

# Properties of the halophyte microbiome and their implications for plant salt tolerance

Silke Ruppel<sup>A,B</sup>, Philipp Franken<sup>A</sup> and Katja Witzel<sup>A</sup>

<sup>A</sup>Leibniz-Institute of Vegetable- and Ornamental Crops Grossbeeren/Erfurt e.V., Theodor-Echtermeyer-Weg 1, 14979 Grossbeeren, Germany.

<sup>B</sup>Corresponding author. Email: ruppel@igzev.de

*This paper originates from a presentation at the COST WG2 Meeting 'Putting halophytes to work – genetics, biochemistry and physiology' Hannover, Germany, 28–31 August 2012.*

**Abstract.** Saline habitats cover a wide area of our planet and halophytes (plants growing naturally in saline soils) are increasingly used for human benefits. Beside their genetic and physiological adaptations to salt, complex ecological processes affect the salinity tolerance of halophytes. Hence, prokaryotes and fungi inhabiting roots and leaves can contribute significantly to plant performance. Members of the two prokaryotic domains Bacteria and Archaea, as well as of the fungal kingdom are known to be able to adapt to a range of changes in external osmolarity. Shifts in the microbial community composition with increasing soil salinity have been suggested and research in functional interactions between plants and micro-organisms contributing to salt stress tolerance is gaining interest. Among others, microbial biosynthesis of polymers, exopolysaccharides, phytohormones and phytohormones-degrading enzymes could be involved.

**Additional keywords:** Archaea, Bacteria, fungi, microbial community, microbial–plant interaction, PGPB, salt stress.

Received 23 November 2012, accepted 6 March 2013, published online 9 April 2013

## Introduction

Saline habitats cover a wide area of our planet and halophytes, which are often able to grow in areas with salt concentration higher than ~400 mM (Flowers 2004; English and Colmer 2011), are increasingly used for human benefits. Salinity tolerance of these plants is genetically and physiologically very complex. It is based on genes whose effects are to limit the rate of salt uptake from the soil and the transport of salt through the plant, that adjust the ionic and osmotic balance of cells in roots and shoots, and that regulate leaf development and the onset of senescence (Munns 2005). Most studies on halophytes have concentrated solely on physiological and genetic regulation of salinity resistance. However, plant tolerance is also connected with complex ecological processes within their rhizosphere and phyllosphere. Thus, micro-organisms inhabiting roots and leaves of halophytes may contribute significantly to their well-being and salinity tolerance. Since microbial–plant interactions in saline habitats are sparsely reported, this review focuses on the contribution of micro-organisms to the plant salinity adaptation process. First, we give an overview of how micro-organisms adapt to high surrounding salinity since these mechanisms enable microbes to establish in the same habitats as halophytic plants. Next, we present a summary of studies aimed at characterising the halophyte microbiome. We highlight the modes of interaction between the micro-organisms and the plant's rhizosphere and phyllosphere and conclude with a

discussion on how these findings can be translated into agriculture.

## Microbial salt tolerance and their adaptation mechanisms

Micro-organisms including fungi and prokaryotes, members of the two domains Bacteria and Archaea, are able to adapt to a range of changes in external osmolarity. Until recently it was assumed that under extreme salt concentrations at or near NaCl saturation, Archaea of the family *Halobacteriaceae* were the only active aerobic heterotrophs (Oren 2002). It is now suggested that bacteria also contribute to the aerobic heterotrophic prokaryotic community at the highest salt concentrations. Salt-tolerant bacteria and cyanobacteria have been isolated from a wide range of biotopes at all latitudes. A salt-tolerant bacterium, *Staphylococcus xylosum*, was isolated from a plant pickled in ~7.2% salt (Abou-Elela *et al.* 2010). Salt-tolerant bacterial strains isolated from an extreme alkali-saline soil in north-east China belong to the genera *Bacillus*, *Nesterenkonia*, *Zhihengliuella*, *Halomonas*, *Stenotrophomonas*, *Alkalimonas* and *Litoribacter* (Shi *et al.* 2012) and isolates from the desert of north-western China were identified as *Mesorhizobium alhagi* (Zhou *et al.* 2012). A new genus and species, *Salinibacter ruber*, an extremely halophilic bacterium, has been recently described and isolated from solar saltern crystalliser ponds in Alicante (Anton *et al.* 2002). Even a yeast-like fungus *Hortaea*

*werneckii* is highly halophilic and survives in nearly salt-saturated solutions (Gunde-Cimerman *et al.* 2000).

The mechanisms that allow micro-organisms to grow and survive in saline habitats are mostly similar among different taxa. The main strategies include avoiding high salt concentrations via specific membrane or cell wall constructions, pumping ions out of the cell by ‘salting out’ processes or adjusting their intracellular environment by accumulating non-toxic organic osmolytes and the adaptation of proteins and enzymes to high concentrations of solute ions (Fig. 1).

### Cell wall constructions

The first strategy in surviving high salinity is to avoid high salt concentrations in the cytoplasm and to prevent water loss and plasmolysis through a specific cell wall construction and composition, as known for Archaea and for Cyanobacteria. The cytoplasmic membrane of a halophilic Archaea contains unique ether lipids that cannot easily be degraded, are temperature- and mechanically resistant and highly salt tolerant. Thermophilic and extreme acidophilic Archaea possess membrane-spanning tetraether lipids that form a rigid monolayer membrane that is nearly impermeable to ions and protons. These properties make the archaeal lipid membranes more suitable for life and survival in extreme environments than the ester-type bilayer lipids of Bacteria or Eukaryota (van de Vossenberg *et al.* 1998). The non-cocoid representatives of the Halobacteriales possess a cell wall of an S-layer, whose main constituent is a high molecular weight glycoprotein regularly arranged on a two dimensional lattice, with 4- or 6-fold symmetry. Glycoprotein makes up to 40–50% of the wall protein (Oren 2006) and requires high NaCl concentrations for stability. Similar to most other proteins of halophilic Archaea, the wall protein denatures when suspended in distilled water.

Cyanobacteria are surrounded by two membrane systems. The cell wall is enclosed by an outer membrane that surrounds the periplasmic space, whereas the cytoplasmic membrane surrounds the cytoplasm. Inside the cytoplasm, cyanobacteria contain a third membrane system, thylakoid membranes, which originate from the cytoplasmic membrane and contain the photosynthetic complex. The respiratory electron transport chain is also mostly situated at the thylakoid membranes (Hagemann 2011). In contrast with the heterotrophic

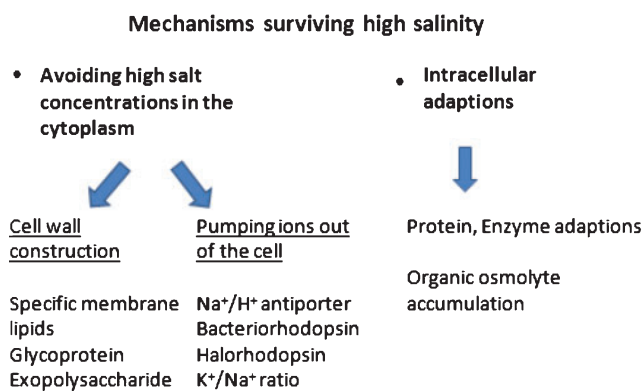
prokaryotes, the mainly photoautotrophic cyanobacteria provide the enhanced energy demand for the extrusion of sodium by an increased photosynthetic activity (Joset *et al.* 1996). *Halococcus* species possess a thick sulfated heteropolysaccharide cell wall that does not require high salt concentrations to maintain its rigidity (Steber and Schleifer 1975). The cocoid *Natronococcus occultus* also has a thick cell wall that retains its shape in the absence of salt, but its structure differs greatly from that of the cell wall polymer of *Halococcus*, consisting of repeating units of a poly(L-glutamine) glycoconjugate (Niemetz *et al.* 1997). Several rhizobacterial species excrete massive amounts of exopolysaccharides which help to mitigate salinity stress by unknown processes (Upadhyay *et al.* 2011). The importance of extracellular polysaccharides (capsular and released polysaccharides) in reducing salt stress was demonstrated by Yoshimura *et al.* (2012) in the cyanobacterium *Nostoc* sp., where the composition ratio of sugars in the extracellular polysaccharide hardly changed under NaCl stress in comparison to normal culture conditions.

Fungal cell walls can become melanised and this has been commonly observed under abiotic stress, when it has been suggested to reduce the loss of compatible solutes (Plemenitaš *et al.* 2008). Comparing different fungi revealed the composition of cell membranes as another adaptation to hypersalinity. In contrast to halosensitive *Saccharomyces cerevisiae* and some halotolerant filamentous fungi, *Hortaea werneckii* is able to maintain its sterol-to-phospholipid ratio at a constant level (Turk *et al.* 2004). This is probably due to the expression of particular fatty acid-modifying enzymes upon salt stress (Gostinčar *et al.* 2009).

### Pumping ions out of the cell

Several bioenergetics processes and ion pumps are involved in the regulation of intracellular ionic concentrations and osmotic adjustment. A proton electrochemical gradient is the driving force for the extrusion of Na<sup>+</sup> from the cell, keeping intracellular Na<sup>+</sup> concentrations relatively low, using Na<sup>+</sup>/H<sup>+</sup> antiporter (Oren 2006). Membranes from halophilic Archaea possess a very high activity of an electrogenic Na<sup>+</sup>/H<sup>+</sup> antiporter. A key role of Na<sup>+</sup> exclusion by different types of Na<sup>+</sup>/H<sup>+</sup> antiporters were also described for the cyanobacterium *Synechococcus* sp. PCC7942 (Waditee *et al.* 2002), the cyanobacterium *Aphanotech halophytica* (Wutipraditkul *et al.* 2005) and the bacterium *Alkalimonas amylolytica* (Zhong *et al.* 2012). In *A. amylolytica* the Na<sup>+</sup>/H<sup>+</sup> antiporter encoding gene *AaNhaD* was able to increase salt tolerance in transgenic tobacco BY-2 cells indicating that *AaNhaD* even in plant cells functions as a pH-dependent tonoplast Na<sup>+</sup>/H<sup>+</sup> antiporter, thus, presenting a new avenue for the genetic improvement of salinity/alkalinity tolerance (Zhong *et al.* 2012).

A crucial function of ion transporters is to maintain and retain favourable cytosolic K<sup>+</sup>/Na<sup>+</sup> ratios in the face of low K<sup>+</sup>/Na<sup>+</sup> ratios in the environment. K<sup>+</sup> is an important monovalent cation inside the cell, where it is not only crucial for salt or turgor acclimation but is also involved in membrane energetics and the regulation of pH, enzyme activities and gene expression (Hagemann 2011). K<sup>+</sup> and Na<sup>+</sup> show similar physiological structures, as the smaller ion Na<sup>+</sup> together with its



**Fig. 1.** Schematic overview of the mechanisms developed by micro-organisms to live and survive in highly saline conditions.

rather large hydration shell mimics the size of  $K^+$ . Therefore, uptake systems for  $K^+$  have difficulties discriminating between these ions, and high  $Na^+$  concentrations in the solution may result in  $K^+$  deficiency (Hagemann 2011). However, the much higher concentration of intracellular  $K^+$  than extracellular  $K^+$  points to an active uptake of this important cation from the solution. Possible regulatory systems are reviewed by Hagemann (2011). Several of the Dead Sea organisms possess unusual properties. A *Halobacterium* sp. has extremely high intercellular  $K^+$  concentration (up to 4.8 M) and extraordinary specificity for  $K^+$  over  $Na^+$ . They adapt to the environment by adjusting their internal inorganic ionic strength, instead of ionic composition, to that of the medium (Nissenbaum 1975).

In contrast with the monovalent cations  $K^+$  and  $Na^+$ , much less is known about the transport of  $Cl^-$ . Similar to  $Na^+$ ,  $Cl^-$  enters cyanobacterial cells in almost equimolar amounts after sudden salt shocks of  $\geq 300$  mM NaCl. Its export, however, is slower than that of  $Na^+$  (Reed *et al.* 1985). In *E. coli*, the majority of  $Cl^-$  transport is done by  $H^+/Cl^-$  exchange transporter and not via channels (Accardi and Miller 2004).

As described for the prokaryotic organisms, fungi use two general strategies to deal with high salt concentrations in the environment. Exclusion of ions have been postulated for fungi, if they are exposed to high salt concentrations and this strategy seems to be more effective for the halophilic *H. werneckii* compared with the only halotolerant *Aureobasidium pullulans* (Kogej *et al.* 2005). Corresponding proteins or genes have not been yet identified, but in *Saccharomyces cerevisiae* gene duplication was detected mostly for genes encoding stress-responsive and transport proteins (Kondrashov *et al.* 2002).

### *Intracellular adaptations*

The presence of high concentrations of solute ions is generally devastating to proteins and other macromolecules, causing aggregation to structural collapse. This is due to the enhancement of hydrophobic interactions, interference with essential electrostatic interactions within or between macromolecules because of charge shielding, and reducing the availability of free water below that required to sustain essential biological processes (Oren 2006). Therefore, the organisms activate various processes: (i) uptake and endogenous biosynthesis of compatible solutes, the nature and amount of which are strain- and salt concentration-dependent; (ii) increased energetic capacity; and (iii) protein and enzyme adaptations. Compatible solutes are low-molecular mass organic compounds, which usually do not have net charge and can be accumulated in high (molar) amounts without negatively interfering with cellular metabolism. The action of compatible solutes is currently best explained by the water exclusion hypothesis (Hagemann 2011). Freshwater cyanobacterial strains with low halotolerance accumulate sucrose or trehalose as their major compatible solutes. Moderately halotolerant (marine) strains are characterised by glycosylglycerol (GG) as their main compatible solute and sometimes glycosylglycerate (GGA) as a secondary compatible solute, whereas halophilic strains that are able to grow in saturated salt concentrations usually synthesise glycine betaine (GB) or glutamate betaine (Hagemann 2011). Only the mostly photoautotrophic cyanobacteria are described

as improving their salt tolerance by an increased photosynthetic activity, which serves as energy source to meet the enhanced energy demand for the extrusion of  $Na^+$  (Joset *et al.* 1996).

Halophilic organisms have to maintain their protein structure and enzymatic activity at high salt concentrations. When comparing amino acid composition of proteins of the Halobacteriaceae to proteins from non-halophilic microorganisms, they contain: (i) a large excess of the acidic amino acids glutamate and aspartate, (ii) a low content of the basic amino acids lysine and arginine, and (iii) a low content of hydrophobic amino acid residues, which is often offset by an increased content of the borderline hydrophobic amino acids serine and threonine (Lanyi 1974). A good reason for increasing the content of acidic amino acids may be the fact that glutamate has the greatest water binding ability of any amino acid residue. This may have important implications when considering the need of any functional protein to maintain a proper hydration shell (Oren 2006). Recently, Bardavid and Oren (2012) performed a comparative analysis of the genome sequences of anaerobic halophilic fermentative bacteria belonging to the order Halanaerobiales, the alkaliphilic *Halanaerobium hydrogeniformans*, and the thermophilic *Halothermothrix orenii* to assess the amino acid composition of their proteomes. Earlier studies demonstrated that members of the Halanaerobiales accumulate KCl rather than organic compatible solutes for osmotic balance and, therefore, the presence of a dominantly acidic proteome was predicted. Past reports indeed showed a large excess of acidic over basic amino acids in whole-cell hydrolysates of selected members of the order. However, the genomic analysis rarely showed unusually high contents of acidic amino acids or low contents of basic amino acids. The apparent excess of acidic amino acids in these anaerobic halophiles reported earlier is due to the high content in their proteins of glutamine and asparagine, which yield glutamate and aspartate upon acid hydrolysis. It is thus suggested that the proteins of the Halanaerobiales, which are active in the presence of high intracellular KCl concentrations, do not possess the typical acidic signature of the 'halophilic' proteins of the Archaea of the order Halobacteriales or of the extremely halophilic bacterium.

Recent analyses of salt-induced changes in proteome maps revealed a more complex insight into the osmolyte accumulation processes of microorganisms. For example, *Halomonas* sp. AAD12 showed significant variations in the expression of proteins involved in osmoregulation, stress response, energy generation and transport under salt stress (Ceylan *et al.* 2012).

Ceylan and colleagues (2012) measured an increase in proline and hydroxyectoine but a decrease in ectoine accumulation at elevated salinity. Fungi also accumulate compatible solutes for dealing with internal high salt concentrations. This has been analysed in the salt sensitive yeast *S. cerevisiae* and in some halotolerant filamentous fungi; it was shown that mostly glycerol is accumulated upon increasing salt concentrations (Blomberg and Adler 1992). Glycerol is also the compatible solute found in highest concentrations in the halophilic black yeast *H. werneckii* (Kogej *et al.* 2007). Other modifications upon exposure to high salt concentrations concern the microsomal HMG-CoA reductase (Vaupotic and Plemenitas 2007) and the glycerol-3-phosphate

dehydrogenase (Lenassi *et al.* 2011). Non-targeted approaches have been also applied for elucidating mechanisms underlying the response of fungi to hypersalinity (e.g. Li *et al.* 2003). By using subtractive hybridisation, numerous *H. werneckii* genes that respond to moderately and extremely high salt concentrations were identified (Vaupotic and Plemenitas 2007). Among those, 13 did not show any similarity to sequences in databases suggesting very specific adaptations of the black yeast to hypersalinity. Further work could aim to discover the functions of the corresponding proteins. The mechanisms of how high salinity is sensed by fungal organisms has been investigated mainly in *S. cerevisiae*. The pathway involved is called 'high osmolarity glycerol' (HOG) and involves a well-studied mitogen-activated protein kinase cascade (Parmar *et al.* 2011). Such a sensing system has been also identified in *H. werneckii* (Plemenitas *et al.* 2008). However, exactly how this contributes to the tolerance to extremely high salt concentrations is unclear.

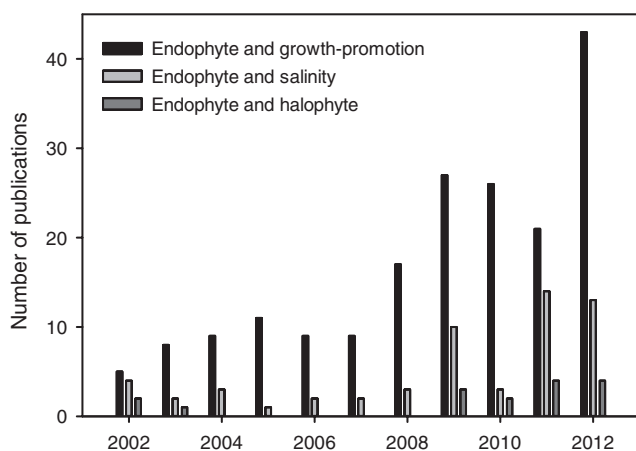
### Interaction of micro-organisms with host plants

The microbiome of glycophytes under normal growth conditions or under salinity stress has become a research focus over the last 10 years (Rosenblueth and Martinez-Romero 2006). However, the prokaryotic community composition of halophytes has only rarely been investigated and the phyllosphere even more sparsely than the rhizosphere (Fig. 2). Therefore, here we can only refer to a limited number of investigations that tried to classify (taxonomically) and count microbial species and numbers (Table 1). The halophyte *Halocnemum strobilaceum*, naturally inhabiting hypersaline coastal areas of the Arabian Gulf, harbour up to  $8.1 \times 10^4 \text{ g}^{-1}$  and  $3 \times 10^2 \text{ g}^{-1}$  extremely halophilic oil-utilising micro-organisms in the rhizosphere and phyllosphere respectively (Al-Mailem *et al.* 2010). Frequent genera in the rhizosphere were affiliated to the Archaea *Halobacterium* sp. and *Halococcus* sp., the firmicute *Brevibacillus borstenlensis*, and the proteobacteria *Pseudoalteromonas ruthenica* and *Halomonas sinaensis*. The phyllospheric microflora consisted of the dimorphic yeast *Candida utilis* and the two proteobacteria

*Ochrobactrum* sp. and *Desulfovibrio* sp. All the strains, except *C. utilis*, which could not tolerate salinities  $>2 \text{ M NaCl}$ , grew also in media with salinities ranging between 1 and 4 M NaCl, with optimum growth between 1 and 2 M NaCl (Al-Mailem *et al.* 2010). That means bacteria inhabiting that halophytic plant rhizosphere and phyllosphere seem to be adapted to high salinities.

Similar salt-related adaptations were assumed in the rhizobium population of *Acacia* spp. (Thrall *et al.* 2009). Studies of *Acacia* spp. in Australia and Algeria, where the shrubby legumes dominate many ecosystems where dryland salinity is a major issue, suggested a high phylogenetic bacterial diversity (Thrall *et al.* 2009; Boukhatem *et al.* 2012). Based on 16S rRNA gene sequence comparisons, 48 isolates ranked into 10 phylogenetic groups representing five bacterial genera, namely, *Ensifer*, *Mesorhizobium*, *Bradyrhizobium* and *Ochrobactrum* (Boukhatem *et al.* 2012). The genetic identification of novel species suggested that the diversity of rhizobia associated with Australian *Accacia* spp. is significantly greater than previously expected and documented a community differentiation in relation to salt stress (Thrall *et al.* 2009). Rueda-Puente *et al.* (2010) detected, for the first time, *Rhizobium* spp. and *Bacillus* spp. species in the rhizosphere of the halophyte *Salicornia bigelovii* (Chenopodiaceae; now in the Amaranthaceae). Recently, the roots and rhizosphere of halophytes have been found to be inhabited by salt-tolerant bacteria. *Haloferula luteola* sp. nov., a gram-negative, non-spore-forming, endophytic (living within plant tissues) bacterium (strain YC6886<sup>5</sup>) was isolated from the root of the halophyte *Rosa rugosa*, which inhabits coastal areas of Namhae Island of the southern coast of Korea and grows optimally with 300–500 mM NaCl (Bibi *et al.* 2011). Another salt-tolerant (growth up to 680 mM NaCl) bacterial strain, *Brachybacterium saurashtrense* sp. nov., was isolated from the roots of *Salicornia brachiata*, an extreme halophyte (Gontia *et al.* 2011).

Most fungi detected in halophytes belong to the phylum *Glomeromycota*, which live with the roots of land plants in an obligate biotrophic symbiosis called arbuscular mycorrhiza (Newman and Reddell 1987). Although spore germination, hyphal growth and root colonisation of arbuscular mycorrhizal (AM) fungi is inhibited by high salt concentrations (Juniper and Abbott 1993; Juniper and Abbott 2006), plants in saline habitats can be highly colonised. The roots of, for example, sea aster (*Aster tripolium*) in marsh lands appeared to be fully colonised by AM fungal structures (Hildebrandt *et al.* 2001), but also plants from other saline ecosystems such as mangroves, in a river delta or in a desert riparian forest were colonised (Sengupta and Chaudhuri 2002; Wang *et al.* 2004; Yang *et al.* 2008). A survey along a salt gradient showed a negative correlation between salt concentrations and mycorrhization of roots of the saltbush *Atriplex* spp. (Aguilera *et al.* 1998). However, cluster analysis in a more detailed investigation revealed that not soil salinity and ion concentrations, but soil pH, the percentage of clay and available P correlates with AM fungal spore numbers (Aliasgharzadeh *et al.* 2001). Another factor that has to be taken into account in such habitats is drought, which can be more important than salt for the abundance of AM fungi in halophytes (Füzy *et al.* 2008).



**Fig. 2.** Publication activity in the area of the plant microbiomes in the last 10 years. Shown are the number of articles published per year in Web of Science for the terms 'endophyte and growth-promotion', 'endophyte and salinity' and 'endophyte and halophyte' (2002–12).

**Table 1. Micro-organisms associated with halophytic plants and their halophilic or halotolerant properties**

Micro-organisms	Halotolerant or halophilic	Associated with halophytes	Reference
<i>Archaea</i>			
<i>Halococcus</i>	Halophilic	<i>Halocnemum strobilaceum</i> rhizosphere	Niemetz <i>et al.</i> (1997), Al-Mailem <i>et al.</i> (2010)
<i>Bacteria</i>			
<i>Aeromonas</i>	Not studied	<i>Sesuvium portulacastrum</i>	Anburaj <i>et al.</i> (2012)
<i>Bacillus</i> sp.	Not studied	<i>Salicornia bigelovii</i>	Rueda-Puente <i>et al.</i> (2010)
		<i>Sesuvium portulacastrum</i>	Bian <i>et al.</i> (2011); Anburaj <i>et al.</i> (2012)
<i>Brachybacterium</i>	Halotolerant	<i>Salicornia brachiata</i> rhizosphere	Jha <i>et al.</i> (2012)
<i>B. saurashtrense</i>	Growth at 0.68 M NaCl	<i>Salicornia brachiata</i>	Gontia <i>et al.</i> (2011)
<i>Bradyrhizobium</i>	Not studied	<i>Acacia</i> spp.	Boukhatem <i>et al.</i> (2012)
<i>Brevibacillus borstenlensis</i>	Halophilic	<i>Halocnemum strobilaceum</i> rhizosphere	Al-Mailem <i>et al.</i> (2010)
<i>Brevibacterium casei</i>	Halotolerant	<i>Salicornia brachiata</i> rhizosphere	Jha <i>et al.</i> (2012)
<i>Corynebacterium</i>	Not studied	<i>Sesuvium portulacastrum</i>	Anburaj <i>et al.</i> (2012)
<i>Cronobacter sakazakii</i>	Halotolerant	<i>Salicornia brachiata</i> rhizosphere	Jha <i>et al.</i> (2012)
<i>Desulf vibrio</i> sp.	Tolerate 1–4 M NaCl	<i>Halocnemum strobilaceum</i> phyllosphere	Al-Mailem <i>et al.</i> (2010)
<i>Ensifer</i>	Not studied	<i>Acacia</i> spp.	Boukhatem <i>et al.</i> (2012)
<i>Escherichia</i>	Not studied	<i>Sesuvium portulacastrum</i>	Anburaj <i>et al.</i> (2012)
<i>Haloferula luteola</i> sp. nov	Halotolerant	<i>Rosa rugosa</i>	Bibi <i>et al.</i> (2011)
<i>Halomonas sinaensis</i>	Tolerate 1–4 M NaCl	<i>Halocnemum strobilaceum</i> rhizosphere	Al-Mailem <i>et al.</i> (2010)
	Halophilic	<i>Salicornia brachiata</i> rhizosphere	Jha <i>et al.</i> (2012)
<i>Haererehalobacter</i>	Halotolerant	<i>Salicornia brachiata</i> rhizosphere	Jha <i>et al.</i> (2012)
<i>Mesorhizobium</i>	Halotolerant	<i>Salicornia brachiata</i> rhizosphere	Jha <i>et al.</i> (2012)
		<i>Acacia</i> spp.	Boukhatem <i>et al.</i> (2012)
<i>Ochrobactrum</i>	Not studied	<i>Acacia</i> spp.	Boukhatem <i>et al.</i> (2012)
<i>Ochrobactrum</i> sp.	Tolerate 1–4 M NaCl	<i>Halocnemum strobilaceum</i> phyllosphere	Al-Mailem <i>et al.</i> (2010)
<i>Pseudomonas</i>	Not studied	<i>Sesuvium portulacastrum</i>	Anburaj <i>et al.</i> (2012)
<i>P. maricaloris</i>	Not studied	<i>Avicennia marina</i>	El-Tarabily and Youssef (2011)
<i>Pseudoalteromonas ruthenica</i>	Halophilic	<i>Halocnemum strobilaceum</i> rhizosphere,	Al-Mailem <i>et al.</i> (2010)
		<i>Salicornia brachiata</i> rhizosphere	Jha <i>et al.</i> (2012)
<i>Rhizobium</i> sp.	Not studied	<i>Acacia</i> spp.	Thrall <i>et al.</i> (2009)
		<i>Salicornia bigelovii</i>	Rueda-Puente <i>et al.</i> (2010)
<i>R. radiobacter</i>	Halotolerant	<i>Salicornia brachiata</i> rhizosphere	Jha <i>et al.</i> (2012)
<i>Salinibacter ruber</i>	Halophilic	Solar saltern crystalliser pond	Anton <i>et al.</i> (2002)
<i>Vibrio</i>	Halotolerant	<i>Salicornia brachiata</i> rhizosphere	Jha <i>et al.</i> (2012)
<i>Zhihengliuella</i>	Halotolerant	<i>Salicornia brachiata</i> rhizosphere	Jha <i>et al.</i> (2012)
<i>Fungi</i>			
<i>Candida utilis</i>	Tolerate <2 M NaCl	<i>Halocnemum strobilaceum</i> phyllosphere	Al-Mailem <i>et al.</i> (2010)
dark septate endophytes	Not studied	Fourwing salt bush rhizosphere	Jumpponen and Trappe (1998); Barrow and Aaltonen (2001); Sonjak <i>et al.</i> (2009); Barrow <i>et al.</i> (2004)
<i>Glomeromycota</i>		<i>Aster tripolium</i> rhizosphere	Hildebrandt <i>et al.</i> (2001); Juniper and Abbott (1993); Juniper and Abbott (2006); Sengupta and Chaudhuri (2002); Wang <i>et al.</i> (2004); Yang <i>et al.</i> (2008);
		Mangroves rhizosphere	Aguilera <i>et al.</i> (1998); Landwehr <i>et al.</i> (2002); Sonjak <i>et al.</i> (2009)
<i>Glomus geosporum</i>		<i>Atriplex</i> spp. rhizosphere	
<i>Glomus caledonium</i>			

Attempts to identify the AM fungal species associated with plants in saline habitats revealed that at least in Europe, most isolates belong to the *Glomus geosporum*/*Glomus caledonium* cluster (Hildebrandt *et al.* 2001; Landwehr *et al.* 2002; Sonjak *et al.* 2009).

In addition to arbuscular mycorrhiza, some papers report the occurrence of so-called dark septate endophytes (DSEs). These root colonisers can be found in diverse habitats (Jumpponen and

Trappe 1998) and have been detected in saline environments (Barrow and Aaltonen 2001; Sonjak *et al.* 2009). These associations can be obligate: it is, for example, impossible to remove DSEs from the fourwing salt bush even if the plants have been grown from calli (Barrow *et al.* 2004). Fungi of the order Sebaciniales (Basidiomycota) are also present in roots of all ecosystems (Weiß *et al.* 2011) and further work is needed to screen plants growing in saline habitats for species of this order.

One representative is the model endophyte *Piriformospora indica*, which has been isolated from the Thar desert in India (Verma *et al.* 1998). Therefore, it might also tolerate higher salt concentrations as it has been shown that it can confer salt tolerance to plants (Waller *et al.* 2005).

One study conducted in a Mediterranean salt marsh from semiarid south-eastern Spain to determine the influence of eight halophytes (*Asteriscus maritimus*, *Arthrocnenium macrostachyum*, *Frankenia corymbosa*, *Halimione portulacoides*, *Limonium cossonianum*, *Limonium caesium*, *Lygeum spartum* and *Suaeda vera Forsskal*) on the soil microbiological and biochemical properties of the rhizosphere (labile C fractions, biomass C, oxidoreductases, hydrolases) and aggregate stabilisation. Results showed that soil microbial activity and microbial-related soil properties, such as aggregate stability, were determined by the species of the halophyte (Caravaca *et al.* 2005). However, microbial community composition and microbial counts were not recorded. From the halophyte *Prosopis strombulifera*, grown under extreme salinity, 29 different bacterial strains were detected, which are grouped into seven clusters according to similarity (Sgroy *et al.* 2009).

From these first microbial investigations of halophytes it seems that, compared with glycophytes, an accumulation of specialised micro-organisms living in the rhizosphere and inside halophytic plants exists. Comprehensive studies and comparison of the halophyte and glycophyte microbiomes are required to evaluate that assumption. Currently the low number of investigations does not allow a general conclusion regarding the microbial impact on the environmental adaptation processes of halophytes. An improved understanding of the microbial community composition in halophilic plants, however, may open new opportunities to broaden plant growth in fragile environments.

### Influence of micro-organisms on salinity tolerance of halophytes

The rhizosphere and phyllosphere of plants is colonised by a range of micro-organisms and growing investments in this research aims at unravelling the mechanisms underlying these beneficial or pathogenic interactions. Microbes are attracted to plant roots by a specific blend of root exudates containing sugars, amino acids and organic acids, which are assimilated and metabolised. The composition of actively and passively released primary and secondary metabolites varies with plant species, developmental stage and environmental conditions. It has been demonstrated that the plant influences the soil microbial communities and its colonising microbiota via the exudate composition (Bais *et al.* 2006; Faure *et al.* 2009; Doornbos *et al.* 2012). The beneficial effects provoked by endophytes result from nitrogen fixation, phytohormone production, supply of nutrients and pathogen suppression (Rosenblueth and Martinez-Romero 2006; Hardoim *et al.* 2008) and those mechanisms also account for the alleviating effects of micro-organisms when host plants face unfavourable environmental conditions. Two recent reviews are devoted to the protective microbial processes conferring abiotic stress tolerance to plants (Dimkpa *et al.* 2009; Dodd and Perez-Alfocea 2012). Halophytic

plants harbour a variety of micro-organisms and in the following we summarise the contribution of micro-organisms to salt tolerance in this specific plant group.

### Plant nutritional status

The growth-promoting effect of most micro-organisms emanates from their ability to increase the availability and uptake of nitrogen, carbon, and minerals. Bacteria residing in halophytic plants are known to (i) produce exopolysaccharide and form rhizosheaths, where mucilage binds a layer of sand grains tightly to the root, providing a special habitat for dinitrogen fixing bacteria (Bergmann *et al.* 2009); (ii) fix atmospheric nitrogen and provide ammonium for plant metabolic processes; and (iii) enrich C and N (Nabeel *et al.* 2010). Hence, the presence of the dinitrogenase reductase (*nif*) gene family is frequently used in microbiota screens for identification of beneficial strains (Juraeva *et al.* 2006). The *nifH* gene has been found in bacterial isolates from roots of *Salicornia brachiata* belonging to the genera *Brachybacterium*, *Brevibacterium* and *Zhihengliuella* (Jha *et al.* 2012).

Other micro-organisms are also referred to as biofertilisers because of their ability to solubilise phosphates and mobilise iron, thereby facilitating plant growth (Vessey 2003).  $\text{Ca}_3(\text{PO}_4)_2$ ,  $\text{AlPO}_4$  and  $\text{FePO}_4$  solubilising bacteria have been isolated from various halophytic plants, from the rhizosphere of four halophytic weeds grown in the Pakistanian Khewra salt range (Yasmin and Bano 2011), the mangrove *Avicennia marina* rhizosphere (El-Tarabily and Youssef 2010) and the oilseed halophyte *Salicornia bigelovii* (Bashan *et al.* 2000). Among the rarely identified bacterial strains are *Arthrobacter*, *Bacillus* (Banerjee *et al.* 2010), *Azospirillum*, *Vibrio*, *Bacillus*, *Phyllobacterium* species (Bashan *et al.* 2000) and *Oceanobacillus picturae* (El-Tarabily and Youssef 2010). When the oilseed halophyte *Salicornia bigelovii* was inoculated with eight species of halotolerant bacteria, including *Azospirillum*, *Vibrio*, *Bacillus* and *Phyllobacterium*, phosphate content in foliage increased compared with non-inoculated plants (Bashan *et al.* 2000). A screen of the mangrove *Avicennia marina* rhizosphere identified 129 bacterial strains with the ability to solubilise rock phosphate, with *Oceanobacillus picturae* being able to mobilise 97% of this mineral (El-Tarabily and Youssef 2010). These activities provide major components in ameliorating the growth-restraining effects of salinity.

The central feature of mycorrhizal symbiosis is the exchange of nutrients between the partners of the symbiosis. This enables plants to receive mineral nutrients even at high salt concentrations where usually the uptake is hampered (for review see Evelin *et al.* 2009). Mycorrhizal plants harbour higher phosphorus contents and are able to keep a better  $\text{K}^+:\text{Na}^+$  ratio than their non-mycorrhizal counterparts (Giri *et al.* 2007). For chloride ions, however, differing results are reported. Mycorrhization of roots can reduce their uptake of  $\text{Cl}^-$  (Zuccarini and Okurowska 2008), but enhanced accumulation of  $\text{Cl}^-$  has been also detected (Buwalda *et al.* 1983). Salt stress impacts on chlorophyll biosynthesis and one reason is the reduced uptake of magnesium. Giri *et al.* (2003) showed that this can be at least partially overcome in mycorrhizal plants. Mineral nutrition in the interaction between plants and other root-endophytic fungi

is a matter of debate and the uptake of mineral nutrients by halophytes has not yet been specifically analysed.

#### Plant hormone status

The production or metabolism of plant hormones and their precursors is widely documented for plant-associated micro-organisms and it is an astonishing demonstration of the close evolution between plants and micro-organisms. A large body of physiological data related to the modulation of abscisic acid (ABA), auxins, cytokinins, ethylene, gibberellins, jasmonic acid (JA) and salicylic acid (SA) in plants upon infection with bacteria proves its significance to plant performance (Dodd *et al.* 2010).

The presence of 1-aminocyclopropane-1-carboxylic acid (ACC) deaminase is frequently described for halotolerant bacteria residing in plants. The enzyme converts the ethylene precursor ACC into ammonia and  $\alpha$ -ketobutyrate, thus, lowering the ethylene concentration within plant tissues and its constraining effect on root elongation and general plant growth. A screen of 140 halotolerant bacterial isolates from coastal soil of the South Korea Yellow Sea for plant-growth-promoting effects led to the identification of 25 strains exhibiting different levels of ACC deaminase activity and those belonging to the genera of *Arthrobacter*, *Bacillus*, *Brevibacterium*, *Corynebacterium*, *Exiguobacterium*, *Halomonas*, *Micrococcus*, *Oceanimonas*, *Planococcus* and *Zhihengliuella* (Siddikee *et al.* 2010). Recent reports on halotolerant ACC-deaminase-producing bacteria isolated from halophytic plants indicate that this is an essential mechanism for salt stress alleviation. Six out of 29 endophytic strains isolated from the halophyte *Prosopis strombulifera* tested positive for ACC deaminase activity (Sgroy *et al.* 2009). Novel diazotrophic halotolerant bacteria from roots of *Salicornia brachiata* featured ACC deaminase activity and isolates included *Brachybacterium saurashtrense*, *Brevibacterium casei*, *Cronobacter sakazakii*, *Haererehalobacter*, *Halomonas*, *Mesorhizobium*, *Pseudomonas*, *Rhizobium radiobacter*, *Vibrio* and *Zhihengliuella* (Jha *et al.* 2012). Additionally, reinoculation of axenically cultured *S. brachiata* with *Brachybacterium saurashtrense* and *Pseudomonas* increased growth parameters significantly under salt stress. The screening of root, stalk and leaf of *Suaeda salsa* allowed for the identification of four ACC deaminase-containing strains: *Pantoea agglomerans*, *Pseudomonas oryzae*, *Pseudomonas putida*, and *Pseudomonas* sp. (Teng *et al.* 2010). Sixty-two different bacterial isolates were extracted from the rhizosphere of the mangrove *Avicennia marina*. One of those, *Pseudomonas maricaloris*, showed high levels of ACC deaminase activity, decreased endogenous levels of ACC in seedlings under salinity stress and improved plant performance (El-Tarably and Youssef 2011). A mutant strain of *P. maricaloris* without ACC deaminase failed to ameliorate the effects of salinity in mangrove seedlings, demonstrating the impact of modulating the plant's ethylene status to confer salt tolerance.

Production of auxins, especially indole-3-acetic acid (IAA), is frequently found in growth-promoting endophytes (Witzel *et al.* 2012). Auxins play a cardinal role in elevation of root growth and development, and act antagonistically to ethylene.

Thus, managing auxin production in halophytic plants by endophytic microbes might be an important tool in conferring salt tolerance. IAA production has been found in (i) salt tolerant rhizobacteria (*Arthrobacter* sp., *Bacillus pumilus*, *Halomonas* sp., *Nitrincola lacisaponensis*, and *Pseudomonas mendocina*) isolated from highly saline habitats (Tiwari *et al.* 2011) and (ii) species of *Bacillus*, *Brevundimonas*, *Exiguobacterium*, *Halobacillus*, *Oceanobacillus*, *Serratia*, *Staphylococcus* and *Vibrio* originating from four halotolerant plants from a Chinese coastal sandbank (Bian *et al.* 2011). Production of IAA, ABA and gibberellins has also been identified in as yet unclassified bacterial strains isolated from the rhizosphere of halophytic weeds from the Pakistani Khewra salt range (Naz *et al.* 2009) as well as from the halophyte *Prosopis strombulifera* (Piccoli *et al.* 2011). Tiwari and colleagues (2011) demonstrated an increase in the fitness of wheat plants grown in salt-affected soil when they were inoculated with salt tolerant IAA producing rhizobacteria.

Mycorrhizal fungi exert impact on nearly all phytohormones and this has been shown for jasmonate and abscisic acid (Hause *et al.* 2007; Herrera-Medina *et al.* 2007). The involvement of phytohormones in the interaction between plants and the root endophyte *Piriformospora indica* is also well investigated (Qiang *et al.* 2012). The role of phytohormones for increasing salt tolerance has, however, neither been analysed for mycorrhizal nor for other root endophytic fungi.

#### Plant antioxidant status

Plants have evolved a range of tools in order to protect their cells from reactive oxygen species formed on the onset of osmotic and salt stress. Oxidation of membrane lipids, proteins or DNA is prevented by scavenging enzymes, including superoxide dismutase, catalase, and ascorbate peroxidase. Micro-organisms use similar approaches to cope with oxidative stress. A recent review focuses on the mediation of reactive oxygen species in plants by fungal endophytes (Hamilton *et al.* 2012). It is likely that micro-organisms use the same mechanisms to alleviate salt stress effects in halophytes as in other plants; however, detailed information remains scarce. The halophytic *Sesuvium portulacastrum* was grown on sterilised and non-sterilised soil during salinity treatment. Plants grown on non-sterilised soil, containing bacteria from the genera *Bacillus*, *Aeromonas*, *Pseudomonas*, *Corynebacterium* and *Escherichia*, revealed lower levels of antioxidant enzymes indicating a reduced degree of oxidative stress (Anburaj *et al.* 2012). Organisms described to alleviate salinity in halophytes are likewise known to colonise glycophytes and often they are described as improving plant growth and plant immunity against pathogens and abiotic stress (Shin *et al.* 2007; Bibi *et al.* 2012).

The production of antioxidants and the expression of enzymes involved in scavenging of reactive oxygen species is probably the mechanism most analysed in seeking explanations of how mycorrhizal fungi are able to increase abiotic stress tolerance of plants (Porcel *et al.* 2012). Mycorrhizal plants contain higher concentrations of ascorbate and glutathione and harbour a greater activity of superoxide dismutase, catalase and ascorbate peroxidase than the corresponding non-mycorrhizal

control plants (Wu *et al.* 2010; Borde *et al.* 2011; Latef and Chaoxing 2011). Since plants show this response to mycorrhization even before they are treated with high salt concentrations, one can suggest that colonisation of the roots by an AM fungus makes the plants more tolerant to high soil salinity and also to other osmotic stresses. Similar responses have been observed in plants when colonised by the non-mycorrhizal endophyte *P. indica* where it was proposed as being involved in general abiotic stress tolerance (Baltruschat *et al.* 2008).

#### Production of exopolysaccharides

Both plant and the plant colonising bacteria may produce exopolysaccharides as a mechanism to shield the root from excessive salt concentrations. Mangroves and some other halophytic plants produce a mixture of viscous exopolysaccharides, so called mucilage, in xylem vessels of roots and shoots that have high water-binding capacity and may act as water reserves during exposure to salinity. Production of mucilage in the halophyte *Kosteletzkya virginica* is positively correlated with salt levels and composition of polysaccharides differs between plant organs and treatments (Ghanem *et al.* 2010). Equally, micro-organisms produce exopolysaccharides, mainly during biofilm formation (Danese *et al.* 2000), but also during the establishment of symbiotic interactions (Jones *et al.* 2007). Microbial biofilms are found on roots of every terrestrial plant (Danhorn and Fuqua 2007) and proper adhesion of microbes to roots through exopolysaccharides may also aid shielding the root from excessive salt concentrations. Exopolysaccharide-producing bacterial strains, including *Aeromonas hydrophila/caviae* and *Bacillus* sp., were isolated from roots of salt-adapted wheat plants and reinoculation restricted the Na<sup>+</sup> uptake by roots (Ashraf *et al.* 2004). Similarly, exopolysaccharide-producing rhizobacteria isolated from salt-adapted wheat plants reduced the plants Na<sup>+</sup> availability and conferred salt tolerance upon inoculation in stress experiments (Upadhyay *et al.* 2011). Although the application of mucilage-producing bacteria might be a promising tool in alleviating salt stress effects, many of the underlying mechanisms still remain unresolved.

#### Biocontrol

The induction of plant systemic resistance by growth-promoting micro-organisms through various pathways led to the application of selected strains for diseases control (van Loon *et al.* 1998). Mechanisms of how microbes reduce plant diseases include production of antibiotics, competition with pathogens for nutrients, and induction of systemic resistance in the host (Lugtenberg and Kamilova 2009). A screen of 17 phyllosphere endophytes isolated from the Karangkadu mangrove ecosystem in India identified eight strains with a broad spectrum of antibacterial activity (Sundaram *et al.* 2011a, 2011b). Induction of resistance against pathogens has been also described for the interaction of plant roots with mycorrhizal fungi (Jung *et al.* 2012), with dark septate endophytes (Andrade-Linares *et al.* 2011) and with the endophyte *Piriformospora indica* (Waller *et al.* 2005). Although a large body of data was generated for the trilateral relationship

between pathogens, growth-promoting microbes, and glycophytes, respective investigations concerning interactions with halophytes are scarce (Fig. 2). As the use of micro-organisms to counteract pathogen attack is environmentally friendly and locally effective, more research activity in this field is expected within the next years.

#### Other mechanisms

Another important mechanism of facing osmotic stress is the accumulation of organic solutes and this has been also found in halophytes (Flowers and Colmer 2008); consequently the amino acid proline has been the subject of research into understanding increases in salt tolerance after colonisation of plants with endophytes. Results with AM fungi, however, have been variable and suggest that proline accumulation is, in most cases, not the cause but the effect of salt tolerance (Ruiz-Lozano *et al.* 2012). Osmoregulation can be also achieved with betaines and with sugars. Both are increased in mycorrhizal plants and were suggested as being involved in salt tolerance (Porcel and Ruiz-Lozano 2004; Manchanda and Garg 2011).

In the case of fungi, the growth of hyphae in the rhizosphere has a particular impact on soil physical properties (Augé *et al.* 2001). Soil aggregates are more stable if colonised with hyphae, this in turn influences water retention (Rillig *et al.* 2010) and ultimately has an impact on the tolerance of plants to osmotic stresses (Augé *et al.* 2007).

#### Agronomic and environmental prospects

Comparative population studies indicate that plants in different habitats contain different microbiomes (Berendsen *et al.* 2012). The identification of halophyte-associated bacteria and fungi, the analysis of their interaction with the host and how this interaction contributes to the survival of both partners will be essential to develop strategies for protecting these plants. Most examples of increased salt tolerance are reported where glycophytes have been inoculated with plant growth promoting bacteria or mycorrhizal fungi (Nabti *et al.* 2010; del Amor and Cuadra-Crespo 2012; Dodd and Perez-Alfocea 2012). Many experiments have been conducted with standard inocula meaning that the micro-organisms being used were not well adapted to hypersaline conditions. Direct comparisons, however, showed (for example, for mycorrhizal fungi) that an isolate from a saline habitat is more able to improve the tolerance of a plant than a corresponding reference strain (Ruiz-Lozano and Azcon 2000). Therefore, it seems necessary to exploit the potential of halophytes and their inhabitants because they could be a valuable resource for plant production systems where soils or irrigation water contain high salt concentrations. This will be a prerequisite for expanding efficient plant production areas into salt affected soils and to get less dependent on fresh water, which will be increasingly important in future agriculture in many regions of the world.

#### Acknowledgements

This research was supported by the COST action FA 0901 'Putting halophytes to work – from genes to ecosystems'. The authors would like to thank Professor Tim Flowers for his critical reading and very helpful comments.



## References

- Abou-Elela SI, Kamel MM, Fawzy ME (2010) Biological treatment of saline wastewater using a salt-tolerant microorganism. *Desalination* **250**(1), 1–5. doi:10.1016/j.desal.2009.03.022
- Accardi A, Miller C (2004) Secondary active transport mediated by a prokaryotic homologue of ClC Cl<sup>-</sup> channels. *Nature* **427**(6977), 803–807. doi:10.1038/nature02314
- Aguilera LE, Gutierrez JR, Moreno RJ (1998) Vesiculo arbuscular mycorrhizae associated with saltbushes *Atriplex* spp. (Chenopodiaceae) in the Chilean arid zone. *Revista Chilena de Historia Natural* **71**(3), 291–302.
- Al-Maillem D, Sorkhoh N, Marafie M, Al-Awadhi H, Eliyas M, Radwan S (2010) Oil phytoremediation potential of hypersaline coasts of the Arabian Gulf using rhizosphere technology. *Bioresource Technology* **101**(15), 5786–5792. doi:10.1016/j.biortech.2010.02.082
- Aliasgharzadeh N, Rastin NS, Towfighi H, Alizadeh A (2001) Occurrence of arbuscular mycorrhizal fungi in saline soils of the Tabriz Plain of Iran in relation to some physical and chemical properties of soil. *Mycorrhiza* **11**(3), 119–122. doi:10.1007/s005720100113
- Anburaj R, Nabeel MA, Sivakumar T, Kathiresan K (2012) The role of rhizobacteria in salinity effects on biochemical constituents of the halophyte *Sesuvium portulacastrum*. *Russian Journal of Plant Physiology: a Comprehensive Russian Journal on Modern Phytophysiology* **59**(1), 115–119. doi:10.1134/S1021443712010025
- Andrade-Linares DR, Grosch R, Restrepo S, Krumbein A, Franken P (2011) Effects of dark septate endophytes on tomato plant performance. *Mycorrhiza* **21**(5), 413–422. doi:10.1007/s00572-010-0351-1
- Anton J, Oren A, Benlloch S, Rodriguez-Valera F, Amann R, Rossello-Mora R (2002) *Salinibacter ruber* gen. nov., sp. nov., a novel, extremely halophilic member of the Bacteria from saltern crystallizer ponds. *International Journal of Systematic and Evolutionary Microbiology* **52**, 485–491.
- Ashraf M, Hasnain S, Berge O, Mahmood T (2004) Inoculating wheat seedlings with exopolysaccharide-producing bacteria restricts sodium uptake and stimulates plant growth under salt stress. *Biology and Fertility of Soils* **40**(3), 157–162. doi:10.1007/s00374-004-0766-y
- Augé RM, Stodola AJW, Tims JE, Saxton AM (2001) Moisture retention properties of a mycorrhizal soil. *Plant and Soil* **230**(1), 87–97. doi:10.1023/A:1004891210871
- Augé RM, Toler HD, Moore JL, Cho K, Saxton AM (2007) Comparing contributions of soil versus root colonization to variations in stomatal behavior and soil drying in mycorrhizal *Sorghum bicolor* and *Cucurbita pepo*. *Journal of Plant Physiology* **164**(10), 1289–1299. doi:10.1016/j.jplph.2006.08.005
- Bais HP, Weir TL, Perry LG, Gilroy S, Vivanco JM (2006) The role of root exudates in rhizosphere interactions with plants and other organisms. *Annual Review of Plant Biology* **57**, 233–266. doi:10.1146/annurev.arplant.57.032905.105159
- Baltruschat H, Fodor J, Harrach BD, Niemczyk E, Barna B, Gullner G, Janeczko A, Kogel K-H, Schäfer P, Schwarczinger I, Zuccaro A, Skoczowski A (2008) Salt tolerance of barley induced by the root endophyte *Piriformospora indica* is associated with a strong increase in antioxidants. *New Phytologist* **180**(2), 501–510. doi:10.1111/j.1469-8137.2008.02583.x
- Banerjee S, Palit R, Sengupta C, Standing D (2010) Stress induced phosphate solubilization by *Arthrobacter* sp. and *Bacillus* sp. isolated from tomato rhizosphere. *Australian Journal of Crop Science* **4**(6), 378–383.
- Bardavid RE, Oren A (2012) The amino acid composition of proteins from anaerobic halophilic bacteria of the order Halanaerobiales. *Extremophiles* **16**(3), 567–572. doi:10.1007/s00792-012-0455-y
- Barrow JR, Aaltonen RE (2001) Evaluation of the internal colonization of *Atriplex canescens* (Pursh) Nutt. roots by dark septate fungi and the influence of host physiological activity. *Mycorrhiza* **11**(4), 199–205. doi:10.1007/s005720100111
- Barrow JR, Osuna-Avila P, Reyes-Vera I (2004) Fungal endophytes intrinsically associated with micropropagated plants regenerated from native *Bouteloua eriopoda* Torr. and *Atriplex canescens* (Pursh) Nutt. *In Vitro Cellular & Developmental Biology. Plant* **40**(6), 608–612. doi:10.1079/IVP2004584
- Bashan Y, Moreno M, Troyo E (2000) Growth promotion of the seawater-irrigated oilseed halophyte *Salicornia bigelovii* inoculated with mangrove rhizosphere bacteria and halotolerant *Azospirillum* spp. *Biology and Fertility of Soils* **32**(4), 265–272. doi:10.1007/s003740000246
- Berendsen RL, Pieterse CMJ, Bakker P (2012) The rhizosphere microbiome and plant health. *Trends in Plant Science* **17**(8), 478–486. doi:10.1016/j.tplants.2012.04.001
- Bergmann D, Zehfus M, Zierer L, Smith B, Gabel M (2009) Grass rhizosheaths: Associated bacterial communities and potential for nitrogen fixation. *Western North American Naturalist* **69**(1), 105–114. doi:10.3398/064.069.0102
- Bian G, Zhang Y, Qin S, Xing K, Xie H, Jiang J (2011) Isolation and biodiversity of heavy metal tolerant endophytic bacteria from halotolerant plant species located in coastal shoal of Nantong. *Acta Microbiologica Sinica* **51**(11), 1538–1547.
- Bibi F, Chung EJ, Yoon HS, Song GC, Jeon CO, Chung YR (2011) *Haloferula luteola* sp. nov., an endophytic bacterium isolated from the root of a halophyte, *Rosa rugosa*, and emended description of the genus *Haloferula*. *International Journal of Systematic and Evolutionary Microbiology* **61**, 1837–1841. doi:10.1099/ijs.0.022772-0
- Bibi F, Chung EJ, Khan A, Jeon CO, Chung YR (2012) *Rhizobium halophytocola* sp. nov., isolated from the root of a coastal dune plant. *International Journal of Systematic and Evolutionary Microbiology* **62**, 1997–2003. doi:10.1099/ijs.0.029488-0
- Blomberg A, Adler L (1992) Physiology of osmotolerance in fungi. *Advances in Microbial Physiology* **33**, 145–212. doi:10.1016/S0065-2911(08)60217-9
- Borde M, Dudhane M, Jite P (2011) Growth photosynthetic activity and antioxidant responses of mycorrhizal and non-mycorrhizal bajra (*Pennisetum glaucum*) crop under salinity stress condition. *Crop Protection* **30**(3), 265–271. doi:10.1016/j.cropro.2010.12.010
- Boukhatem ZF, Domergue O, Bekki A, Merabet C, Sekkour S, Bouazza F, Duponnois R, de Lajudie P, Galiana A (2012) Symbiotic characterization and diversity of rhizobia associated with native and introduced acacias in arid and semi-arid regions in Algeria. *FEMS Microbiology Ecology* **80**(3), 534–547. doi:10.1111/j.1574-6941.2012.01315.x
- Buwalda JG, Stribley DP, Tinker PB (1983) Increased uptake of bromide and chloride by plants infected with vesicular-arbuscular mycorrhizas. *New Phytologist* **93**(2), 217–225. doi:10.1111/j.1469-8137.1983.tb03426.x
- Caravaca F, Aiguacil MM, Torres P, Roldan A (2005) Plant type mediates rhizospheric microbial activities and soil aggregation in a semiarid Mediterranean salt marsh. *Geoderma* **124**(3–4), 375–382. doi:10.1016/j.geoderma.2004.05.010
- Ceylan S, Yilan G, Akbulut BS, Poli A, Kazan D (2012) Interplay of adaptive capabilities of *Halomonas* sp AAD12 under salt stress. *Journal of Bioscience and Bioengineering* **114**(1), 45–52. doi:10.1016/j.jbiosc.2012.02.030
- Danese PN, Pratt LA, Kolter R (2000) Exopolysaccharide production is required for development of *Escherichia coli* K-12 biofilm architecture. *Journal of Bacteriology* **182**(12), 3593–3596. doi:10.1128/JB.182.12.3593-3596.2000
- Danhorn T, Fuqua C (2007) Biofilm formation by plant-associated bacteria. In 'Annual Review of Microbiology. Vol. 61'. pp. 401–422. (Annual Reviews: Palo Alto, CA)

- del Amor FM, Cuadra-Crespo P (2012) Plant growth-promoting bacteria as a tool to improve salinity tolerance in sweet pepper. *Functional Plant Biology* **39**(1), 82–90. doi:10.1071/FP111173
- Dimkpa C, Weinand T, Asch F (2009) Plant-rhizobacteria interactions alleviate abiotic stress conditions. *Plant, Cell & Environment* **32**(12), 1682–1694. doi:10.1111/j.1365-3040.2009.02028.x
- Dodd IC, Perez-Alfocea F (2012) Microbial amelioration of crop salinity stress. *Journal of Experimental Botany* **63**(9), 3415–3428. doi:10.1093/jxb/ers033
- Dodd IC, Zinovkina NY, Safronova VI, Belimov AA (2010) Rhizobacterial mediation of plant hormone status. *Annals of Applied Biology* **157**(3), 361–379. doi:10.1111/j.1744-7348.2010.00439.x
- Doornbos RF, van Loon LC, Bakker P (2012) Impact of root exudates and plant defense signaling on bacterial communities in the rhizosphere. A review. *Agronomy for Sustainable Development* **32**(1), 227–243. doi:10.1007/s13593-011-0028-y
- El-Tarabily KA, Youssef T (2010) Enhancement of morphological, anatomical and physiological characteristics of seedlings of the mangrove *Avicennia marina* inoculated with a native phosphate-solubilizing isolate of *Oceanobacillus picturæ* under greenhouse conditions. *Plant and Soil* **332**(1–2), 147–162. doi:10.1007/s11104-010-0280-y
- El-Tarabily KA, Youssef T (2011) Improved growth performance of the mangrove *Avicennia marina* seedlings using a 1-aminocyclopropane-1-carboxylic acid deaminase-producing isolate of *Pseudoalteromonas maricaloris*. *Plant Growth Regulation* **65**(3), 473–483. doi:10.1007/s10725-011-9618-6
- English JP, Colmer TD (2011) Salinity and waterlogging tolerances in three stem-succulent halophytes (*Tecticornia* species) from the margins of ephemeral salt lakes. *Plant and Soil* **348**(1–2), 379–396. doi:10.1007/s11104-011-0924-6
- Evelin H, Kapoor R, Giri B (2009) Arbuscular mycorrhizal fungi in alleviation of salt stress: a review. *Annals of Botany* **104**(7), 1263–1280. doi:10.1093/aob/mcp251
- Faure D, Vereecke D, Leveau JHJ (2009) Molecular communication in the rhizosphere. *Plant and Soil* **321**(1–2), 279–303. doi:10.1007/s11104-008-9839-2
- Flowers TJ (2004) Improving crop salt tolerance. *Journal of Experimental Botany* **55**(396), 307–319. doi:10.1093/jxb/erh003
- Flowers TJ, Colmer TD (2008) Salinity tolerance in halophytes. *New Phytologist* **179**(4), 945–963. doi:10.1111/j.1469-8137.2008.02531.x
- Füzy A, Biro B, Toth T, Hildebrandt U, Bothe H (2008) Drought, but not salinity, determines the apparent effectiveness of halophytes colonized by arbuscular mycorrhizal fungi. *Journal of Plant Physiology* **165**(11), 1181–1192. doi:10.1016/j.jplph.2007.08.010
- Ghanem ME, Han RM, Classen B, Quetin-Leclerq J, Mahy G, Ruan CJ, Qin P, Perez-Alfocea F, Lutts S (2010) Mucilage and polysaccharides in the halophyte plant species *Kosteletzkya virginica*: localization and composition in relation to salt stress. *Journal of Plant Physiology* **167**(5), 382–392. doi:10.1016/j.jplph.2009.10.012
- Giri B, Kapoor R, Mukerji KG (2003) Influence of arbuscular mycorrhizal fungi and salinity on growth, biomass, and mineral nutrition of *Acacia auriculiformis* *Biology and Fertility of Soils* **38**(3), 170–175. doi:10.1007/s00374-003-0636-z
- Giri B, Kapoor R, Mukerji KG (2007) Improved tolerance of *Acacia nilotica* to salt stress by arbuscular mycorrhiza, *Glomus fasciculatum* may be partly related to elevated K/Na ratios in root and shoot tissues. *Microbial Ecology* **54**(4), 753–760. doi:10.1007/s00248-007-9239-9
- Gontia I, Kavita K, Schmid M, Hartmann A, Jha B (2011) *Brachybotrium saurashtrense* sp. nov., a halotolerant root-associated bacterium with plant growth-promoting potential. *International Journal of Systematic and Evolutionary Microbiology* **61**, 2799–2804. doi:10.1099/ijs.0.023176-0
- Gostinčar C, Turk M, Plemenitaš A, Gunde-Cimerman N (2009) The expressions of  $\Delta^9$ -,  $\Delta^{12}$ -desaturases and an elongase by the extremely halotolerant black yeast *Hortaea werneckii* are salt dependent. *FEMS Yeast Research* **9**(2), 247–256. doi:10.1111/j.1567-1364.2009.00481.x
- Gunde-Cimerman N, Zalar P, de Hoog S, Plemenitas A (2000) Hypersaline waters in salterns – natural ecological niches for halophilic black yeasts. *FEMS Microbiology Ecology* **32**(3), 235–240.
- Hagemann M (2011) Molecular biology of cyanobacterial salt acclimation. *FEMS Microbiology Reviews* **35**(1), 87–123. doi:10.1111/j.1574-6976.2010.00234.x
- Hamilton CE, Gundel PE, Helander M, Saikkonen K (2012) Endophytic mediation of reactive oxygen species and antioxidant activity in plants: a review. *Fungal Diversity* **54**(1), 1–10. doi:10.1007/s13225-012-0158-9
- Hardoim PR, van Overbeek LS, van Elsland JD (2008) Properties of bacterial endophytes and their proposed role in plant growth. *Trends in Microbiology* **16**(10), 463–471. doi:10.1016/j.tim.2008.07.008
- Hause B, Mrosk C, Isayenkov S, Strack D (2007) Jasmonates in arbuscular mycorrhizal interactions. *Phytochemistry* **68**(1), 101–110. doi:10.1016/j.phytochem.2006.09.025
- Herrera-Medina MJ, Steinkellner S, Vierheilig H, Bote JAO, Garrido JMG (2007) Abscisic acid determines arbuscule development and functionality in the tomato arbuscular mycorrhiza. *New Phytologist* **175**(3), 554–564. doi:10.1111/j.1469-8137.2007.02107.x
- Hildebrandt U, Janetta K, Ouziad F, Renne B, Nawrath K, Bothe H (2001) Arbuscular mycorrhizal colonization of halophytes in Central European salt marshes. *Mycorrhiza* **10**(4), 175–183. doi:10.1007/s005720000074
- Jha B, Gontia I, Hartmann A (2012) The roots of the halophyte *Salicornia brachiata* are a source of new halotolerant diazotrophic bacteria with plant growth-promoting potential. *Plant and Soil* **356**(1–2), 265–277. doi:10.1007/s11104-011-0877-9
- Jones KM, Kobayashi H, Davies BW, Taga ME, Walker GC (2007) How rhizobial symbionts invade plants: the *Sinorhizobium–Medicago* model. *Nature Reviews. Microbiology* **5**(8), 619–633. doi:10.1038/nrmicro1705
- Joset F, Jeanjean R, Hagemann M (1996) Dynamics of the response of cyanobacteria to salt stress: deciphering the molecular events. *Physiologia Plantarum* **96**(4), 738–744. doi:10.1111/j.1399-3054.1996.tb00251.x
- Jumpponen A, Trappe JM (1998) Dark septate endophytes: a review of facultative biotrophic root-colonizing fungi. *New Phytologist* **140**(2), 295–310. doi:10.1046/j.1469-8137.1998.00265.x
- Jung SC, Martinez-Medina A, Lopez-Raez JA, Pozo MJ (2012) Mycorrhiza-induced resistance and priming of plant defenses. *Journal of Chemical Ecology* **38**(6), 651–664. doi:10.1007/s10886-012-0134-6
- Juniper S, Abbott L (1993) Vesicular-arbuscular mycorrhizas and soil salinity. *Mycorrhiza* **4**(2), 45–57. doi:10.1007/BF00204058
- Juniper S, Abbott LK (2006) Soil salinity delays germination and limits growth of hyphae from propagules of arbuscular mycorrhizal fungi. *Mycorrhiza* **16**(5), 371–379. doi:10.1007/s00572-006-0046-9
- Juraeva D, George E, Davranov K, Ruppel S (2006) Detection and quantification of the *nifH* gene in shoot and root of cucumber plants. *Canadian Journal of Microbiology* **52**(8), 731–739. doi:10.1139/w06-025
- Kogej T, Ramos J, Plemenitas A, Gunde-Cimerman N (2005) Halophilic fungus *Hortaea werneckii* and the halotolerant fungus *Aureobasidium pullulans* maintain low intracellular cation concentrations in hypersaline environments. *Applied and Environmental Microbiology* **71**(11), 6600–6605. doi:10.1128/AEM.71.11.6600-6605.2005
- Kogej T, Stein M, Volkmann M, Gorbushina AA, Galinski EA, Gunde-Cimerman N (2007) Osmotic adaptation of the halophilic fungus *Hortaea werneckii*: role of osmolytes and melanization. *Microbiology* **153**, 4261–4273. doi:10.1099/mic.0.2007/010751-0

- Kondrashov FA, Rogozin IB, Wolf YI, Koonin EV (2002) Selection in the evolution of gene duplications. *Genome Biology* **3**, research0008–research0008.9. doi:10.1186/gb-2002-3-2-research0008
- Landwehr M, Hildebrandt U, Wilde P, Nawrath K, Toth T, Biro B, Bothe H (2002) The arbuscular mycorrhizal fungus *Glomus geosporum* in European saline, sodic and gypsum soils. *Mycorrhiza* **12**(4), 199–211. doi:10.1007/s00572-002-0172-y
- Lanyi JK (1974) Salt-dependent properties of proteins from extremely halophilic bacteria. *Bacteriological Reviews* **38**(3), 272–290.
- Latef AAHA, Chaoxing H (2011) Effect of arbuscular mycorrhizal fungi on growth, mineral nutrition, antioxidant enzymes activity and fruit yield of tomato grown under salinity stress. *Scientia Horticulturae* **127** (3), 228–233. doi:10.1016/j.scienta.2010.09.020
- Lenassi M, Zajc J, Gostincar C, Gorjan A, Gunde-Cimerman N, Plemenitas A (2011) Adaptation of the glycerol-3-phosphate dehydrogenase GPD1 to high salinities in the extremely halotolerant *Hortaea werneckii* and halophilic *Wallemia ichthyophaga*. *Fungal Biology* **115**(10), 959–970. doi:10.1016/j.funbio.2011.04.001
- Li JX, Steen H, Gygi SP (2003) Protein profiling with cleavable isotope-coded affinity tag (cICAT) reagents – the yeast salinity stress response. *Molecular & Cellular Proteomics* **2**(11), 1198–1204. doi:10.1074/mcp.M300070-MCP200
- Lugtenberg B, Kamilova F (2009) Plant-growth-promoting Rhizobacteria. In 'Annual Review of Microbiology. Vol. 63.' pp. 541–556. (Annual Reviews: Palo Alto, CA)
- Manchanda G, Garg N (2011) Alleviation of salt-induced ionic, osmotic and oxidative stresses in *Cajanus cajan* nodules by AM inoculation. *Plant Biosystems* **145**(1), 88–97. doi:10.1080/11263504.2010.539851
- Munns R (2005) Genes and salt tolerance: bringing them together. *New Phytologist* **167**(3), 645–663. doi:10.1111/j.1469-8137.2005.01487.x
- Nabeel MA, Kathiresan K, Rajendran N, Ohnishi H, Hamaoka H, Omori K (2010) Contribution by microbes to the foodweb of a mangrove biotope: the approach of carbon and nitrogen stable isotopes. *African Journal of Marine Science* **32**(1), 65–70. doi:10.2989/18142321003714492
- Nabti E, Sahnoun M, Ghoul M, Fischer D, Hofmann A, Rothballer M, Schmid M, Hartmann A (2010) Restoration of growth of durum wheat (*Triticum durum* var. waha) under saline conditions due to inoculation with the rhizosphere bacterium *Azospirillum brasilense* NH and extracts of the marine alga *Ulva lactuca*. *Journal of Plant Growth Regulation* **29** (1), 6–22. doi:10.1007/s00344-009-9107-6
- Naz I, Bano A, Tamoor Ul H (2009) Isolation of phytohormones producing plant growth promoting rhizobacteria from weeds growing in Khewra salt range, Pakistan and their implication in providing salt tolerance to *Glycine max* L. *African Journal of Biotechnology* **8**(21), 5762–5768.
- Newman EI, Reddell P (1987) The distribution of mycorrhizas among families of vascular plants. *New Phytologist* **106**, 745–751. doi:10.1111/j.1469-8137.1987.tb00175.x
- Niemetz R, Karcher U, Kandler O, Tindall BJ, König H (1997) The cell wall polymer of the extremely halophilic archaeon *Natronococcus occultus*. *European Journal of Biochemistry* **249**(3), 905–911. doi:10.1111/j.1432-1033.1997.00905.x
- Nissenbaum A (1975) The microbiology and biogeochemistry of the Dead Sea. *Microbial Ecology* **2**(2), 139–161. doi:10.1007/BF02010435
- Oren A (2002) Molecular ecology of extremely halophilic Archaea and Bacteria. *FEMS Microbiology Ecology* **39**(1), 1–7. doi:10.1111/j.1574-6941.2002.tb00900.x
- Oren A (2006) The order Halobacteriales. In 'The prokaryotes. Vol. 3.' (3rd edn) (Eds M Dworkin, S Falkow, E Rosenberg, K-H Schleifer, E Stackebrandt) pp. 113–164. (Springer: Singapore)
- Parmar JH, Bhartiya S, Venkatesh KV (2011) Characterization of the adaptive response and growth upon hyperosmotic shock in *Saccharomyces cerevisiae*. *Molecular BioSystems* **7**(4), 1138–1148. doi:10.1039/c0mb00224k
- Piccoli P, Travaglia C, Cohen A, Sosa L, Comejo P, Masuelli R, Bottini R (2011) An endophytic bacterium isolated from roots of the halophyte *Prosopis strombulifera* produces ABA, IAA, gibberellins A(1) and A(3) and jasmonic acid in chemically-defined culture medium. *Plant Growth Regulation* **64**(2), 207–210. doi:10.1007/s10725-010-9536-z
- Plemenitas A, Vaupotic T, Lenassi M, Kogej T, Gunde-Cimerman N (2008) Adaptation of extremely halotolerant black yeast *Hortaea werneckii* to increased osmolarity: a molecular perspective at a glance. *Studies in Mycology* **61**(1), 67–75. doi:10.3114/sim.2008.61.06
- Porcel R, Ruiz-Lozano JM (2004) Arbuscular mycorrhizal influence on leaf water potential, solute accumulation, and oxidative stress in soybean plants subjected to drought stress. *Journal of Experimental Botany* **55**(403), 1743–1750. doi:10.1093/jxb/erh188
- Porcel R, Aroca R, Ruiz-Lozano JM (2012) Salinity stress alleviation using arbuscular mycorrhizal fungi. A review. *Agronomy for Sustainable Development* **32**(1), 181–200. doi:10.1007/s13593-011-0029-x
- Qiang X, Weiss M, Kogel KH, Schafer P (2012) *Piriformospora indica* a mutualistic basidiomycete with an exceptionally large plant host range. *Molecular Plant Pathology* **13**(5), 508–518. doi:10.1111/j.1364-3703.2011.00764.x
- Reed RH, Warr SRC, Richardson DL, Moore DJ, Stewart WDP (1985) Multiphasic osmotic adjustment in a euryhaline cyanobacterium. *FEMS Microbiology Letters* **28**(3), 225–229. doi:10.1111/j.1574-6968.1985.tb00796.x
- Rillig MC, Mardatin NF, Leifheit EF, Antunes PM (2010) Mycelium of arbuscular mycorrhizal fungi increases soil water repellency and is sufficient to maintain water-stable soil aggregates. *Soil Biology & Biochemistry* **42**(7), 1189–1191. doi:10.1016/j.soilbio.2010.03.027
- Rosenblueth M, Martinez-Romero E (2006) Bacterial endophytes and their interactions with hosts. *Molecular Plant-Microbe Interactions* **19**(8), 827–837. doi:10.1094/MPMI-19-0827
- Rueda-Puente E, Castellanos-Cervantes T, Diaz de Leon-Alvarez J, Preciado-Rangel P, Almaguer-Vargas G (2010) Bacterial community of rhizosphere associated to the annual halophyte *Salicornia bigelovii* (Torr.). *Terra Latinoamericana* **28**(4), 345–353.
- Ruiz-Lozano JM, Azcon R (2000) Symbiotic efficiency and infectivity of an autochthonous arbuscular mycorrhizal *Glomus* sp. from saline soils and *Glomus deserticola* under salinity. *Mycorrhiza* **10**(3), 137–143. doi:10.1007/s005720000075
- Ruiz-Lozano JM, Porcel R, Azcon C, Aroca R (2012) Regulation by arbuscular mycorrhizae of the integrated physiological response to salinity in plants: new challenges in physiological and molecular studies. *Journal of Experimental Botany* **63**(11), 4033–4044. doi:10.1093/jxb/ers126
- Sengupta A, Chaudhuri S (2002) Arbuscular mycorrhizal relations of mangrove plant community at the Ganges river estuary in India. *Mycorrhiza* **12**(4), 169–174. doi:10.1007/s00572-002-0164-y
- Sgroj V, Cassan F, Masciarelli O, Del Papa MF, Lagares A, Luna V (2009) Isolation and characterization of endophytic plant growth-promoting (PGPB) or stress homeostasis-regulating (PSHB) bacteria associated to the halophyte *Prosopis strombulifera*. *Applied Microbiology and Biotechnology* **85**(2), 371–381. doi:10.1007/s00253-009-2116-3
- Shi W, Takano T, Liu S (2012) Isolation and characterization of novel bacterial taxa from extreme alkali-saline soil. *World Journal of Microbiology & Biotechnology* **28**(5), 2147–2157. doi:10.1007/s11274-012-1020-7
- Shin D-S, Park MS, Jung S, Lee MS, Lev KH, Bae KS, Kim SB (2007) Plant growth-promoting potential of endophytic bacteria isolated from roots of coastal sand dune plants. *Journal of Microbiology and Biotechnology* **17**(8), 1361–1368.
- Siddikee MA, Chauhan PS, Anandham R, Han GH, Sa T (2010) Isolation, characterization, and use for plant growth promotion under salt stress,

- of ACC deaminase-producing halotolerant bacteria derived from coastal soil. *Journal of Microbiology and Biotechnology* **20**(11), 1577–1584. doi:10.4014/jmb.1007.07011
- Sonjak S, Udovic M, Wraber T, Likar M, Regvar M (2009) Diversity of halophytes and identification of arbuscular mycorrhizal fungi colonising their roots in an abandoned and sustained part of Secovlje salterns. *Soil Biology & Biochemistry* **41**(9), 1847–1856. doi:10.1016/j.soilbio.2009.06.006
- Steber J, Schleifer KH (1975) *Halococcus morrhuae* sulfated heteropolysaccharide as structural component of bacterial cell wall. *Archives of Microbiology* **105**(1), 173–177. doi:10.1007/BF00447133
- Sundaram R, Inbaneson SJ, Muthu U, Priya SR, Andy R, Banerjee MB (2011a) Diversity of endophytic actinomycetes from Karangkadu mangrove ecosystem and its antibacterial potential against bacterial pathogens. *Journal of Pharmacy Research* **4**(1), 294–296.
- Sundaram R, Inbaneson SJ, Muthu U, Ramakrishnan K, Andy R, Banerjee MB, Jayaprakasham R (2011b) Antibacterial activity of heterotrophic endophytes from Karangkadu mangrove ecosystem, India. *Journal of Pharmacy Research* **4**(1), 195–198.
- Teng S, Liu Y, Zhao L (2010) Isolation, identification and characterization of ACC deaminase-containing endophytic bacteria from halophyte *Suaeda salsa*. *Weishengwu Xuebao* **50**(11), 1503–1509.
- Thrall PH, Broadhurst LM, Hoque MS, Bagnall DJ (2009) Diversity and salt tolerance of native *Acacia* rhizobia isolated from saline and non-saline soils. *Austral Ecology* **34**(8), 950–963. doi:10.1111/j.1442-9993.2009.01998.x
- Tiwari S, Singh P, Tiwari R, Meena KK, Yandigeri M, Singh DP, Arora DK (2011) Salt-tolerant rhizobacteria-mediated induced tolerance in wheat (*Triticum aestivum*) and chemical diversity in rhizosphere enhance plant growth. *Biology and Fertility of Soils* **47**(8), 907–916. doi:10.1007/s00374-011-0598-5
- Turk M, Mejanelle L, Sentjurs M, Grimalt JO, Gunde-Cimerman N, Plemenitas A (2004) Salt-induced changes in lipid composition and membrane fluidity of halophilic yeast-like melanized fungi. *Extremophiles* **8**(1), 53–61. doi:10.1007/s00792-003-0360-5
- Upadhyay S, Singh J, Singh D (2011) Exopolysaccharide-producing plant growth-promoting rhizobacteria under salinity condition. *Pedosphere* **21**(2), 214–222. doi:10.1016/S1002-0160(11)60120-3
- van de Vossen JLCM, Driessen AJM, Konings WN (1998) The essence of being extremophilic: the role of the unique archaeal membrane lipids. *Extremophiles* **2**(3), 163–170. doi:10.1007/s007920050056
- van Loon LC, Bakker PAHM, Pieterse CMJ (1998) Systemic resistance induced by rhizosphere bacteria. *Annual Review of Phytopathology* **36**(1), 453–483. doi:10.1146/annurev.phyto.36.1.453
- Vaupotic T, Plemenitas A (2007) Differential gene expression and Hog1 interaction with osmoresponsive genes in the extremely halotolerant black yeast *Hortaea werneckii*. *BMC Genomics* **8**, 280. doi:10.1186/1471-2164-8-280
- Verma S, Varma A, Rexer KH, Hassel A, Kost G, Sarbhoy A, Bisen P, Bütehorn B, Franken P (1998) *Piriformospora indica*, gen. nov. sp. nov., a new root-colonizing fungus. *Mycologia* **90**(5), 896–903. doi:10.2307/3761331
- Vessey JK (2003) Plant growth promoting rhizobacteria as biofertilizers. *Plant and Soil* **255**(2), 571–586. doi:10.1023/A:1026037216893
- Waditee R, Hibino T, Nakamura T, Incharoensakdi A, Takabe T (2002) Overexpression of a Na<sup>+</sup>/H<sup>+</sup> antiporter confers salt tolerance on a freshwater cyanobacterium, making it capable of growth in sea water. *Proceedings of the National Academy of Sciences of the United States of America* **99**(6), 4109–4114. doi:10.1073/pnas.052576899
- Waller F, Achatz B, Baltrusch H, Fodor J, Becker K, Fischer M, Heier T, Hüchelhoven R, Neumann C, von Wettstein D, Franken P, Kogel K-H (2005) The endophytic fungus *Piriformospora indica* reprograms barley to salt-stress tolerance, disease resistance, and higher yield. *Proceedings of the National Academy of Sciences of the United States of America* **102**(38), 13 386–13 391. doi:10.1073/pnas.0504423102
- Wang FY, Liu RJ, Lin XG, Zhou JM (2004) Arbuscular mycorrhizal status of wild plants in saline-alkaline soils of the Yellow River Delta. *Mycorrhiza* **14**(2), 133–137. doi:10.1007/s00572-003-0248-3
- Weiß M, Sykorova Z, Garnica S, Riess K, Martos F, Krause C, Oberwinkler F, Bauer R, Redecker D (2011) Sebaciales everywhere: previously overlooked ubiquitous fungal endophytes. *PLoS ONE* **6**(2), e16793. doi:10.1371/journal.pone.0016793
- Witzel K, Gwinn-Giglio M, Nadendla S, Shefchek K, Ruppel S (2012) Genome sequence of *Enterobacter radicincitans* DSM16656<sup>T</sup>, a plant growth-promoting endophyte. *Journal of Bacteriology* **194**(19), 5469. doi:10.1128/JB.01193-12
- Wu QS, Zou YN, Liu W, Ye XF, Zai HF, Zhao LJ (2010) Alleviation of salt stress in citrus seedlings inoculated with mycorrhiza: changes in leaf antioxidant defense systems. *Plant, Soil and Environment* **56**(10), 470–475.
- Wutipraditkul N, Waditee R, Incharoensakdi A, Hibino T, Tanaka Y, Nakamura T, Shikata M, Takabe T (2005) Halotolerant cyanobacterium *Aphanothece halophytica* contains NapA-type Na<sup>+</sup>/H<sup>+</sup> antiporters with novel ion specificity that are involved in salt tolerance at alkaline pH. *Applied and Environmental Microbiology* **71**(8), 4176–4184. doi:10.1128/AEM.71.8.4176-4184.2005
- Yang YH, Chen YN, Li WH (2008) Arbuscular mycorrhizal fungi infection in desert riparian forest and its environmental implications: a case study in the lower reach of Tarim River. *Progress in Natural Science* **18**(8), 983–991. doi:10.1016/j.pnsc.2008.02.009
- Yasmin H, Bano A (2011) Isolation and characterisation of phosphate solubilizing bacteria from rhizosphere soil of weeds of Khewra salt range and attack. *Pakistan Journal of Botany* **43**(3), 1663–1668.
- Yoshimura H, Kotake T, Aohara T, Tsumuraya Y, Ikeuchi M, Ohmori M (2012) The role of extracellular polysaccharides produced by the terrestrial cyanobacterium *Nostoc* sp. strain HK-01 in NaCl tolerance. *Journal of Applied Phycology* **24**(2), 237–243. doi:10.1007/s10811-011-9672-5
- Zhong NQ, Han LB, Wu XM, Wang LL, Wang F, Ma YH, Xia GX (2012) Ectopic expression of a bacterium NhaD-type Na<sup>+</sup>/H<sup>+</sup> antiporter leads to increased tolerance to combined salt/alkali stresses. *Journal of Integrative Plant Biology* **54**(6), 412–421. doi:10.1111/j.1744-7909.2012.01129.x
- Zhou M, Chen W, Chen H, Wei G (2012) Draft genome sequence of *Mesorhizobium alhagi* CCNWXJ12-2(Tau), a novel salt-resistant species isolated from the desert of north-western China. *Journal of Bacteriology* **194**(5), 1261–1262. doi:10.1128/JB.06635-11
- Zuccarini P, Okurowska P (2008) Effects of mycorrhizal colonization and fertilization on growth and photosynthesis of sweet basil under salt stress. *Journal of Plant Nutrition* **31**(3), 497–513. doi:10.1080/01904160801895027