Functional Plant Biology

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Special Issue: Halophytes

<i>Foreword</i> : Putting halophytes to work – genetics, biochemistry and physiology <i>Bernhard Huchzermeyer and Tim Flowers</i>	v–viii	In 2009 the COST Action <i>Putting halophytes to work – from</i> <i>genes to ecosystems</i> was established and it was from contributions to a conference held at the Leibniz University, Hannover, Germany, in 2012 that this Special Issue has been produced. The 17 contributions cover the fundamentals of salt tolerance and aspects of the biochemistry and physiology of tolerance in the context of advancing the development of salt- tolerant crops.
<i>Evans Review</i> : The integration of activity in saline environments: problems and perspectives <i>John M. Cheeseman</i>	759–774	Plants have adapted to life in saline environments in a myriad of ways, some more broadly successful than others. These adaptations involve the integration of all activities at levels ranging from genes to physiology to life cycles. With the availability of new '-omic' resources, the tools of systems biology and perhaps forgotten tools of physiology and biophysics, we may now be poised to decipher the complexities of the integration of organismal activities as never before.
Review: Plant proteome responses to salinity stress – comparison of glycophytes and halophytes Klára Kosová, Pavel Vítámvás, Milan Oldřich Urban and Ilja Tom Prášil	775–786	Proteome studies can provide important insights into plant responses to salinity stress and their mechanism of tolerance. In this review, recent knowledge of proteome response to salinity is summarised with a focus on comparative studies revealing similarities and differences between related plant species with contrasting salinity tolerance – glycophytes and halophytes. The contribution of proteomic studies to a complex picture of plant salinity response is discussed.
<i>Review</i> : The effect of hyper-osmotic salinity on protein pattern and enzyme activities of halophytes <i>Hans-Werner Koyro, Christian Zörb,</i> <i>Ahmed Debez and Bernhard Huchzermeyer</i>	787–804	Proteomic approaches allow the analysis of salt-induced changes in protein patterns at any given moment in time. Here we summarise such data from halophytes and closely related plants differing in salt resistance and physiology respectively. Results indicate that, in general, keeping structural integrity in the presence of salt is of the highest priority, but plants differ in their strategies of how to tune metabolism and reach a new equilibrium subsequent to exposure to salt.

Cover illustration: Energy and metabolite flow in photosynthesis (see Koyro *et al.* pp. 787–804). Branching points of the photosynthetic pathway essential for efficient energy use are indicated and numbered. Ribbon shaped arrows show regulatory effects such as rearrangement of membrane protein structures (green and red), redox control of Calvin cycle enzymes (blue), metabolite (sugars and sugar phosphates) control of gene expression (orange). Since the number of coenzyme molecules inside a chloroplast, for instance, is limited, when the absorption of light quanta is high, we have to consider turnover as well as transport rates of intermediates. Diagram by Hans-Werner Koyro, Christian Zörb, Ahmed Debez and Bernhard Huchzermeyer.

Review: Are soluble carbohydrates ecologically relevant for salt tolerance in halophytes? Ricardo Gil, Monica Boscaiu, Cristina Lull, Inmaculada Bautista, Antonio Lidón and Oscar Vicente	805–818	Soil salinity is one of the most important environmental factors that reduce crop yields in agriculture and limit plant distribution in nature. In this review, we discuss evidence supporting a functional role of soluble carbohydrates in salt tolerance mechanisms, although their ecological relevance remains largely unknown. We propose that more effort should be invested in field studies of salt-tolerant plants, as a complement to more common experimental approaches based on the analysis of salt- sensitive models under artificial laboratory conditions.
<i>Review</i> : Balancing salinity stress responses in halophy and non-halophytes: a comparison between <i>Thellungiella</i> and <i>Arabidopsis thaliana</i> <i>Dorothea Bartels and Challabathula Dinakar</i>	rtes 819–831	The halophyte <i>Thellungiella salsuginea</i> has been used as a model for studying plant salt tolerance. In this review, <i>T. salsuginea</i> and the glycophyte <i>Arabidopsis thaliana</i> are compared with regards to their biochemical, physiological and molecular responses to salinity. Recent developments are presented for improvement of salinity tolerance in glycophytic plants using genes from halophytes.
<i>Review</i> : Reactive oxygen species regulation and antioxidant defence in halophytes <i>Rengin Ozgur, Baris Uzilday, Askim Hediye Sekmen</i> <i>and Ismail Turkan</i>	832–847	Halophytes deploy a range of responses to salinity that confers on them more tolerance to salt than seen in glycophytes. Induction of an antioxidant defence system is one of these responses, which protects plants against reactive oxygen species and regulates their level for stress signalling. An understanding of these mechanisms in halophytes may provide information for increasing stress tolerance of crop plants.
<i>Review</i> : Salt stress, signalling and redox control in seeds <i>Ilse Kranner and Charlotte E. Seal</i>	848–859	Surprisingly little is known about the effects of salt stress upon seeds given their pivotal role in plant reproduction and dispersal. This review provides information on redox control in seeds, detoxification mechanisms and tolerance in relation to seed metabolism and performance. Implications of redox control in seeds on the physiological, biochemical and molecular level are discussed; the review concludes with a perspective on future research in relation to salt stress and seed biology.
The influence of genes regulating transmembrane transport of Na ⁺ on the salt resistance of <i>Aeluropus lagopoides</i> <i>Muhammad Zaheer Ahmed, Takayoshi Shimazaki,</i> <i>Salman Gulzar, Akira Kikuchi, Bilquees Gul,</i> <i>M. Ajmal Khan, Hans–W. Koyro,</i> <i>Bernhard Huchzermeyer and Kazuo N. Watanabe</i>	860–871	To investigate the role of compartmentation and secretion rate in the avoidance of Na ⁺ toxicity in the halophyte <i>Aeluropus</i> <i>lagopoides</i> , we report that Na ⁺ was successfully compartmentalised at salinities up to 373 mM NaCl by upregulating the gene expression of membrane linked transport proteins V-NHX and PM- NHX. At higher salinity a reduction in the expression of <i>V</i> - <i>NHX</i> and <i>PM</i> - <i>NHX</i> in leaves without any change in the rate of salt secretion is a possible cause of toxicity of NaCl.
<i>Review</i> : The waterlogging/salinity interaction in higher plants revisited – focusing on the hypoxia-induced disturbance to K ⁺ homeostasis <i>Edward G. Barrett-Lennard and Sergey N. Shabala</i>	872–882	Salinity and waterlogging (oxygen deficiency around the roots) are plant stresses that often occur together on saltland. This combination of stresses impacts on plant growth by decreasing the concentration of potassium and increasing the concentrations of sodium and chloride in shoots. The synchronicity between these changes in ion concentrations has important implications for our understanding of the mechanisms of ion regulation in plants.
Review: Physiological response of halophytes to multiple stresses Karim Ben Hamed, Hasna Ellouzi, Ons Zribi Talbi, Kamel Hessini, Ines Slama, Tahar Ghnaya, Sergi Munné Bosch, Arnould Savouré and Chedly Abdelly	883–896	Saline lands are often affected by a wide range of constraints rather than salinity alone. Often, only halophytes are able to survive in these conditions by amplifying the mechanisms of salt tolerance, mainly proline accumulation, K:Na homeostasis and antioxidant defence. Cross-tolerance, anticipation and memory are also involved in the tolerance of halophytes to combined stresses.

Tolerance of extreme salinity in two stem-succulent halophytes (<i>Tecticornia</i> species) <i>Jeremy P. English and Timothy D. Colmer</i>	897–912	Some stem-succulent halophytes inhabit areas of very high salinity, such as inland salt lakes. Tolerance and physiological responses to extreme salinity (2000 mM NaCl) were evaluated for two <i>Tecticornia</i> species; both were highly tolerant. Growth patterns of halophytic species on the margins of salt lakes are likely influenced both by soil salinity and water availability (periodic floods and water deficits).
<i>Review</i> : Bioaccumulation of heavy metals in <i>Spartina</i> <i>Susana Redondo-Gómez</i>	913–921	Heavy metal pollution is a major environmental problem that is rapidly gaining importance due to its impact on human health through the food chain. Phytoremediation is considered an effective, low cost, preferred cleanup option for moderately contaminated areas. In this context, the available literature on heavy metal bioaccumulation by <i>Spartina</i> sp. was compiled and compared.
Halophyte anti-oxidant feedback seasonality in two salt marshes with different degrees of metal contamination: search for an efficient biomarker <i>Bernardo Duarte, Dinis Santos</i> <i>and Isabel Caçador</i>	922–930	In contaminated estuaries, halophytes can be subjected to high levels of metal contamination that inevitably affect their metabolism, namely, their anti-oxidant systems. Considering the more abundant halophyte species in Tagus estuary salt marshes, <i>Spartina maritima</i> proved to be potentially efficient biomonitor species. Also its enzymatic anti-oxidant system revealed a substantial increase of activity under contaminated conditions. Considering this, <i>Spartina maritima</i> and its anti-oxidant enzymatic defences arise as potential biomonitor species and biomarker for heavy metal contamination studies.
Halophytes as sources of metals in estuarine systems with low levels of contamination <i>Thiago Couto, Bernardo Duarte, Dimitri Barroso,</i> <i>Isabel Caçador and João C. Marques</i>	931–939	In this work the metal concentration in three plant species (<i>Scirpus maritimus, Spartina maritima</i> and <i>Zostera noltii</i>) of the Mondego Estuary in Portugal was analysed. From the concentration of metals in the aboveground and belowground organs and in the sediment it was possible to conclude that the Mondego Estuary, although having a low level of contaminants, could be a source of metals for nearby aquatic systems.
<i>Review</i> : Properties of the halophyte microbiome and their implications for plant salt tolerance <i>Silke Ruppel, Philipp Franken and Katja Witzel</i>	940–951	Plant-inhabiting micro-organisms have a crucial impact on plant growth and health. Specialised bacterial and fungal communities live inside and on the surface of halophytes and may significantly contribute to the salt tolerance of their host. This review analyses the opportunity that the native microbial world offers crop plants to enlarge their growing space into salt affected areas.
<i>Review</i> : An economic point of view of secondary compounds in halophytes <i>Anne Buhmann and Jutta Papenbrock</i>	952–967	A broad variety of secondary compounds of economic interest is present in halophytes, with potential uses in various fields such as pharmaceuticals and nutraceuticals. Salt-tolerant plants are potential sources of valuable products that are largely unexploited. Our overview identifies open research questions and gives suggestions for future applications of secondary compounds of halophytes.
The importance of iron supply during repetitive harvesting of Aster tripolium Yvonne Ventura, Malika Myrzabayeva, Zerekbay Alikulov, Shabtai Cohen, Zion Shemer and Moshe Sagi	968–976	In an attempt to develop <i>Aster tripolium</i> L. as a halophyte vegetable for saline irrigation on dune sand, it was observed that sequential harvesting resulted in leaf chlorosis, yield reduction, reduced nitrate reductase activity (NRA) and enhanced nitrate concentration. Application of suitable Fe-chelates restored leaf colour, NRA and nitrate content indicating that NRA can be an indicator for iron deficiency in <i>A. tripolium</i> .