger 7	3	8165119–8185196	Wang X et al., 2007
A. thaliana L.	*AtMYBL*	*Arabidopsis*	HORVU5Hr1G077100.1	56	MYB domain protein 3R-3	5	552718664–552726337	Zhang et al., 2011
A. thaliana L.	*RAP2.6L*	*Arabidopsis*	HORVU2Hr1G071270.4	60	Ethylene-responsive transcription factor 1	2	507785971–507787466	Krishnaswamy et al., 2011
A. thaliana L.	*AtERF96*	*Arabidopsis*	HORVU4Hr1G000960.1	59	Ethylene-responsive transcription factor 14	4	1356682–1357123	Wang et al., 2017
A. thaliana L.	*AtCYSa*	*Arabidopsis*	HORVU1Hr1G067870.2	56	Cysteine proteinase inhibitor	1	479563716–479564368	Zhang et al., 2008
A. thaliana L.	*AtCYSb*	*Arabidopsis*	HORVU3Hr1G038190.1	66	Cysteine proteinase inhibitor 12	3	219953557–219956556	Zhang et al., 2008
A. thaliana L.	*AtNHX1*	Cotton	HORVU2Hr1G021020.4	69	Sodium hydrogen exchanger 2	2	59025629–59030226	Cheng C et al., 2018
A. thaliana L.	*AtPP2-B11*	*Arabidopsis*	HORVU6Hr1G090000.1	42	F-box protein PP2-B1	6	571135647–571137859	Jia et al., 2015
A. thaliana L.	*AnnAt8*	*Arabidopsis*	HORVU6Hr1G074440.1	50	Annexin 7	6	514097241–514103959	Yadav et al., 2016
A. thaliana L.	*AtDIF1*	*Arabidopsis*	HORVU5Hr1G079500.1	42	Sister chromatid cohesion 1 protein 4	1	557145143–557147352	Gao et al., 2017
A. thaliana L.	*NF-YA1-9*	*Arabidopsis*	HORVU5Hr1G007890.11	66	Nuclear transcription factor Y subunit A-10	5	16694492–16699091	Mu et al., 2013
Maize (*Zea mays*)	*ZmCBL4*	*Arabidopsis*	HORVU1Hr1G080820.6	72	Calcineurin B-like protein 8	1	526318770–526320885	Wang MY et al., 2007
Maize (*Z. mays*)	*ZmMKK4*	*Arabidopsis*	HORVU0Hr1G038850.2	88	Protein kinase superfamily protein	0	247582088–247583184	Kong et al., 2011
Maize (*Z. mays*)	*ZmMPK5*	Tobacco	HORVU7Hr1G023760.3	89	Mitogen-activated protein kinase 3	7	37300015–37306217	Zhang et al., 2014
Rice (*Oryza sativa*)	*OSISAP1*	Tobacco	HORVU5Hr1G072920.1	70	Zinc finger A20 and AN1 domain-containing stress-associated protein 1	5	536933399–536936238	Mukhopadhyay et al., 2004
Rice (*O. sativa*)	*OsDREB2A*	Soybean	HORVU6Hr1G050520.2	78	Ethylene-responsive transcription factor 4	6	306973236–306973949	Zhang et al., 2013
Rice (*O. sativa*)	*OsiSAP8*	Tobacco/rice	HORVU2Hr1G053670.4	43	Zinc finger A20 and AN1 domain-containing stress-associated protein 9	2	328713964–328714708	Kanneganti and Gupta, 2008

To be continued

Table 2

Gene source	Gene ID	Transgenic host	Homolog ID in barley	Similarity (%)	Gene name in barley	Chromosome	Location	Reference
Rice (*O. sativa*)	*OsMYB48-1*	Rice	HORVU1Hr1G008810.3	82	MYB domain protein 59	1	19369578–19370912	Xiong et al., 2014
Rice (*O. sativa*)	*OsSAP11*	*Arabidopsis*	HORVU7Hr1G050270.3	66	Zinc finger A20 and AN1 domain-containing stress-associated protein 11	7	180473211–180476075	Giri et al., 2011
Rice (*O. sativa*)	*OsRLCK253*	*Arabidopsis*	HORVU6Hr1G061280.1	69	Protein kinase superfamily protein	6	410507581–410509354	Giri et al., 2011
Rice (*O. sativa*)	*OsGSTU4*	*Arabidopsis*	HORVU6Hr1G026810.3	71	Glutathione S-transferase family protein	6	103574244–103575543	Sharma et al., 2014
Rice (*O. sativa*)	*OsDREB1D*	*Arabidopsis*	HORVU5Hr1G080420.1	71	C-repeat-binding factor 4	5	560569797–560571193	Zhang et al., 2009
Rice (*O. sativa*)	*OsNAC9*	Rice	HORVU7Hr1G060310.1	75	NAC domain protein	7	276430981–276436993	Redillas et al., 2012
Rice (*O. sativa*)	*OsZFP179*	Rice	HORVU5Hr1G055970.1	85	RING/U-box superfamily protein	5	438292337–438301123	Sun et al., 2010
Rice (*O. sativa*)	*OsOPT10*	*Arabidopsis*/rice	HORVU6Hr1G067430.2	30	Oligopeptide transporter 4	6	467362064–467373338	Jung et al., 2010
Rice (*O. sativa*)	*OsMYB3R-2*	*Arabidopsis*	HORVU3Hr1G086270.3	71	MYB domain protein 3R-5	3	616465321–616471572	Dai et al., 2007
Soybean (*Glycine max*)	*GmbZIP44*	*Arabidopsis*	HORVU5Hr1G023000.1	43	Basic-leucine zipper transcription factor family protein	5	119817528–119818004	Liao et al., 2008
Soybean (*G. max*)	*GmbZIP62*	*Arabidopsis*	HORVU6Hr1G031330.2	49	Basic-leucine zipper transcription factor family protein	6	132098841–132101167	Liao et al., 2008
Soybean (*G. max*)	*GmbZIP78*	*Arabidopsis*	HORVU2Hr1G055230.4	61	Basic-leucine zipper 8	2	342114231–342120751	Liao et al., 2008
Soybean (*G. max*)	*GmDREB2*	*Arabidopsis*/tobacco	HORVU4Hr1G015350.1	66	Ethylene-responsive transcription factor 2	4	59331360–59332535	Chen M et al., 2007
Soybean (*G. max*)	*GmDREB1*	Wheat	HORVU7Hr1G026940.1	67	Ethylene-responsive transcription factor 5	7	47357790–47359063	Jiang et al., 2014
Soybean (*G. max*)	*GmNARK*	*Arabidopsis*	HORVU5Hr1G098840.2	54	Leucine-rich receptor-like protein kinase family protein	5	608904210–608907733	Cheng CH et al., 2018
Soybean (*G. max*)	*GmFDL19*	Soybean	HORVU2Hr1G110500.1	76	ABSCISIC ACID-INSENSITIVE 5-like protein 5	2	720057018–720058296	Li et al., 2017
Wheat (*Triticum aestivum*)	*TaNAC29*	*Arabidopsis*	HORVU2Hr1G017470.1	93	NAC domain protein	2	42672748–42675686	Huang et al., 2015
Wheat (*T. aestivum*)	*TaSC*	*Arabidopsis*	HORVU5Hr1G067740.1	99	Transmembrane protein 50A	5	514305842–514309764	Huang et al., 2012
Wheat (*T. aestivum*)	*TaNAC2D*	*Arabidopsis*	HORVU5Hr1G111590.2	95	NAC domain protein	5	636772274–636774317	Huang and Wang, 2016
Wheat (*T. aestivum*)	*TaARGOS*	*Arabidopsis*	HORVU4Hr1G043960.1	88	Eukaryotic aspartyl protease family protein	4	351442597–351444197	Zhao et al., 2017

To be continued

Table 2

Gene source	Gene ID	Transgenic host	Homolog ID in barley	Similarity (%)	Gene name in barley	Chromosome	Location	Reference
Wheat (*T. aestivum*)	*TaCRT1*	Tobacco	HORVU3Hr1G089830.2	98	Calreticulin 3	3	630 039 636–630 043 684	Xiang et al., 2015
Wheat (*T. aestivum*)	*TaSRG*	*Arabidopsis*/rice	HORVU2Hr1G072420.11	97	Family of unknown function (DUF662)	2	519 528 221–519 529 717	He et al., 2011
Wheat (*T. aestivum*)	*TaSTRG*	Tobacco	HORVU4Hr1G063430.1	90	Salt-tolerance-related protein	4	531 361 349–531 362 720	Kavas et al., 2016
Wheat (*T. aestivum*)	*DHN-5*	*Arabidopsis*	HORVU5Hr1G103460.2	79	Dehydrin Rab15	5	616 115 076–616 116 086	Brini et al., 2007
Wheat (*T. aestivum*)	*TaAQP8*	Tobacco	HORVU2Hr1G096360.13	91	Aquaporin-like superfamily protein	2	674 156 225–674 158 128	Hu et al., 2012
Wheat (*T. aestivum*)	*TaWRKY10*	Tobacco	HORVU2Hr1G109330.1	87	WRKY family transcription factor	2	716 404 110–716 405 772	Wang et al., 2013
Wheat (*T. aestivum*)	*TaDi19A*	*Arabidopsis*	HORVU3Hr1G061690.1	97	Protein DEHYDRATION-INDUCED 19 homolog 3	3	469 768 135–469 771 916	Li et al., 2010
Wheat (*T. aestivum*)	*TaWD40D*	*Arabidopsis*	HORVU0Hr1G016450.1	99	Transducin/WD40 repeat-like superfamily protein	0	88 366 914–88 373 289	Kong et al., 2015
Wheat (*T. aestivum*)	*TaAIDFa*	*Arabidopsis*	HORVU5Hr1G105980.4	72	Histone-lysine *N*-methyltransferase NSD3	5	623 061 366–623 067 662	Xu et al., 2008a
Wheat (*T. aestivum*)	*TaCIPK29*	Tobacco	HORVU2Hr1G018340.3	92	Protein kinase family protein	2	46 669 169–46 672 779	Deng et al., 2013
Wheat (*T. aestivum*)	*TaERF3*	Wheat	HORVU2Hr1G098330.1	85	Ethylene-responsive transcription factor 1	2	682 511 166–682 511 937	Rong et al., 2014
Wheat (*T. aestivum*)	*TaPUB1*	Tobacco	HORVU4Hr1G083960.3	95	Pre-mRNA-processing factor 19	3	627 004 064–627 010 259	Zhang et al., 2017
Wheat (*T. aestivum*)	*TaWRKY44*	Tobacco	HORVU4Hr1G048400.12	92	WRKY DNA-binding protein 3	4	390 705 028–390 708 928	Wang et al., 2015
Wheat (*T. aestivum*)	*TaVB*	*Arabidopsis*	HORVU4Hr1G033760.1	97	Sodium hydrogen exchanger 2	4	238 472 323–238 482 634	Wang et al., 2011
Wheat (*T. aestivum*)	*TaSRHP*	*Arabidopsis*	HORVU7Hr1G037410.4	90	Protein of unknown function	7	89 779 039–89 780 525	Hou et al., 2013
Wheat (*T. aestivum*)	*TaNHXS1*	Tobacco	HORVU2Hr1G021020.4	70	Sodium hydrogen exchanger 2	2	59 025 629–59 030 226	Gouiaa et al., 2012
Wheat (*T. aestivum*)	*TaVP1*	Tobacco	HORVU7Hr1G031480.1	97	K^+-insensitive pyrophosphate-energized proton pump	7	63 936 492–63 936 858	Gouiaa et al., 2012
Wheat (*T. aestivum*)			HORVU7Hr1G114250.2	88	Pyrophosphate-energized vacuolar membrane proton pump	7	639 161 697–639 164 555	Gouiaa et al., 2012
Wheat (*T. aestivum*)	*TaPLDα*	*Arabidopsis*	HORVU1Hr1G048970.4	100	Phospholipase D P2	1	363 556 495–363 563 036	Wang et al., 2014
Wheat (*T. aestivum*)	*TaOPR1*	*Arabidopsis*	HORVU1Hr1G001850.3	82	12-Oxophytodienoate reductase 2	1	4 131 150–4 132 543	Dong et al., 2013
Wheat (*T. aestivum*)	*TaNF-YA10-1*	*Arabidopsis*	HORVU6Hr1G081080.12	89	Nuclear transcription factor Y subunit A-5	6	544 207 949–544 211 747	Ma et al., 2015
Wheat (*T. aestivum*)	*TaPI4KIIγ*	*Arabidopsis*	HORVU2Hr1G118320.7	94	Phosphatidylinositol 3- and 4-kinase family protein	2	742 201 795–742 204 374	Liu et al., 2013

RING, really interesting new gene; MYB, myeloblastosis; NAC, no apical meristem, ATAF1,2 and cup-shaped cotyledon; NSD, nuclear receptor-binding SET domain

2012). Such proteins are involved in relationships with the transmembrane (TM) helix (Kleist et al., 2014) including *HvCBL8*. Reports about other CBLs from different plant species reflected similar trends to that of *HsCBL8*, such as transgenic *Arabidopsis* having *35S-AtCBL5* (Cheong et al., 2010) and poplar harbouring *35S-PeCBL10* (Li DD et al., 2013). *OsCBL2* is likely to be involved in GA-signalling that facilitates the vacuolation of aleurone cells (Hwang et al., 2005), and *AtCBL1* is involved in upregulation of GA (Li ZY et al., 2013) and downregulation of ABA (Pandey et al., 2008) during seed germination.

4.2.4 SERKs

Three orthologs of somatic embryogenesis receptor-like kinase (SERK) genes (*HvSERK1*/*2*/*3*) isolated from barley were induced in microspore-derived embryogenic callus under salt stress (Li et al., 2016), indicating their protective role for developing embryos during salinity stress. SERKs are a subfamily of the leucine-rich repeat receptor-like kinase II group (LRR-RLKII) with proline-rich SPP motifs between the LRRs and the TM domain (Hecht et al., 2001). These genes are present during somatic embryogenesis in plants before declining in later stages (Schmidt et al., 1997; Somleva et al., 2000; Nolan et al., 2003; Singla et al., 2008; Li, 2010). They have been characterized in many plants, including maize (Baudino et al., 2001), wheat (Singla et al., 2008), soybean (Yang et al., 2011), rice (Singla et al., 2009), cotton (Pandey and Chaudhary, 2014), and *Arabidopsis* (Hecht et al., 2001). In rice (*Oryza sativa* L.), BRs reverse the inhibitory effect of salinity during germination (Anuradha and Rao, 2001), and in *Arabidopsis* are reportedly signalled by *SERK1*, *SERK3*, and *SERK4* (Albrecht et al., 2008), while ABA stimulates *OsSERK1* during stress (Hu et al., 2005).

4.2.5 DREBs

A gene that encodes DREB proteins in *H. vulgare* (*HvDREB1*) is induced by exogenous ABA to enhance germination and early root growth in *Arabidopsis* plants under salinity stress (Xue et al., 2004). TF *HvDREB1* is a member of the AP2 group of the *DREB* subfamily that is vital for regulating responses to various stresses (Agarwal et al., 2006; Xu et al., 2008b) and reportedly improves salt, drought, and cold responses in transgenic plants (Oh et al., 2007). Overexpressing rice *OsDREB1A* in *Arabidopsis* enhanced tolerance to drought and freezing stresses (Dubouzet et al., 2003), and barley's *HvCBF4* in rice transgenes increased drought, salt, and cold stress tolerance (Oh et al., 2007). DREB proteins isolated from several plants including rice, maize, soybean, and wheat are involved in several signal transduction pathways during abiotic stress (Dubouzet et al., 2003; Agarwal et al., 2006). Of particular interest are those belonging to the A-2 group that respond to dehydration and salinity stress (Liu et al., 1998; Dubouzet et al., 2003) and regulate ABA-independent gene expression in target plants under stress (Chinnusamy et al., 2006; Nakashima and Yamaguchi-Shinozaki, 2006). It is possible that *HvDREB1* may take part in both ABA-independent and -dependent pathways concurrently (Xue et al., 2004).

4.2.6 ERFs

Barley ERF-type TF *HvRAF* improved seed germination and root growth under salinity stress but was not induced by ABA treatment in transgenic *Arabidopsis* plants (Jung et al., 2007). TF *HvRAF* is a member of the *AP2* group in the *ERF* family (Sakuma et al., 2002; Gutterson and Reuber, 2004), which is involved in regulating both biotic and abiotic stress-responsive genes in plants (Lee et al., 2004; Yi et al., 2004). However, the response of *Arabidopsis* transgenic lines with *HvRAF* was specific to salinity stress, where it acted as a regulator for ABA-independent signalling in root growth and seed germination (Jung et al., 2007). Similar ABA regulation responses to salinity have been documented in *Arabidopsis* for *DREB2A* and *DREB2B* (Chinnusamy et al., 2005). A tolerance response in terms of root growth and seed germination was observed when *CaERFLP1* and *JERF1* from pepper and tomato, respectively, were overexpressed in transgenic tobacco plants in response to salt stress (Lee et al., 2004; Zhang et al., 2004).

4.2.7 Aquaporin genes

Overexpression of a barley aquaporin gene *HvPIP2;5* in yeast enhanced salt and osmotic stress tolerance, and transgenic *Arabidopsis* with the gene showed better seed germination and root growth than the wild type under salinity stress (Alavilli et al., 2016). Aquaporins form part of the major intrinsic proteins (MIPs) found in living organisms that enable the transportation of water and small nonpolar molecules across living membranes (Zardoya et al., 2002; Maurel et al., 2015). In plants, all but the GlpF-like intrinsic proteins show water-specific channel movement. Hence, the collective name for MIPs in plants is aquaporins (Maurel et al., 2008), even though they can transport additional small molecules such as CO_2 and ammonia inside cells (Uehlein et al., 2003; Jahn et al., 2004). There are five groups of aquaporins in plant genomes, reflective of their diverse physiological roles. Of importance are the plasma membrane intrinsic proteins (PIPs) that are further subdivided into PIP1 and PIP2, each with several isoforms (Javot et al., 2003; Postaire et al., 2010). Overexpression of *PIP* genes from various plants (*O. sativa*, *Nicotiana tabacum*, *Vicia faba*, *Arabidopsis*, and *Triticum aestivum*) enhanced dehydration stress tolerance in their respective transgenic lines (Alavilli et al., 2016).

4.3 Diversity of barley salinity tolerance genes at germination

In this review, we have compared studies to determine whether any of the eight genes (Table 3) that have been reported and functionally characterized for salinity tolerance in barley at germination are unique or similar to their homologs from wheat and rice. All the sequences producing a significant match, based on length and total relationship hits, were downloaded and recorded. The following total significant homolog hits from barley, wheat, and rice were recorded: dehydrins (17), dehydrogenase/reductase SDR family member 4 (20), 6PGDH, (29), ERFs (31), CBL protein (72), DREB protein (164), SERKs (215), and aquaporin gene (227).

Three genes families—DREB protein, SERKs and aquaporin gene—were considered for further analysis based on their high numbers of hits. The proteins from the three genes were blasted on the Phytozome (https://phytozome.jgi.doe.gov/pz/portal.html) to download matched homologs (>30%) in 40 different plant species. Mega software (https://www.megasoftware.net) was used to align the 40 species' sequences, and a phylogenetic tree was constructed to estimate the evolutionary distances between the genes using MEGA-X software (https://www.megasoftware.net) (Kumar et al., 2018). Gene alignments showed three distinct regions across the sequences of the gene families. The start and end sections of the sequences were more divergent than the middle segments. The phylogenetic tree of the DREB proteins divided the genes into two major groups that were further divided into two subgroups (Fig. 2a). The groups were distinguished by the presence or absence of genes from wheat, barley, and rice. Among the four sub-groups, barley genes appeared three times in two categories while genes from the three cereals were missing in two sub-groups (Fig. 2a). The phylogenetic tree shows that DREB proteins are no more diverse in barley than in wheat or rice. The SERK phylogenetic tree (Fig. 2b) was similar to that of the DREB proteins, but with more hits. However, the four subgroups contained genes from the three cereals with five hits for barley and wheat, and three hits for rice. The aquaporin gene phylogenetic tree differed from the other two trees in which the genes were first divided into three major groups, two small and one major, containing representative genes from the three cereals (Fig. 3).

5 Conclusions and future prospects

Among the most destructive abiotic stresses, salinity causes massive yield losses in crops in arid, semi-arid, coastal regions, and humid and sub-humid landscapes. Thus, more effort is needed to increase crop yields in these areas to produce enough food for the increasing global population. Growing salt-adapted cultivars requires knowledge of the donating characters at different growth stages. It involves the use of many disciplines to identify and functionally characterize the genes contributing to tolerance, and then to transfer them to commercially acceptable cultivars. Barley is one of the hardiest crops that can grow in saline environments, but its germination is severely affected by salinity stress. Development of cultivars that can acclimatise to salinity at this stage is essential in regions like Western Australia that experience hot and dry summers and increasing salt levels in the topsoil before sowing in autumn. The identification and characterization of salinity tolerance genes, enzymes, and compounds during germination in barley have been ongoing, and some transgenic "salt-tolerant" plants have been developed. However, the seeds of these genotypes have had little success in

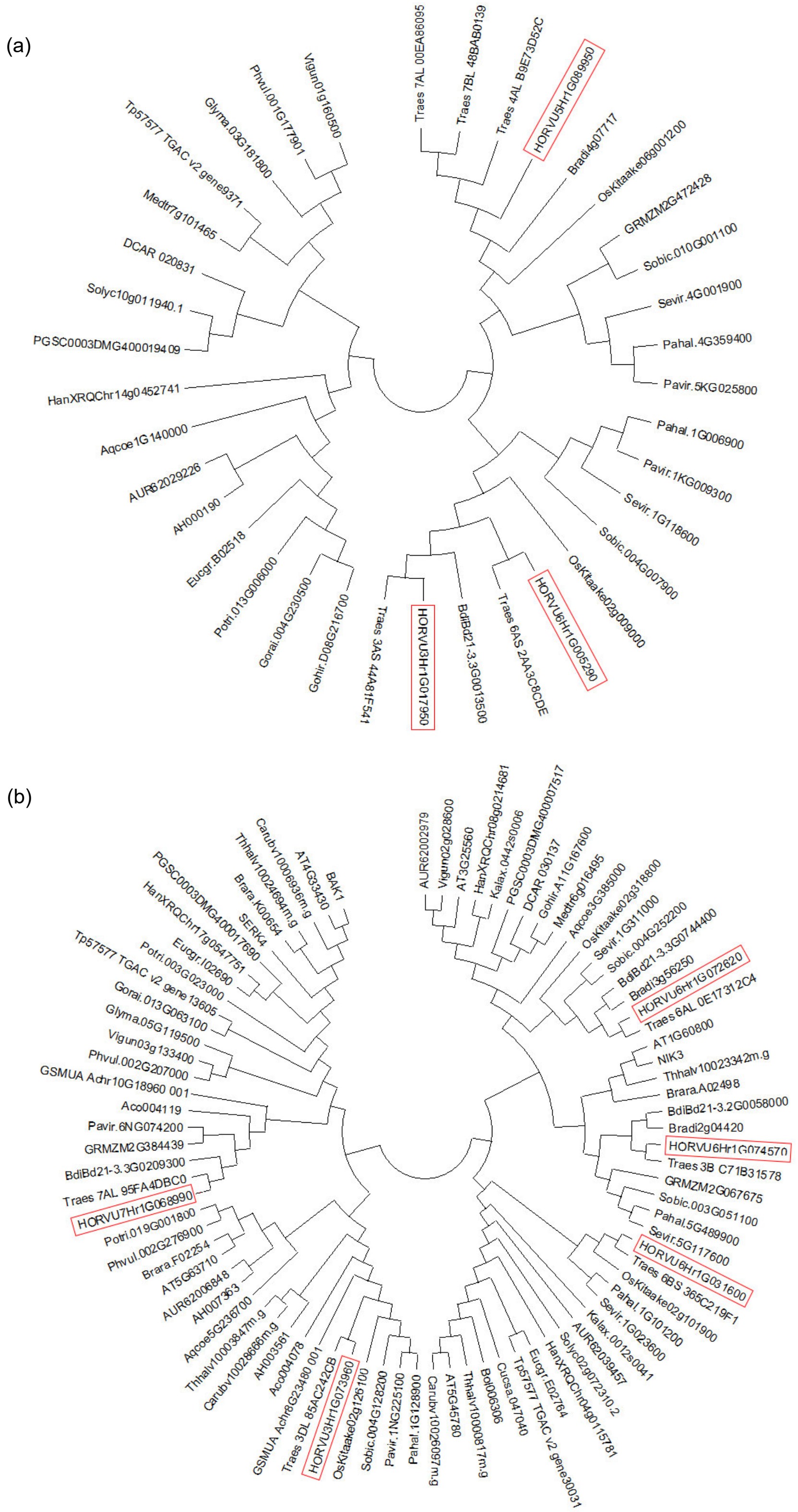

Fig. 2 Phylogenetic analyses of barley homolog genes

(a) Dehydration-responsive element binding proteins. (b) Somatic embryogenesis receptor-like kinases. The unrooted phylogenetic trees of 37 (a) and 92 (b) domains comprising four (a) and five (b) domains, respectively, from barley were constructed using MEGA-X

Table 3 Barley salinity tolerance functional transcriptional factors and genes at germination

Reported functional barley gene	Gene ID in barley	Gene name in barley
6-Phosphogluconate dehydrogenase	HORVU7Hr1G006160.4	6-Phosphogluconate dehydrogenase, decarboxylating 1
Glucose/ribitol dehydrogenase	HORVU1Hr1G018140.5	Dehydrogenase/reductase SDR family member 4
Dehydrin	HORVU7Hr1G099800.5	Dihydroneopterin aldolase
Calcineurin B-like protein 8	HORVU1Hr1G064470.4	Calcineurin B-like protein 1
Somatic embryogenesis receptor-like kinase	HORVU7Hr1G068990.2	Receptor-like protein kinase 4
Dehydration-responsive element binding protein	HORVU3Hr1G017950.4	Chromodomain-helicase-DNA-binding protein 5
Ethylene response factor	HORVU4Hr1G077310.1	Ethylene-responsive transcription factor 1
Aquaporin gene	HORVU2Hr1G089940.1	Aquaporin-like superfamily protein

Reported functional barley gene	Reported gene ID	Chromosome	Location	Reference
6-Phosphogluconate dehydrogenase	*6PGDH*	7	8000958–8002650	Witzel et al., 2010
Glucose/ribitol dehydrogenase	*Glc/RibDH*	1	65592292–65593858	Witzel et al., 2010
Dehydrin	*aba2*	7	602554874–602555971	Calestani et al., 2015
Calcineurin B-like protein 8	*HvCBL8*	1	461521906–461524442	Guo et al., 2016
Somatic embryogenesis receptor-like kinase	*HvSERK1/2/3*	7	366099333–366114129	Li et al., 2016
Dehydration-responsive element binding protein	*HvDREB1*	3	46482481–46494788	Xue et al., 2004
Ethylene response factor	*HvRAF*	4	603804858–603809470	Jung et al., 2007
Aquaporin gene	*HvPIP2;5*	2	640763978–640768942	Alavilli et al., 2016

The protein sequences of identified functional barley genes retrieved from BARLEX (https://apex.ipk-gatersleben.de/apex/f?p=284:10) and blasted on barley (https://webblast.ipk-gatersleben.de/barley_ibsc/viroblast.php), wheat (https://urgi.versailles.inra.fr/blast_iwgsc/?dbgroup=wheat_iwgsc_refseq_v1_chromosomes&program=blastn), and rice (https://www.plantgdb.org/OsGDB) genome explorers

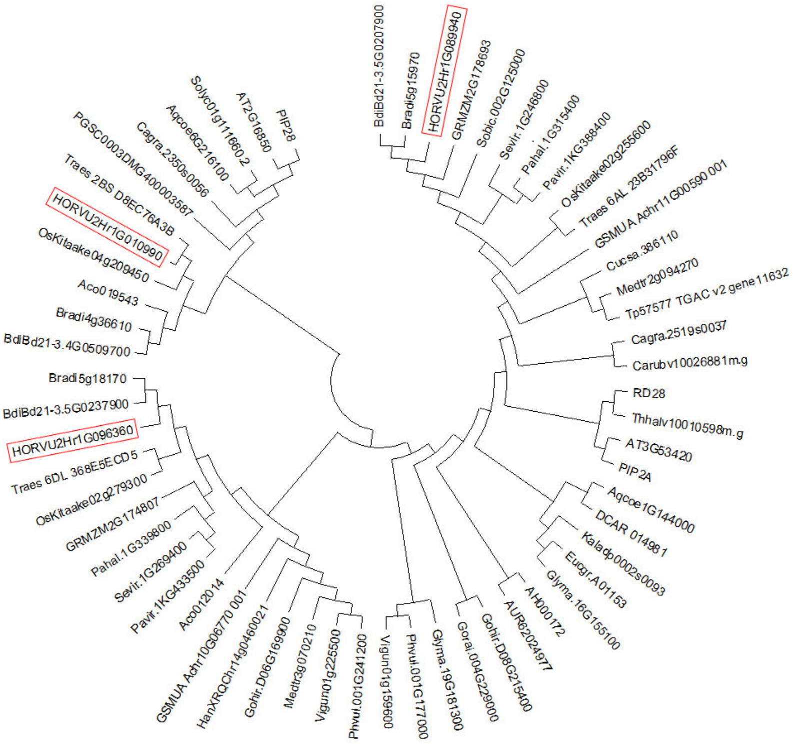

Fig. 3 Phylogenetic analysis of barley homolog aquaporin genes

The unrooted phylogenetic tree of 74 domains comprising five domains from barley was constructed using MEGA-X commercial production because they are not equipped with holistic genes or the mechanisms required for successful germination and growth under saline field conditions.

This review summarized the agronomic/morphological, physiological, and biochemical traits related to salinity stress. The best trait or combination of traits needs to be identified which can be used to accurately screen for salinity stress tolerance at germination to identify and characterize novel genes. Homolog salinity tolerance genes in barley during germination have been reported, but they need to be validated in barley and other transgenic plants that carry them. Functional characterization by blending genetic, agronomic, biochemical, and physiological indicators can facilitate proof of identity of the genes, leading to the development of barley cultivars with improved salt tolerance at germination and better performance in the field.

Contributors

Edward MWANDO performed literature search, data analysis, interpretation of information, and drafting the manuscript. Tefera Tolera ANGESSA and Yong HAN gave guidance on relevant literature search, information and data interpretation. Chengdao LI conceived the projects idea. All authors revised the paper and approved the final version to be published.

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Compliance with ethics guidelines

Edward MWANDO, Tefera Tolera ANGESSA, Yong HAN, and Chengdao LI declare that they have no conflict of interest.

This article does not contain any studies with human or animal subjects performed by any of the authors.

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List of electronic supplementary materials

Table S1 Expression levels in different tissues and growth stages of candidate genes for barley salinity tolerance at germination

中文概要

题 目：大麦芽期耐盐相关的同源和候选基因

概 要：土壤盐害影响了全球 6%以上的陆地面积，并导致了大量的农作物减产。盐害主要通过渗透和离子胁迫抑制植物的生长和发育，而植物相应地通过渗透调节、转移或外排积累的钠和氯离子以增强适应性。目前，生产上尚未有实用、经济的方法治理盐害，因而最为可行的途径是增强植物自身的耐盐性。盐胁迫严重抑制种子萌发，而作为全球第四大禾谷类作物的大麦与其他谷物相比耐盐性更强。本文综述了大麦芽期耐盐性的遗传机制，总结了已报道的相关数量性状位点和功能基因，比对了拟南芥、大豆、玉米、小麦和水稻中耐盐候选基因在大麦中的同源基因并映射到参考基因组。此外，本文还讨论了三个耐盐功能基因家族的遗传多样性，包括脱水应答元件结合蛋白（DREB）、类体细胞胚胎发生受体激酶和水通道蛋白。上述三个基因家族在植物中都存在丰富的多样性，但 DREB 家族在大麦中的多样性高于水稻和小麦。后续研究中，芽期耐盐性的简便筛选方法仍有待开发，耐盐基因及相关机理机制仍需鉴定、验证，并整合到栽培品种中，以实现盐土上作物的生产。

关键词：遗传；大麦；数量性状位点；发芽；耐盐性；同源基因；多样性