

REVIEW ARTICLE

Salinity and crop yield

C. Zörb^{1,*} , C.-M. Geilfus^{2,*} & K.-J. Dietz^{3,*}

¹ Institute of Crop Science, University of Hohenheim, Stuttgart, Germany

² Albrecht Daniel Thaer-Institute of Agricultural and Horticultural Sciences, Division of Controlled Environment Horticulture, Humboldt Universität Berlin, Berlin, Germany

³ Biochemistry and Physiology of Plants, Universität Bielefeld, Bielefeld, Germany

Keywords

crop plant; ROS; salinity; yield.

Correspondence

C. Zörb, Institute of Crop Science, University of Hohenheim, 340e, Schloss Westflügel, 70593 Stuttgart, Germany.

E-mail: christian.zoerb@uni-hohenheim.de

*All authors contributed equally.

Editor

A. Weber

Received: 14 May 2018; Accepted: 27 July 2018

doi:10.1111/plb.12884

ABSTRACT

Thirty crop species provide 90% of our food, most of which display severe yield losses under moderate salinity. Securing and augmenting agricultural yield in times of global warming and population increase is urgent and should, aside from ameliorating saline soils, include attempts to increase crop plant salt tolerance. This short review provides an overview of the processes that limit growth and yield in saline conditions. Yield is reduced if soil salinity surpasses crop-specific thresholds, with cotton, barley and sugar beet being highly tolerant, while sweet potato, wheat and maize display high sensitivity. Apart from Na^+ , also Cl^- , Mg^{2+} , SO_4^{2-} or HCO_3^- contribute to salt toxicity. The inhibition of biochemical or physiological processes cause imbalance in metabolism and cell signalling and enhance the production of reactive oxygen species interfering with cell redox and energy state. Plant development and root patterning is disturbed, and this response depends on redox and reactive oxygen species signalling, calcium and plant hormones. The interlink of the physiological understanding of tolerance processes from molecular processes as well as the agronomical techniques for stabilizing growth and yield and their interlinks might help improving our crops for future demand and will provide improvement for cultivating crops in saline environment.

INTRODUCTION

Plants for agriculture have been evolved and cultivated on arable land and, therefore, most of our crop plants are salt-sensitive. These crop plants were referred to be ‘glycophytes’ in comparison to halophytes which have the ability to complete their life cycle in a salt ion-rich environment where almost 99% of salt sensitive species die because of salt toxicity (Panta *et al.* 2014). Salinity is one of the most decisive environmental factors limiting the productivity of crop plants especially in arid and semi-arid regions. Water scarcity and inadequate drainage of irrigated lands severely reduce growth and productivity of crops, which has negative economic, environmental and social impacts (Pannell 2001; Munns & Gilliham 2015). Salt accumulation in soil solution reduces water and nutrient uptake. This leads to osmotic stress, ion toxicity, nutrient imbalances and water-deficit. Excessive concentrations of salt ions also injure photosynthetically active leaves, and may lead to chlorosis and early leaf senescence (Hanin *et al.* 2016).

At present about 30 crop plant species provide 90% of plant-based human food. Under conditions of moderate salinity ($\text{EC } 4\text{--}8 \text{ dS m}^{-1}$), all important glycophytic crops reduce average yields by 50–80% (Panta *et al.* 2014). Problems associated to soil salinity are anticipated to worsen in many regions because of the changing climate. A wide range of adaptations and mitigation strategies are required to cope with such impacts (Shrivastava & Kumar 2014). The world’s human population is expected to reach 9.1 billion by 2050, and global food

production will need to increase by about 70% to match this population growth by this time (FAO 2011, Panta *et al.* 2014). For improving crop performance under saline conditions, it is of utmost importance to identify the physiological, biochemical, molecular, and genetic basis of salt tolerance. This review provides an overview of the processes that limit growth and yield in saline conditions. This review aims to provide a balanced introduction to this important topic. The reader is referred to other reviews for comprehensive coverage (Miller *et al.* 2010; Hanin *et al.* 2016; Liang *et al.* 2018).

SALINITY INDUCES DECLINE OF BIOMASS AND YIELD LOSSES

Crop plants generate high yields and produce high quality of grain, fibre, as well as high sugar, oil, or protein content if the growth requirements are properly matched, e.g. adequate management during the growth season, and nutrient- and water management, as well as light and temperature must fit to their optimum growth requirements. Yield-associated traits are inversely related to abiotic stress conditions such as salt or drought during plant development. If salt stress reduces growth in an early phase of plant development, the yield strongly declines and plant products will be compromised in quality and quantity. It is important to note that salinity can cause crop yield losses even though the effects of salinity may not be obvious. Both salt tolerance and sensitivity of a specific crop depend on its ability to extract water and nutrients from saline

soils and to avoid excessive tissue accumulation of salt ions (Ahmad *et al.* 2017; Khan *et al.* 2017; Kaleem *et al.* 2018)

The majority of vegetable crops is highly salt sensitive. In the model of Maas & Hoffman (1977), relative crop yield is not affected until a salinity threshold (EC_t) is exceeded, according to the following equation: $Y = 100 - S (EC_e - EC_t)$, where Y is the relative crop yield with 100 being the maximum yield, EC_e is the salinity of saturated soil extract, and EC_t ($dS\ m^{-1}$) is the threshold defined as the value of the electrical conductivity (EC) that is expected to cause the initial significant reduction in the maximum expected yield, and S is the slope that represents the percentage of yield expected to be reduced for each unit of added salinity above the EC_t . Salt crop tolerance is rated by salinity threshold (EC_t) and the percent of reduction of relative yield per unit increase in soil salinity above the threshold (S).

Na^+ and Cl^- at high amounts are toxic to plants, especially if they increase in the cytosol. Despite this relevance, not much is known about cytosolic processes that are impaired by excessive concentrations of salt ions. For instance, toxicity effects of chloride in the cytosol remain to be elucidated (Geilfus 2018a). Plants that are exposed to excessive concentrations of salt ions are poisoned and eventually die. The ion-toxicities have diverse consequences resulting in ionic imbalance *i.e.* in terms of uptake competition of Na^+ with K^+ , Ca^{2+} and Mg^{2+} and may accelerate senescence of transpiring leaves, not only because of toxic concentrations of deleterious ions in photosynthetic active tissues but also reduced availability of the beneficial nutrients. The energy gain of a crop under salinity stress is schematized in Fig. 1. At any given time, a finite amount of energy and resources that can be harvested by the plant through photosynthesis or metabolically utilized (Munns & Gilliham 2015). Under non-stressed conditions, plants use the majority of the energy in processes necessary for maintenance and vegetative and generative growth. However, resource allocation changes with increasing levels of salinity as increasing resources are invested in the mitigation of stress (Fig. 1).

Salinity-induced yield losses have high economic impacts on agriculture and other bio-based-industries. The estimated economic impact of soil salinity on irrigated land has been extrapolated to surpass 27 billion US\$ per year (Qadir *et al.* 2014). Actually, many agricultural areas are running at risk of zero yields in some years. Once degraded by salts, agricultural utilization of that land is almost impossible (Qadir *et al.* 2006).

An area of $6 \cdot 10^9$ ha out of total $14 \cdot 10^9$ ha of agricultural land available in the world, is arid or semi-arid and 10^8 ha are affected by excessive salt concentrations (Christiansen 1982). In former studies, crop yield was estimated for various degrees of soil salinity. Moderate soil salinity in the range of 8 to $10\ dS\ m^{-1}$ results in yield losses of 55%, 28%, and 15% in corn, wheat and cotton, respectively. A high soil salinity of $18\ dS\ m^{-1}$ resulted in a 55% yield loss in cotton (Satir & Berberoglu 2016). An assessment of dryland areas indicated that 5.7 Mha of cropland and pastureland are affected by or are at risk of developing dryland salinity from shallow water tables [National Land and Water Resources Audit (NLWRA), 2001]. This area could increase to 17 Mha by 2050 unless effective strategies are implemented (Scanlon *et al.* 2007). In the next section the focus lies on vegetables and fleshy fruits which were less referred to in literature and their somehow specific problems under saline field conditions.

SALINITY TOLERANCE OF VEGETABLE CROPS AND FLESHY FRUITS

The majority of vegetable crops have a very low salinity threshold that is $2.5\ dS\ m^{-1}$ (Snapp *et al.* 1991). Thus, the area of soils with restrictions for vegetable crop production is therefore greater than the area that is defined as 'salinized', since a saline soil is generally defined as showing an EC value of the saturation extract (EC_e) in the root zone that exceeds $4\ dS\ m^{-1}$ (approximately 40 mM NaCl) at 25 °C and having an exchangeable Na^+ level of 15% (Shrivastava & Kumar 2014). The performance of sensitive and tolerant crops in dependence of soil salinity can be summarized in a simplified scheme as shown in Fig. 1B.

The salt sensitivity changes during the various plant growth stages. Often plants at early growth stages (seedling, establishment) are more sensitive to salt stress than plants at later stages. During germination and emergence, determination of tolerance is based on percent survival, while during later developmental stages, tolerance is usually measured as relative growth (Läuchli & Grattan 2007). For instance, salinity affected cauliflower growth mainly when imposed in the first growth phase (Giuffrida *et al.* 2016). The EC of irrigation water also affects salt tolerance (Grattan 2002). The lowest threshold level of irrigation water not restricting crop growth was $0.7\ dS\ m^{-1}$. The majority of vegetable crops show low tolerance to saline irrigation water when applied continuously. In the study of Machado and Serralheiro (2017), asparagus has been considered the most salt-tolerant vegetable crop. For main crops such as wheat or maize there is a 10% yield decrease at soil extract salinity (EC_e) of 2.5 or $7.2\ dS\ m^{-1}$; and a yield decrease of 50% occurs at EC_e levels of 5.5 or $13\ dS\ m^{-1}$ (for more details refer to the review of Panta *et al.* 2014). The next section focuses to physiological ion adjustments of some examples of grain crops and their mechanisms to withstand salt stress.

PERTURBATION OF CELLULAR ION HOMEOSTASIS

Under non-saline conditions, nutrient ion net fluxes in crops such as maize, wheat, barley and broad bean are adjusted according to developmental and cellular requirements, thus establishing an ion homeostasis (Niu *et al.* 1995; Fig 2). However, ion homeostasis can be disturbed under conditions of salinity when excessive amounts of salt ions (e.g. Na^+ and Cl^- or Mg^{2+} and SO_4^{2-}) accumulate in the soil solution. Excessive increases of the cation Na^+ disturb uptake of cationic nutrients such as K^+ (Wakeel *et al.* 2011; Zörb *et al.* 2014) or Ca^{2+} (Ehret *et al.* 1990; Gardner 2016) leading to nutrient imbalances. For example, Na^+ -induced Ca^{2+} deficiency symptoms comprise lesions and reduced dry weights of leaf blades (Maas & Grieve 1977). A Na^+ -induced reduction in the K^+ uptake reduced shoot growth (Zörb *et al.* 2014). Excessive concentrations of Cl^- can also impair nutrient uptake by affecting uptake of anions (Geilfus 2018b). Antagonistic anion-anion uptake interactions are thought to be meaningful as the Cl^- concentration in the soil solution can be rather high under conditions of NaCl-salinity. Cl^- is greatly mobile in the soil as the negative charges of kaolin and other clay minerals repel Cl^- , causing it to accumulate in the soil solution or macropores (Thomas & Swoboda 1970) whereas cations such as Na^+ are weakly adsorbed by the negative surface charges (Borggaard 1984). An

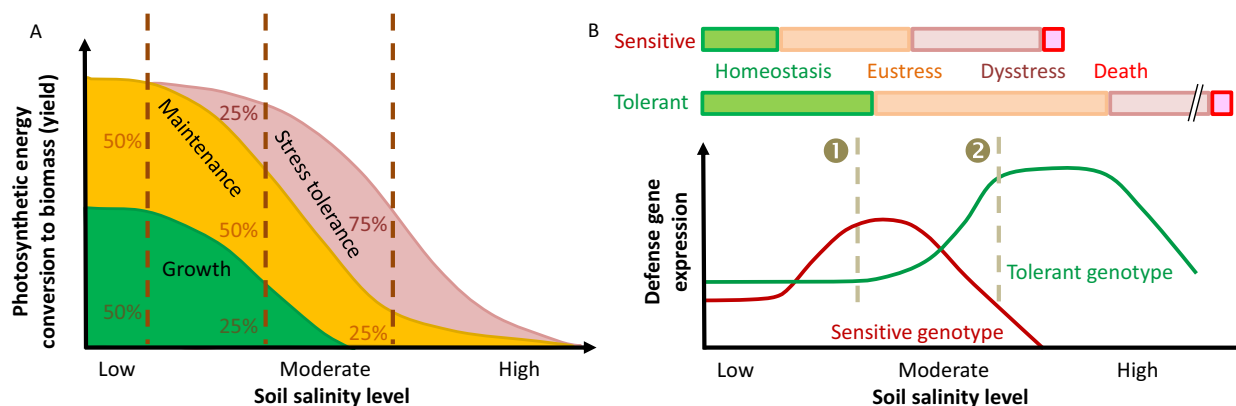


Fig. 1. Schematic of energy gain and energy use by a crop plant and performance of crops under salinity stress. (A) The proportion of energy used for maintenance, growth and stress defense is portrayed. The relative proportions will change depending on the developmental stage of the plant and exposure to salt stress – maintenance costs will be greater when plants are larger. Total energy gain will decrease with greater salinity by decreasing photosynthetic rate following induced closure of stomata and damage to cellular and photosynthetic machinery. Stress tolerance mechanisms represent additional costs to the plant required to deal with the salt load in the soil (for example, but not limited to, greater costs in ion exclusion or compartmentation, maintaining ion homeostasis and reactive oxygen species (ROS) detoxification). At high salinity there will be zero growth, as the total costs to the plant equal energy gain; when costs exceed energy gained, then tissue will senesce. Source; adapted from a concept by A. H. Millar and H. Lambers, based on data and reasoning of Amthor (2000) and Van der Werf *et al.* (1988) Munns & Gilliam (2015). (B) Response of a sensitive and a tolerant crop to soil salinity. Both crop types display response to salinity which can be grouped in phases: homeostasis maintains high growth rate, eustress elicits defense gene expression and dysstress causes stagnation and death. The salinity range is narrow in sensitive crops and broad in tolerant ones. The induction of defense in sensitive crops occurs early, with less magnitude.

antagonism between Cl^- and nitrate (NO_3^-) uptake was reported when the external Cl^- concentrations was very high (Cerezo *et al.* 1999; Abdelgadir *et al.* 2005) and this can reduce growth and yield in wheat (Hu & Schmidhalter 1998), whereas this could not be confirmed in maize (Hütsch *et al.* 2016). Anion-anion uptake competitions were also described between Cl^- and phosphate (PO_4^{3-}). Studies on tomato (Papadopoulos & Rendig 1983) and roses (Massa *et al.* 2009) substantiate the existence of a specific competitive inhibition of PO_4^{3-} uptake by Cl^- , while such an effect was not observed in melon (Navarro *et al.* 2001). Even less is known about a competition between Cl^- and sulphate (SO_4^{2-}), which might exist in pea (Mor & Manchanda 1992). It appears that Cl^- may hamper growth under NaCl-salinity by imposing phosphorous and sulfur deficiency through inhibited uptake of PO_4^{3-} and SO_4^{2-} , however generalizable conclusions cannot be easily drawn from the published data. For the conclusiveness of such studies it is important to distinguish between the effects of Cl^- and those of the counter-cation. Experiments with membrane-impermeable counter-cations of the particular salt are needed. Moreover, the molecular mechanism underlying the antagonistic nutrient-nutrient uptake effects is not very well studied. It might be possible that the antagonism is based on a specific competition for a binding site at the PO_4^{3-} or SO_4^{2-} transport proteins. Another school of thought considers that Cl^- is leaking through these protein pores, quantitatively displacing PO_4^{3-} or SO_4^{2-} from being taken up. Both scenarios are based on physicochemical attributes of the transmembrane pores (e.g. their charge and size). For example, the radius of hydrated Cl^- ion is very similar to that of SO_4^{2-} (Table 1). It seems that during evolution and breeding, most of our 'glycophytic' crops never encountered a need to avoid excessive uptake of Na^+ or Cl^- , thus never developed selectivity mechanisms at the transporter site to discriminate the required nutrient against

unwanted salt ion (e.g. Cl^-). This might be due to the fact that most glycophytic crops originated and were domesticated in non-saline habitats (Cheeseman 2015), with the exception of e.g. sugar beet which has halophytic ancestors (Rozema *et al.* 2015).

Presently there appears to be a lack of knowledge on Cl^- , in particular concerning the way how high Cl^- tissue concentrations cause physiological dysfunctions and how (ii) Cl^- stress events are sensed and used to trigger responses that adjust the metabolism to resist Cl^- -toxicities. Many aspects of Cl^- transport and distribution still await clarification, while a bulk of research into Na^+ influx- and efflux-relations has led to a significant understanding of the underlying transmembrane Na^+ transport processes. In contrast, many molecular and electrophysiological properties of transmembrane proteins that mediate Cl^- fluxes (under Cl^- stress) have yet to be elucidated.

PHYSIOLOGY OF YIELD LOSSES

Salinity stress is often dominated by the presence of NaCl, while other ions also contribute to the stress level. The toxicity effects vary among different ions and ion combinations (Kaiser *et al.* 1988; Hawkins & Lewis 1993). At low salinity levels, transport of the salt ions into the vacuole copes with the ion flux across the plasma membrane into the cell (Blumwald *et al.* 2000). At higher influx rates, cellular ion homeostasis is compromised and anions such as Cl^- , SO_4^{2-} or PO_4^{3-} and cations such as Na^+ and sometimes Mg^{2+} or even Ca^{2+} accumulate in the plasmatic compartments of the cell, i.e. in the cytosol, matrix and stroma, rather than in the vacuole. Also critical is the ion accumulation in the apoplast which occurs e.g. in leaves if the leaf cells fail to drain ions from the apoplast to the symplast. Apoplastic accumulation of ions has been identified as causal mechanism of salinity induced leaf necrosis in pea

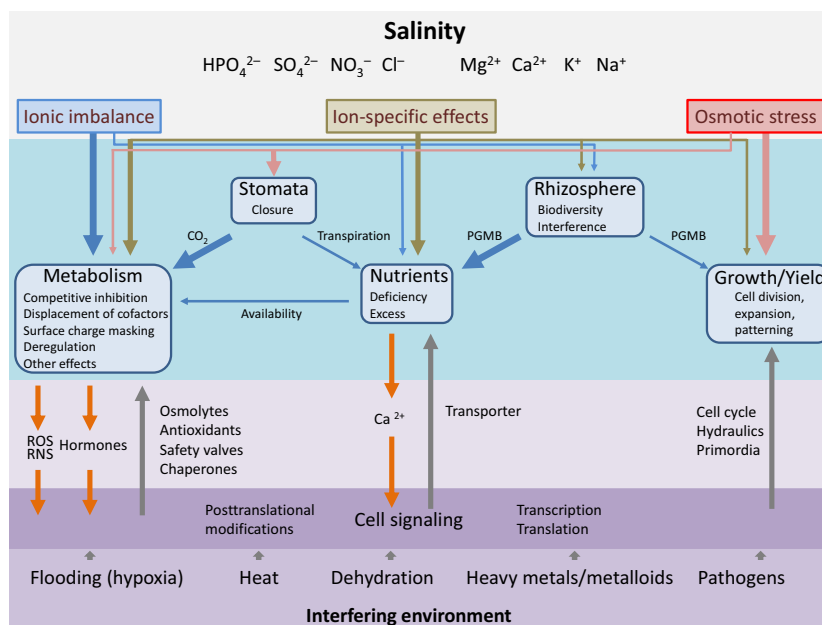


Fig. 2. Interaction network of salinity stress with cellular processes. Excessive concentrations of several salts present in the rooting medium may cause toxicity symptoms. Both divalent and monovalent anions and cations contribute to salinity effects and display distinct toxicity intensity as given as tentative order from left to right. Ions entering the plant organs in excess interfere with ion balance, exert ion-specific effects and establish osmotic stress. The lines and their thickness illustrate how these stress components distinctly affect metabolism, stomatal function, nutrient homeostasis, processes in the rhizosphere and growth and yield. Changes in these processes interfere with each other, initiate cell signaling and affect transcription, translation and posttranslational state which in the case of eustress allows for activation of tolerance mechanisms and readjustment of homeostasis or in the case of dystress is insufficient or even promotes cellular disequilibria and cell death. Other stresses such as flooding, temperature changes and light interfere with the salinity stress network and response.

Table 1. Ion radii of salt ions.

ion	ion radius [nm]	
	not hydrated	hydrated
Na ⁺	0.098	0.360–0.386
K ⁺	0.133	0.301–0.315
Ca ²⁺	0.106	0.348
Cl [−]	0.181	0.270–0.291
SO ₄ ^{2−}	0.147	0.300

Source: Taken from Tanganov (2013), Baldanov et al. (2006), Moelwyn-Hughes (1962)

(Speer & Kaiser 1991). Salt accumulation in the leaf apoplast disturbs cellular water relations causing wilting (Flowers *et al.* 1991).

Inorganic ions often act as competitive inhibitors of enzymes that receive ionic substrates, but also interfere with protein surface charges and destabilize molecular interactions. Na⁺ displaces K⁺ from essential binding sites. The two best-known examples for K⁺ dependency in biochemistry are pyruvate kinase and ribosomes. Pyruvate kinase activity (V_{\max}) increases 400-fold in the presence of K⁺ (Oria-Hernández *et al.* 2005) and replacement of K⁺ by Na⁺ leads up to 92% inhibition (Kayne 1971). The peptidyl transferase activity of eukaryotic ribosomes depends on high K⁺ concentration reaching then a turnover of 20 s^{−1} (Ioannou & Coutsoegeorgopoulos 1997). If the K⁺-concentration drops and Na⁺ concentration increases, such inhibitory processes cause metabolic imbalances, including redox and energy metabolism.

In leaves of sensitive plants, photosynthesis is inhibited. Photosynthetic electron transport turns over-reduced in the light and reactive oxygen species (ROS) are released (Miller *et al.* 2010). Likewise mitochondrial respiration is perturbed which enhances ROS production in respiratory electron transport (Jacoby *et al.* 2010). In addition, rates of photorespiration increase if stomata close and intracellular CO₂ concentration drops. Enhanced photorespiration produces an additional load of ROS (Voss *et al.* 2013). It is also very likely that salt ions accumulate in mitochondria and chloroplasts disturbing electron flow and causing electrons to leak to molecular oxygen, thereby triggering O₂[−] production. Apart from loss of ionic homeostasis, the rise in osmotic potential and salts interferes with specific processes like cell expansion, stomata development and stomatal movement (Kumari *et al.* 2014; Chen *et al.* 2015; Zörb *et al.* 2015; Geilfus *et al.* 2017) (Fig. 1).

Widely used biochemical markers of abiotic stress including salinity are ROS, lipid peroxidation products, carbonylated proteins and enhanced ion leakage (Dietz 2010). On the other hand, salinity tolerance usually correlates with high amounts of compatible solutes, high activity of antioxidant enzymes and efficient compartmentation as shown in a large set of studies (Munns & Tester 2008). For instance, superoxide dismutase and glutathione reductase activities increased in a NaCl-tolerant cotton cultivar Pora, while being unchanged in the sensitive cultivar Guazuncho (Meloni *et al.* 2003).

The correlation between tolerance on the one hand and increased activities of antioxidant enzymes and repair mechanisms on the other hand is not straight forward, because it highly depends on the salinity dose and exposure time (Fig. 1B)

or on the circadian rhythm. At lower stress intensity, tolerant species maintain homeostasis e.g. by efficient compartmentation and nutrient uptake and do not up-regulate defense mechanisms, while sensitive species may already encounter disturbance of homeostasis and activate general defense responses. However, as a rule of thumb, tolerant species often specifically tune their antioxidant system. Thus in the rather salt-sensitive pea, successful long-term acclimation to salinity correlates with enhanced antioxidant defense (Hernandez *et al.* 2000). Likewise, in sugar beet, exposure to salt induces upregulation of antioxidant enzymes such as superoxide dismutase, alternative oxidase and plastid terminal oxidases, while NADPH oxidase transcripts decrease leading to the peculiar state of less ROS production in salt exposed tissue than in control plants (Hossain *et al.* 2017).

Efficient ion distribution and compartmentation at the sub-cellular, cellular, tissue, and organ level is also important to protect growing meristems and cambia from excessive and thus inhibitory accumulation of ions and to decrease ion deposition in photosynthetically active or harvested tissues in crop plants (Blumwald *et al.* 2000). Thus Na⁺-unloading of the xylem vessels by AtHKT1 decreases the Na⁺ content of the xylem sap and leaves, and thereby contribute to protects shoots (Sunarpi Horie *et al.* 2005). The genome-encoded sets of ion transporters involved in these processes essentially are known for many crops, but further scrutiny is needed in many cases to establish the biochemical specificity of transported ion species, the subcellular localization, the activity regulation, the transport direction and the cell-specific expression under optimal as well as stress conditions (Yamaguchi *et al.* 2013). All these data show that salt ion transport, compartmentation and recycling, and efficient nutrient acquisition are of prime importance for salinity tolerance, but that in addition a strong antioxidant defense and repair systems support growth performance on saline soil. For a more detailed description of involved gene expression and its regulation under saline conditions, other stress markers and metabolic implications, the reader is referred to other reviews, e.g. by Panta *et al.* (2014), Munns & Tester (2008), Munns & Gilliam (2015), Yang & Guo (2018), Li *et al.* (2017), and Liang *et al.* (2018).

SIGNALING AND CONTRIBUTION OF PLANT HORMONES

Salinity without mentioning signalling and hormones would be indefensible. However, only a few recent insights are highlighted here. The discovery of the salt overly sensitive (SOS) signalling pathway in a seedling-based screening for Na⁺-sensitive *Arabidopsis thaliana* mutants in 1997 (Liu & Zhu 1997; Zhu *et al.* 1998) marked the beginning of a deep mechanistic dissection of cellular signalling processes involved in salt acclimation. The Ca²⁺ sensor SOS3/CBL4 binds Ca²⁺ which then interacts with the protein kinase SOS2/CIPK24 and this protein complex activates the Na⁺ antiporter SOS1 for export of Na⁺ from the cytosol. Many other signalling compounds and signalling elements have been described since then. Thus Ca²⁺ plays a central role in counteracting salinity toxicity, and the SOS pathway has been expanded to an intricate network for ion homeostasis (Köster *et al.* 2018); the reader is referred to this excellent review to get insight into this Ca²⁺-dependent

signalling network which constitutes a core element in plant salinity responses.

Apart from halophytes with constitutive expression of the tolerance genes, most species including crops activate the tolerance mechanisms only upon exposure to the particular stress. The activation of the tolerance program leads to salinity acclimation and involves altered physiological responses, redirection of metabolism, reinforcement of defense and repair, and changes in developmental programs to adapt morphological and anatomical features. Such a profound reorganization implicates different signals and regulation pathways. A large set of studies in particular with *Arabidopsis* mutants and using transcript profiling has assigned essential roles of all plant hormones in the acclimation process, growth and organ patterning under salinity. Only a few recent insights can be highlighted here.

One focus of recent research addressed root patterning. The root endodermis has been recognized as a sensory tissue integrating ABA as inhibitory signal and the antagonizing gibberellic acid signal. ABA represses lateral root formation in soil regions with high salinity (Duan *et al.* 2013). Moreover, root endodermis acts as a guard, involving abscisic acid, to prevent the plant from growing into salt pools (Geng *et al.* 2013). Additional components in ABA signalling have been recognized which control the positive regulator of the ABA response, the transcription factor ABI5 (ABSCISIC ACID INSENSITIVE 1). SDIR1 (SALT- AND DROUGHT-INDUCED RING FINGER1) causes ubiquitination and destabilization of its target protein SDIRIP1 (SDIR1-INTERACTING PROTEIN 1) which is needed to activate ABI5 expression and salt acclimation (Zhang *et al.* 2015). Root elongation is inhibited in saline soil. Nitric oxide mediates the inhibition of root meristem growth by downregulation of PINFORMED genes involved in directed auxin delivery to the growing root tip (Liu *et al.* 2015). The participation of brassinosteroids in proteostasis under salinity (Cui *et al.* 2012), salicylic acid and ethylene in tuning ion uptake, antioxidant defense and concomitant gene expression (Jayakannan *et al.* 2015; Zhang *et al.* 2015) are other examples highlighting the important roles of hormones in shaping the plant response to salinity.

IMPROVEMENT OF CROPS IN THE LAST DECADE

For crop production, tolerance ultimately means higher yields. As a result, although experiments with seedlings, hydroponics or greenhouse experiments reveal mechanisms, they unfortunately do not allow a proof of concept to be derived for crop performance in the field. Such attempts across the scale levels are rare, and even impossible to apply at the field level in Europe if genetically modified crops are involved. It is surprising that, in spite of the complexity of salt tolerance, there are commonly claims in the literature that the transfer of a single or a few genes can increase the tolerance of plants to saline conditions (for review see: Parmar *et al.* 2017). In a review of the former decade, examples of genetically improved crops were evaluated with information available for only 19 reports including quantitative estimates of plant growth. The author concluded that such experiments may provide insights into components of tolerance, but are not grounds for claims of enhanced tolerance at the whole plant level (Flowers 2004).

In general, many breeding technologies are used to stabilize crop yields during salinity (Tester & Langridge 2010). Crossing of a gene for Na⁺ exclusion (*Nax2*) from the wheat relative *Triticum monococcum* into durum wheat (*Triticum durum*) reduced its leaf Na⁺ concentration by removing it from the xylem (James *et al.* 2006). Field trials on saline soils that overexpress *TmHKT1;5-A*, which is a gene in the *Nax2* locus, reduces leaf Na⁺ concentration and increases durum wheat grain yield (Munns *et al.* 2012). Unfortunately, we were not able to find many recent examples of success in increasing salt tolerance of genetically modified crops verified in field trials. A major problem in efforts to engineer salt-tolerant crops is that many screening experiments focus on the salt stress performance of the candidate plant during a very limited time, often during the vegetative period (e.g. stressing and evaluating plants during germination or within the first weeks during the vegetative phase). However, what is needed are screening approaches that estimate performance during both the vegetative phase and the reproductive stage, as it was done for the salt tolerant rice variety BRRI Dhan 10 (Islam *et al.* 2008). Ismail & Horie (2017) that summarizes progress in breeding approaches for improving salt tolerance in rice, wheat and barley refer the reader to the recent review.

PERSPECTIVES AND TRENDS

The severity of salinity stress depends on additional environmental factors such as, water availability or thermal stress which recently moved into the focus of systems research. This concerns the complexity of the organismic interactions in the rhizosphere and combinatorial stress situations, many

of which have not been scrutinized yet in controlled laboratory experiments. Salinity toxicity strongly depends on the pH environment in the soil, thus alkali stress has more severe effects on germination, growth and photosynthesis (Li *et al.* 2010). Flooding-induced hypoxia and salinity can occur as combined stress. Breeding efforts for salt-tolerant rice demonstrate that it is worthwhile to introduce salt tolerance landraces that are traditionally used by local farmers in coastal saline areas into breeding programs, as they enrich the genetic diversity of our modern high yield crops with novel genes and alleles for salt tolerance (Ismail & Horie 2017). The use of halophytes as valuable cash crops or the development of crops from halophytes might be an additional option (Flowers & Muscolo 2015). Eating halophytes such as *Atriplex triangulata*, or *Salicornia bigelovii* served as salad or vegetable might contribute to the future strategies to meet the higher demand of plant-based food (Rozema & Schats 2013; Panta *et al.* 2014). The physiological complexity of the salinity syndrome and the underlying polygenic tolerance mechanisms imply that while some improvement in yield on saline soils may be achieved as a consequence of single gene transfer (the 'silver bullet approach' advocated by molecular breeders), real progress may be achieved only via a complex slow pyramiding of essential physiological traits (Panta *et al.* 2014). The interlink of the deep physiological understanding of tolerance processes at molecular, cellular, and whole physiological level as well as the agronomical techniques for stabilizing growth and yield and their interlinks might help improving our crops for future demand and might provide improvement for cultivating crops in saline environment.

REFERENCES

- Abdelgadir E.M., Oka M., Fujiyama H. (2005) Characteristics of nitrate uptake by plants under salinity. *Journal of Plant Nutrition*, **28**, 33–46.
- Ahmad R., Jamil S., Shahzad M., Zörb C., Irshad U., Khan N., Younas M., Khan S.A. (2017) Metabolic profiling to elucidate genetic elements due to salt stress. *Clean - Soil Air Water*, **45**, 1600574.
- Baldanov M., Baldanova D., Zhigzhitova S., Tanganov B. (2006) To the problem of the radii of hydrated ions. *Reports of the Russian High School Academy of Science*, **2**, 32–34.
- Blumwald E., Aharon G.S., Apse M.P. (2000) Sodium transport in plant cells. *Biochimica et Biophysica Acta*, **1465**, 140–151.
- Borggaard O.K. (1984) Influence of iron oxides on the non-specific anion (chloride) adsorption by soil. *Journal of Soil Science*, **35**, 71–78.
- Cerezo M., Garcia-Atustin P., Primo-Millo E. (1999) Influence of chloride and transpiration on net ¹⁵NO₃⁻ uptake rate by *Citrus* roots. *Annals of Botany*, **84**, 117–120.
- Cheeseman J.M. (2015) The evolution of halophytes, glycophytes and crops, and its implications for food security under saline conditions. *New Phytologist*, **206**, 557–570.
- Chen T.W., Kahlen K., Stützel H. (2015) Disentangling the contributions of osmotic and ionic effects of salinity on stomatal, mesophyll, biochemical and light limitations to photosynthesis. *Plant Cell & Environment*, **38**, 1528–1542.
- Christiansen M.B. (1982) World environmental limitation to food and fibre culture. In: Christiansen M.B., Lew C.F. (Eds), *Breeding Plants for Less Favourable Environments*. John Wiley and Sons, New York, USA, pp 1–24.
- Cui F., Liu L., Zhao Q., Zhang Z., Li Q., Lin B., Wu Y., Tang S., Xie Q. (2012) Arabidopsis ubiquitin conjugase UBC32 is an ERAD component that functions in brassinosteroid-mediated salt stress tolerance. *Plant Cell*, **24**, 233–244.
- Dietz K.J. (2010) Redox-dependent regulation, redox control and oxidative damage in plant cells subjected to abiotic stress. *Methods in Molecular Biology*, **639**, 57–70.
- Duan L., Dietrich D., Ng C.H., Chan P.M., Bhalerao R., Bennett M.J., Dinneny J.R. (2013) Endodermal ABA signaling promotes lateral root quiescence during salt stress in Arabidopsis seedlings. *Plant Cell*, **25**, 324–341.
- Ehret D.L., Redmann R.E., Harvey B.L., Cipywnyk A. (1990) Salinity-induced calcium deficiencies in wheat and barley. *Plant and Soil*, **128**, 143–151.
- Flowers T.J. (2004) Improving crop salt tolerance. *Journal of Experimental Botany*, **55**, 307–319.
- Flowers T. J., Muscolo A. (2015) Introduction to the Special Issue: halophytes in a changing world. *AoB Plants*, **7**. <https://doi.org/10.1093/aobpla/plv020>
- Flowers T.J., Hajibagheri M.A., Yeo A.R. (1991) Ion accumulation in the cell walls of rice plants growing under saline conditions: evidence for the Oerdt hypothesis. *Plant, Cell & Environment*, **14**, 319–325.
- Gardner W.K. (2016) Sodium, calcium and magnesium ratios in soils of NW Victoria, Australia may restrict root growth and crop production. *Journal of Plant Nutrition*, **39**, 1205–1215.
- Geilfus C.M. (2018a) Chloride— From nutrient to toxicant. *Plant and Cell Physiology*, **59**, 877–886.
- Geilfus C.M. (2018b) Review on the significance of chlorine for crop yield and quality. *Plant Science*, **270**, 114–122.
- Geilfus C.M., Tenhaken R., Carpentier S.C. (2017) Transient alkalinization of the leaf apoplast stiffens the cell wall during onset of chloride salinity in corn leaves. *Journal of Biological Chemistry*, **292**, 18800–18813.
- Geng Y., Wu R., Wee C.W., Xie F., Wei X., Chan P.M.Y., Dinneny J.R. (2013) A spatio-temporal understanding of growth regulation during the salt stress response in Arabidopsis. *The Plant Cell*, **25**, 2132–2154.
- Giuffrida F., Carla C., Angelo M., Cherubino L. (2016) Effects of salt stress imposed during two growth phases on cauliflower production and quality. *Journal of the Science of Food Agriculture*, **97**, 1552–1560.
- Grattan S. (2002) *Irrigation water salinity and crop production*. UCANR Publications, University of California, Oakland, CA, USA, p 9.
- Hanin M., Ebel C., Ngom M., Laplace L., Masmoudi K. (2016) New insights on plant salt tolerance mechanisms and their potential use for breeding. *Frontiers in Plant Science*, **7**, 1787.
- Hawkins H.J., Lewis O.A.M. (1993) Combination effect of NaCl salinity, nitrogen form and calcium

- concentration on the growth, ionic content and gaseous exchange properties of *Triticum aestivum* L. cv Gamtoos. *New Phytologist*, **124**, 161–170.
- Hernandez J.A., Jimenez A., Mullineaux P., Sevilla F. (2000) Tolerance of pea (*Pisum sativum* L.) to long-term salt stress is associated with induction of antioxidant defences. *Plant Cell & Environment*, **23**, 853–862.
- Hossain M.S., El Sayed A.I., Moore M., Dietz K.J. (2017) Redox and reactive oxygen species network in acclimation for salinity tolerance in sugar beet. *Journal of Experimental Botany*, **68**, 1283–1298.
- Hu Y., Schmidhalter U. (1998) Spatial distributions and net deposition rates of mineral elements in the elongating wheat (*Triticum aestivum* L.) leaf under saline soil conditions. *Planta*, **204**, 212–219.
- Hütsch B.W., He W., Schubert S. (2016) Nitrogen nutritional status of young maize plants (*Zea mays*) is not limited by NaCl stress. *Journal of Plant Nutrition and Soil Science*, **179**, 775–783.
- Ioannou M., Coutsoygeorgopoulos C. (1997) Kinetic studies on the activation of eukaryotic peptidyltransferase by potassium. *Archives of Biochemistry and Biophysics*, **345**, 325–331.
- Islam M.R., Salam M.A., Bhuiyan M.A.R., Rahman M.A., Yasmeen R., Rahman M.S., Uddin M.K., Gregorio G.B., Ismail A.M. (2008) BRRI Dhan 47: a salt tolerant rice variety for Boro season isolated through participatory variety selection. *International Journal of Biological Research*, **5**, 1–6.
- Ismail A.M., Horie T. (2017) Genomics, physiology, and molecular breeding approaches for improving salt tolerance. *Annual Review of Plant Biology*, **68**, 405–434.
- Jacoby R.P., Millar A.H., Taylor N.L. (2010) Wheat mitochondrial proteomes provide new links between antioxidant defense and plant salinity tolerance. *Journal of Proteome Research*, **9**, 6595–6604.
- James R.A., Davenport R.J., Munns R. (2006) Physiological characterization of two genes for Na⁺ exclusion in durum wheat, Nax1 and Nax2. *Plant Physiology*, **142**, 1537–1547.
- Jayakannan M., Bose J., Babourina O., Shabala S., Mas-sart A., Poschenrieder C., Rengel Z. (2015) The NPRI-dependent salicylic acid signalling pathway is pivotal for enhanced salt and oxidative stress tolerance in Arabidopsis. *Journal of Experimental Botany*, **66**, 1865–1875.
- Kaiser W.M., Kaiser G., Martinoia E., Heber U. (1988) Salt toxicity and mineral deficiency in plants: cytoplasmic ion homeostasis, a necessity for growth and survival under stress. In: Kleinkauf H., von Döhren H., Jaenicke L. (Eds), *The Roots of Modern Biochemistry*. De Gruyter, Berlin, pp 721–733.
- Kaleem F., Shabir G., Aslam K., Rasul S., Manzoor H., Shah S.M., Khan A.R. (2018) An overview of the genetics of plant response to salt stress: present status and the way forward. *Applied Biochemistry and Biotechnology*. <https://doi.org/10.1007/s12010-018-2738-y> [Epub ahead of print]
- Kayne F.J. (1971) Thallium (I) activation of pyruvate kinase. *Archives of Biochemistry and Biophysics*, **143**, 232–239.
- Khan A., Tan D.K.Y., Afridi M.Z., Luo H., Tung S.A., Ajab M., Fahad S. (2017) Nitrogen fertility and abiotic stresses management in cotton crop: a review. *Environmental Science and Pollution Research*, **24**, 14551–14566.
- Köster P., Wallrad L., Edel K.H., Faisal M., Alatar A.A., Kudla J. (2018) The battle of two ions: Ca²⁺ signalling against Na⁺ stress. *Plant Biology*. <https://doi.org/10.1111/plb.12704> [Epub ahead of print]
- Kumari A., Jewaria P.K., Bergmann D.C., Kakimoto T. (2014) Arabidopsis reduces growth under osmotic stress by decreasing SPEECHLESS protein. *Plant Cell Physiology*, **55**, 2037–2046.
- Läuchli A., Grattan S. (2007) Plant growth and development under salinity stress. In: Jenks M. A., Hasegawa P. M., Jain S. M. (Eds), *Advances in molecular breeding toward drought and salt tolerant crops*. Springer, Dordrecht, The Netherlands, pp 1–32.
- Li R.L., Shi F.C., Fukuda K., Yang Y.L. (2010) Effects of salt and alkali stresses on germination, growth, photosynthesis and ion accumulation in alfalfa (*Medicago sativa* L.). *Soil Science and Plant Nutrition*, **56**, 725–733.
- Li B., Tester M., Gilliam M. (2017) Chloride on the move. *Trends in Plant Science*, **22**, 236–248.
- Liang W., Ma X., Wan P., Liu S. (2018) Plant salt-tolerance mechanisms: a review. *Biochemical and Biophysical Research Communication*, **495**, 286–291.
- Liu J., Zhu J.K. (1997) An Arabidopsis mutant that requires increased calcium for potassium nutrition and salt tolerance. *Proceedings of the National Academy of Sciences USA*, **94**, 14960–14964.
- Liu W., Li R.J., Han T.T., Cai W., Fu Z.W., Lu Y.T. (2015) Salt stress reduces root meristem size by nitric oxide-mediated modulation of auxin accumulation and signaling in Arabidopsis. *Plant Physiology*, **168**, 343–356.
- Maas E.V., Grieve C. M. (1977) Sodium-induced calcium deficiency in salt-stressed corn. *Plant, Cell & Environment*, **10**, 559–564.
- Maas E.V., Hoffman G.J. (1977) Crop salt tolerance – current assessment. *Journal of the Irrigation and Drainage Division*, **103**, 115–134.
- Machado R.M.A., Serralheiro R.P. (2017) Soil salinity: effect on vegetable crop growth. Management practices to prevent and mitigate soil salinization. *Horticulturae*, **3**, 30.
- Massa D., Mattson N.S., Lieth H.J. (2009) Effects of saline root environment (NaCl) on nitrate and potassium uptake kinetics for rose plants: a Michaelis-Menten modelling approach. *Plant and Soil*, **318**, 101–115.
- Meloni D.A., Oliva M.A., Martinez C.A., Cambraia J. (2003) Photosynthesis and activity of superoxide dismutase, peroxidase and glutathione reductase in cotton under salt stress. *Environmental and Experimental Botany*, **49**, 69–76.
- Moelwyn-Hughes E.A. (1962) *Physical Chemistry*, Second revised edition. Pergamon Press, New York.
- Miller G., Suzuki N., Ciftci-Yilmaz S., Mittler R. (2010) Reactive oxygen species homeostasis and signalling during drought and salinity stresses. *Plant Cell & Environment*, **33**, 453–467.
- Mor R.P., Manchanda H.R. (1992) Influence of phosphorus on the tolerance of table pea to chloride and sulfate salinity in a sandy soil. *Arid Land Research and Management*, **6**, 41–52.
- Munns R., Gilliam M. (2015) Salinity tolerance of crops – what is the cost? *New Phytologist*, **208**, 668–673.
- Munns R., Tester M. (2008) Mechanisms of salinity tolerance. *Annual Review of Plant Biology*, **59**, 651–681.
- Munns R., James R. A., Xu B., Athman A., Conn S. J., Jordans C., Byrt C.S., Hare R.A., Tyerman S.D., Tester M., Plett D., Gilliam M. (2012) Wheat grain yield on saline soils is improved by an ancestral Na⁺ transporter gene. *Nature Biotechnology*, **30**, 360–364.
- Navarro J.M., Botella M.A., Cerdá A., Martinez V. (2001) Phosphorus uptake and translocation in salt-stressed melon plants. *Journal of Plant Physiology*, **158**, 375–381.
- Niu X., Bressan R.A., Hasegawa P.M., Pardo J.M. (1995) Ion homeostasis in NaCl stress environments. *Plant Physiology*, **109**, 735.
- Oria-Hernández J., Cabrera N., Pérez-Montfort R., Ramírez-Silva L. (2005) Pyruvate kinase revisited: the activating effect of K⁺. *Journal of Biological Chemistry*, **280**, 37924–37929.
- Pannell D.J. (2001) Dryland salinity: economic, scientific, social and policy dimensions. *Australian Journal of Agricultural and Resource Economics*, **45**, 517–546.
- Panta S., Flowers T.J., Lane P., Doyle R., Haros G., Shabala S. (2014) Halophyte agriculture: success stories. *Environmental and Experimental Botany*, **107**, 71–83.
- Papadopoulos I., Rendig V.V. (1983) Interactive effects of salinity and nitrogen on growth and yield of tomato plants. *Plant and Soil*, **73**, 47–57.
- Parmar N., Singh K.H., Sharma D., Singh L., Kumar P., Nanjundan J., Khan Y.J., Chauhan D.K., Thakur A.K. (2017) Genetic engineering strategies for biotic and abiotic stress tolerance and quality enhancement in horticultural crops: a comprehensive review. *3 Biotech*, **7**, 239.
- Qadir M., Noble A.D., Schubert S., Thomas R.J., Arslan A. (2006) Sodicity-induced land degradation and its sustainable management: problems and prospects. *Land Degradation & Development*, **17**, 661–676.
- Qadir M., Quillérue E., Nangia V., Murtaza G., Singh M., Thomas R.J., Drechsel P., Noble A.D. (2014) Economics of salt-induced land degradation and restoration. *Natural Resources Forum*, **38**, 282–295.
- Rozema J., Schats H. (2013) Salt tolerance of halophytes, research questions reviewed in the perspective of saline agriculture. *Environmental and Experimental Botany*, **92**, 83–95.
- Rozema J., Cornelisse D., Zhang Y., Li H., Bruning B., Katschnig D., Broekman R., Ji B., van Bodegom P. (2015) Comparing salt tolerance of beet cultivars and their halophytic ancestor: consequences of domestication and breeding programmes. *AoB Plants*, **7**, pii: plu083.
- Satir O., Berberoglu S. (2016) Crop yield prediction under soil salinity using satellite derived vegetation indices. *Field Crops Research*, **192**, 134–143.
- Scanlon B.R., Jolly I., Sophocleous M., Zhang L. (2007) Global impacts of conversions from natural to agricultural ecosystems on water resources: quantity versus quality. *Water Resources Research*, **43**, 3.
- Shrivastava P., Kumar R. (2014) Soil salinity: a serious environmental issue and plant growth promoting bacteria as one of the tools for its alleviation. *Saudi Journal of Biological Science*, **22**, 123–131.
- Snapp S.S., Shennan C., Bruggen A.V. (1991) Effects of salinity on severity of infection by *Phytophthora parasitica* Dast., ion concentrations and growth of tomato, *Lycopersicon esculentum* Mill. *New Phytologist*, **119**, 275–284.
- Speer M., Kaiser W.M. (1991) Ion relations of symplastic and apoplastic space in leaves from *Spinacia oleracea* L. and *Pisum sativum* L. under salinity. *Plant Physiology*, **97**, 990–997.
- Sunarpri Horie T., Motoda J., Kubo M., Yang H., Yoda K., Horie R., Chan W.Y., Leung H.Y., Hattori K., Konomi M., Osumi M., Yamagami M., Schroeder J.I., Uozumi N. (2005) Enhanced salt tolerance mediated by ATHKT1 transporter-induced Na

- unloading from xylem vessels to xylem parenchyma cells. *The Plant Journal*, **44**, 928–938.
- Tanganov B.B. (2013) About sizes of the hydrated salt ions—the components of sea water. *European Journal of Natural History*, **1**, 36–37.
- Tester M., Langridge P. (2010) Breeding technologies to increase crop production in a changing world. *Science*, **327**, 818–822.
- Thomas G.W., Swoboda A.R. (1970) Anion exclusion effects on chloride movement in soils. *Soil Science*, **110**, 163–166.
- Van der Werf A., Kooijman A., Welschen R., Lambers H. (1988) Respiratory energy costs for the maintenance of biomass, for growth and for ion uptake in roots of *Carex diandra* and *Carex acutiformis*. *Physiologia Plantarum*, **72**, 483–491.
- Voss I., Sunil B., Scheibe R., Raghavendra A.S. (2013) Emerging concept for the role of photorespiration as an important part of abiotic stress response. *Plant Biology*, **15**, 713–722.
- Wakeel A., Farooq M., Qadir M., Schubert S. (2011) Potassium substitution by sodium in plants. *Critical Reviews in Plant Sciences*, **30**, 401–413.
- Yamaguchi T., Hamamoto S., Uozumi N. (2013) Sodium transport system in plant cells. *Front Plant Science*, **4**, 410.
- Yang Y., Guo Y. (2018) Elucidating the molecular mechanisms mediating plant salt-stress responses. *New Phytologist*, **217**, 523–539.
- Zhang H., Cui F., Wu Y., Lou L., Liu L., Tian M., Ning Y., Shu K., Tang S., Xie Q. (2015) The RING finger ubiquitin E3 ligase SDIR1 targets SDIR1-INTERACTING PROTEIN1 for degradation to modulate the salt stress response and ABA signaling in Arabidopsis. *Plant Cell*, **27**, 214–227.
- Zhu J.K., Liu J., Xiong L. (1998) Genetic analysis of salt tolerance in Arabidopsis. Evidence for a critical role of potassium nutrition. *Plant Cell*, **10**, 1181–1191.
- Zörb C., Senbayram M., Peiter E. (2014) Potassium in agriculture—status and perspectives. *Journal of Plant Physiology*, **171**, 656–669.
- Zörb C., Mühling K.H., Kutschera U., Geilfus C.M. (2015) Salinity stiffens the epidermal cell walls of salt-stressed maize leaves: is the epidermis growth-restricting? *PLoS ONE*, **10**, e0118406.