REVIEW PAPER

Molecular control to salt tolerance mechanisms of woody plants: recent achievements and perspectives

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Abstract

Key message Woody plants have salt-tolerant mechanisms similar to those developed by non-woody plants. Among others, compartmentalization of ions, production of compatible solutes, synthesis of specific proteins and metabolites, and induction of transcriptional factors are the most relevant. Woody plant-associated microbial interactions as well as naturally stress-adapted trees are resources that deserve to be deepened to fully understand the tolerance mechanisms.

Context The high variability of salinity responses found in woody plants implies a high potentiality for germplasm selection and breeding. Salt tolerance mechanisms of plants are regulated by numerous genes, which control ion homeostasis, production of compatible solutes and specific proteins, and activation or repression of specific transcription factors. Despite the fact that numerous studies have been done on herbaceous model plants, knowledge about salt tolerance mechanisms in woody plants is still scarce.

Aims The present review critically evaluates molecular control of salt tolerance mechanisms of woody plants, focusing on the regulation and compartmentalization of ions, production of compatible solutes, activation of transcription factors, and differential expression of stress response-related proteins, including omics-based approaches and the role of plant-microbial interactions. The potential identification of genes from naturally stress-adapted woody plants and the integration of the massive omics data are also discussed.

Conclusion In woody plants, salt tolerance mechanisms seem not to diverge to those identified in non-woody plants. More comparative studies between woody and non-woody salt tolerance plants will be relevant to identify potential molecular mechanisms specifically developed for wood plants. In this sense, the activation of metabolic pathways and molecular networks by novel genetic engineering techniques is key to establish strategies to improve the salt tolerance in woody plant species and to contribute to more sustainable agricultural and forestry systems.

Keywords Salt tolerance mechanisms · Omics responses · Salt tolerance stress-related proteins · Transcription factors · Naturally stress-adapted woody plants

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1 Introduction

New developments in agriculture have allowed obtaining higher crop yield and quality, which has optimized the cultivable land area around the world. Soil salinization is a widespread environmental constraint for plants, in which salts are highly deposited in the soil to an extent that affects plant biomass production and agricultural economies (FAO 2017). Given the growing water scarcity and the increasing salt-affected land area, the ability of crop plants to tolerate high levels of salinity in the soils is an agriculturally useful trait (Flowers et al. 2015; Khan and Hemalatha 2016;

Morton et al. 2019). In general, plants have different levels of susceptibility to salinity, which causes osmotic and ionic stress (Munns and Tester 2008; Zhang and Shi 2013). Thus, plants have evolved intricate tolerance mechanisms for dealing with salt stress. The understanding of these physiological and molecular mechanisms of salt tolerance increased in the last years. Some of these mechanisms involve genes regulating different pathways, such as ion regulation and compartmentalization and osmotic adjustment by synthesis of compatible solutes and redox homeostasis (Hanin et al. 2016; Muchate et al. 2016; Martínez-Andújar et al. 2019). Most of these studies have been done on herbaceous model plants, such as *Arabidopsis*, barley, rice, and wheat, among others. However, the knowledge about salt tolerance mechanisms in woody plants is still scarce. Deepening their molecular mechanisms of salt tolerance would allow the identification of new genes that play a key role in plant salt responses.

Woody plants have long juvenile phases and often reproduce over multiple years. These plants have secondary growth, which is a major difference with herbaceous plants. The ability to generate secondary xylem (dicots) or thickened vascular bundles that accumulate to form wood-like tissue (monocots) enables woody plants to increase transport capacity when it is needed (Liesche et al. 2017). In addition, long-lived woody species require complex dynamic mechanisms controlling their developmental changes and growth, when compared with short-lived herbaceous plants. Woody plants have traits, such as high rates of outcrossing, long distance pollen and seed dispersal, large effective population sizes, arborescent stature, low population density, longevity, overlapping generations, more chromosomes, and occurrence in late successional communities, as compared to herbaceous plants (Petit and Hampe, 2006; Sork et al. 2013; Olson et al. 2016). These traits allow woody species to be less sensitive to genetic bottlenecks and more tolerant to habitat fragmentation or climate changes, such as conditions of high salinity. However, both woody and non-woody plants share certain basic physiological and biochemical mechanisms of salt tolerance. Following the perception of salinity, multiple cell signaling pathways are activated, which is reflected in a gene expression reprogramming salt responses. However, plant species differ in their tolerance to salt stress, and particularly, most species are salt-sensitive (Munns et al 2020). Therefore, it is of crucial importance to focus on the identification of key genes of salt-tolerant woody plants and on the application of molecular approaches that allow to elucidate the complex responses to salinity in this type of plants.

Many woody species grow under adverse environmental conditions, as those present in salinized soils. In this type of soils, woody plants have evolved specific mechanisms controlling their salt tolerance. Thereby, some woody plants might be used as model plants to discover and identify new

molecular mechanisms underlying salt tolerance of plants. In this regard, *Populus* species have arisen as model trees in woody plant studies because, among other reasons, this genus contains approximately 30 species inhabiting different types of habitats (e.g., *Populus euphratica* Olivier grows naturally in saline environments); it has relatively small genome size (~ 500 Mbp), which has been completely sequenced in *Populus trichocarpa* Torr. & A.Gray ex. Hook. (Tuskan et al 2006); it has a fast growth in vitro and ex vitro; and it is easy to transform genetically.

This review summarizes the recent achievements in molecular control of salt tolerance in woody plants, focusing on the regulation and compartmentalization of ions, production of compatible solutes, activation of transcription factors, and differential expression of salt stress response-related proteins, including "omics" approaches and the role of plant-microbial interactions. The value of naturally stress-adapted woody plants as biological and genetic resources for sustainable agriculture and forestry to get a better knowledge of salt tolerance mechanisms in woody species is also discussed.

2 Salinity effect on ion regulation and compartmentalization in woody plants

The salt depends on the ability to regulate uptake, transport, and compartmentalization of ions (Munns et al. 2016; Peng et al. 2016; Shabala et al. 2019). The regulation of different pathways, involving the plasma membrane and tonoplast $Na+/H+$ antiporter transporters, membrane-related cation channels, and co-transporters, is essential to tolerance to salt stress in woody plants (Table 1). Thus, except for some halophytes that can successfully maintain low $Na+$ influx (Munns and Tester 2008), a crucial plant response to salinity is the maintenance of ionic homeostasis in cells through preventing $Na+$ accumulation (Martínez-Alcántara et al. 2015). This ionic homeostasis is reached by action of several genes encoding plasma membrane and vacuolar $H+$-ATPases, vacuolar $H+$-pyrophosphatase, cation/proton antiporters on the plasma membrane and vacuolar membrane, and other genes involved in salt tolerance mechanisms (Ma et al. 2016), which allowed to display a set of potential genes to be used in breeding programs.

Studies in *Populus euphratica*, a salt-tolerant tree species, allowed to identify genes involved in salt tolerance that participate in the control of $Na+$ uptake and extrusion, ion compartmentalization into vacuoles, xylem loading of salt solution, and simultaneously maintaining potassium levels in the cells (Brosché et al. 2005; Chen and Polle 2010). In addition, one of the first studies about the transcriptional profiles of distinct *Populus alba* L. genotypes varying in salt

Table 1 List of genes isolated and characterized from woody plant species linked to ion homeostasis, production of compatible solutes, synthesis of specific proteins, and induction of transcriptions factor in the regulation of salt tolerance responses

Gene	Species	Function	References
MaNHX (1–7)	*Morus atropurpurea* L	Na+/H+ exchanger (NHX) tonoplast	Cao et al. 2016
PtNHX (1–5)	*Populus trichocarpa* Torr. & A.Gray ex. Hook	NHX tonoplast	Tian et al. 2017
PtNH6	*Populus trichocarpa*	NHX endo	
PtNH8-9	*Populus trichocarpa*	NHX PM	
PeNHX3	*Populus euphratica* Olivier	NHX tonoplast	Pan et al. 2017
MdNHX1	*Malus domestica* Borkh	NHX tonoplast	Li et al. 2010
PtrCCC	*Poncirus trifoliata* (L.) Raf	Cation-chloride cotransporter	Wei et al. 2018
Putative *SOS1*, *HKT1*, and *NHX1* genes	*Citrus reshni* Tan *Poncirus trifoliata* (L.) Raf	SOS1, HKT1, and NHX1 exchangers	Martínez-Alcántara et al. 2015
JcProDH	*Jatropha curcas* L	Proline dehydrogenase	Wang et al. 2015a, b, c
VnPRP	*Vitis vinifera* L	Proline-rich cell wall protein like	Guan et al. 2018
OeMaT1	*Olea europaea* L	Mannitol transporter	Conde et al. 2007
PeMIPS1	*Populus euphratica*	Myo-inositol phosphate synthase	Zhang et al. 2018
LcDHAR	*Liriodendron chinense* (Hemsl.) Sarg	Dehydrogenase ascorbic reductase	Hao et al. 2019
JcDHAR	*Jatropha curcas* L	Dehydrogenase ascorbic reductase	Chang et al. 2017
PsLEA3	*Prosopis strombulifera* (Lam.) Benth	Late-embryogenesis abundant protein	Llanes et al. 2016a, b
PeuPP2C (PP2CA-M families)	*Populus euphratica*	Phosphatase 2Cs proteins	Li et al. 2018
MnEIL3	*Morus notabilis* Schneid	Ethylene-insensitive3 (EIN3)/EIN3-like (EIL) protein	Liu et al. 2019a, b
MnACO1, MnACO2, MnACS1, and MnACS3	*Morus notabilis*	Ethylene biosynthesis proteins	Liu et al. 2015
PtRab (RabA-H families)	*Populus trichocarpa*	Small GTP-binding proteins	Zhang et al. 2018
MiREM	*Morus indica* L	Remorin	Checker and Khurana 2013
ThDREB	*Tamarix hispida* Willd	Dehydration-responsive element-binding transcription factor	Yang et al. 2017
BpDREB2	*Broussonetia papyrifera* (L.) Vent	Dehydration-responsive element-binding transcription factor	Sun et al. 2014
PeNAC	*Populus euphratica*	NAC transcription factor	Lu et al. 2017
ThNAC13	*Tamarix hispida* Willd	NAC transcription factor	Wang et al. 2017
PalNAC002 PalRD26	*Populus alba var. pyramidalis* L	ABA signaling-related genes	Jiang et al. 2020

tolerance showed differential regulatory patterns of vacuolar and plasma membrane H+-ATPase genes, with tonoplast-ATPase genes up-regulated at an intermediate salinity level but down-regulated at high salinity in the more salt-tolerant genotypes. In contrast, in the most salt-sensitive genotype, no regulation in transcript levels of both plasma membrane-ATPase and tonoplast-ATPase genes was observed, suggesting the absence of salt-sensitive signal transduction pathways in the sensitive genotype, which seems to be necessary to trigger an active response to salinity changes (Beritognolo et al. 2007). Similarly, studies on the response to salt stress in *P. euphratica* cell suspensions showed an increase of both the H+ pumping and H+-ATPase hydrolytic activity (Ma et al. 2016).

In *Citrus* species, it has been proposed that the salt overly sensitive (SOS) pathway (comprising SOS3, SOS2, and SOS1) mediates the signal transduction network for ion homeostasis regulation under salinity (Martínez-Alcántara et al. 2015) as it occurs in close non-woody species. The SOS1 gene encodes a putative sodium/proton antiporter, it was originally identified in *Arabidopsis* (Shi et al. 2000), and then it was also reported in salt response in woody species such as *P. euphratica* (Wu et al. 2007) and *Populus trichocarpa* (Tang et al. 2010). Overexpression of SOS2 protein, a calcineurin B-like protein (CBL)-interacting protein kinase, in apple (*Malus domestica* (Suckow) Borkh.) induced several proteins involved in reactive oxygen species (ROS) scavenging, procyanidin

biosynthesis and malate metabolism, enhancing its salt tolerance (Hu et al. 2015), suggesting that overexpression of SOS pathway genes might be an interesting tool for breeding of fruit trees or other woody plants.

Antiporters like the NHX-type, which are located in the tonoplast of cells, also have an important role in salt tolerance of woody plants. Overexpression of the vacuolar Na + /H + antiporter gene MdNHX1 in apple rootstocks (*M. domestica*) resulted in increased salt tolerance in transgenic plants compared with non-transformed plants, and this was correlated with a higher Na + compartmentalization in roots and higher K + /Na + ratio in leaves (Li et al. 2010). In addition, Martínez-Alcántara et al. (2015) analyzed the differential response to salt stress between two citrus rootstocks ("trifoliate orange" and "cleopatra mandarin") differing in their Na + exclusion capacity. They found that salt tolerance in *Citrus* species involved an accumulation of Na + concentration in the roots and lower allocation of this ion in the shoots through an increased retrieval of Na + from the xylem and a reduced translocation to the shoot tissues. These mechanisms could be a consequence of the overexpression of SOS1, high transcriptional levels of NHX1, and enhanced activity of the tonoplast proton pumps in roots, demonstrating that the mechanism to face ion excess is a complex process. Cao et al. (2016) identified and cloned seven NHX gene sequences from mulberry (*Morus atropurpurea* Roxb.), based on an analysis of the *Morus* genome database. These NHXs were classified into three groups based on a phylogenetic analysis and the exon–intron organization. The expression profiles of NHX family genes (MaNHXs) from three different subgroups were analyzed in response to adverse environmental conditions, phytohormones, and plant signaling molecules (abscisic acid (ABA), salicylic acid, hydrogen peroxide, and methyl jasmonate). Results of this study demonstrated that these genes could be induced by salt, drought, abscisic acid, and other signal molecules. Therefore, the NHXs show diverse and complicated expression patterns in different tissues under varying conditions (abiotic stresses, hormones, and signaling molecules). Recently, García et al. (2019) analyzed the expression of a specific gene (NHX1) from *Eucalyptus grandis* W.Hill ex Maiden plants subjected to salt, drought, and ABA effects. Results of this study suggested that the expression of NHX1 increases both in shoots and roots depending on abscisic acid, confirming the participation of NHX family genes in the responses to abiotic conditions of *E. grandis* plants (García et al. 2019). Additional characterizations of NHX family genes are necessary to provide insights into new and emerging cellular and physiological functions of these exchanger groups in order to be used as new tools for forest breeding.

In plants, chloride (Cl–) plays an important micronutrient role, and it acts as co-factor in photosynthesis, stomatal regulation, and regulation of enzyme activities in the cytoplasm. However, Cl– ions can be metabolically toxic at high concentrations in plants under salinity conditions. The voltage-gated chloride channel (CLC) has been implicated in transporting chloride and other monovalent anions (Herdean et al. 2016). A number of studies have demonstrated that the expression of CLC genes increases tolerance to various types of stress in non-woody plants (Wang et al. 2015a, b, c). The expression of two CLC genes, SaCLCa1 and SaCLCc1, in the non-woody euhalophyte *Suaeda altissima* (L) Pall., was altered in response to changes in the anionic composition of the growth medium, and it might be characterized as organ-specific (Nedelyaeva et al. 2019). In woody plants, Xing et al. (2020) demonstrated that some CLC genes isolated from tea plants (*Camellia sinensis* (L.) Kuntze) are implicated in the absorption and long distance transport of Cl–, probably as a physiological strategy to avoid chloride toxicity. All these results suggest that chloride homeostasis involves a fine regulation of several genes, and it might be interesting to study the role of chloride transporters in woody plants under salinity conditions.

Taken together, these ionic studies demonstrate that ion regulation and compartmentalization systems play an essential role in salt tolerance, with many of these genes being conserved among some woody species. Nevertheless, further approaches should be carried out in order to understand the molecular mechanisms of salt tolerance in woody plants by analyzing the role of these membrane proteins in the whole process.

3 Salinity effect on transcription factors

Plants have complex and interconnected mechanisms to protect or reduce damage caused by adverse environmental conditions. In these mechanisms, transcription factors (TFs) play regulatory roles affecting gene expression in response to abiotic stress, by binding to cis-elements in the promoters of target genes, or other functional modular structures. Plant genomes have a high content of TFs, such as dehydration-responsive element binding (DREB), basic region/leucine zipper motif (bZIP), APETALA 2/ethylene-responsive element binding factor (AP2/ERF), WRKY, myeloblastosis (MYB) family, no apical meristem (NAC), and NAM/ATAF/CUC family, which directly or indirectly regulate responses to different stresses (Alves et al. 2014; Shao et al. 2015; Wang et al. 2016; Banerjee and Roychoudhury 2017).

WRKY transcription factors play an important role in regulating salt stress responses in plants (Mohanta et al. 2016; Xu et al. 2018). In recent years, several WRKY genes have been reported in non-woody plants, but there are few studies on salinity effects on these TFs in woody plants. Wang et al. (2019) isolated and functionally characterized 48 WRKY sequences obtained from the transcriptome of

Hippophae rhamnoides L., an important tree to extract metabolites with strong antioxidant activity. The evaluation of the expression pattern of eight of these HrWRKYS showed that they are involved in abiotic stress responses. Therefore, WRKY might be used as a valid TF to improve or complement the production of plants tolerant to drought and salt stresses. Recently, Jiang et al. (2020) isolated and characterized a WRKY gene in *Populus alba* var. pyramidalis. They found that *PalWRKY77* gene was repressed by salt stress, decreasing salt tolerance in this tree. Interestingly, this transcription factor gene was found to be a repressor of ABA response, which unveils ABA regulation mechanism that negatively signals the PalWRKY77 pathway, resulting in a more sensitive poplar tree to salinity.

Many studies have focused on the structure and function in stress-associated networks of the NAC family genes in herbaceous plants, such as *Arabidopsis* (Gladman et al. 2016; Welner et al. 2016), soybean (Hao et al. 2011), tomato (Zhu et al. 2014), rice (Nakashima et al. 2012; Hu et al. 2008), and wheat (Mao et al. 2012; Tang et al. 2012), but again, few studies have focused on woody species (Table 1). According to high-throughput sequencing data, *P. euphratica* NAC (PeNAC) genes were confirmed to be involved in responses to salt and osmotic stresses (Tang et al. 2013). Lu et al. (2017) also demonstrated that salt tolerance is differentially regulated by several stress-responsive PeNAC transcription factors in transgenic plants. In addition, twenty-one full-length NAC genes were identified in *Tamarix hispida* Willd., a woody halophyte. Most of these NACs contained a complete NAC DNA-binding domain and a variable transcriptional regulation domain. Results of real-time qPCR analysis showed that all these ThNAC genes are expressed in roots, stems, and leaves of *T. hispida* in response to salinity, indicating that they play regulatory roles in salt stress responses and ABA-dependent stress signaling pathways through the whole plant (Wang et al. 2014). Similarly, overexpression of another NAC gene, ThNAC13, induced superoxide dismutase and peroxidase activities, chlorophyll and proline contents, decreased ROS and malondialdehyde levels, and reduced electrolyte leakage rates in both transgenic Tamarix and *Arabidopsis* plants after the exposure to salt and drought stress (Wang et al. 2017). In addition, overexpression of two ABA signaling related NAC genes, PalNAC002 and PalRD26, enhanced salt tolerance in *Populus alba* var. *pyramidalis* (Jiang et al. 2020). Taken together, these studies suggest that NAC family genes could improve salt tolerance in woody plants by different mechanisms, such as enhancing the ROS scavenging capacity, participating in ABA signaling and adjusting osmotic potential. More efforts should be pursued to include NAC genes in regular breeding programs of trees due to their multiple roles in controlling abiotic stresses. A future challenge will be to produce cisgenic or transgenic trees overexpressing NAC genes and other transcription factors, to corroborate their potential role in salt tolerance in woody plants.

4 Salinity effect on compatible solutes in woody plants

Salt tolerance in plants involves the regulation of intracellular Na + homeostasis to reduce the toxicity of ions and to achieve osmotic adjustment (Slama et al. 2015; Suprasanna et al. 2016; Blum 2017). The osmotic adjustment involves the accumulation of compatible solutes that confers protection against dehydration, maintaining cellular structures and functions, even if their concentration is not high enough to achieve osmotic adjustment. Compatible solutes such as proline, glycine-betaine, trehalose, fructose, sucrose, glucose, and sugar alcohols (e.g., mannitol and sorbitol) are synthetized and accumulated in saline-treated cells and contribute significantly to plant salt responses (Méndez-Alonzo et al. 2016; Negrão et al. 2017).

The role of proline in cellular homeostasis, including redox balance and energy status, is widely known (Szabados and Savoure 2010; Kaur and Asthir 2015; Vives-Peris et al. 2017). Notably, the expression of a gene encoding a proline-rich protein was strongly reduced by salinity in different *Populus alba* genotypes (Beritognolo et al. 2011), suggesting that in this tree species, the down-regulation of metabolic pathways could impair some protection mechanisms. Recently, Guan et al. (2018) proposed four genes as candidates to be used as molecular markers for salt stress in grapevine; among them, a proline-rich cell wall protein-like (PRPs) was highlighted. Many studies have been performed on the metabolism of proline in plants growing under adverse conditions, and the use of transgenic and mutant plants allowed the demonstration that proline metabolism produces a complex effect on development and stress responses (Per et al. 2017). Proline catabolism takes place in mitochondria via proline dehydrogenase or proline oxidase (ProDH or POX); these enzymes produce pyrroline-5-carboxylate (P5C), which is further converted to glutamate by P5C dehydrogenase (P5CDH; Ribarits et al. 2007; Szabados and Savoure 2010). The ProDH enzyme and its complementary DNA (cDNA) were isolated from *Jatropha curcas* L., a woody oil plant important for biodiesel production (Wang et al. 2015a, b, c). The phylogenetic analysis indicated that JcProDH showed a high similarity with ProDH from other plants, and it was classified as a member of the ProDH family. In addition, JcProDH expression was increased in leaves of this woody plant growing under stressed conditions such as cold (5 °C), heat (42 °C), salt (300 mM), and drought (30% PEG 6000), indicating that proline dehydrogenase

contributes to regulate the deleterious effect of abiotic stress. Due to its promissory role in facing abiotic stress, proline needs to be deepened in woody plants.

Knowledge about the role of carbohydrates on osmotic adjustment in woody plants under salinity is still scarce (Table 1). The role of carbohydrates as compatible solutes may be masked by their multiple functions like direct products of photosynthesis and components of primary metabolism and signaling and regulatory molecules, making it sometimes difficult to analyze specific contribution to osmotic adjustment in plants under salt conditions. Among the few studies, Conde et al. (2007) showed that the NaCl applications to cell suspensions of olive tree (*Olea europaea* L.) increased the mannitol transporter 1 (OeMaT1) transcripts and repressed mannitol dehydrogenase activity providing intracellular accumulation of mannitol. Similarly, *Populus nigra* x *P. tomentosa* hybrids were genetically modified to synthesize mannitol through the introduction of an *Escherichia coli* mannitol-1-phosphate dehydrogenase (mtlD), which participates in the conversion of fructose to mannitol, resulting in mannitol accumulation and improved salt tolerance (Lin et al. 2016). Interestingly, an increased galactinol synthase gene expression was observed in *P. euphratica* under salt stress. This enzyme catalyzes the first step in the synthesis of raffinose family oligosaccharides (RFOs) which have been demonstrated to have a role as osmoprotectants in several plants by stabilization of the membranes and protects against oxidative stress (Zhang et al. 2017a, b). However, the increase of these oligosaccharides was not related to osmotic adjustment in this species (Ottow et al. 2005). In contrast, the transcripts of galactinol synthase gene were decreased by salinity in *Populus alba* genotypes (Beritognolo et al. 2011), which indicates that the role of galactinol synthase in woody plants needs to be more studied. Recently, Lima et al (2021) evaluated whether the time of day at the onset of salt stress influences the dynamics of leaf Na + content and non-structural carbohydrates accumulation in the foliar tissue of *Cenostigma pyramidale* (Tul.) Gagnon & G.P.Lewis, a woody species of a tropical dry forest. Thus, morning-stressed *C. pyramidale* plants showed a reduction in gas exchange and large amounts of Na + reached in leaves, and these plants accumulated higher amounts of proline and sugars than those plants stressed at night. Therefore, these authors suggest that details about the stress time should be taken into account in salt tolerance studies.

As a conclusion, salt tolerance improvement in woody plants could be achieved through accumulation of carbohydrates, by mechanisms that protect or reduce cell damage caused by salinity, which could be modified depending on the time of salt stress. Nevertheless, because certain results of gene and enzyme expression of compatible solutes seem to be contradictory, more research is needed to understand the potential role of carbohydrates in woody plant salt tolerance.

5 Salinity effect on stress response-related proteins

Dehydration-responsive element binding (DREB) are important abiotic stress response-related proteins, and many studies have been reported on these proteins involved in stress tolerance in non-woody species. Although studies on DREB proteins stress response in woody plants are still few (Table 1), the role of DREB in abiotic stress tolerance in the woody *Tamarix hispida* was explored, and a ThDREB gene was isolated and cloned. ThDREB expression was highly induced by salt, alkali, drought, and heavy metal stress showing various transcription patterns. Moreover, transient overexpression of ThDREB improved tolerance to NaCl and mannitol in transgenic plants of tobacco and *T. hispida* (Yang et al. 2017). Similarly, Sun et al. (2014) cloned a BpDREB2 gene from the woody plant *Broussonetia papyrifera* (L.) LHér. ex Vent. that BpDREB2 protein specifically binds to DRE sequence and is able to activate the expression of reporter genes and that BpDREB2 gene expression is greatly induced by drought and salt. Finally, these studies showed that DREB genes represent potential candidate genes for molecular breeding to increase plant stress tolerance.

Protein tyrosine phosphatases (PTPs) have important roles in signaling pathways related to cell differentiation, cell division, and cell growth (Hunter 2009). In plants, the role of PTP is important in response to abiotic stress, hormone and development, nutrient deficiency, biotic stress, and starch metabolism. In relation to salt stress, Lu et al. (2020) identified a tyrosine (Tyr)-specific phosphatase (PdPTP1) gene from *Populus nigra* × (*P. deltoides* × *P. nigra*), which was significantly up-regulated by salt and oxidative stress. When this gene was overexpressed (OxPdPTP1), the transgenic woody plants showed hypersensitivity to salt, accumulating more Na + in leaves and stems but less K + in roots, as well as more oxidative damage in leaves and roots. Interestingly, in the OxPdPTP1 trees, ROS scavenging enzymes such as CAT and SOD showed lower activities than wild-type plants. Taken together, these results showed that PdPTP1 gene has an important role to maintain a proper antioxidant activity and ion homeostasis in this *Populus* species. Due to PTPs that have been involved in the activation of mitogen-activated protein kinase (MAPK) cascades signal transduction pathways controlling ROS homeostasis and SOS1 antiporter activity, further investigation to dissect more precisely the role of PTPs in MAPK dephosphorylation in woody plants will be required.

Remorin proteins (REMs) belong to an interesting multigenic family of plant-specific membrane-bound proteins playing an essential role in biotic responses (Gui et al. 2014; Jamann et al. 2016; Gronnier et al. 2017). Although their physiological role in response to abiotic stresses has been less characterized in plants, tolerance to water deficit and salt stress was improved in transgenic *Arabidopsis* plants overexpressing a remorin gene during germination and seedling growth (Yue et al. 2014). Regarding woody plants, Checker and Khurana (2013) have isolated a gene from mulberry tree (*Morus indica* L) that encodes a remorin protein (MiREM). Expression analysis of MiREM revealed that its transcript increases under different abiotic stress conditions mainly under water deficit and salt stress, suggesting a role in the regulation of stress signaling pathways.

6 Omics approaches in woody plants under salt-stress

Omics-based technologies and approaches are useful for deciphering the entire genome, transcriptome, proteome, or metabolome of plant species, and thus gaining insights into plant molecular responses, which will offer specific strategies for sustained productivity of woody plants, and to incorporate genes in suitable species to yield salt-tolerant varieties. Until now, many advances have been achieved through the completion of genome sequencing of different species of woody plants, such as poplar (*Populus trichocarpa*; Tuskan et al. 2006), peach (*Prunus persica* (L) Batsch; Verde et al. 2013), *Eucalyptus grandis* (Myburg et al. 2014), *Salix suchowensis* W.C.Cheng (Dai et al. 2014), Chinese chestnut (*Castanea mollissima* Blume; Staton et al. 2015), sweet cherry (*Prunus avium* (L.) L.; Shirasawa et al. 2017), oak (*Quercus robur* L.; Plomion et al. 2018), camphor tree (*Cinnamomum kanehirae* Hayata; Chaw et al. 2019), *Malania oleifera* Chung & S.K.Lee (Xu et al. 2019), and different citrus species including the diploid sweet orange ridge pineapple and the haploid clementine, among others (Wu et al. 2014; Gmitter et al. 2020).

In connection with this, Ma et al. (2015) developed a new database web called salinity tolerant poplar database (STPD) (http://me.lzu.edu.cn/stpd/) to assist studies of salt tolerance in trees and poplar genomics. The database incorporates new genome-wide data of related poplar species. This database is useful for studies on the molecular function of genes, comparative genomics, and evolution in closely related species as well as for promoting the development of molecular breeding in *Populus*. Similarly, Makita et al. (2018) developed a rubber tree (*Hevea brasiliensis* (Willd. ex A.Juss.) Müll.Arg.) genome and transcriptome database web (http://matsui-lab.riken.jp/rubber/home.html).

The database provides the whole-genome information of *H. brasiliense* plants, including gene functional annotations and multi-transcriptome data of RNA-seq, full-length cDNAs including PacBio Isoform sequencing (Iso-Seq), ESTs, and genome-wide transcription start sites (TSSs) (Makita et al. 2018). Recently, Jin et al. (2019) analyzed the genome-wide expression profiles of tea plant (*C. sinensis*) under three dehydration levels using RNA-Seq and digital gene expression (DGE) technologies. They performed de novo assembly and obtained a total of 91,925 non-redundant genes, of which 58,472 were extensively annotated. Some of these genes were involved in ABA biosynthesis and signal transduction, transcription factor, antioxidant enzyme, LEA protein, and proline metabolism, indicating that they play regulatory roles in dehydration situations, which corroborate previous studies performed in woody trees using non-omics approaches. Thus, this genome-wide study elucidates the possible molecular mechanisms associated with dehydration tolerance in woody plants, and it may contribute to exploring the mechanism of other conditions like salinity. In addition, the production of expressed sequence tags (ESTs) from mulberry (*Morus* spp.) has laid the basis for functional genomics studies in these plants under abiotic stress conditions (Sarkar et al. 2017). Although these expressed sequence tags from mulberry sequencing contribute to the knowledge about the participation and possible function of genes involved in salt tolerance, the functional validation of these expressed genes needs to be carried out. The transcriptomic analyses of some woody plants investigated by its salt tolerance are presented in Table 2.

Integrated approaches with other omics technologies could contribute to a better understanding of salt tolerance mechanisms in woody plants. Proteomics is the large-scale study of proteins in biological systems and constitutes a powerful tool for describing the complete proteomes in different organelles, cells, organs, or tissues (Hossain 2020). Proteomics is not only used for quantitative profiling, analysis of dynamic post-translational modifications, subcellular localization and compartmentalization, protein complexes, signaling pathways, and protein–protein interactions (Agarwal et al. 2013), but high-throughput proteomics is also useful to compare proteomes under different stress conditions such as salinity. Using proteomic technologies, many proteins involved in salt tolerance have been identified in plants. Salt stress-related proteomic analyses conducted in woody plants such as *Bruguiera gymnorhiza* (L.) Lam. (Zhu et al. 2012), *Tangut nitraria* Maxim. (Cheng et al. 2015), *Kandelia candel* (L.) Druce (Wang et al. 2015a, b, c), and *Robinia pseudoacacia* L. (Meng et al. 216) have allowed to identify salt-responsive proteins which are related to osmotic and ionic homeostasis, signal transduction, ROS scavenging activity, photosynthesis, regulation/defense, energy and metabolism, and redox homeostasis. These proteomic results

Table 2 Transcriptomic approaches from different woody plant species describing the main findings linked to salt tolerance responses

Species	Omic approach	Findings	References
Avicennia officinalis L	RNA-seq and de novo assembly and annotation	22, 254 transcripts and 613 microsatellite markers. They identified different copies and isoforms of three candidate genes, AoPIP, AoTIP, and AoDHN1, which might be involved in salt excretion via salt glands	Lyu et al. 2018
Camellia sinensis (L.) Kuntze	RNA-seq/DEG	3715 differentially salt stress expressed genes were identified	Zhang et al. 2017a, b
Picea wilsonii Mast	RNA-seq/DEG	3438 (1592 up-regulated and 1706 down-regulated) differentially expressed genes were identified under salt treatments. qRT-PCR analyses showed that the expression of PwNAC genes were induced by salt treatment, suggesting that these genes are involved in salt stress resistance	Guo et al. 2020
Populus alba × *Populus glandulosa* and *Populus simonii* × *Populus nigra*	RNA-seq/DEG	A total of 276 up-regulated DEGs and 159 down-regulated DEGs were identified to be shared in the four species. Overexpression of a transcription factor (NAC57) gene conferred salt tolerance in transgenic *Arabidopsis*	Yao et al. 2018
Populus pruinosa, *Populus euphratica*, *Populus trichocarpa*, and *Populus tomentosa*	RNA-seq/DEG	On the basis of the 7822 1:1 orthologs between the four poplar species, a total of 1335 differentially expressed genes were identified	Luo et al. 2017
Populus tomentosa Carrière	RNAseq/DEG	3991, 4603, and 4903 genes were up-regulated, and 1408, 2206, and 3461 genes were down-regulated at 6, 12, and 24 h under salt treatments, mainly identified with ROS and hormone regulatory networks	Zheng et al. 2015
Prosopis juliflora (Sw) DC	De novo assembly of transcriptome/DEG	666 genes were responsive to salt stress in leaf tissue, of which 110 were responsive to drought stress too, and 20 were responsive to salt stress in root tissue also. Similarly, 1044 were responsive to salt stress in root tissue, of which 832 were responsive to drought stress too, and 20 were responsive to salt stress in leaf tissue also. More transcriptome changes in root tissue compared to leaf under the stress, drought stress caused more differential gene expression than salt stress	George et al. 2017
Vitis vinifera L	RNA-seq/DEG	2472 differentially expressed genes in salt-responsive grapevine leaves were identified	Guan et al. 2018
Vitis vinifera (Thompson seedless variety)	RNA-seq/DEG	714 differentially expressed genes were identified under 150 mM salinity stress, where 311 genes were down-regulated and 406 genes were up-regulated. 20 salt stress-induced DEGs were selected for validation through qRT-PCR analysis; these genes were involved in pathways related to salt tolerance (signaling transduction, transcription factor, defense metabolism, antioxidant genes, cell wall, and growth)	Das and Majumder 2019

could be used to improve plant salt tolerance (Meng et al. 2016). For instance, Xing et al. (2019) analyzed the root proteome of *K. candel* exposed to 600 mM NaCl, identifying 110 up-regulated and 117 down-regulated differentially abundant proteins, which were related to the main biological processes affected by salt stress (i.e., carbohydrate and energy metabolism, stress response and defense, cell wall structure and secondary metabolism). Further, they found that this mangrove tree can tolerate high salinity by stabilization of the Embden-Meyerhof-Parnas and tricarboxylic acid (EMP-TCA) pathway, providing enough energy to sustain the higher metabolic activity occurring in plant cells due to salt stress. The stabilization of the EMP-TCA pathway seems to increase the activity of antioxidant enzymes such as peroxidase, catalase, superoxide dismutase, ascorbate peroxidase, and glutathione reductase. Overexpression of enzymes participating in the EMP-TCA pathway might be an interesting approach that deserves to be studied more deeply due to its promissory effects to control the pleiotropic impact provoked by salt stress in plants.

Recently, a study on proteomic responses of *Morus alba* to both salt and drought stress allowed to identify a total of 577 and 270 differentially expressed proteins from the salt-stressed leaves and roots, respectively. These proteins

were associated with different metabolic pathways, including carbon metabolism, photosynthesis, redox, secondary metabolism, and hormone metabolism. Among these, the sucrose metabolism pathway was enriched in both stressed leaves and roots, demonstrating the importance of this pathway in this woody plant under stress conditions (Liu et al. 2019a, b). Taken together, these studies are providing a comprehensive understanding of plant salt responses at protein level and will lead to further studies on the development of salt-tolerant plants. It is worth mentioning that it is necessary to emphasize that these proteomic approaches (in silico) need to be validated in plants.

Metabolomics involves the study of the global profile of the low molecular weight metabolites in cells, tissues, and even the whole organism (Jorge et al. 2016). The identification of metabolites provides information about the metabolic status of an organism, and it is useful to evaluate the biological responses to different conditions. Therefore, metabolomics constitutes a powerful tool in plant research, improving the knowledge of dynamic metabolic networks. However, because of the discrepancy and large number of metabolites identified in each study, the role of each metabolite in salt stress responses of plants may be difficult to interpret (Kumari et al. 2015). Thus, the diversity of compounds has to be interpreted as a picture of the metabolic pathways moving on in the tissue under a specific condition. There are few studies of metabolic pathways affected by salinity in woody trees. In this aspect, Rao et al. (2017), using an untargeted metabolomic profiling approach, highlighted the up-regulation of phenylpropanoid, monolactam, indole alkaloid, and flavonoid biosynthetic pathways in young leaves of olive tree (*O. europaea*). Their findings suggest that these metabolites could be involved in resistance to abiotic stress. In accordance, several metabolites similar to those reported in olive trees were already associated with salt tolerance in the halophytic woody species *Prosopis strombulifera* (Lam.) Benth. (Llanes et al. 2016a, b). Indeed, metabolomics profiles of *P. strombulifera* plants, grown hydroponically in iso-osmotic solutions of NaCl and Na_2SO_4, showed that several metabolites, such as organic acids, are associated with cell damage probably caused by an increased respiration induced by the presence of sulfate anion. Specific amino acids and carbohydrates were induced only by NaCl, suggesting that they play an important role in osmotic adjustment in *P. strombulifera* plants during salt stress. In *Malus halliana* Koehne, a metabolomic approach combined with a proteome analysis demonstrated that 140 metabolites were differentially expressed due to saline-alkali stress, such as enzymes related to photosystem II (PSII) repair cycle and chlorophyll metabolism, metabolites triggered by carbohydrates, proteins related to aspartate and glutamate, and flavonoids. All these metabolites seem to play a key role in osmotic balance and cell detoxification due to excess ROS (Jia et al. 2019). Therefore, these high-throughput technologies are allowing us to unravel more quickly the role of metabolites in salt tolerance of woody plants.

7 Salinity effect on the woody plant-microbial interactions

Beyond inherent plant salt tolerance mechanisms, the plant-associated microbial communities play a key role in the adaptation of plants to extreme environments (Lumibao et al. 2020; Sharma et al. 2021). Plant growth-promoting rhizobacteria (PGPR), endophytes, and arbuscular mycorrhizal fungi (AMF) can interact and mediate plant tolerance to environmental stressors such as salinity (Zhang et al. 2021b) by interacting and colonizing plant roots, root tissue, and plant endosphere (Thiem et al. 2018). Root-mediated changes in the soil environment provide soil microorganisms with oxygen or other substrates, altering microbial community structure (Lipson et al. 2015). Recently, Barreto et al. (2018) investigated the bacterial community composition in soils from plots dominated by either woody mangroves or herbaceous salt marshes and positioned across a mangrove-marsh ecotone. They found that both woody and herbaceous plants have different sediment microbial communities and that future mangrove encroachment into salt marshes could alter soil microbial communities with potential implications for soil carbon storage.

Woody plant-microbial interactions can promote salt tolerance by enhancing several mechanisms in plants such as the accumulation of compatible solutes and the reduction of sodium uptake in plant tissues (Fig. 1). In some woody species symbiotic associations with AMF, such as *Hebeloma crustuliniforme*, *Laccaria bicolor*, *Paxillus involutus*, *Pisolithus tinctorius*, *Scleroderma bermudense*, and *Suillus tomentosus*, that enhanced tolerance to salinity by the accumulation of osmolytes has been identified (Muhsin and Zwiazek 2002a, b; Bandou et al. 2006; Bois et al. 2006; Nguyen et al. 2006; Calvo-Polanco et al. 2008a, b; Yi et al. 2008; Luo et al. 2009). In *Cenostigma pyramidale*, the use of AMF *Acaulospora longula* and *Claroideoglomus etunicatum* combined with application of superphosphate (P2O5) partially alleviates salinity effects on stomatal conductance, photosynthesis, and biomass parameters. When only AMF was applied, *C. pyramidale* showed an increased shoot biomass and high net photosynthesis under non-saline and saline conditions (Frosi et al. 2017). On the other hand, PGPR, such as *Pseudomonas putida* and *Novosphingobium* sp., can increase the accumulation of proline in plants under salinity, which reduces sodium uptake and enhances potassium assimilation as observed in *Citrus macrophylla* (Numan et al. 2018;
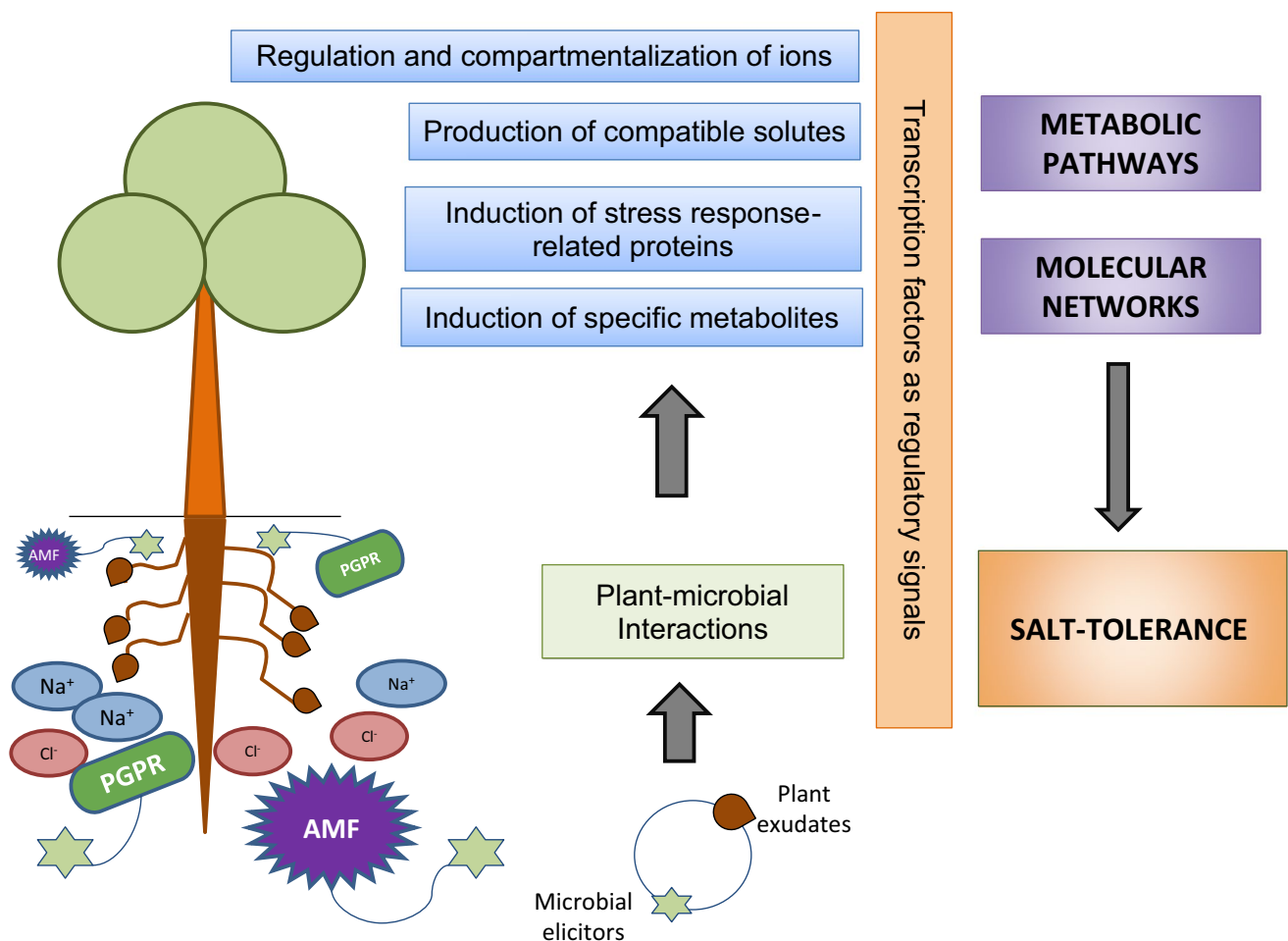
Fig. 1 Overview of salinity effects on roots of woody plants. Salinity generates a regulation and compartmentalization of ions, production of compatible solutes, specific proteins and metabolites at the rizhosphere level. The plant-microbial interactions promote some physiological and molecular responses by microbial elicitors, such as reactive oxygen species scavengers (i.e., catalases, superoxide dismutase, peroxidase), hormone-related compounds (i.e., abscisic acid, 1-aminocyclopropane-1-carboxylate (ACC) deaminase, cytokinins, zeatin, gibberellic acid). On the other hand, roots exude mainly car- bohydrates, amino acids, and other organic acids that are used by microbial communities for its development. In the plant, a group of transcription factors play regulatory roles of these salinity responses, activating metabolic and molecular networks for the salt tolerance. Therefore, understanding metabolic pathways and molecular networks are key players to establish strategies to improve the salt-tolerance in plant species. AMF, arbuscular mycorrhizal fungi; PGPR, plant growth-promoting rhizobacteria

Vives-Peris et al. 2018; El Moukhtari et al. 2020; Sharma et al. 2021). The sodium uptake regulation in plants might include a strong extrusion by fungi and bacteria to protect the roots (Guerrero-Galán et al. 2019); however, the specific mechanisms for reducing sodium uptake are still unclear.

PGPR can increase the accumulation of compatible solutes by allowing plants to absorb them through their roots, which aids in balancing osmolarity and protecting against oxidative damage (Casanovas et al. 2003; Zarea et al. 2012; Akhtar 2019; Yadav et al., 2020). The capacity of rhizobia to confer osmoprotectant mechanisms to woody plants was observed in *Acacia gummifera* Willd., *Acacia raddiana* Savi, *Ceratonia siliqua* L., and *Adenocarpus decorticans* Boiss. (Abdelmoumen et al. 1999; Essendoubi et al. 2007).

Besides, PGPR (*Rhizobacterium* and *Bacillus subtilis*) and AMF (*Claroideoglomus etunicatum*, *Rhizophagus intraradices*, and *Funneliformis mosseae*) increased osmoprotectants in *Acacia gerrardii* (Hashem et al. 2016). Production of phytohormones by plant-microbial communities such as indole-3-acetic acid (IAA), cytokinins, and abscisic acid (ABA) is involved in changes in root morphology and transportation activity in response to saline conditions. In root endophytes, production of IAA, zeatin, gibberellic acid, and ABA was observed as a protective mechanism of salt tolerance in woody plants such as *P. strombulifera*, *C. sinensis*, *Persea americana* Mill., and *Populus* sp. (Xin et al. 2009; Trivedi et al. 2011; Barra et al. 2016; Sgroy et al. 2009; Kushwaha et al. 2020). Specifically, IAA produced

by PGPR and endophytes from genera *Bacillus*, *Marino-bacterium*, *Sinorhizobium*, *Paenibacillus*, *Rhizobium*, *Stenotrophomonas*, *Pseudomonas*, and *Pantoea*, among others, can promote root proliferation and root architecture changes, which are required when plants need to cope with salt stress (Rodríguez-Llorente et al. 2019). ABA is produced by several endophytic bacteria (e.g., *Achromobacter*, *Bacillus*, *Brevibacterium*, *Lysinibacillus*, and *Pseudomona*s) in *P. strombulifera* as well as gibberellic acid in saline-rich environments (Sgroy et al. 2009; Gerhardt et al. 2017). The decrease in ethylene levels by regulation of 1-aminocyclopropane-1-carboxylate (ACC) deaminase has been observed in plant-microbial interactions. The ACC deaminase enzyme can cleave ethylene precursor ACC, producing ammonia and α-keto butyrate, which contributes to enhance salinity tolerance (Ha-Tran et al. 2021). Examples of ACC deaminase activity have been observed in root endophytic bacteria of the halophyte *P. strombulifera* and rhizosphere bacteria from *Cocos nucifera* under salinity (Sgroy et al. 2009; Glick 2014; Pandey and Gupta 2020). The effects of ACC deaminase (Glick et al. 2007; Glick 2014) and phytohormones production by microbial communities (Akhtar 2019) have been widely studied.

Another salt tolerance mechanism involving plant-microbial interactions is the production of antioxidant enzymes that counteract oxidative stress as result of increased reactive oxygen species (ROS) (El Moukhtari et al. 2020). Some PGPR, endophytes from genera *Enterobacter*, *Serratia*, *Microbacterium*, *Pseudomonas*, and *Achromobacter*, and AMF species, such as *Funneliformis mosseae*, *Rhizophagus intraradices*, and *Claroideoglomus etunicatum*, can produce several antioxidant enzymes such as superoxide dismutase (SOD), peroxidase (POX), and catalase (CAT) in response to salinity as observed in the woody plants *Phoenix dactylifera* L., *Persea americana*, and *Panicum turgidum* Forssk. (Hashem et al. 2015; Barra et al. 2016; El Moukhtari et al. 2020). The ROS mechanisms are shared among microbes, which involve enhancing enzymatic activity for ROS scavenging as well as stimulating plant antioxidant production (Bharti and Barnawal 2019).

Formerly, to know the composition, function, and interaction of all these microorganism communities, laborious methods of isolation and culture were required (Shen and Fulthorpe 2015; Szymanska et al. 2016; Yaish et al. 2016). Nevertheless, massive analysis and characterization of all these organisms can now be possible thanks to the metagenomic approach, a molecular technique that eludes the unculturability of microbiomes, the most significant barrier to advance in environmental microbiology. It involves DNA sequencing directly from soil or plant tissues, which has opened the gate for current plant microbiome research (Jansson and Hofmockel 2018). Metagenomic studies of rhizosphere and endosphere microorganisms in salt tolerance

woody plants are limited. Among the few metagenomic studies, differential microbial communities can be observed from the endosphere of roots and rhizosphere under salinity (Thiem et al. 2018; Vanegas et al. 2019; Lumibao et al. 2020). These metagenomics studies showed enriched metabolic capabilities related to stress tolerance such as signaling transduction turnover and post-translational modification of proteins. Besides, known salinity tolerance genes encoding for glycerol transporter and glycine betaine metabolism, as well as proton pump, have been observed from hypersaline rhizosphere. Microbial communities, comprising fungi and bacteria, associated with roots of woody plants have demonstrated protection capabilities in salt-rich environments (Min et al. 2014; González-Teuber et al. 2019; Pandey and Gupta 2020).

Taken together, there is no doubt that studies of salinity effects on the woody plant-microbial interactions are accelerating our understanding of the molecular strategies developed by plants to deal with adverse environmental conditions. The limitations for cultivation of woody plants in laboratories are now being overcome by high-throughput screening of their genes, proteins, metabolites, or microbiomes. Nevertheless, even with these important advances, the complex salt tolerance mechanisms in woody plants still need to be deepened as well as plant-microbial interactions should be included in these omics approaches in order to capture the entire genetic diversity displayed by woody plants to deal with salinity.

8 Naturally stress-adapted woody plants (NSAW) as a source for stress-adapted gene discovery

Naturally stress-adapted woody plants (NSAW) are able to survive and reproduce in environments with low resource availability (Pantha and Dassanayake, 2020). NSAW inhabiting extreme environments on Earth are called extremophiles, which according to the environmental conditions can be classified a 476 cryophytes and thermophytes (adapted to very low or very high temperatures, respectively), hydrophytes and xerophytes (adapted to high or low water level, respectively), and halophytes (adapted to high salinity), including the interesting subgroup of secretohalophytes which have glandular structures that secrete salt, among other categories (Zhang et al. 2019). In this regard, mangroves species are an interesting group of extremely NSAW found in tropical coastline environments with tolerance to high salinity, hypoxia, daily fluctuating tides, strong UV light, high temperature, high sedimentation, and muddy anaerobic soils. Their morphological and physiological features can be accounted for the exceptional salt adaptations such as thickening of leaves with increased water content, leaves with salt

glands for Na + efflux, aerial roots, viviparous sexual reproduction, and a high concentration of mucilage in roots and stem that prevents water loss and improves the efficiency of water usage (Zhang et al., 2004; Liang et al., 2008). Among molecular adaptation, the salinity tolerance of mangroves species is associated with secretion, exclusion, and salt accumulation by the gathering of compatible solutes, utilization of antioxidant enzymes, and salt induce genes in high salinity conditions (Parida and Jha, 2010; Zhang et al., 2021a). Regulation of gene expression under saline stress can be related to up-regulation of betaine/proline metabolism genes, ethylene and auxin signaling genes, and down-regulation of ABA signaling genes, among others (Xu et al., 2017). Understanding these highly specialized characters of mangrove plants offers the opportunity to expand the tolerance mechanisms possessed by some of the more salt-tolerant woody plant species on earth (Liang et al., 2008; Parida and Jha, 2010; Palmgren et al. 2015; Krishnamurthy et al., 2017). In this sense, native populations of mangroves, as well as others NSAW, would be valuable to discover stress-related genes, which combined with new omics technologies and genetic engineering approaches, such as CRISPR-Cas9-sgRNA ribonucleoprotein complex fused to magnetic nanoparticles (MNPs) (Zhao et al. 2017; Cunningham et al. 2018; Zhang et al. 2015), and would improve and accelerate domestication of woody species, including those with important economic and ecological impacts (e.g., Fabaceae family; Castro et al. 2017; Watson et al. 2018).

In arid environments, where woody species such as *Populus* spp., *Prosopis* spp., *Atriplex* spp., and *Eucalyptus* spp. are naturally found, these plants utilize the scarce rainfall inputs very efficiently, either in near real time or with seasonal deferrals. Even during periods when precipitation exceeds evapotranspiration, these plants avoid any drainage by taking advantage of occasional water surpluses in subsequent dry spells due to large water storage capacity and deep root development systems. These water flows are less important for removing salts, but it can play a relevant role in the local positioning of salt accumulating zones and, therefore, for the subsequent gaining of salt tolerance. For example, *Prosopis* spp. in the arid region of Argentina (Chaco) is considered salt-tolerant (Villagra et al. 2017). Research in these species indicates that the ability to regulate and control Na + uptake and prevent its build-up in metabolically active tissues (Meloni et al. 2008) or production of specific metabolites (Llanes et al. 2016a, b) is contributing to its adaptation. In wild *Vitis* spp., the search for salt-tolerant genotypes showed that the shoot ion exclusion may contribute to salt tolerance (Vila et al. 2016).

Other benefit of NSAW is that they would contribute to mitigate soil erosion and conserve plant–microbe soil interactions. It is known that the rhizosphere microbiome is essential for plant and animal health (Balestrini et al. 2015).

Therefore, knowledge of the interactions between native NSAW and these microorganisms will offer great opportunities to improve crop performance. In addition, NSAW could be useful for increasing crop diversity and for providing a better understanding of stress tolerance mechanisms in a climate change context. The integrated approaches of genomic, transcriptomic, proteomic, and metabolomic data of naturally stress-adapted woody plants will allow us to identify mechanisms involved in their stress tolerance. In addition, the development of basic knowledge of NSAW biology (i.e., seed germination, viability and recalcitrance of seeds, growth requirements under greenhouse conditions) and woody plant DNA, RNA, protein, and metabolite isolation protocols still remains as a challenge. A deep understanding of the natural adaptation to salinity in woody plants can speed up the integration of suitable genes into crop species to produce salt-tolerant varieties and/or to maintain the productivity of commercial woody species. However, there are debates about the use and regulation of genetically modified crops in today's society. Different countries have their own regulations and opinions on the use of genome editing technologies, which can be delayed or even prohibited in their territories. For example, the US Department of Agriculture (USDA) announced that there are no regulations for genome-edited plants. On the contrary, the European Union (EU) considers that genome-edited plants must be subject to the same regulation as conventional genetically modified plants. The development of new salt-tolerant plants using new approaches and technologies will depend on each country's laws, which would delay the commercialization of these salt-tolerant crops.

In spite of this, we are convinced that studies of woody plants growing in salinized soils (and other harsh environments) should be continued, and it will be desirable that NSAW will receive more attention from researchers in the coming years, especially because they are valuable biological resources for sustainable agroecosystem management and as a reservoir of genetic information.

9 Conclusions

Expanding knowledge on woody plant responses to salinity represents a valuable option to increase the productive capacity of salt-affected land areas and to reverse the degradation trends in different environments. Woody plant responses to salinity involve the participation of numerous genes which putatively provide stress protection and whose expression is not controlled by one specific pathway. Part of these salt tolerance mechanisms in woody plants involves the maintenance of cellular ion homeostasis, which is associated with numerous genes encoding the plasma membrane and vacuolar transporters, and with a fine and complex

Fig. 2 Model summarizing the current understanding of recent achievements and perspectives about salt tolerance mechanisms in woody plants. Naturally stress-adapted woody plants (NSAW) are proposed as a new source for stress-adapted gene discovery. AMF, arbuscular mycorrhizal fungi; PGPR, plant growth-promoting rhizobacteria
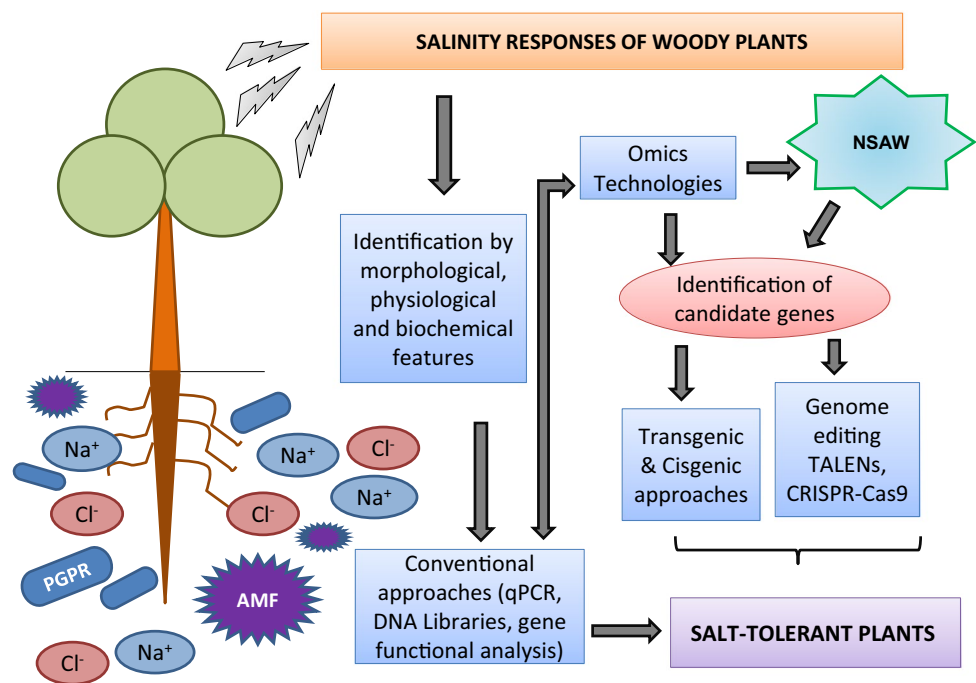
regulation of compartmentalization systems (Fig. 1). In addition, the osmotic adjustment through synthesis and accumulation of compatible solutes contributes significantly to salt tolerance mechanisms, protecting subcellular structures against oxidative stress caused by salinity. Moreover, stress response-related proteins and transcription factors play key roles in the regulation of gene expression in response to salinity in woody plants. Studies of molecular and physiological aspects of these mechanisms are particularly interesting due to their potential contribution to the breeding of new salt-tolerant varieties and to accelerate the domestication of wild salt-tolerant species. Nevertheless, there are numerous research gaps on salt tolerance of woody plants that need to be fulfilled. The identification of specific genes isolated from salt-tolerant woody plants represents a good predictor of stress tolerance phenotypes that may lead to the development of plants with improved stress tolerance. Omics approaches should be included in integral studies of salt responses in woody plants. Thus, the combination of transcriptomics, proteomics, and metabolomics will provide a global view of the plant responses to salinity and will enable us to develop strategies to enhance salt tolerance in different plants (Fig. 2). Nevertheless, this abundant omics information is still at the *in silico* stage, provoking that their validation and functional application in woody plants remain as an unresolved challenge. In addition, more comparative studies are needed between woody and non-woody salt tolerance plants in order to identify potential molecular mechanisms specifically developed by woody plants. We believe that the development of new techniques for the identification of gene networks from naturally stress-adapted woody plants

and the integration of data from multiple sources will shed light on salt tolerance mechanisms particularly developed in woody plants. Furthermore, incorporating these salt tolerance traits into plant breeding programs is a challenge for sustainable agriculture and forestry development during the next decades.

Declarations

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