Plant Growth Regulation (2019) 89:1–17
https://doi.org/10.1007/s10725-019-00519-w

REVIEW PAPER

Genetic sources for the development of salt tolerance in crops

Stanislav V. Isayenkov[1]

Received: 18 January 2019 / Accepted: 27 June 2019 / Published online: 4 July 2019

Abstract

Salinity is one of major threats to modern agriculture. The problem of soil salinization is especially important for the agricultural areas suffering from water scarcity and inadequate irrigation. This type of environmental stress can severely reduce crop yield since it inhibits and impairs plant growth and development. During evolution, a wide range of adaptation strategies and tolerance mechanisms have evolved in plants to survive in harsh saline environments. Moreover, some other eukaryotes such as lower plants, fungi and animals demonstrate outstanding capabilities to adapt to saline conditions. The deep knowledge of these tolerance mechanisms of halophytes, halophytic crop relatives and other living organisms could be a useful tool for new crop breeding strategies and genetic engineering. The study of adaptation strategies to high salinity including gene networks involved in these process in different plant species and other organisms may help to develop and transfer salt tolerance to the major agricultural crops.

Keywords Salinity stress · Mechanisms of salt tolerance · Adaptation strategies · Genetic resources · Halophytes · Wild crop relatives · Lower plants · Eukaryotes

Introduction

High soil salinity is a worldwide problem. Increased salt concentration in the soil affects crop productivity, changes the microbial community, and consequently negatively impacts on agricultural economy (FAO 2016). Over 2% of the total and nearly 20% of agricultural irrigated lands suffer from high salinity (FAO 2016). It is expected that soil salinization further increases due to global climate changes and as consequences of wrong irrigation techniques (Munns and Tester 2008a, b). Expansion of salinity on arable areas might reduce agricultural lands up to 30% by 2050 (FAO 2016). Huge economic losses of over 10 billion USD occur annually due to the soil salinization (Qadir et al. 2014).

High soil salinity can inhibit and impair plant development and productivity because of the decrease of water potential of plant cell and ion cytotoxicity, mainly sodium (Na^+) and chloride (Cl^-), causing metabolic dysfunction, alteration of membrane integrity and function as well as the nutritional disorders due to the excess of Na^+ and Cl^- in soil (Tester and Davenport 2003). Additionally, salinity is very often accompanied by oxidative stress due to generation of reactive oxygen species (ROS) (Tsugane et al. 1999).

During evolution many plant species developed unique ways to resist and to survive in harsh saline environments. Moreover, lower plants, fungi and animals reveal outstanding capabilities to adapt to the saline conditions due to the development of specific mechanisms of salt tolerance. Unravelling these salt tolerance mechanisms and identification of key salt tolerance genes can be used for the further biotechnological improvement of our major agricultural crops.

In order to improve salt tolerance of crops a broad spectrum of methods and approaches has been introduced such as high throughput phenotypic screening methods, molecular genetics, genetic engineering, different types of "omics" (genomics, transcriptomics, proteomics, microbiomics, ionomics, etc.). However, it is still challenging to transfer the identified desirable trait into cultivated crop plants. Both the exploration of gene sources and an introduction of novel genes from other types of living organisms is one of the important and essential ways to uphold the enormous challenges for the design and creation of modern crop cultivars. Molecular biology and genetics can supply the tools for the

---

Stanislav V. Isayenkov
stan.isayenkov@gmail.com

[1] Institute of Food Biotechnology and Genomics NAS of Ukraine, Osipovskogo str., 2a, Kyiv-123, Kyiv 04123, Ukraine

gene identification and isolation. The genes of interest have to be transferred either through conventional introgression methods or through advanced genetic engineering methods including genome editing techniques.

In this review the halophytic plants, wild crop relatives, as well as some types of eukaryotes are discussed as the resources for the salt stress tolerance genes. The most important and promising candidate genes from this network and also their possible application and delivery in molecular breeding and genetic engineering are presented here.

Types of salt tolerance

Plant salinity tolerance is governed by action of many physiological and molecular mechanisms. Usually these mechanisms are classified into three major categories: osmotic tolerance, ionic tolerance, tissue tolerance (Roy et al. 2014).

According to the growth performance in saline environments, plants can characterised as salt-tolerant (halophytes) and salt-sensitive (glycophytes) (Fig. 1). Halophytes are capable to tolerate high Na^+ and Cl^- concentrations in their shoots in comparison with the glycophytic plants. The salt tolerance of halophytes and other plants is mediated by two major mechanisms—salt exclusion or inclusion. According to these mechanisms plants can be grouped into two types—includers and excluders. The representatives of the first group are capable to accumulate high NaCl concentrations in their tissues equal or higher as then water salinity level. In turn, glycophytic plants are mostly regarded as salt excluders due to their capacity to prevent accumulation of salts in photosynthetic tissues. In contrast to glycophytes, the majority of halophytes belongs to includers and are able to transport Na^+ actively from root to shoot (Flowers et al. 1977; Läuchli 1984). Numerous data suggests that the majority of halophytic monocot species are strong exluders (Colmer et al. 1995; Garthwaite et al. 2005). Interestingly, the cultivated common barley (*Hordeum vulgare*) belongs to halophytic includer type. It is believed that the includers employ progressive mechanisms of intracellular NaCl compartmentation and effectively regulate cytoplasmic homeostasis and synthesis of compatible solutes. The majority of the plant species belong to salt excluders employing the mechanisms of salt avoidance and revealing wide range of adaptations aimed to minimize the cytosolic salt concentrations or physiological exclusion by root membranes.

Halophytes

Halophytes are capable to grow and reproduce themselves on salt concentration equal to 200 mM NaCl or even higher (Flowers and Colmer 2008, 2015). Only 500 species, comprising 0.14% of the world's floristic diversity, are able to live in saline areas (Flowers et al. 2010). Thus every individual halophytic plant species evolved their own adaptation

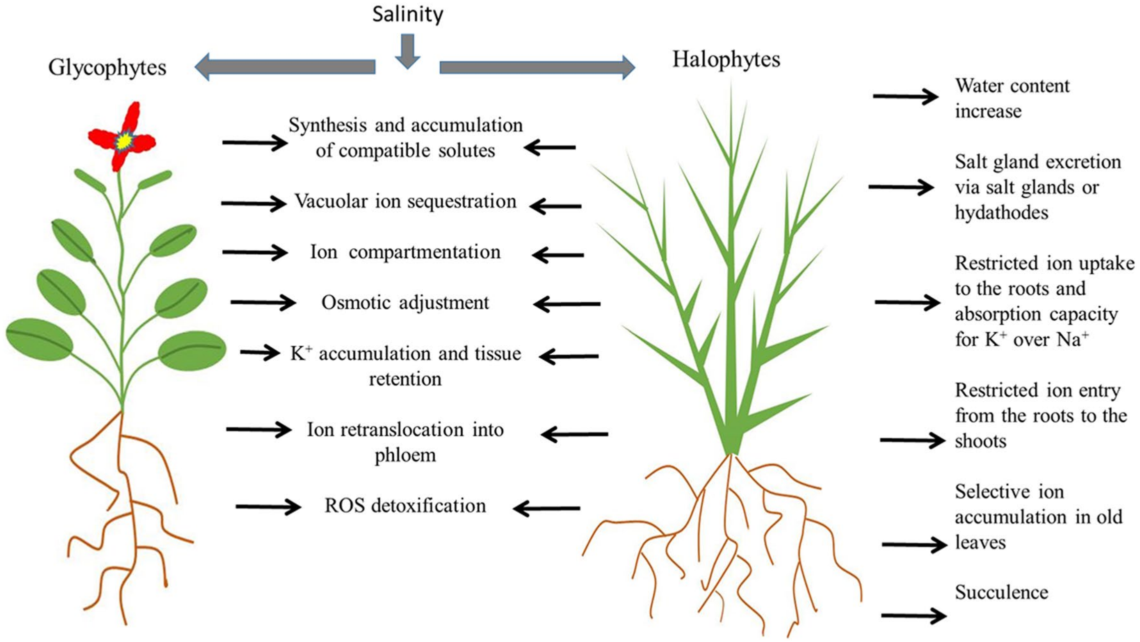

Fig. 1 Comparative diagram and overview of major plant salt tolerance mechanisms in glycophytic and halophytic plants. In comparison with glycophytes, halophytic plants exhibit efficient salt excretion systems (salt glands or hydathodes) and absorption capacity for K^+ over Na^+. Halophytes are capable to accumulate toxic ions in older leaves and restrict ion uptake to the roots or ion migration from the roots to the shoots. The salt tolerance of halophytic is often accompanied by succulence and improved capacity to maintain increased water content

mechanism to survive in saline conditions. The mechanisms of salt tolerance in halophytic plants emerged via the consequent accumulation of beneficial mutations leading to physiological and adaptive changes required to survive in harsh environments of high salinity (Rozema and Flowers 2005; Bromham and Bennett 2014). In turn, halophytic plants can be subdivided into two different groups—obligate halophytes (require salt for their growth) and facultative halophytes (can grow without salt) (Braun-Blanquet 1932; Polunin 1960). Halophytes play an important role as a valuable resource for livestock and are good candidates for the phytoremediation of degraded lands (Flowers et al. 2010). It seems that the domestication of new crops from halophytic species would be also a good solution to solve many problems associated with the intense agriculture and promote agricultural diversity. For example, the halophytic crop Quinoa (*Chenopodium quinoa*) whose cultivation is expanding globally, because of high resistance to multiple abiotic stresses and good nutritional value (Zou et al. 2017). Moreover, grain of Quinoa has high nutritious value due to its exceptional protein quality and wide range of minerals and vitamins. The Quinoa grain proteins are enriched in amino acids like lysine and methionine that are deficient in many cereals (Bhargava et al. 2006). This plant species is also considered as a future crop for food security improvement and model halophytic plant to study the molecular mechanisms of salt bladder function to generate novel salt tolerant crops (Zou et al. 2017). The domestication and production of new crop varieties will support diversity of the sustainable provision of food in the nearest future. Besides this, halophytic plants are a good option to study the adaptation strategies to high salinity as well as an important genetic pool for improvement of tolerance to saline environments and other abiotic stresses (Mishra and Tanna 2017) (Fig. 1). Moreover, the salt-tolerant genes from halophytes could be potential key players of salt tolerance in glycophytic plants including crops (Himabindu et al. 2016). Successful gene transfer from halophytes for salt tolerance improvement has been shown for many plant species (Mishra and Tanna 2017). Therefore, the introduction of halophytic genes via genetic engineering or conventional breeding aimed to develop modern salt-tolerant crop varieties is an important approach for plant scientists and breeders (Munns and Tester 2008a, b; Bose et al. 2015).

Halophytes are capable to tolerate high Na^+ and Cl^- concentrations in their shoots in comparison with glycophytic plants. The mechanisms of salt tolerance of halophytes rely on the adjustment of cellular water potential, enhancement of the exclusion and sequestration of excess salt, and control of uptake and compartmentalization of ions (Mishra and Tanna 2017). Moreover, many halophytic plant species developed specialized organs such as salt glands and bladders for additional salt accumulation and removal. Halophytes are capable to maintain a high K^+ to Na^+ selectivity, produce a wide range of organic solutes, detoxify ROS, and use water efficiently. All these mechanisms are important contributions to efficiency of salt tolerance of halophytes (Shabala and Mackay 2011; Ozgur et al. 2013; Shabala et al. 2014; Shabala and Pottosin 2014). Accordingly, there is no single salinity tolerance mechanism of halophytes. Instead, they employ a range of adaptation mechanisms such as osmotic tolerance, ion exclusion or inclusion, tissue tolerance, and ROS detoxification (Shabala and Pottosin 2014).

It is worth to mention that some genes from halophytes are of exquisite interest because they might be more efficient than their glycophytic homologs regarding salinity stress (Himabindu et al. 2016; Mishra and Tanna 2017) (Table 1). Thus, big attention is now given to the evaluation of the molecular mechanisms of halophyte adaptation to saline environments. For instance, the halophytic plant *Thellungiella parvula* is a dicotyledonous species closely related to *A. thaliana*. The study of its salinity tolerance and the comparison with the model species *A. thaliana* has revealed some differences in the adaptation mechanisms and ion transport in saline conditions (Orsini et al. 2010). It was shown that TsHKT1;2 from the related halophyte *T. salsuginea* acts as a potassium transporter even under salinity stress in comparison with *A. thaliana* AtHKT1. It is noteworthy that the TsHKT1;2 includes a conserved Asp (D) residue in the 2nd pore-loop domain. Most other HKT1 sequences, including AtHKT1, contain an Asn (N) in this position. According to this data the complementation of *A. thaliana athkt1-1* mutants by *TsHKT1;2* under control of the native AtHKT1 promoter resulted in improved salt tolerance. On the other hand, the substitution of Asp (D207) by Asn significantly reduced the resistance to salinity (Ali et al. 2017). Thus, during the evolution process, *T. salsuginea* acquired the Asp (D207) substitution that substantially changed the cation selectivity of the HKT1-type transporter and significantly increased the salt tolerance of the plant (Ali et al. 2017). Another study demonstrated that transgenic *A. thaliana* lines expressing *PutAKT1* from the halophytic relative *Puccinellia tenuiflora* exhibit lower Na^+ and elevated K^+ contents in plant tissues under salinity stress or normal growing conditions (Ardie et al. 2010). Further study of the physiological role of PutAKT1suggested that PtAKT1 is a key factor regulating selective uptake capacity for K^+ over Na^+ in *P. tenuiflora* under saline conditions (Wang et al. 2015a, b). In addition, a recent study reported that SsHKT1;1 from the halophytic plant *Suaeda salsa* mainly functions as K^+ transporter in heterologous expression systems and in *S. salsa*. The main role of this HKT transporter is the maintenance of K^+ nutrition and cytosolic cation homeostasis under high salinity (Shao et al. 2014). Thus, this HKT1 may contribute to halophytism by the enhancement of K^+ transport (Ali et al. 2017). It is noteworthy that

Table 1 Examples of gene transfer associated with salinity tolerance from halophytes

Species (gene source)	Genetic targets	Transgenic plant	References
Ion homeostasis			
Salicornia brachiata	*SbSOS1*	*Nicotiana tabaccum*	Yadav et al. (2012)
Thellungiella halophila	*ThSOS1*	*Arabidopsis thaliana*	Oh et al. (2009)
Chenopodium quinoa	*CqSOS1A* *CqSOS1B*	*A. thaliana*	Maughan et al. (2009)
Puccinellia tenuiflora	*PtSOS1*	*A. thaliana*	Kobayashi et al. (2012)
Aeluropus littoralis	*AlNHX1*	*Glycine max*	Zhang et al. (2008), Liu et al. (2014)
Atriplex gmelini	*AgNHX1*	*Oriza sativa*	Ohta et al. (2002)
S. brachiata	*SbNHX1*	*N. tabaccum*	Jha et al. (2011)
S. europaea	*SeNHX1*	*N. tabaccum* *Medicago sativa*	Zhou et al. (2008) Zhang et al. (2014), Chen et al. (2015)
Salsola soda	*SsNHX1*	*M. sativa*	Li et al. (2011)
P. tenuiflora	*PtNHX1*	*O. sativa*	Kobayashi et al. (2012)
Suaeda salsa	*SsNHX1*	*O. sativa*	Zhao et al. (2006a, b)
Agropyron elongatum	*AeNHX1*	*A. thaliana* *Festuca glauca*	Qiao et al. (2007)
Th. halophila	*ThNHX1*	*A. thaliana*	Wu et al. (2009)
A. littoralis	*AlNHX*	*N. tabaccum* *G. max*	Zhang et al. (2008) Liu et al. (2014)
Spartina anglica	*SaNHX1*	*O. sativa*	Lan et al. (2011)
Halostachys caspica	*HcNHX1*	*A. thaliana*	Guan et al. (2011)
P. tenuiflora	*PtNHX*	*O. sativa*	Kobayashi et al. (2012)
Suaeda corniculata	*ScNHX1*	*M. sativa*	Liu et al. (2013)
Leptochloa fusca	*LfNHX1*	*N. tabaccum*	Rauf et al. (2014)
S. salsa	*SsHKT1;1*	*A. thaliana*	Shao et al. (2014)
Thellungiella salsuginea	*TsHKT1;2*	*A. thaliana*	Ali et al. (2017)
P. tenuiflora	*PutHKT2;1*	*A. thaliana*	Ardie et al. (2009)
P. tenuiflora	*PutAKT1*	*A. thaliana*	Ardie et al. (2010)
T. halophila	*ThVP*	*N. tabaccum* *Gossypium hirsutum*	Gao et al. (2006) Lv et al. (2008, 2009)
Suaeda salsa	*SsVP*	*A. thaliana*	Guo et al. (2006)
Suaeda corniculata	*ScVP*	*A. thaliana*	Liu et al. (2011)
Kalidium foliatum	*KfVP1*	*A. thaliana*	Yao et al. (2012)
Zoysia matrella	*ZmVP1*	*A. thaliana*	Chen et al. (2015)
Halostachys caspica	*HcVP1 and HcVHA-B*	*A. thaliana*	Hu et al. (2011)
Spartina alterniflora	*SaVHAc1*	*O. sativa*	Baisakh et al. (2012)
Detoxifixation, antioxidant systems and stress-induced proteins			
S. brachiata	*SbGSTU*	*N. tabaccum*	Jha et al. (2011)
S. brachiata	*SbpAPX*	*N. tabaccum* *Arachis hypogaea*	Tiwari et al. (2014) Singh et al. (2014)
Avicennia marina	*AmSod1*	*O. sativa*	Prashanth et al. (2008)
Tamarix androssowii	*TaMnSOD*	*Populus nigra*	Wang et al. (2010)
Eutrema halophilum	*ThMSD*	*A. thaliana*	Xu et al. (2014)
S. brachiata	*SbMT-2*	*N. tabaccum*	Chaturvedi et al. (2014)
Avicennia marina	*AmMDAR*	*N. tabaccum*	Kavitha et al. (2010)
Th. salsuginea	*TsLEA1*	*A. thaliana*	Zhang et al. (2012)
Tamarix androssowii	*TaLEA*	*Populus nigra*	Gao et al. (2013)
Osmolite biosynthesis			
Atriplex hortensis	*AhProT1*	*A. thaliana*	Guo et al. (2002)
A. hortensis	*AhBadh*	*O. sativa*	Guo et al. (1997)
A. hortensis	*AhBadh*	*Solanum lycopersicum*	Jia et al. (2002)

Table 1 (continued)

Species (gene source)	Genetic targets	Transgenic plant	References
Inositol biosynthesis			
Mesembryanthemum crystallinum	*McIMT1*	*N. tabaccum*	Sheveleva et al. (1997), Patra et al. (2010)
Spartina alterniflora	*SaINO1*	*A. thaliana*	Joshi et al. (2013)
Transcription factors			
Atriplex halimus	*AtDREB*	*N. tabaccum*	Khedr et al. (2012)
A. hortensis	*AhDREB*	*N. tabaccum*	Shen et al. (2003)
S. brachiata	*SbSI-2*	*N. tabaccum*	Yadav et al. (2014)
Suaeda liaotungensis	*SlNAC1* *SlNAC2*	*A. thaliana*	Yang et al. (2014)
S. liaotungensis	*SlPAPA1*	*A. thaliana*	Li et al. (2014)
A. hortensis	*AhAL1*	*A. thaliana*	Tao et al. (2018)

S. salsa is considered to be a promising model to understand the mechanisms of salt tolerance and to develop saline agriculture (Song and Wang 2015). A number of salt tolerance-related genes including *SsNHX1, SsHKT1, SsAPX, SsCAT1, SsP5CS* and *SsBADH* from *S. salsa* have been cloned and analysed (Song and Wang 2015) (Table 1). The genes related to the biosynthesis of osmolytes play an important role in tolerance mechanisms of halophytes (Table 1). For example, *SsP5CS* and *SsBADH* are involved in biosynthesis of proline and betaine, respectively, in *S. salsa*.

The study of differences in sequences and structures between the homologs from halophytic and glycophytic relatives has a high potential to reveal novel adaptation mechanisms and physiological strategies to tolerate high salinity. For instance, NHX1 from the halophyte *Aeluropus littoralis* comprises ten putative hydrophobic regions, which differ from the nine transmembrane domains of OsNHX1 and AtNHX1 (Zhang et al. 2008). The expression of *AlNHX1* in transgenic soybean leads to a reduced accumulation of Na^+ in shoots and enhanced K^+ levels in both roots and shoots, suggesting a role of AlNHX1 in K^+ homeostasis instead of vacuolar Na^+ sequestration (Liu et al. 2014) (Table 1). Another study showed that transgenic rice expressing *Puccinellia tenuiflora* NHX exhibited higher K^+ content in shoots under NaCl treatment (Kobayashi et al. 2012). It was shown that expression of *SeNHX1* from *Salicornia europaea* leads to improvement of both salt tolerance and disease resistance in tobacco (Chen et al. 2015).

The lack of whole-genome sequence data presents difficulties in considering these unique plant species for understanding their response to salt stress on molecular basis. Only few studies comparing salt response between the glycophytes and the halophytes at transcript and protein levels involve A. *thaliana* and *Thellungiella halophila* (Taji et al. 2004; Gong et al. 2005; Amtmann 2009; Pang et al. 2010), common wheat (*Triticum aestivum)* and *Thinopyrum ponticum* (Wang et al. 2008; Peng et al. 2009) as well as rice and its wild relative *Porteresia coarctata* (Sengupta and Majumder 2009). These studies suggest that salt-tolerant species have higher constitutive levels of stress- and anabolism-related proteins, the former including ROS scavenging enzymes, salt ion transporters, or V-ATPases. In contrast, salt-sensitive species demonstrate a relatively higher abundance of catabolism-related proteins.

There are relations between activities of antioxidant enzymes, stress-induced proteins and mechanisms of salt tolerance. Genes encoding ascorbate peroxidase (APX) or superoxide dismutase (SOD) from halophytic plants could be potential targets for gene transfer to crops. For example, it was demonstrated that SbpAPX from *Salicornia brachiata* plays an important role in the protection against oxidative stress. Unlike wild type plants, transgenic *SbpAPX*-expressing peanut lines were capable to grow and reproduce under salt stress conditions (Table 1) (Singh et al. 2014). Another study demonstrates the role of SbMT-2 metallothionein from *S. brachiata* in abiotic stress tolerance and ROS scavenging in transgenic tobacco (Chaturvedi et al. 2014). There are some other successful applications of halophytic genes encoding antioxidant enzymes for salt tolerance improvement (Table 1). Stress-related proteins such as LEA may also contribute to abiotic stress tolerance. It was demonstrated that the expression level of *TsLEA1* gene in seedlings of halophytic plant *T. salsuginea* increased upon salt treatment. Expression of *TsLEA1* in yeast and Arabidopsis resulted in an improvement of salinity tolerance of both organisms. Thus LEA proteins may play an important role in stress responses (Table 1) (Zhang et al. 2012).

Recently, high-throughput transcript sequencing techniques were used as a powerful approach for the study of the molecular basis of salinity stress regulation in halophytes. Transcript profiling for several halophytic species, such as *Sporobolus virginicus* (Yamamoto et al. 2015), *Porteresia coarctata* (Garg et al. 2014), *Salicornia europaea* (Ma et al. 2013), *Mesembryanthemum crystallinum* (Tsukagoshi et al.

2015), *Suaeda fruticose* (Diray-Arce et al. 2015), *Zostera marina* (Kong et al. 2014), *Halogeton glomeratus* (Wang et al. 2015a, b), *Kosteletzkya virginica* (Tang et al. 2015), *Suaeda maritime* (Gharat et al. 2016), *Cakile maritima* (Megdiche et al. 2008) and *Salicornia brachiata* (Singh et al. 2016; Udawat et al. 2016, 2017) was reported.

Since the majority of agricultural crops are monocots, this type of halophytic species is discussed here. Interestingly, monocotyledonous halophytes contain lower Na$^+$ concentrations and exhibit higher selectivity for K$^+$ uptake as compared to dicotyledonous halophytes (Flowers and Colmer 2008, 2015). Among monocots, there are plenty of plant species including *Bromus danthoniae*, *Hordeum glaucum*, *H. marinum* and others showing exceptional salinity tolerance, suggested for the detailed research aimed to the development of salinity stress-tolerant crops for sustainable agriculture.

Wild crop relatives and their potential use

The development of new salt-tolerant crops is an essential part of biotechnological plant improvement. The domestication of crops resulted the truncation of genetic variation present in the population of wild crop relatives. Closely related species of cereals are valuable genetic resources for modern agriculture and plant biotechnology, and the progenitors and other wild crop relatives provide a solid platform to promote new gene discoveries and mechanisms of physiological adaptations. The introduction of genes from wild relatives into crop cultivars is of primary importance for global food security (Hajjar and Hodgkin 2007). The study of the salinity tolerance in wild crop relatives could significantly facilitate the improvement of common agricultural plants. Many successful breeding efforts involving wild relatives for the significant improvement of drought and salinity tolerance in crops have been conducted.

Wheat, barley and rice are the major cereal crops in the world. Usually domesticated crop cultivars and varieties lack the genetic resources for the development and production of new salt-tolerant genotypes. Among the *Triticeae* tribe exist around 38 species, belonging to *Triticum, Aegilops, Hordeum, Elytrigia, Elymus, Leymus* and *Thinopyrum* genera as potential sources of salinity tolerance (Colmer et al. 2006). One of the easiest possibilities is to create amphidiploid hybrids as new crops being implicated in the saline areas. However, many of these amphidiploid hybrids did not perform well argonomically and exhibited low yield potential. For instance, it was shown that *Hordeum chilense*/*Triticum turgidum* ssp. *durum* and *T. turgidum* ssp. *durum/Thinopyrum bessarabicum* amphidiploids did not show good productivity (Martin and Chapman 1977; King et al. 1997). The accumulation of high Na$^+$ concentrations in plant tissues significantly inhibits leaf function in cereal crops. In order to overcome this problem, the enhancement of shoot Na$^+$ exclusion capacity of cereal crops may be very useful for salt tolerance improvement (Munns and Tester 2008a, b, Horie et al. 2009) (Table 2).

Wheat

The modern wheat species used for bread production and feed have a hexaploid (*Triticum aestivum* L.) or tetraploid (*Triticum turgidum*) genome. The tetraploid *T. turgidum* is a natural hybrid between a *T. urartu* with genome A (Khlestkina and Salina 2001) and an unknown diploid caring genome B. *Aegilops* is the closest relative of *Triticum* genus. It is believed that the *Aegilops* genus is most

Table 2 Examples of gene transfer or crosses associated with salinity tolerance from wild crop relatives

Species (gene source)	Genetic targets/crosses	Transgenic plant/introgressions	References
Wheatgrass species			
Thinopyrum bessarabicum	*T. turgidum—Th. bessarabicum*	*Triticum turgidum* ssp. *durum*	Colmer et al. (2006)
Thinopyrum ponticum	*T.aestivum—Th. ponticum*	*Triticum aestivum*	Xia et al. (2003), Chen et al. (2004)
Lophopyrum elongatum	*T. aestivum—L. elongatum*	*T. aestivum*	Colmer et al. (1995)
Wild barley species			
Hordeum brevisubulatum	*HbCIPK2*	*A. thaliana*	Li et al. (2012)
H. brevisubulatum	*HbNHX1*	*N. tabaccum*	Lu et al. (2005)
Hordeum marinum	*T. aestivum—H. marinum*	*T. aestivum*	Colmer et al. (2005a, b)
Hordeum chilense	*T. turgidum—H. chilense*	*T. turgidum* ssp. *durum*	Forster et al. (1990)
Wide rice species			
Oryza rufipogon	*O. sativa—O. rufipogon*	*O. sativa*	Quan et al. (2018)
Porteresia coarctata	*PcMIP*	*N. tabaccum*	Majee et al. (2004)
P. coarctata	*PcINO1*	*N. tabaccum* *O. sativa* *Brassica juncea*	Patra et al. (2010) Das-Chatterjee et al. (2006)

probably the B genome donor species (Kerby and Kuspira 1987). From the 22 wild *Aegilops* species, *A. cylindrica* has the biggest potential for salt tolerance improvement (Arzani and Ashraf 2016). The hexaploid genome of *T. aestivum* comprises genomes of the diploid species *A. tauschii* (DD) and the tetraploid species *T. turgidum* (AABB) (Colmer et al. 2006). The estimation of salt tolerance capacity of *A. tauschii* revealed lower Na^+ accumulation and higher K^+/Na^+ ratios in their leaves in comparison with durum wheat (Gorham 1990). According to experimental data *A. cylindrica* demonstrates its halophytic capacity to secrete salt on leaves under high salinity (400 mM NaCl) (Arabbeigi et al. 2014). It was shown that the enhanced K^+/Na^+ discrimination in *A. tauschii* is associated with chromosome 4D (Shah et al. 1987). The plant species containing the D genome (*Ae. tauschii*, *T. ventricosum*, and *T. crissum*) displayed high salt tolerance capacity (Xu et al. 1993).

The "primitive" wild wheat species, *T. turgidum spp. diccocum* and *T. monocotum,* might have desirable traits and genes for the improvement of the salinity tolerance (James et al. 2006; Shavrukov et al. 2010; Munns et al. 2012; Table 2). Among wheat progenitors, wild relatives and halophytic species of *Triticeae,* variation in mechanisms of Na^+ 'exclusion' and K^+/Na^+ discrimination is observed (Gorham 1994; Garthwaite et al. 2005). The mechanisms of salt tolerance among wheat species comprises the ability to maintain low Na^+ and high K^+ concentrations in leaves (Maas and Grieve 1990; Dvorak et al. 1994; Munns and James 2003; Poustini and Siosemardeh 2004). However, relatively small variation in Cl^- accumulation in leaves among cultivated wheat species was observed (Gorham 1990; Husain et al. 2004; Colmer et al. 2005a). The crossing of Nax2, a gene locus in the wheat relative *Triticum monococcum* into a commercial durum wheat (*T. turgidum* ssp. *durum* var. Tamaroi) significantly reduced Na^+ contents in leaves (James et al. 2011). Further studies revealed that a gene in the Nax2 locus is *TmHKT1;5-A* encoding Na^+-selective transporter in the plasma membrane of root cells around the xylem vessels, which, therefore, is ideally localized to withdraw Na^+ from the xylem and reduce transport of Na^+ to leaves (Munns et al. 2006). The transfer of the Kna1 locus from D genome of hexaploid wheat into tetraploid *T. turgidum* significantly enhanced K^+/Na^+ ratios (Dvorak et al. 1994; Byrt et al. 2007). Interestingly, under salinity stress (150 mM NaCl) *T. aestivum* excludes nearly 99% of the Na^+ from the transpiration stream. In contrast with bread wheat, *T. turgidum* has lower Na^+ exclusion capacity (95–94%) (Munns 2005). Another study of wheat demonstrates that during salinity stress the key enzymes of the TCA cycle are physiochemically inhibited by salt. In order to compensate this enzyme inhibition wheat increases the GABA shunt activity. An increase of GABA shunt activity provides an alternative carbon source for mitochondria (Che-Othman et al. 2019).

Among halophytic plants of the *Triticeae* tribe, tall wheatgrass species, *Elytrigia elongata*, *Thinopyrum bessarabicum*, *Thinopyrum ponticum* and *Thinopyrum junceum*, have to be mentioned. These wild species of wheatgrass are considered as valuable genetic sources for the improvement of salt tolerance in wheat (Colmer et al. 2005a). It was demonstrated that amphiploid *T. aestivum–E. elongata* exhibits an enhanced capacity of Na^+ and Cl^- exclusion and elevated levels of K^+ in leaves (Schachtman et al. 1989; Omielan et al. 1991). Moreover, some studies indicate a fivefold lower Na^+ concentration, better maintenance of K^+ concentrations, and enhanced levels of glycinebetaine, in the youngest leaf blades of the *T. aestivum–E. elongata* amphiploid in conditions of salinity stress (200 mM NaCl) in comparison with parent *T. aestivum* (Colmer et al. 1995). A salinity tolerance trait originating from *T. bessarabicum* (King et al. 1997) has been introgressed into durum wheat (Colmer et al. 2006). The capability to survive on 750 mM NaCl was shown for several accessions of *T. ponticum* (McGuire and Dvorak 1981). The mechanisms of salt tolerance of many halophytic wheatgrass species are associated with their capacity to restrict the Na^+ and/or Cl^- accumulation in shoots (Shannon 1978; Weimberg and Shannon 1988), and elevated levels of glycine-betaine accumulation in leaves (Weimberg and Shannon 1988). The transfer of *T. ponticum* chromosomes into bread wheat resulted in growth improvement of two introgression lines on 250 mM NaCl in comparison with bread wheat (Xia et al. 2003; Chen et al. 2004) (Table 2).

There are no clear data available regarding the salt tolerance of *T. junceum*. However, in sap from mature leaves after 4 months of growth on 200 mM NaCl, concentration for Na^+ was 146 mM, that of Cl^- was 248 mM, and the K^+/Na^+ ratio was only 1.0 (Gorham 1994) Thus, more data have to be obtained to evaluate this species as genetic source for salt tolerance.

Barley

Hordeum vulgare is considered as salt-tolerant crop in comparison with wheat and other cultivated species of *Triticeae*. Cultivated barley is able to grow on 150 mM NaCl, but in these conditions the loss of biomass is nearly 55–58% (Greenway 1962). Recently it was demonstrated that, in contrast with rice, barley plants are capable to quickly increase their xylem Na^+ concentration and subsequent Na^+ delivery to the shoot. However, barley plants were able to reduce this process later and keep most accumulated Na^+ in the root. Thus, cultivated barley was able to maintain non-toxic shoot Na^+ levels. Differences in control of xylem Na^+ loading between rice and barley may explain their different capacities to tolerate salinity (Ishikawa and Shabala 2019). The salt tolerance may vary among the different *Hordeum vulgare* cultivars. For example, recent study suggest that salt-tolerant barley cultivars rely on the ability to counter Na^+-induced oxidative stress by increasing antioxidant enzyme levels, on possible intensification of vacuolar Na^+ sequestration, and on the prevention of cellular K^+ leakage (Elsawy et al. 2018).

The genetic resources of wild *Hordeum* species for salt tolerance traits are largely unexplored. The ecogeographical study of *Hordeum* spp. demonstrates that more than a half of the barley species are capable to grow and develop on saline habitats, for example, *H. patagonicum* (von Bothmer et al. 1995) and *H. brevisubulatum* (Li et al. 2012). Previously, it was suggested that wild barley—*H. vulgare* ssp. *spontaneum* may serve as a source of the salinity tolerance (Nevo et al. 1993). Nonetheless, other studies demonstrated just limited enhancement of salinity tolerance in *H. vulgare* ssp. *spontaneum* (Forster et al. 1994; Ellis et al. 2000). Perhaps, the wild barley *H. vulgare* ssp. *spontaneum* has to be considered as a drought- and heat-tolerant, rather than a salt-tolerant species.

Among *Hordeum* species, *H. marinum (*sea barley grass or sea side barley) is considered to be one of the major genetic sources for salinity tolerance. *H. marinum* is a halophytic wild relative of the cultivated barley. This typical species of salt marshes and coastal areas is known to inhabit saline areas owing to its considerable tolerance to waterlogging and salinity (Garthwaite et al. 2005). The sea side barley is capable to control concentrations of Na^+ and Cl^- in leaves, even after exposure to 450 mM NaCl in the root-zone. Moreover, the analysis of plant water content and osmotic potential under high salinity revealed a relatively higher water saturation deficiency in *H. marinum* in comparison with *H. vulgare*. In contrast, *H. vulgare* had a lower osmotic potential, corresponding to high levels of proline and dehydrins (Maršálová et al. 2016). Analysis of salt-treated *H. marinum* plants displays enhanced levels of proteins involved in energy metabolism (glycolysis, ATP metabolism, photosynthesis) (Maršálová et al. 2016). These data indicate the high fitness capability of *H. marinum* in saline environments. Recently, a *H. marinum*–bread wheat amphiploid was created (Colmer et al. 2005b) (Table 2) demonstrating intermediate salt and waterlogging tolerance as compared to its parents (Colmer et al. 2005b). Another wild relative of barley, *H. brevisubulatum,* also needs elaborated research, since some reports indicating successful utilization of genes involved in salinity tolerance of this species aimed to improve salt tolerance in other plant species (Lu et al. 2005; Li et al. 2012) (Table 2). It is noteworthy that the salinity tolerance originating from another halophytic barley species, *H. chilense,* has been introgressed into durum wheat (Forster et al. 1990). Thus, wild *Hordeum* species may serve as a good source for the genetic salt tolerance improvement of our crops. Moreover, these halophytic barley species deserve more intense and detailed attention to reveal their adaptation mechanisms to harsh saline environments.

Rice

Rice (*Oryza sativa* L.) is supposed to be one of the most salt-sensitive crop species. The majority of the relatively salt-tolerant rice varieties originated from coastal areas and belong to the *Indica* group (Negrão et al. 2011). The *O. sativa* cv. *Japonica* cultivar Moroberekan originated from Guinea. Due to the specific environment of this country, with mangrove forests nearby cultivated areas, it has been used as a donor of salinity tolerance for other rice cultivars (Kim et al. 2009).

Recently, a large-scale genetic study was conducted to isolate a salt-tolerant introgression line, Dongxiang/Ningjing 15 (DJ 15), from a population of the salt tolerant wild rice *Oryza rufipogon* (Quan et al. 2018; Table 2). Using QTL mapping analysis, 9 QTLs for salt tolerance at the seedling stage located on chr. 1, 3, 4, 5, 6, 8, and 10 were found. Moreover, a sequence variation analysis within the QTL regions revealed that SKC1, HKT8, HKT1;5, and HAK6 transporters together with various transcription factors were candidate genes for the salt tolerance trait (Quan et al. 2018).

Among wild rice species *Oryza glaberrima* has to be mentioned. This plant is the second cultivated species of the *Oryza* genus and potentially grows in mangrove and brackish marshes (Linares 2002). However, the *O. glaberrima* salt tolerance is controversial and seems to be lower than that of *O. sativa* (Awala et al. 2010; Gregorio et al. 2002). Of the rice wild relatives only *Porteresia coarctata* has been extensively studied for its potential as genetic source of salt tolerance for rice (Flowers et al. 1990). This plant species is abundant near coastal areas and mangrove forests, where soils are subjected to salinity twice a day by sea tides or saline rivers (Bal and Dutt 1986).

Porteresia is an important genetic source of salt-tolerant genes/traits for the development of novel tolerant rice varieties (Latha et al. 2004). The use of *P. coarctata* for rice breeding programs is limited by the difficulties to obtain viable embryos (Gregorio et al. 2002) (Table 2). Nevertheless, several studies have shown that the application of some genes from *Porteresia* can improve the salinity tolerance of cultivated rice. These genes are involved in the inositol metabolic pathway (Majee et al. 2004; Sengupta et al. 2008; Morozova et al. 2009). Transcriptome analysis of *P. coarctata* under the salinity stress revealed upregulation of genes encoding stress-responsive transcription factors from different families including MYB, bHLH, AP2-EREBP, WRKY, bZIP and NAC (Garg et al. 2014). It has to be emphasised that *Porteresia* transcripts showed low similarity to the rice orthologs. The similarity levels of *P. coarctata* genes to rice were lower than those of other sequenced wild rice species

(Sakai et al. 2011; Chen et al. 2013; Garg et al. 2014). Moreover, the analysis of ion content and physiological status of *Porteresia* plants have shown accumulation of less sodium and more potassium in leaves and roots in comparison to the Pokkali and IR64 rice varieties (Sengupta and Majumder 2009). Further studies of genes involved in metabolic pathways of salt stress in wild rice species may be a promising approach to improve salinity tolerance in cultivated rice.

Other crops

There are few economically important crops salt-tolerant wild relatives were described. Several halophytic wild relatives exhibit desirable characteristics that can be introgressed into the crop plants through conventional breeding. It was shown, that salt tolerance of sunflower could be substantially enhanced by the introduction of genes originated from their wild relative *Heliantus paradoxus* (Lexer et al. 2003; Kane et al. 2013). The other crop species are tomato (*Lycopersicum cheesmanii and L. pimpinellifolium*; Asins et al. 1993), and *Beta vulgaris* ssp. vulgaris (*B. vulgaris* ssp. Maritime; Rozema et al. 1993). It was demonstrated, that *L. pimpinellifolium* exhibit high productivity under saline condition as much as 15 dS/m. It is one of the closest related species to *L. eseulentum* and could be considered as potential donor of salt tolerance traits for tomato (Asins et al. 1993). The comparative analysis of growth capacities between the coastal halophyte *Beta vulgaris* ssp. Maritima (seabeet) (L.) Arcang and the fodder beet (*Beta vulgaris* ssp. Vulgaris L. cv. Majoral) under salinity has shown that relative growth rate of sea beet decreased by 20% and of fodder beet by 30% with salinity increasing to 400 mol m^{-3} NaCI (Rozema et al. 1993). Perhaps, it would be an option to look for salinity tolerance traits in *Beta vulgaris* ssp. Maritima. However, the further detailed study of this wild crop relatives have to be conducted. Moreover, the crosses of cultivated plant varieties with their halophytic relatives will provide possibility to raise salt tolerance in the amphiploids.

Lower plants, yeasts and animals

One strategy to engineer salt-tolerant plants is to keep cytosolic Na^+ concentrations below toxic levels. To achieve this goal, genetic manipulations with native or heterologous ion transporters involved in Na^+ extrusion and sequestration may be performed (Shi et al. 2002; Munns et al. 2012). Many attempts to generate salt-resistant high-yielding crops by the manipulation of plant membrane ion transporters genes have been unsuccessful (Roy et al. 2014).

Lower plants, including algae, have ion transporters, channels, and pumps potentially unknown in land plants. Fungi and animals could be a good source of useful transporters absent in plant kingdom as well. For example, expression of a yeast Na^+/H^+ antiporter (SOD2) resulted in increased salt tolerance in transgenic rice plants (Zhao et al. 2006a, b).

Animal cells have a completely different approach to handle Na^+ than plants, since they are much more tolerant to saline conditions because of the capability to extrude Na^+ by an efficient Na^+/K^+-ATPase (Pedersen and Palmgren 2017). The Na^+/K^+-ATPase system is exceptionally efficient, since the export of three Na^+ ions and import of two K^+ by this enzyme requires only one ATP (Pedersen and Palmgren 2017). The result of the Na^+/K^+-ATPase activity is developing of chemical Na^+ and K^+ gradients and subsequent creation of difference in electrical charge across the plasma membrane. The created electrochemical gradient could be used by many transport processes (Pedersen and Palmgren 2017). For animal growth the Na^+ extrusion is an essential part of metabolism (Fig. 2). In contrast to this, canonical plant Na^+/H^+-antiporters indirectly consume one ATP molecule per one exported Na^+. Thus, this type of Na^+ export is considered to be costlier in terms of energy (Pedersen and Palmgren 2017) (Table 3). Some lower plants could also have Na^+/K^+-ATPases. For example, *Chlamydomonas reinhardtii* has a Na^+/K^+-ATPase, A8HX15 (Pedersen and Palmgren 2017). However, this type of gene does not exist in fungi and mosses (Pedersen and Palmgren 2017).

Furthermore, Na^+-ATPases, similar to those in fungi, have been identified in mosses (Pardo et al. 2006). It was shown that moss ENA Na^+-ATPases work together with the SOS1-like Na^+/H^{+-}-antiporters. Although in fungi, ENA Na^+-ATPases play the major role in Na^+ export (Prista et al. 1997). It was reported that some green algae have genes encoding homologues of animal Na^+/K^+-ATPases (Pedersen et al. 2012). Therefore, one of the differences between the lower plants (green algae and mosses) and vascular plants is absence of genes that encode Na^+/K^+-ATPases or Na^+-ATPases. It is postulated that Na^+/K^+-ATPases or Na^+-ATPases may give an advantage under salt stress for green algae and mosses (Pedersen and Palmgren 2017). Perhaps, these ATPases were lost during evolution of flowering plants (Pedersen and Palmgren 2017). It is very likely that the first land plants which colonised land originated from freshwater (Kenrick and Crane 1997). Some experimental studies reveal a positive correlation between salt tolerance and *ENA1* expression in the moss *Physcomitrella patens* (Pedersen and Palmgren 2017). Thus, it is possible that plants transformed with animal, moss, or algal type of Na^+/K^+-ATPase or Na^+–ATPase could have a significantly improved salt tolerance. For example, the expression of ENA1 from *P. patens* in rice leads to greater biomass production under salinity stress (Jacobs et al. 2011). Consequently, it is obvious that the strategy to produce transgenic plants heterologously expressing these types of genes

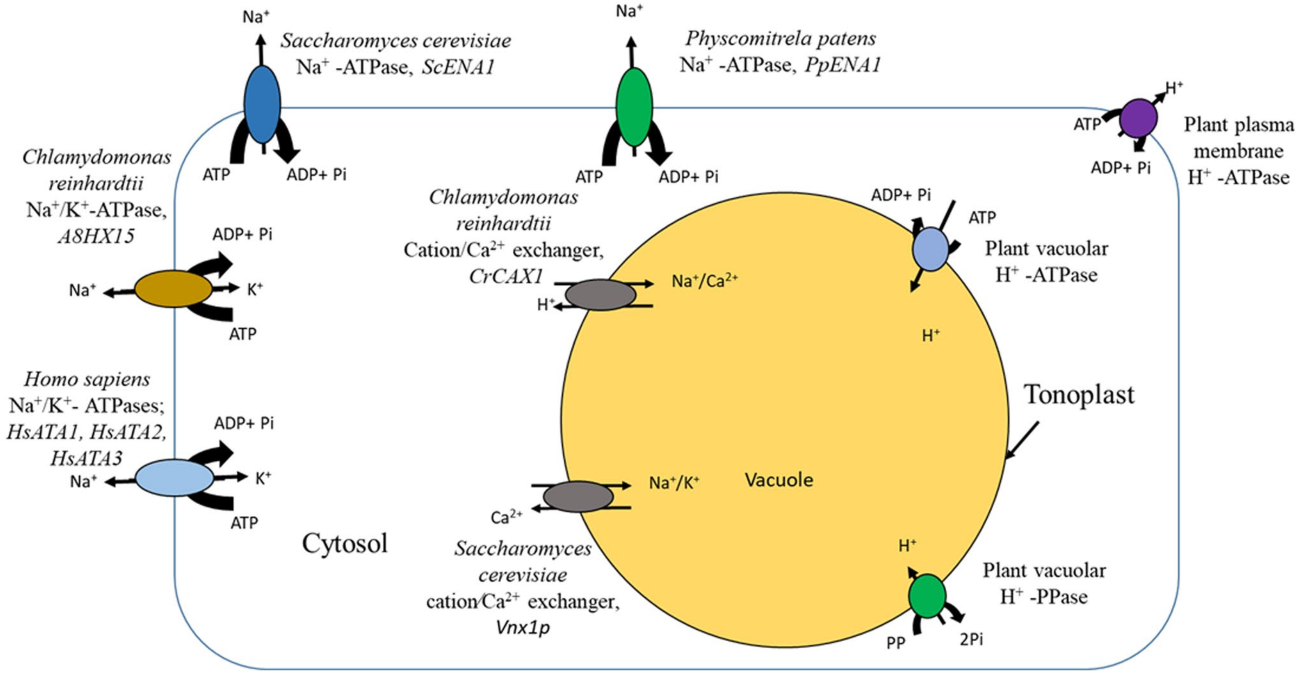

Fig. 2 The perspective targets from animals, yeast and lower plants to increase salt tolerance in plants. Overexpression of exogenous genes encoding Na^+-ATPases (*ScENA1*, *PpENA1*), Na^+/K^+-ATPases (*A8HX15, HsATA1, HsATA2, HsATA3*), vacuolar cation/Ca^{2+} exchangers (*CrCAX1, Vnx1p*) may favour to an increased salt tolerance

Table 3 Examples of gene transfer resulted improvement of plant salinity tolerance from lower plants or fungi

Species (gene source)	Genetic targets	Transgenic plant	Reference
Lower plants			
Chlamydomonas reinhardtii	*CrCAX1*	*A. thaliana*	Pittman et al. (2009)
Physcomitrella patens	*PpENA1*	*O. sativa*	Jacobs et al. (2011)
Yeast			
Saccharomyces cerevisiae	*Na^+/H^+ antiporter (SOD2)*	*O. sativa*	Zhao et al. (2006a, b)
S. cerevisiae	*ScENA1*	*N. tabacum*	Nakayama et al. (2004)

for salinity tolerance improvement needs to be considered (Fig. 2).

It seems that the yeast protein Vnx1p, belonging to the CAX Type II subfamily, is capable to mediate transport of Na^+ and K^+ into the vacuole (Cagnac et al. 2007). Higher plants do not have those type II cation/proton exchangers. In contrast to higher plants, mammals and fungi (yeasts) have CAX proteins exhibiting Na^+/Ca^{2+} and Na^+/H^+ exchange activities (Manohar et al. 2011). Moreover, another member of CAX proteins, CrCAX1 from *C. reinhardtii,* has Ca^{2+}/H^+ and Na^+/H^+ exchange activities (Pittman et al. 2009) (Table 3). A role of CrCAX1 in providing tolerance to cation stress, including Na^+, based on heterologous expression experiments in yeast and Arabidopsis (Pittman et al. 2009), has suggested. The identification of CrCAX1 as a Na^+ transporter may help to understand the osmotic stress regulation by this unicellular organism (Fig. 2).

It would be a good opportunity to test if the application of these type of CAX proteins with Na^+/Ca^{2+} and Na^+/H^+ exchange activities can improve salinity tolerance of higher plants. Alternatively, the use of synthetic biology approaches to generate novel CAX transporters with the desired transport and selectivity properties will be a promising option as well.

Salt tolerance genes

There are several possibilities to use genetic sources to improve salt tolerance. In order to succeed in salt tolerance improvement, the careful selection of candidate genes for gene transfer or manipulation have to be conducted. Moreover, detailed functional analysis of gene products and determination of place of these genes in the molecular network of salinity tolerance is required. Among the prospective genes for genetic engineering and molecular breeding the several functional groups have to be highlighted.

First group comprises the genes encoding ion transporters. These group is most prominent and well-studied. The ion transporters are involved in many mechanisms of salinity tolerance including osmotic adjustment; accumulation of toxic ions into intracellular compartments; ion retranslocation to the non-active metabolically tissues; toxic ions removal from cells and plant tissues; limitation of Na^+ and Cl^- uptake; maintenance of low Na^+/K^+ (Cl^-/NO^{3-}) ratio in cytosol (Isayenkov 2012; Isayenkov and Maathuis 2019). The wide range of genes were identified and characterised for salt tolerance improvement, among these genes the SOS (Salt-Overly-Sensitive) genes, the Na^+ transporter genes NHX1 and HKT1, genes encoding K^+ transporters and channels (HAK, SKOR, AKT, KAT, TPK), family of Ca^{2+}/cation exchangers, H^+:monovalent cation exchanger family (CHX) (Maathuis and Amtmann 1999; Schachtman 2000; Hasegawa et al. 2000; Flowers and Colmer 2008; Ashraf and Akram 2009; Shabala and Cuin 2007; Pardo et al. 2006; Fuchs et al. 2005; Obata et al. 2007; Shabala and Mackay 2011; Wang et al. 2012; Isayenkov 2012). Moreover, the genes encoding the tonoplast and plasma membrane proton-pumps are crucial for generating the electric potential and proton gradients (Ashraf and Akram 2009). Beside this, it should be noted big potential of genes encoding anion, in particular Cl^-, transport (Li et al. 2017). According to the experimental data the major gate of Na^+ entry belong to NCCC channels. Therefore, knock out or limitation of some NCCC genes expression could be beneficial for salinity tolerance (Tester and Davenport 2003; Horie and Schroeder 2004; Demidchik and Maathuis 2007).

Second gene group is related to osmolyte biosynthesis proteins. However, the application of this type genes may solve the problems of osmotic adjustment, but not ion toxicity. Therefore application of genes involved in biosynthesis of betaine, proline, myo-inositol, sugars or other types of osmolyte would beneficial for plant tolerance (Rhodes et al. 2002; Flowers and Colmer 2008; Kalinina et al. 2012). However, the experimental data suggest that from the point of energy use, cellular osmotic adjustment is more efficient by application of ions than organic solutes (Greenway and Munns 1980; Flowers et al. 2010).

Third group of genes is involved in antioxidant machinery. In the battle with ROS, plants recruit an efficient antioxidant system comprising enzymatic antioxidants including superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX), peroxidase (POX), redox regulatory enzymes such as monodehydroascorbate reductase (MDAR), glutathione reductase (GR), glutathione peroxidase (GPX), glutathione S- transferases (GST) (Gao et al. 2008; Isayenkov 2012; Negrão et al. 2011). Therefore, gene transfer or modulation of gene expression for plant protection against ROSs deserves our attention.

Forth group of genes is encoding stress-induced proteins such as LEA. The LEA proteins is involved in protection of molecules under the water deficiency. These group of proteins is providing a water-like rich environment to their target enzymes (Negrão et al. 2011). Among the different LEA proteins, the group 2 of LEAs (dehydrins) is very important for plant tolerance improvement to various stresses (Hanin et al. 2011). Therefore, application of genes encoding these type proteins deserve to be considered.

Last functional group belong to the genes is encoding transcription factors known to be involved in salinity stress response. This group comprise MYB, bHLH, AP2-EREBP, WRKY, bZIP and NAC families. Many transcription factors were successfully tested in various glycophytic crops including tobacco, maize, rice, wheat, potato, tomato, cabbage (Joshi et al. 2015).

Conclusion

From the more than 300,000 plant species in the world, less than 200 are commercially important. It remains still challenging to create and commercialize crops with the increased tolerance to salinity or any other abiotic stress and also laboratory growth and experiment setup are far different from field conditions. However, to create successful salt-tolerant crop the large-scale and long-term field trials under the monitored conditions have to be conducted. Besides field trials there are the plethora of challenges still waiting to be solved. However, different halophytic plant species, lower plants and fungi use different mechanisms to respond on salt stress, since a single species as a model for study salt tolerance is not enough. Therefore, the detailed studies of the molecular mechanisms of salt stress regulation for the wide range of halophytic species from plant, animal and fungi kingdoms might significantly improve our understanding of the salinity tolerance nature. The identification and characterization of the novel specific genes involved in the regulation of the plant salinity tolerance from different plants and other organism will significantly improve quality of the engineered salt tolerant crops. High-throughput phenotyping, expression profiling, genome sequencing of both economically important crops and their relatives, as well as halophytic plants are required to achieve desirable goals in salt tolerance engineering. An alternative approach is the synthetic biology tools for the modification of the existing membrane transport proteins or other key proteins of salt tolerance. Engineering of the completely novel proteins, with the desired properties, for the regulation of salt crop tolerance will be a good option. It has to be mentioned that the several traits in crops crucial for their domestication are results of mutations, which can be easily reproduced by genome-editing techniques, offering the potential for the enhanced domestication of the new crops. Thus, the engineering of salt tolerance mechanisms via the genome editing will progress in the upcoming years, and, in the meanwhile, the domestication of new crops might increase agricultural diversity and provide an alternative solution to solve various problems of modern agriculture.

Compliance with ethical standards

Conflict of interest The author declares no conflict of interest.

References

Ali A, Yun D-J (2017) Salt stress tolerance; what do we learn from halophytes? J Plant Biol 60:431–439

Ali A, Park HC, Aman R, Ali Z, Yun DJ (2013) Role of HKT1 in *Thellungiella salsuginea*, a model extremophile plant. Plant Signal Behav 8(8):e25196

Amtmann A (2009) Learning from evolution: *Thellungiella* generates new knowledge on essential and critical components of abiotic stress tolerance in plants. Mol Plant 2:3–12

Arabbeigi M, Arzani A, Majidi MM, Kiani R, Tabatabaei BES, Habibi F (2014) Salinity tolerance of *Aegilops cylindrica* genotypes collected from hyper-saline shores of Uremia Salt Lake using physiological traits and SSR markers. Acta Physiol Plant 36:2243–2251

Ardie SW, Xie L, Takahashi R, Liu S, Takano T (2009) Cloning of a high-affinity K^+ transporter gene PutHKT2;1 from *Puccinellia tenuiflora* and its functional comparison with OsHKT2;1 from rice in yeast and Arabidopsis. J Exp Bot 60(12):3491–3502

Ardie SW, Liu S, Takano T (2010) Expression of the AKT1-type K^+ channel gene from *Puccinellia tenuiflora*, PutAKT1, enhances salt tolerance in Arabidopsis. Plant Cell Rep 29:865–874

Arzani A, Ashraf M (2016) Smart engineering of genetic resources for enhanced salinity tolerance in crop plants. Crit Rev Plant Sci 35:146–189

Ashraf M, Akram NA (2009) Improving salinity tolerance of plants through conventional breeding and genetic engineering: an analytical comparison. Biotechnol Adv 27:744–752

Asins MJ, Bretó MP, Cambra M, Carbonell EA (1993) Salt tolerance in *Lycopersicon* species. I. Character definition and changes in gene expression. Theor Appl Genet 86:737–743

Awala SM, Nanhapo PI, Sakagami JI, Kanyomeka L, Iijima M (2010) Differential salinity tolerance among *Oryza glaberrima*, *Oryza sativa* and their interspecies including NERICA. Plant Prod Sci 13:3–10

Baisakh N, RamanaRao MV, Rajasekaran K, Subudhi P, Janda J, Galbraith D, Vanier C, Pereira A (2012) Enhanced salt stress tolerance of rice plants expressing a vacuolar H^+ -ATPase subunit c1 (SaVHAc1) gene from the halophyte grass *Spartina alterniflora* Löisel. Plant Biotechnol J 10:453–464

Bal AR, Dutt SK (1986) Mechanism of salt tolerance in wild rice (*Oryza coarctata* Roxb). Plant Soil 92:399–404

Bhargava A, Shukla S, Ohri D (2006) *Chenopodium quinoa*—an Indian perspective. Ind Crops Prod 23:73–87

Bose J, Rodrigo-Moreno A, Lai D, Xie Y, Shen W, Shabala S (2015) Rapid regulation of the plasm membrane H^+-ATPase activity is essential to salinity tolerance in two halophyte species, *Atriplex lentiformis* and *Chenopodium quinoa*. Annu Bot 115:481–494

Braun-Blanquet J (1932) Plant sociology: the study of plant communities. MacGraw Hill, New York, pp 1–439

Bromham L, Bennett TH (2014) Salt tolerance evolves more frequently in C4 grass lineages. J Evol Biol 27:653–659

Byrt CS, Platten DJ, Spielmeyer W, James RA, Lagudah ES, Dennis ES, Tester M, Munns R (2007) HKT1;5-like cation transporters linked to Na^+ exclusion loci in wheat, Nax2 and Kna11. Plant Physiol 143:1918–1928

Cagnac O, Leterrier M, Yeager M, Blumwald E (2007) Identification and characterization of Vnx1p, a novel type of vacuolar monovalent cation/H^+ antiporter of *Saccharomyces cerevisiae*. J Biol Chem 282:24284–24293

Chaturvedi AK, Patel MK, Mishra A, Tiwari V, Jha B (2014) The SbMT-2 gene from a halophyte confers abiotic stress tolerance and modulates ROS scavenging in transgenic tobacco. PLoS ONE 9(10):e111379

Chen SY, Xia GM, Quan TY, Xiang FN, Yin J, Chen HM (2004) Introgression of salt-tolerance from somatic hybrids between common wheat and *Thinopyrum ponticum*. Plant Sci 167:773–779

Chen J, Huang Q, Gao D, Wang J, Lang Y, Liu T, Li B, Bai Z, Luis Goicoechea J, Liang C, Chen C, Zhang W, Sun S, Liao Y, Zhang X, Yang L, Song C, Wang M, Shi J, Liu G, Liu J, Zhou H, Zhou W, Yu Q, An N, Chen Y, Cai Q, Wang B, Liu B, Min J, Huang Y, Wu H, Li Z, Zhang Y, Yin Y, Song W, Jiang J, Jackson SA, Wing RA, Wang J, Chen M (2013) Whole-genome sequencing of *Oryza brachyantha* reveals mechanisms underlying *Oryza* genome evolution. Nat Commun 4:1595

Chen X, Bao H, Guo J, Jia W, Li Y (2015) Overexpression of SeNHX1 improves both salt tolerance and disease resistance in tobacco. Plant Signal Behav 10(4):e993240

Che-Othman MH, Jacoby RP, Millar AH, Taylor NL (2019) Wheat mitochondrial respiration shifts from the tricarboxylic acid cycle to the GABA shunt under salt stress. New Phytol 1:4. https://doi.org/10.1111/nph.15713

Colmer TD, Epstein E, Dvorak J (1995) Differential solute regulation in leaf blades of various ages in salt-sensitive wheat and a salt-tolerant wheat × *Lophopyrum elongatum* (Host) A Love amphiploid. Plant Physiol 108:1715–1724

Colmer TD, Munns R, Flowers TJ (2005a) Improving salt tolerance of wheat and barley: future prospects. Aust J Exp Agric 45:1425–1443

Colmer TD, Garthwaite AJ, Islam AKMR, Islam S, Malik AI, von Bothmer R (2005b) Salinity and waterlogging tolerance in wild *Hordeum* species: physiological basis and prospects for use in cereal improvement. In: Li CJ et al (eds) Plant nutrition for food security, human health and environmental protection. Tsinghua University Press, Beijing, pp 8–9

Colmer TD, Flowers TJ, Munns R (2006) Use of wild relatives to improve salt tolerance in wheat. J Exp Bot 57:1059–1078

Das-Chatterjee A, Goswami L, Maitra S, Dastidar KG, Ray S, Majumder AL (2006) Introgression of a novel salt-tolerant L-myo-inositol 1-phosphate synthase from *Porteresia coarctata* (Roxb.) Tateoka (PcINO1) confers salt tolerance to evolutionary diverse organisms. FEBS Lett 580:3980–3988

Demidchik V, Maathuis FJM (2007) Physiological roles of nonselective cation channels in plants: from salt stress to signaling and development. New Phytol 175:387–404

Diray-Arce J, Clement M, Gul B, Khan MA, Nielsen BL (2015) Transcriptome assembly, profiling and differential gene expression analysis of the halophyte *Suaeda fruticosa* provides insights into salt tolerance. BMC Genomics 16:353

Dvorak J, Noaman MM, Goyal S, Gorham J (1994) Enhancement of the salt tolerance of *Triticum turgidum* L. by the Kna1 locus transferred from *Triticum aestivum* L. chromosome 4D by homologous recombination. Theor Appl Genet 87:872–877

Ellis RP, Foster BP, Robinson D, Handley LL, Gordon DC, Russell JR, Powell W (2000) Wild barley: a source of genes for crop improvement in the 21st century? J Exp Bot 51:9–17

Elsawy HIA, Mekawy AMM, Elhity MA, Abdel-Dayem SM, Abdelaziz MN, Assaha DVM, Ueda A, Saneoka H (2018) Differential responses of two Egyptian barley (*Hordeum vulgare* L.) cultivars to salt stress. Plant Physiol Biochem 127:425–435

FAO (2016)

Flowers TJ, Colmer TD (2008) Salinity tolerance in halophytes. New Phytol 179:945–963

Flowers TJ, Colmer TD (2015) Plant salt tolerance: adaptations in halophytes. Annu Bot 115:327–331

Flowers TJ, Troke PF, Yeo AR (1977) The mechanism of salt tolerance in halophytes. Annu Rev Plant Physiol 28:89–121

Flowers TJ, Flowers SA, Hajibagheri MA, Yeo AR (1990) Salt tolerance in the halophytic wild rice, *Porteresia coarctata* Tateoka. New Phytol 114:675–684

Flowers TJ, Galal HK, Bromham L (2010) Evolution of halophytes: multiple origins of salt tolerance in land plants. Funct Plant Biol 37:604–612

Forster BP, Phillips MS, Miller TE, Baird E, Powell W (1990) Chromosome location of genes controlling tolerance to salt (NaCl) and vigour in *Hordeum vulgare* and *H. chilense*. Heredity 65:99–107

Forster BP, Pakniyat H, Macaulay M, Matheson W, Philips MS, Thomas WTB, Powell W (1994) Variation in the leaf sodium content of the *Hordeum vulgare* (barley) cultivar Maythorpe and its derived mutant cv. Golden promise. Heredity 73:249–253

Fuchs I, Stölzle S, Ivashikina N, Hedrich R (2005) Rice K^+ uptake channel OsAKT1 is sensitive to salt stress. Planta 221:212–221

Gao F, Gao Q, Duan X, Yue G, Yang A, Zhang J (2006) Cloning of an H^+-PPase gene from *Thellungiella halophila* and its heterologous expression to improve tobacco salt tolerance. J Exp Bot 57:3259–3270

Gao S, Ouyang C, Wang S, Xu Y, Tang L, Chen F (2008) Effects of salt stress on growth, antioxidant enzyme and phenylalanine ammonia-lyase activities in *Jatropha curcas* L. seedlings. Plant Soil Environ 54:374–381

Gao W, Bai S, Li Q, Gao C, Liu G, Li G, Tan F (2013) Overexpression of TaLEA gene from Tamarix androssowii improves salt and drought tolerance in transgenic poplar (*Populus simonii* × *P. nigra*). PLoS ONE 8(6):e67462

Garg R, Verma M, Agrawal S, Shankar R, Majee M, Jain M (2014) Deep transcriptome sequencing of wild halophyte rice, *Porteresia coarctata*, provides novel insights into the salinity and submergence tolerance factors. DNA Res 21:69–84

Garthwaite AJ, von Bothmer R, Colmer TD (2005) Salt tolerance in wild Hordeum species is associated with restricted entry of Na^+ and Cl^- into the shoots. J Exp Bot 56:2365–2378

Gharat SA, Parmar S, Tambat S, Vasudevan M, Shaw BP, Subudhi PK (2016) Transcriptome analysis of the response to NaCl in *Suaeda maritima* provides an insight into salt tolerance mechanisms in halophytes. PLOS ONE 11(9):e0163485

Gong Q, Li P, Ma S, Rupassara SI, Bohnert HJ (2005) Salinity stress adaptation competence in the extremophile *Thellungiella halophila* in comparison with its relative *Arabidopsis thaliana*. Plant J 44:826–839

Gorham J (1990) Salt tolerance in the *Triticeae*: K/Na discrimination in *Aegilops* species. J Exp Bot 41:615–621

Gorham J (1994) Salt tolerance in the Triticeae: K/Na discrimination in some perennial wheatgrasses and their amphiploids with wheat. J Exp Bot 45(4):441–447

Greenway H (1962) Plant response to saline substrates. I. Growth and ion uptake of several varieties of *Hordeum* during and after sodium chloride treatment. Aust J Biol Sci 15:16–38

Greenway H, Munns R (1980) Mechanisms of salt tolerance in nonhalophytes. Annu Rev Plant Physiol 31(1):149–190

Gregorio GB, Senadhira D, Mendoza RD, Manigbas NL, Roxas JP, Guerta CQ (2002) Progress in breeding for salinity tolerance and associated abiotic stresses in rice. Field Crops Res 76:91–101

Guan B, Hu Y, Zeng Y, Wang Y, Zhang F (2011) Molecular characterization and functional analysis of a vacuolar Na(+)/H(+) antiporter gene (HcNHX1) from *Halostachys caspica*. Mol Biol Rep 38:1889–1899

Guo Y, Zhang L, Xiao G, Cao S, Gu D, Tian W, Chen S (1997) Expression of betaine aldehyde dehydrogenase gene and salinity tolerance in rice transgenic plants. Sci China Ser C 40:496–501

Guo YS, Wan-Ke Z, Dong-Qing Y, Bao-Xing D, Jin-Song Z, Shou-Yi C (2002) Overexpression of proline transporter gene isolated from halophyte confers salt tolerance in Arabidopsis. Acta Bota Sinica 44:956–962

Guo S, Yin H, Zhang X, Zhao F, Li P, Chen S, Zhao Y, Zhang H (2006) Molecular cloning and characterization of a vacuolar H^+-pyrophosphatase gene, *SsVP*, from the halophyte *Suaeda salsa* and its overexpression increases salt and drought tolerance of Arabidopsis. Plant Mol Biol 60:41–50

Hajjar R, Hodgkin T (2007) The use of wild relatives in crop improvement: a survey of developments over the last 20 years. Euphytica 156:1–13

Hanin M, Brini F, Ebel C, Toda Y, Takeda S, Masmoudi K (2011) Plant dehydrins and stress tolerance: versatile proteins for complex mechanisms. Plant Signal Behav 6(10):1503–1509

Hasegawa PM, Bressan RA, Zhu JK, Bohnert HJ (2000) Plant cellular and molecular responses to high salinity. Annu Rev Plant Physiol Plant Mol Biol 51:463–499

Himabindu Y, Chakradhar Th, Reddy MC, Kanygin A, Redding KE, Chandrasekhar T (2016) Salt-tolerant genes from halophytes are potential key players of salt tolerance in glycophytes. Environ Exp Bot 124:39–63

Horie T, Schroeder JI (2004) Sodium transporters in plants. Diverse genes and physiological functions. Plant Physiol 136:2457–2462

Horie T, Hauser F, Schroeder JI (2009) HKT transporter-mediated salinity resistance mechanisms in Arabidopsis and monocot crop plants. Trends Plant Sci 14:660–668

Hu YZ, Zeng YL, Guan B, Zhang FC (2011) Overexpression of a vacuolar H^+-pyrophosphatase and a B subunit of H^+-ATPase cloned from the halophyte *Halostachys caspica* improves salt tolerance in *Arabidopsis thaliana*. Plant Cell Tiss Organ Cult 108:63–71

Husain S, von Caemmerer S, Munns R (2004) Control of salt transport from roots to shoots of wheat in saline soil. Funct Plant Biol 31:1115–1126

Isayenkov SV (2012) Physiological and molecular aspects of salt stress in plants. Cytol Gen 46:302–318

Isayenkov SV, Maathuis FJM (2019) Plant salinity stress: many unanswered questions remain. Front Plant Sci 10:80

Ishikawa T, Shabala S (2019) Control of xylem Na^+ loading and transport to the shoot in rice and barley as a determinant of differential salinity stress tolerance. Physiol Plant 165:619–631

Jacobs A, Ford K, Kretschmer J, Tester M (2011) Rice plants expressing the moss sodium pumping ATPase PpENA1 maintain greater biomass production under salt stress. Plant Biotechnol J 9:838–847

James RA, Davenport RJ, Munns R (2006) Physiological characterisation of two genes for Na^+ exclusion in durum wheat: Nax1 and Nax2. Plant Physiol 142:1537–1547

James RA, Blake C, Byrt CS, Munns R (2011) Major genes for Na^+ exclusion Nax1 and Nax2 (wheat HKT1;4 and HKT1;5) decrease Na^+ accumulation in bread wheat under saline and waterlogged conditions. J Exp Bot 62:2939–2947

Jha B, Sharma A, Mishra A (2011) Expression of *SbGSTU* (tau class glutathione S-transferase) gene isolated from *Salicornia* *brachiata* in tobacco for salt tolerance. Mol Biol Rep 38:4823–4832. https://doi.org/10.1007/s11033-010-06

Jia GX, Zhu ZQ, Chang FQ, Li YX (2002) Transformation of tomato with the BADH gene from *Atriplex* improves salt tolerance. Plant Cell Rep 21:141–146

Joshi R, Ramanarao MV, Baisakh N (2013) Arabidopsis plants constitutively overexpressing a myo-inositol 1-phosphate synthase gene (*SaINO1*) from the halophyte smooth cordgrass exhibits enhanced level of tolerance to salt stress. Plant Physiol Biochem 65:61–66

Joshi R, Ramanarao MV, Bedre B, Sanchez L, Pilcher W, Zandkarimi H, Baisakh N (2015) Salt adaptation mechanisms of halophytes: improvement of salt tolerance in crop plants. In: Pandey GK (ed) Elucidation of abiotic stress signaling in plants. Springer, New York, pp 243–279

Kalinina EB, Keith BK, Kern AJ, Dyer WE (2012) Salt-and osmotic stress-induced choline monooxygenase expression in *Kochia scoparia*, is ABA-independent. Biol Plant 56:699–704

Kane NC, Burke JM, Marek L, Seiler G, Vear F, Baute G, Knapp SJ, Vincourt P, Rieseberg LH (2013) Sunflower genetic, genomic and ecological resources. Mol Ecol Resour 13:10–20

Kavitha K, Usha B, George S, Venkataraman G, Parida A (2010) Molecular characterization of a salt-inducible monodehydroascorbate reductase from the halophyte *Avicennia marina*. Int J Plant Sci 171:457–465

Kenrick P, Crane PR (1997) The origin and early evolution of plants on land. Nature 389:33–39

Kerby K, Kuspira J (1987) The phylogeny of the polypoloid wheats *Triticum aestivum* (bread wheat) and *Triticum durum* (macaroni wheat). Genome 29:722–737

Khedr AHA, Serag MS, Nemat-Alla MM, Abo El-Naga AZ, Nada RM, Quick WP, Abogadallah GM (2012) A DREBgene from the xero-halophyte *Atriplex halimusis* induced by osmotic but not ionic stress and shows distinct differences from glycophytic homologues. Plant Cell Tiss Organ Cult 106:191–206

Khlestkina EK, Salina EA (2001) Genome-specific markers of tetraploid wheats and their putative diploid progenitor species. Plant Breed 120:227–232

Kim DM, Ju HG, Kwon TR, Oh CS, Ahn SN (2009) Mapping QTLs for salt tolerance in an introgression line population between japonica cultivars in rice. J Crop Sci Biotech 12:121–128

King IP, Law CN, Cant KA, Orford SE, Reader SM, Miller TE (1997) *Tritipyrum,* a potential new salt-tolerant cereal. Plant Breed 116:127–132

Kobayashi S, Abe N, Yoshida KT, Liu S, Takano T (2012) Molecular cloning and characterization of plasma membrane and vacuolar type Na^+/K^+ antiporters of an alkaline salt tolerant monocot *Puccinellia tenuiflora*. J Plant Res 125:587–594

Kong F, Li H, Sun P, Zhou Y, Mao Y (2014) De Novo assembly and characterization of the transcriptome of seagrass *Zostera marina* using Illumina paired-end sequencing. PLoS ONE 9:e112245

Lan T, Duan Y, Wang B, Zhou Y, Wu W (2011) Molecular cloning and functional characterization of a Na^+/H^+ antiporter gene from halophyte *Spartina anglica*. Turk J Agric For 35:535–543

Latha R, Rao CS, Subramaniam HMS, Eganathan P, Swaminathan MS (2004) Approaches to breeding for salinity tolerance—a case study on *Porteresia coarctata*. Annu Appl Biol 144:177–184

Läuchli A (1984) Salt exclusion: an adaptation of legumes for crops and pastures under saline conditions. In: Staples RC (ed) Salinity tolerance in plants: strategies for crop improvement. Wiley, New York, pp 171–187

Lexer C, Lai Z, Rieseberg LH (2003) Candidate gene polymorphisms associated with salt tolerance in wild sunflower hybrids: implications for the origin of *Helianthus paradoxus*, a diploid hybrid species. New Phytol 161:225–233

Li W, Wang D, Jin T, Chang Q, Yin D, Xu S, Liu B, Liu L (2011) The vacuolar Na^+/H^+ antiporter gene SsNHX1 from the halophyte *Salsola soda* confers salt tolerance in transgenic Alfalfa (*Medicago sativa* L.). Plant Mol Biol Rep 29:278

Li R, Zhang J, Wu G, Wang H, Chen J, Wei J (2012) HbCIPK2, a novel CBL-interacting protein kinase from halophyte *Hordeum brevisubulatum*, confers salt and osmotic stress tolerance. Plant Cell Environ 35:1582–1600

Li XL, Hu YX, Yang X, Yu XD, Li QL (2014) A novel zinc-finger HIT protein with an additional PAPA-1-like region from *Suaeda liaotungensis* K. enhanced transgenic Arabidopsis drought and salt stresses tolerance. Mol Biotechnol 56:1089–1099

Li B, Tester M, Gilliham M (2017) Chloride on the move. Trends Plant Sci 22(3):236–248. https://doi.org/10.1016/j.tplants.2016.12.004

Linares OF (2002) African rice (*Oryza glaberrima*): history and future potential. Proc Natl Acad Sci USA 99:16360–16365

Liu L, Wang Y, Wang N, Dong YY, Fan XD, Liu XM, Yang J, Li HY (2011) Cloning of a vacuolar H(+)-pyrophosphatase gene from the halophyte *Suaeda corniculata* whose heterologous overexpression improves salt, saline-alkali and drought tolerance in Arabidopsis. J Integr Plant Biol 53:731–742

Liu L, Fan XD, Wang FW, Wang N, Dong YY, Liu X-M, Yang J, Wang Y-F, Li H-Y (2013) Coexpression of ScNHX1 and ScVP in transgenic hybrids improves salt and saline-alkali tolerance in alfalfa (*Medicago sativa* L.). J Plant Growth Regul 32:1–8

Liu J, Zhang S, Dong L, Chu J (2014) Incorporation of Na^+/H^+ antiporter gene from *Aeluropus littoralis* confers salt tolerance in soybean (*Glycine max* L.). Indian J Biochem Biophys 51:58–65

Lu S-Y, Jing Y-X, Shen S-H, Zhao H-Y, Ma L-Q, Zhou X-J, Ren Q, Li Y-F (2005) Antiporter gene from *Hordum brevisubulatum* (Trin.) link and its overexpression in transgenic tobaccos. J. Integr Plant Biol 47:343–349

Lv S, Zhang K, Gao Q, Lian L, Song Y, Zhang J (2008) Overexpression of an H^+-PPase gene from *Thellungiella halophile* in cotton enhances salt tolerance and improves growth and photosynthetic performance. Plant Cell Physiol 49:1150–1164

Lv SL, Lian LJ, Tao PL, Li ZX, Zhang KW, Zhang JR (2009) Overexpression of *Thellungiella halophile* H(+)-PPase (TsVP) in cotton enhances drought stress resistance of plants. Planta 229:899–910

Ma J, Zhang M, Xiao X, You J, Wang J, Wang T, Yao Y, Tian C (2013) Global transcriptome profiling of *Salicornia europaea* L. shoots under NaCl treatment. PLoS ONE 8(6):e65877

Maas EV, Grieve CM (1990) Spike and leaf development in salt stressed wheat. Crop Sci 30:1309–1313

Maathuis FJM, Amtmann A (1999) K^+ nutrition and Na^+ toxicity: the basis of cellular K^+/Na^+ ratios. Ann Bot 84:123–133

Majee M, Maitra S, Dastidar KG, Pattnaik S, Chatterjee A, Hait NC, Das KP, Majumder AL (2004) A novel salt-tolerant l-myo-inositol-1-phosphate synthase from *Porteresia coarctata* (Roxb.) Tateoka, a halophytic wild rice: molecular cloning, bacterial overexpression, characterization, and functional introgression into tobacco-confering salt tolerance phenotype. J Biol Chem 279:28539–28552

Manohar M, Shigaki T, Hirschi KD (2011) Plant cation/H^+ exchangers (CAXs): biological functions and genetic manipulations. Plant Biol 13:561–569

Maršálová L, Vítámvás P, Hynek R, Prášil IT, Kosová K (2016) Proteomic response of *Hordeum vulgare* and *H. marinum* to salinity. Front Plant Sci 7:1154

Martin A, Chapman V (1977) A hybrid between *Hordeum chilense* and *Triticum aestivum*. Cereal Res Commun 5:365–368

Maughan PJ, Turner TB, Coleman CE, Elzinga DB, Jellen EN, Morales JA, Udall JA, Fairbanks DJ, Bonifacio A (2009) Characterization of salt overly sensitive 1 (SOS1) gene homologs in quinoa (*Chenopodium quinoa* Willd.). Genome 52:647–657

McGuire GE, Dvorak J (1981) High salt tolerance potential in wheat grasses. Crop Sci 21:702–705

Megdiche W, Passaquet C, Zourrig W, Zuily Fodi Y, Abdelly C (2008) Molecular cloning and characterization of novel cystatin gene in leaves *Cakile maritima* halophyte. J Plant Physiol 166:739–749

Mishra A, Tanna B (2017) Halophytes: potential resources for salt stress tolerance genes and promoters. Front Plant Sci 8:829

Morozova O, Hirst M, Marra MA (2009) Applications of new sequencing technologies for transcriptome analysis. Annu Rev Genomics Hum Genet 10:135–151

Munns R (2005) Genes and salt tolerance: bringing them together. New Phytol 167:645–663

Munns R, James RA (2003) Screening methods for salinity tolerance: a case study with tetraploid wheat. Plant Soil 253:201–218

Munns R, Tester M (2008) Mechanisms of salinity tolerance. Annu Rev Plant Biol 59:651–681

Munns R, James RA, Läuchli A (2006) Approaches to increasing the salt tolerance of wheat and other cereals. J Exp Bot 57:1025–1043

Munns R, James RA, Xu B, Athman A, Conn SJ, Jordans C, Byrt CS, Hare RA, Tyerman SD, Tester M, Plett D, Gilliham M (2012) Wheat grain yield on saline soils is improved by an ancestral Na^+ transporter gene. Nat Biotechnol 30:360–364

Nakayama H, Yoshida K, Shinmyo A (2004) Yeast plasma membrane Ena1p ATPase alters alkali-cation homeostasis and confers increased salt tolerance in tobacco cultured cells. Biotechnol Bioeng 85:776–789

Negrão S, Courtois B, Ahmadi N, Abreu I, Saibo N, Oliveira M (2011) Recent updates on salinity stress in rice: from physiological to molecular responses. Crit Rev Plant Sci 30:329–377

Nevo E, Krugman T, Beiles A (1993) Short communication: genetic resources for salt tolerance in the wild progenitors of wheat (*Triticum dicoccoides*) and barley (*Hordeum spontaneum*) in Israel. Plant Breed 110:338–341

Obata T, Kitamoto HK, Nakamura A, Fukuda A, Tanaka Y (2007) Rice shaker potassium channel OsKAT1 confers tolerance to salinity stress on yeast and rice cells. Plant Physiol 144(4):1978–1985

Oh DH, Gong Q, Ulanov A, Zhang Q, Li Y, Ma W, Yun D-J, Bressan RA, Bohnert HJ (2007) Sodium stress in the halophyte *Thellungiella halophila* and transcriptional changes in a thsos1-RNA interference line. J Integr Plant Biol 49:1484–1496

Ohta M, Hayashi Y, Nakashima A, Hamada A, Tanaka A, Nakamura T, Hayakawa T (2002) Introduction of a Na^+/H^+ antiporter gene from *Atriplex gmelini* confers salt tolerance to rice. FEBS Lett 532:279–282

Omielan JA, Epstein E, Dvorak J (1991) Salt tolerance and ionic relations of wheat as affected by individual chromosomes of salttolerant *Lophopyrum elongatum*. Genome 34:961–974

Orsini F, D'Urzo MP, Inan G, Serra S, Oh DH, Mickelbart MV, Consiglio F, Li X, Jeong JC, Yun DJ, Bohnert HJ, Bressan RA, Maggio A (2010) A comparative study of salt tolerance parameters in 11 wild relatives of *Arabidopsis thaliana*. J Exp Bot 61:3787–3798

Ozgur R, Uzilday B, Sekmen AH, Turkan I (2013) Reactive oxygen species regulation and antioxidant defence in halophytes. Funct Plant Biol 40:8–9

Pang Q, Chen S, Dai S, Chen Y, Wang Y, Yan X (2010) Comparative proteomics of salt tolerance in *Arabidopsis thaliana* and *Thellungiella halophila*. J Proteome Res 9:2584–2599

Pardo JM, Cubero B, Leidi EO, Quintero FJ (2006) Alkali cation exchangers: roles in cellular homeostasis and stress tolerance. J Exp Bot 57:1181–1199

Patra B, Ray S, Richter A, Majumder AL (2010) Enhanced salt tolerance of transgenic tobacco plants by co-expression of PcINO1 and McIMT1 is accompanied by increased level of myo-inositol and methylated inositol. Protoplasma 245:143–152

Pedersen JT, Palmgren MB (2017) Why do plants lack sodium pumps and would they benefit from having one? Funct Plant Biol 44:473–479

Pedersen CN, Axelsen KB, Harper JF, Palmgren MG (2012) Evolution of plant P-type ATPases. Front Plant Sci 3:31

Peng Z, Wang M, Li F, Lv H, Li C, Xia G (2009) A proteomic study of the response to salinity and drought stress in an introgressions train of bread wheat. Mol Cell Proteomics 8:2676–2686

Pittman JK, Edmond C, Sunderland PA, Bray CM (2009) A cation-regulated and proton gradient-dependent cation transporter from *Chlamydomonas reinhardtii* has a role in calcium and sodium homeostasis. J Biol Chem 284:525–533

Polunin N (1960) Introduction to plant geography. McGraw-Hill Book Company Inc, New York

Poustini K, Siosemardeh A (2004) Ion distribution in wheat cultivars in response to salinity stress. Field Crops Res 85:125–133

Prashanth SR, Sadhasivam V, Parida A (2008) Overexpression of cytosolic copper/zinc superoxide dismutase from a mangrove plant *Avicennia marina* in indica rice var Pusa Basmati-1 confers abiotic stress tolerance. Transgenic Res 17:281–291

Prista C, Almagro A, Loureiro-Dias MC, Ramos J (1997) Physiological basis for the high salt tolerance of *Debaryomyces hansenii*. Appl Environ Microbiol 63:4005–4009

Qadir M, Quillerou E, Nangia V, Murtaza G, Singh M, Thomas RJ, Drechsel P, Noble AD (2014) Economics of salt-induced land degradation and restoration. Nat Resour Forum 38:282–295

Qiao WH, Zhao XY, Li W, Luo Y, Zhang XS (2007) Overexpression of AeNHX1, a root-specific vacuolar Na^+/H^+ antiporter from *Agropyron elongatum*, confers salt tolerance to Arabidopsis and Festuca plants. Plant Cell Rep 26:1663–1672

Quan R, Wang J, Hui J, Bai H, Lyu X, Zhu Y, Zhang H, Zhang Z, Li S, Huang R (2018) Improvement of salt tolerance using wild rice genes. Front Plant Sci 8:2269

Rauf M, Shahzad K, Ali R, Ahmad M, Habib I, Mansoor S, Berkowitz GA, Saeed NA (2014) Cloning and characterization of Na^+/H^+ antiporter (LfNHX1) gene from a halophyte grass *Leptochloa fusca* for drought and salt tolerance. Mol Biol Rep 41(3):1669–1682

Rhodes D, Nadolska-Orczyk A, Rich PJ (2002) Salinity, osmolytes and compatible solutes. In: Lauchli A, Luttge U (eds) Salinity: environment pbnt-molecuks. Kluwer, Dordrecht, pp 181–204

Roy SJ, Negrão S, Tester M (2014) Salt resistant crop plants. Curr Opin Biotechnol 26:115–124

Rozema J, Flowers TJ (2005) Crops for a salinized world. Science 322:1478

Rozema J, Zaheer S, Niazi B, Linders H, Broekman R (1993) Salt tolerance of *Beta vulgaris* L.: a comparison of the growth of seabeet and fodderbeet in response to salinity. In: Lieth H, Masoom A (eds) Towards the rational use of high salinity tolerant plants, V 2. Kluwer Academic, Dordrecht, pp 193–198

Sakai H, Ikawa H, Tanaka T, Numa H, Minami H, Fujisawa M, Shibata M, Kurita K, Kikuta A, Hamada M, Kanamori H, Namiki N, Wu J, Itoh T, Matsumoto T, Sasaki T (2011) Distinct evolutionary patterns of *Oryza glaberrima* deciphered by genome sequencing and comparative analysis. Plant J 66:796–805

Schachtman DP (2000) Molecular insights into the structure and function of plant K^+ transport mechanisms. Biochem Biophys Acta 1465:127–139

Schachtman DP, Bloom AJ, Dvorak J (1989) Salt-tolerant *Triticum*x-*Lophopyrum* derivatives limit the accumulation of sodium and chloride ions under saline stress. Plant Cell Environ 12:47–55

Sengupta S, Majumder AL (2009) Insight into the salt tolerance factors of a wild halophytic rice, *Porteresia coarctata*: a physiological and proteomic approach. Planta 229:911–929

Sengupta S, Patra B, Ray S, Majumder AL (2008) Inositol methyl transferase from a halophytic wild rice, *Porteresia coarctata*

Roxb. (Tateoka) regulation of pinitol synthesis under abiotic stress. Plant Cell Environ 31:1442–1459

Shabala S, Cuin TA (2007) Potassium transport and plant salt tolerance. Physiol Plant 133:651–669

Shabala S, Mackay A (2011) Ion transport in halophytes. Adv Bot Res 57:151–199

Shabala S, Pottosin I (2014) Regulation of potassium transport in plants under hostile conditions: implications for abiotic and biotic stress tolerance. Physiol Plant 151:257–279

Shabala S, Bose J, Hedrich R (2014) Salt bladders: do they matter? Trends Plant Sci 19:687–691

Shah SH, Gorham J, Forster BP, Wyn Jones RG (1987) Salt tolerance in the *Triticeae*: the contribution of the D-genome to cation selectivity in hexaploid wheat. J Exp Bot 38:254–269

Shannon MC (1978) Testing salt tolerance variability among tall wheatgrass lines. Agron J 10:719–722

Shao Q, Han N, Ding T, Zhou F, Wang B (2014) SsHKT1;1 is a potassium transporter of the C3 halophyte *Suaeda salsa* that is involved in salt tolerance. Funct Plant Biol 41:790–802

Shavrukov Y, Langridge P, Tester M, Nevo E (2010) Wide genetic diversity of salinity tolerance, sodium exclusion and growth in wild emmer wheat, *Triticum dicoccoides*. Breed Sci 60:426–435

Shen YG, Zhang WK, Yan DQ, Du BX, Zhang ZS, Liu Q, Chen SY (2003) Characterization of a DRE-binding transcription factorfrom a halophyte *Atriplex hortensis*. Theor Appl Gene 107:155–161

Sheveleva E, Chmara W, Bohnert HJ, Jensen J (1997) Increased salt and drought tolerance by D-Ononitol production in transgenic *Nicotiana tabacum* L. Plant Physiol 115:1211–1219

Shi H, Quintero F, Pardo J, Zhu JK (2002) The putative plasma membrane Na^+/H^+ antiporter SOS1 controls long-distance Na^+ transport in plants. Plant Cell 14:465–477

Singh N, Mishra A, Jha B (2014) Ectopic over-expression of peroxisomal ascorbate peroxidase (SbpAPX) gene confers salt stress tolerance in transgenic peanut (*Arachis hypogaea*). Gene 547:119–125

Singh D, Yadav NS, Tiwari V, Agarwal PK, Jha B (2016) A SNARE-Like superfamily protein SbSLSP from the halophyte *Salicornia brachiata* confers salt and drought tolerance by maintaining membrane stability, K(+)/Na(+) ratio, and antioxidant machinery. Front Plant Sci 7:737

Song J, Wang B (2015) Using euhalophytes to understand salt tolerance and to develop saline agriculture: *Suaeda salsa* as a promising model. Ann Bot 115:541–553

Taji T, Seki M, Satou M, Sakurai T, Kobayashi M, Ishiyama K, Narusaka Y, Narusaka M, Zhu JK, Shinozaki K (2004) Comparative genomics in salt tolerance between Arabidopsis and Arabidopsis related halophyte salt cress using Arabidopsis microarray. Plant Physiol 135:1697–1709

Tang X, Wang H, Shao C, Shao H (2015) Global gene expression of *Kosteletzkya virginica* seedlings responding to salt stress. PLoS ONE 10:e0124421

Tao JJ, Wei W, Pan WJ, Lu L, Li QT, Ma JB, Zhang WK, Ma B, Chen SY, Zhang JS (2018) An Alfin-like gene from *Atriplex hortensis* enhances salt and drought tolerance and abscisic acid response in transgenic Arabidopsis. Sci Rep 8(1):2707

Tester M, Davenport R (2003) Na^+ tolerance and Na^+ transport in higher plants. Ann Bot 91:503–527

Tiwari V, Chaturvedi AK, Mishra A, Jha B (2014) The transcriptional regulatory mechanism of the peroxisomal ascorbate peroxidase (pAPX) gene cloned from an extreme halophyte, *Salicornia brachiate*. Plant Cell Physiol 55:201–217

Tsugane K, Kobayashi K, Niwa Y, Ohba Y, Wada K, Kobayashi H (1999) A recessive Arabidopsis mutant that grows photoautotrophically under salt stress shows enhanced active oxygen detoxification. Plant Cell 11:1195–1206

Tsukagoshi H, Suzuki T, Nishikawa K, Agarie S, Ishiguro S, Higashiyama T (2015) RNA-seq analysis of the response of the halophyte, *Mesembryanthemum crystallinum* (ice plant) to high salinity. PLoS ONE 10:e0118339

Udawat P, Jha RK, Sinha D, Mishra A, Jha B (2016) Overexpression of a cytosolic abiotic stress responsive universal stress protein (SbUSP) mitigates salt and osmotic stress in transgenic tobacco plants. Front Plant Sci 7:518

Udawat P, Jha RK, Mishra A, Jha B (2017) Overexpression of a plasma membrane-localized SbSRP-like protein enhances salinity and osmotic stress tolerance in transgenic tobacco. Front. Plant Sci 8:582

Von Bothmer R, Jacobsen N, Baden C, Jørgensen RB, Linde-Laursen I (1995) An ecogeographical study of the genus *Hordeum*, 2nd edn. International Plant Genetic Resources Institute, Rome, pp 1–127

Wang MC, Peng ZY, Li CL, Li F, Liu C, Xia GM (2008) Proteomic analysis on a high salt tolerance introgressions train of *Triticum aestivum*/T*hinopyrum ponticum*. Proteomics 8:1470–1489

Wang YC, Qu GZ, Li HY, Wu YJ, Wang C, Liu GF, Yang CP (2010) Enhanced salt tolerance of transgenic poplar plants expressing a manganese superoxide dismutase from *Tamarix androssowii*. Mol Biol Rep 37:1119–1124

Wang YY, Hsu PK, Tsay YF (2012) Uptake, allocation and signaling of nitrate. Trends Plant Sci 17:458–467

Wang J, Li B, Meng Y, Ma X, Lai Y, Si E, Yang K, Ren P, Shang X, Wang H (2015a) Transcriptomic profiling of the salt-stress response in the halophyte *Halogeton glomeratus*. BMC Genomics 16:169

Wang S, Su SZ, Wu Y, Li SP, Shan XH, Liu HK, Wang S, Yuan YP (2015b) Overexpression of maize chloride channel gene *ZmCLC*-d in *Arabidopsis thaliana* improved its stress resistance. Biol Plant 59:55–64

Weimberg R, Shannon MC (1988) Vigor and salt tolerance in 3 lines of tall wheatgrass. Physiol Plant 73:232–237

Wu C, Gao X, Kong X, Zhao Y, Zhang H (2009) Molecular cloning and functional analysis of a Na^+/H^+ antiporter gene ThNHX1 from a halophytic plant *Thellungiella halophile*. Plant Mol Biol Rep 27:1

Xia GM, Xiang FN, Zhou AF, Wang H, He SX, Chen HM (2003) Asymmetric somatic hybridization between wheat (*Triticum aestivum* L.) and *Agropyron elongatum* (Host) Nevski. Theor Appl Genet 107:299–305

Xu X, Monneveux P, Damania AB, Zahavieva M (1993) Evaluation of salt tolerance in genetic resoures of *Triticum* and *Aegilops* species. Plant Genet Resour News Lett 96:11–16

Xu XJ, Zhou YJ, Ren DT, Ren HH, Bu JC, Feng GY (2014) Cloning and characterization of gene encoding a Mn-containing superoxide dismutase in *Eutrema halophilum*. Biol Plant 58:105–113

Yadav NS, Shukla PS, Jha A, Agarwal PK, Jha B (2012) The SbSOS1 gene from the extreme halophyte *Salicornia brachiata* enhances Na(+) loading in xylem and confers salt tolerance in transgenic tobacco. BMC Plant Biol 12:188

Yadav NS, Singh VK, Singh D, Jha B (2014) A novel gene SbSI-2 encoding nuclear protein from a halophyte confers abiotic stress tolerance in *E coli* and tobacco. PLoS ONE. 9(7):e101926

Yamamoto N, Takano T, Tanaka K, Ishige T, Terashima S, Endo C, Kurusu T, Yajima S, Yano K, Tada Y (2015) Comprehensive analysis of transcriptome response to salinity stress in the halophytic turf grass *Sporobolus virginicus*. Front Plant Sci 6:241

Yang X, Hu YX, Li XL, Yu XD, Li QL (2014) Molecular characterization and function analysis of SlNAC2 in *Suaeda liaotungensis* K. Gene 543:190–197

Yao M, Zeng Y, Liu L, Huang Y, Zhao E, Zhang F (2012) Overexpression of the halophyte *Kalidium foliatum* H^+-pyrophosphatase gene confers salt and drought tolerance in *Arabidopsis thaliana*. Mol Biol Rep 39:7989–7996

Zhang GH, Su Q, An LJ, Wu S (2008) Characterization and expression of a vacuolar Na(+)/H(+) antiporter gene from the monocot halophyte *Aeluropus littoralis*. Plant Physiol Biochem 46:117–126

Zhang Y, Li Y, Lai J, Zhang H, Liu Y, Liang L, Xie Q (2012) Ectopic expression of a LEA protein gene *TsLEA1* from *Thellungiella salsuginea* confers salt-tolerance in yeast and Arabidopsis. Mol Biol Rep 39:4627–4633

Zhang LQ, Niu YD, Huridu H, Hao JF, Qi Z, Hasi A (2014) *Salicornia europaea* L. Na^+/H^+ antiporter gene improves salt tolerance in transgenic alfalfa (*Medicago sativa* L.). Gen Mol Res 13:5350–5360

Zhao F, Guo S, Zhang H, Zhao Y (2006a) Expression of yeast SOD2 in transgenic rice results in increased salt tolerance. Plant Sci 170:216–224

Zhao FY, Zhang XJ, Li PH, Zhao Y-X, Zhang H (2006b) Co-expression of the *Suaeda salsa SsNHX1* and Arabidopsis *AVP1* confer greater salt tolerance to transgenic rice than the single SsNHX1. Mol Breed 7:341

Zhou S, Chen X, Zhang X, Li Y (2008) Improved salt tolerance in tobacco plants by co-transformation of a betaine synthesis gene BADH and a vacuolar Na^+/H^+ antiporter gene SeNHX1. Biotechnol Lett 30:369–376

Zou C, Chen A, Xiao L, Muller HM, Ache P, Haberer G, Zhang M, Jia W, Deng P, Huang R, Lang D, Li F, Zhan D, Wu X, Zhang H, Bohm J, Liu R, Shabala S, Hedrich R, Zhu JK, Zhang H (2017) A high-quality genome assembly of quinoa provides insights into the molecular basis of salt bladder-based salinity tolerance and the exceptional nutritional value. Cell Res 27:1327–1340