Chapter 16
Environmental and Economical Opportunities for the Valorisation of the Genus *Atriplex*: New Insights

Maali Benzarti, Kilani Ben Rejeb, Ahmed Debez and Chedly Abdelly

Abstract *Atriplex* species are members of the Chenopodiaceae. There are more than 400 species growing naturally in arid and semi arid regions of the world, most of which are highly tolerant to drought and salt. *Atriplex* species contain high levels of protein and economically valuable compounds. These characteristics could make *Atriplex* a suitable food for livestock in saline or arid/ semi-arid area. Furthermore, *Atriplex* can take up salt ions from saline soil and sequester it into the salt glands at the leaf surface. This trait is of high significance since it allows them to be used for revegetation of saline or arid/semi-arid lands. *Atriplex* species have also been used for cloning some genes related to drought and salt tolerance. This review is a new contribution that updates knowledge on the ecological and socio-economical potential of some plant genus *Atriplex*.

Introduction

Many arid and semi-arid regions in the world have soils and water resources that are too saline for most of the common conventional crop systems (Pitman and Lauchli 2002). Halophytes are plants that have been naturally selected in saline environments and are distinguishable from glycophytes by their capacity to cope with ex-

---

C. Abdelly (✉) · M. Benzarti · K. B. Rejeb · A. Debez
Laboratoire des Plantes Extrêmophiles, Centre de Biotechnologie de Borj-Cedria (CBBC),
BP 901, 2050 Hammam-Lif, Tunisia
e-mail: chedly.abdelly@cbbc.rnrt.tn

M. Benzarti
e-mail: maali23@yahoo.fr

A. Debez
e-mail: ahmed_debez@yahoo.com

K. B. Rejeb
Physiologie Cellulaire et Moléculaire des Plantes, UR5,
EAC 7180 CNRS, Université Pierre et Marie Curie (UPMC),
Case 156, 4 place Jussieu, 75252 Paris cedex 05, France
e-mail: kilanib@yahoo.com

K. R. Hakeem et al. (eds.), *Crop Improvement,* DOI 10.1007/978-1-4614-7028-1_16,

cessive levels of ions by various eco-physiological mechanisms. Some halophytes possess unique adaptations, such as salt glands or bladders that alleviate the deleterious effects of high ion concentrations. However, intrinsically cellular processesmust make the major contribution to the capacity of plants for salt adaptation. At the molecular level, the higher salt-adaptive plasticity of halophytes may be due to constitutive expression of genes that encode salt-tolerance determinants (Casas et al. 1992) or the better aptitude to regulate the expression of these genes in response to salt. This hypothesis makes halophytes a source of exclusive genes or new genetic mechanisms that could be applied in genetic manipulation of crops. Cultivation of salt-tolerant crops, or halophytes, on saline soil has significant social and economical potential that needs to be further explored and developed (Debez et al. 2011).

Among the halophytes extensively used in physiological and molecular biological investigations is the *Atriplex* genus. The genus *Atriplex* (Chenopodiaceae) contains various species distinguishable by different morphology, biological cycles and ecological adaptations (Le Houérou 1992). Tolerance to salinity, drought, heavy metals and temperature are important characteristics of species of *Atriplex*. However, the value of certain *Atriplex* species has been recognized by their incorporation in the rangelands improvement programs in many salt-affected regions throughout the world. In this contribution, we review the literature regarding the ecological and agronomic importance of the plant genus *Atriplex* in arid and semi arid regions.

Geographical Distribution of the Genus *Atriplex*

Atriplex species constitute the largest and most diversified genus of the family Chenopodiaceae (Kadereit et al. 2010). *Atriplex* species (saltbushes) are dominant in many arid and semi-arid regions of the world, particularly in habitats that combine relatively high soil salinity with aridity (Ortíz-Dorda et al. 2005). Over 400 species of *Atriplex* have been found to be geographically distributed on all continents. *Atriplex* species are mainly found in the deserts and semi-deserts in North America, South Australia, South Central Asia, West and South East America, and the Mediterranean basin. *A. nummularia*, and *A. halimus* are the most widely distributed species of the genus *Atriplex*. *A. halimus* is a perennial native shrub of the Mediterranean region (Ortíz-Dorda et al. 2005). This species has two subspecies: the subsp. *halimus*, which is present on the northern shores of the Mediterranean basin and the subsp. *schweinfurthii* (Boiss.) common on the southern shores of the Mediterranean basin, North Africa and Near East. *A. nummularia* occurs naturally in the semi arid and arid zone of southern and central Australia where it was divided in three subspecies (subsp. *nummularia*; subsp. *Omissa* and subsp. *Spathulata*). Molecular genetic and taxonomic evidence suggests that *Atriplex* was transported to Australia during the late Miocene (Kadereit et al. 2010). *A. nummularia* is proposed to have evolved from a common octoploid ancestor *A. paludosa* ssp. *moquiniana* (Moq.) Parr-Smith in the coastal semi-arid fringe of southwestern Australia. Sampson and Byrne

(2012) suggested that many species spread and diversified from this zone to exploit the arid and saline habitats that were increasingly becoming available as a result of changing climatic conditions through the Pliocene and Pleistocene in inland areas of Australia. There are two species that are considered to be closely related to *A. nummularia* that are found in the arid zones of Western and South Australia, respectively: *A. amnicola* Paul G. Wilson and *A. incrassate* F Muell (Sampson and Byrne 2012). *A. breweri* and *A. cansecens* are relatively close to *A. halimus*. Between 1920 and 1930, *A. nummularia*, *A. semibaccata* from Australia and *A. canescens* from USA were introduced to Tunisia and Morocco (Ben Salem et al. 2010). Only 13 species and subspecies are used for rangeland rehabilitation and fodder production: *A. halimus* subsp. *halimus*, *A. halimus* subsp. *schweinfurthii*, *A. mollis*, *A. glauca*, *A. leucoclada*, *A. nummularia*, *A. canescens* subsp. *canescens*, *A. canescens* subsp. *linearis*, *A. amnicola*, *A. undulata*, *A. repanda*, *A. semibaccata*, and *A. barclayana* (Ben Salem et al. 2010).

The Importance of *Atriplex* Species for Saline Soil Reclamation

Salt affected soils are widely spread in many arid and semi-arid regions of the world and increasingly threatening agricultural expansion and productivity. Yet, in many arid environments, high quality water in not available to support the establishment of plants for revegetation projects. The removal of sodium salts from saline soils by halophytes plants, as alternative for costly chemical amendments, has emerged as an efficient low cost technology (Gharaibeh et al. 2011). It is well known that *Atriplex* species actively accumulate soluble salts in leaves, especially sodium, in association with a drought tolerance mechanism. For this reason it is also considered as an excellent species for reducing soil salinity in drylands, if cut and collected (Ben Salem et al. 2005). It was found that the dehydrated *A. halimus* accumulated more Na^+ than the control plants even without the addition of NaCl to the stressed plants (Martinez et al. 2003). Glenn and Brown (1998) concluded that tolerance of *A. canescens* to water and salt stress was linked through a common mechanism of accumulating Na^+ for osmotic adjustment. By comparing salinity tolerance of three *Atriplex* species in well-watered and drying soil Glenn et al. (2012) found that *A. hortensis* was able to complete its life cycle on drying soil with a final salt content 85 g/l NaCl. *A. lentiformis* was able to survive on drying soils with salinities five times higher than seawater, whereas *A. canescens* had high survival on drying soils but was less salt tolerant than either *A. hortensis* or *A. lentiformis*. It has been demonstrated that there is a relationship between the habitat of the Mediterranean xero-halophyte species *A. halimus* and the strategy adopted for NaCl and osmotic stress resistance. The coastal (Monastir, salt-affected site) population is more tolerant of salinity than the inland (Sbikha, non saline semi-arid area) population and displays a higher ability to accumulate glycinebetaine (GB) in response to this constraint. In contrast, the inland population, exposed in its natural habitat to transient periods of drought, is more resistant to osmotic stress induced by 15 % PEG, and mainly accumulates proline in response to this treatment (Ben Hassine et al. 2008). Some *Atriplex* species grown under rangeland conditions has leaf ash concentrations of 13–27 % (Welch 1978; Hyder 1981; Berrett-Lennard 2002) and *Atriplex* species grown in saline soils can have leaf ash concentrations up to 39 % (Malcolm et al. 1988). Khan et al. (2000) reported that *A. halimus* was more salt-tolerant than *A. calotheca* and *A. nitens*, when grown at 750 mM NaCl (−40, −67 and −80 % of biomass production) but interestingly, all three species were able to survive at this salt concentration. Recently, Benzarti et al. (2012) found that *A. portulacoides* was able to grow in medium containing 1,000 mM NaCl without displaying salt-induced toxicity symptoms. The salinity resistance of some *Atriplex* species is often attributed to the presence of vesiculated trichomes covering the leaf surface and containing large amounts of salt (Smaoui et al. 2011). These trichomes play a significant role in removing salt from the the leaf tissues, thereby preventing the accumulation of toxic salts in the parenchyma and vascular tissues. For many *Atriplex* species, more than 50 % of the salt transported to the shoots is excreted via these epidermic trichomes (Belkheiri and Mulas 2011). These attributes have led some workers to suggest that *Atriplex* species could be grown to remove salt from the soil (Barrett-Lennard 2002).

Atriplex species (*A. canescens*) has been especially recommended for arid zone restoration projects (Fitzsimmons et al. 1998). In a field experiment Chisci et al. (2001) demonstrated the use of *A. halimus* in improving physical characteristics of a clay soil in Italy and to provide environmental protection by controlling runoff and reducing soil erosion on slopes. *Atriplex* plant litter can modify the top soil salinity, along with other soil properties. Maganhotto de Souza Silva et al. (2008) found that soils cultivated with *A. nummularia* and irrigated with saline effluents, in semi-arid conditions in Brazil, improved their fertility (organic carbon, nitrogen and phosphorus contents) and microbiological properties (enzymes activity). Sameni and Soleimani (2007) studied the distribution of salinity and of some soil physico-chemical properties, observing significant changes in salinity and pH and found that *A. nummularia* may actually facilitate growth of plants under their canopy. The work by Zucca et al. (2011) in a study site in Morocco also confirmed that the significant relationship between soil properties and *A. nummularia* development can be mostly observed within the first 10 cm. *A. nummularia* is one of the most important species used for the revegetation of degraded land in low rainfall areas. Slavich et al. (1999) planted *A. nummularia* as a vegetative cover in a salt affected land in southeast Australia. Brown et al. (1999) showed that *A. barclayana* could be used as a biofilter to remove nutrients from saline aquaculture effluents. Gharaibeh et al. (2011) showed that amelioration of a calcareous saline sodic soil can be achieved efficiently by growing *A. halimus* without applying an amendment. Planting *A. halimus* reduced soil sodicity and electrical conductivity considerably to values comparable to that of gypsum treatments.

The *Atriplex* species may also be used for wildfire prevention purposes. The high salt concentration found in its leaves increases their moisture content, which makes this species behave as a fire retardant in the event of wildfire (Montgomery and Cheo 1969).

Table 16.1 Potential candidates for phytoremediation approach

Species	Metal contaminants	Reference
A. halimus	Cd/Zn/Pb	Lutts et al. 2004
A. portulacoides	Cd/Cu/Zn/Fe/Ti	Luque et al. 1999; Rebordea and Caçador 2007; Cambrollé et al. 2012a, b
A. canescens	Cd/Cr	Sawalha et al. 2006
A. hortensis spp purpurea	Pb/Zn	Kachout et al. 2012
A. hortensis spp rubra	Cu/Ni	Kachout et al. 2012
A. atacamensis Phil	Ar	Vromman et al. 2011
A. conodocarpa	Hg	Lomonte et al. 2010
A. palula	Se	Vickerman et al. 2002
A. spongiosa	Se	Vickerman et al. 2002

The Importance of *Atriplex* Species in Heavy Metal Phytoremediation

The contamination of soil by heavy metals is one of the most serious environmental problems and has significant implications for human health. The clean up of heavy metals contaminated soils is one of the most difficult tasks for environmental engineering. In most cases, traditional physiochemical methods are quite expensive and may lead to soil alterations (Gardea-Torresdey et al. 2005). Phytoremediation based on the use of plants to remove or degrade inorganic and organic pollutants, has been proposed as a promising, environmentally friendly and relatively cheap. The success of phytoremediation depends upon the identification of suitable plant species those hyperaccumulate heavy metals. The use of deep-rooting xero-halophyte species is may be of special interest in this context to remediate salty contaminated area, especially in arid and semi-arid regions. Several species of the genus *Atriplex*, which are naturally salt- and drought-tolerant have been also suggested as potential candidates for a phytoremediation approach (Table 16.1) because of their high biomass production associated with a deep root system. *A. portulacoides* was suggested as a suitable species for the phytoremediation owing to the high translocation rates of Cd and Cu towards the aboveground tissues (Reboreda and Caçador 2007). *A. portulacoides* can tolerate external Cu levels of up to 15 mmol/l (1,000 mg Cu/l) without suffering adverse physiological effects (Cambrollé et al. 2012a). Furthermore, despite the fact that Cu concentrations of between 20 and 100 mg Cu/kg DW in leaf tissue are generally considered excessive or toxic (Kabata-Pendias and Pendias 2001), growth parameters of this species are unaffected by leaf tissue concentrations as high as 80 mg Cu/kg DW. *A. portulacoides* is able to survive with external Cu levels of 35 mmol/l and can be found growing in sediments that contain 300–3,000 ppm Cu. Sousa et al. (2008) stated that compartmentalization and detoxification mechanisms are crucial to allow *A. portulacoides* to tolerate high levels of heavy metals, and found that this species is able to retain a considerable quantity of metals in the root cell wall. Cambrollé et al. (2012b) reported also that this salt-marsh shrub may represent a valuable tool in the restoration of Zn-polluted areas since the plant can tolerate high tissue concentrations of Zn without suffering adverse physiological effects, and can produce a significant amount of biomass while sequestrating high concentrations of this metal. Other species that belong to the *Atriplex* genus, such as *Atriplex halimus*, have already been studied for their level of resistance to heavy metals (Cd, Zn, Pb). These species have been recommended as a promising species for the phytoremediation of heavy-metal contaminated areas based on their high biomass production, deep root systems and ability to tolerate high concentrations of toxic elements (Lutts et al. 2004; Lefèvre et al. 2009; Manousaki and Kalogerakis 2009). Precipitation of heavy-metal with oxalate and/or its excretion into trichomes and increased synthesis of glycine betaine may contribute to the tolerance of *A. halimus*. Among the heavy metals frequently present in contaminated soils, mercury is arguably of the greatest environmental and public health concern. *A. conodocarpa* proved to be the most suitable candidates for mercury phytoextraction because of its ability to translocate mercury from roots to the above-ground tissues (Lomonte et al. 2010). Vickerman et al. (2002) evaluated 30 *Atriplex* lines for potential habitat improvement and phytoremediation of selenium contaminated sites. *A. patula* was found to be one of the top selenium accumulators and grew well in saline soil. *A. atacamensis Phil* has been proposed as possible candidates for phytoremediation of Ar (Vromman et al. 2011).

Atriplex Species Forage Production

The main limitations to animal production in the arid and semi-arid regions, is the scarcity of green forage. The use of native or introduced halophytes for livestock production is an important issue in many semi-arid and arid areas. Several halophytes plants have been used as fodder crops under saline conditions in order to produce green forage during the dry season (El Shaer 2010). These include planting perennial salt marsh plant species, mainly *Atriplex* species, in numerous regions. In several experiments, the Mediterranean *Atriplex* species has been the most successful shrub species in terms of establishment and productivity. Research conducted in north-east Morocco showed an average production of 920 Kg DM/ha (1,000 plants/ha density), with variations from 406 to 2,140 Kg DM/ha depending on the species studied. *A. vesicaria*, *A. semibaccata*, *A. nummularia* and *A. paludosa* scored the high levels of production. Other reports indicate that forage production from a 2-year old *Atriplex* plantation was 5 t under 150 and 200 mm rainfall.

The pastoral value of fodder shrubs depends not only upon their biomass but also upon their nutritive value and their palatability and digestibility (Salem et al. 2012). The low concentrations of metabolizable energy and high concentrations of soluble salt in herbage of *Atriplex* species as well as the presence of anti-nutritional compounds, including tannins, flavonoids, oxalate tends to reduce fodder palatability and feed intake of sheep and goats. Several methods have been devised to lessen adverse effects of phenols and to alleviate deleterious effects of sodium chloride found in tree and shrub fodder foliages. These include treatment with alkalis such as urea, ammonia and calcium hydroxide and oxidizing agents such as potassium dichromate. Addition of exogenous enzymes is also a method to improve the nutritive value of tree leaves. The study of Salem et al. (2012) showed that there are beneficial impacts of sun-drying and/or dietary exogenous enzyme addition for sheep fed *A. halimus*.

Despite the limited nutritional values, the use of *Atriplex* species as an important component of the diet should be considered in arid and semi-arid regions since this plant produces 2.5–20 t of dry matter per hectare per year and it is available most of the year. Given the low nutritional value of the *Atriplex* species, various authors have proposed supplementing them with other types of feed like barley grain, barly straw or spineless cactus so that the animals could obtain the energy from the hay and grain, and the protein and minerals from *Atriplex* species. Abu-Zanat (2005) reported that grazing a combination of salt-tolerant grasses, legumes and *Atriplex* species improved feeding value and maximize animal production (feed intake and growth rates) from saline land. Norman et al. (2008) reported that 170 g/day of grain was the minimum required to ensure sheep fed *A. nummularia* and *A. amnicola* maintained live weight. In the study of Ben Salem et al. (2005) lambs fed *A. nummularia* and supplemented with barley achieved a growth rate of 67 g/day over an 85-day period. Data presented by van der Baan et al. (2004) clearly demonstrate that supplementation with grains such as barley or maize significantly increases the digestibility of *A. nummularia* and this leads to an increase in growth rate of ruminant. Mixing alfalfa with *Atriplex* as green fodders to sheep may increase the palatability and consequently intake and utilization of *Atriplex* which lead to improvement of the performance of animal. Abu-Zanat (2005) reported that it is possible to replace up to 50 % of alfalfa hay by *A. nummularia* without negative effects on intake and digestibility of dry matter by Awassi lambs. Jacobs and Smith (1977) reported significant differences in chemical composition between (*Atriplex nummularia, A. Canescens, A. Brewerii* and *A. Lentiformis*) species and between seasons. Kandil and El-Shaer (1989) reported that *Atriplex nummularia* had higher nutritive value in spring and winter than in summer and autumn. Riasi et al. (2008) reported that *A. dimorphostegia* have more number of beneficial chemical nutritive components and digestible values than *Suaeda arcuata* as forage for ruminants. Farmers in some arid areas of the world have already begun to cultivate *Atriplex* as a salt-tolerant forage crop on lands where other crops are difficult to grow.

Characterization of Bioactive Compounds from Some *Atriplex* Species

Several salt marsh plants have traditionally been used for medical, nutritional, and even artisanal purposes. Currently, an increasing interest is granted to these species because of their high content in bioactive compounds (Ksouri et al. 2011). Various *Atriplex* species have medicinal values, e.g. *A. semibaccata* has been used as an antifungal agent and *A. vestita* in the traitement of bronchitis. *A. hortensis* has been

Table 16.2 Some *Atriplex* species and their isolated compounds

Species	Chemical content	Reference
A. portulacoides	Phenolic compounds	Boughalleb et al. 2009
A. inflata	Phenolic compounds	Boughalleb et al. 2009
A. halimus	Tanins, alkaloids, saponins, ascorbic acid	Benhammou et al. 2009
A. lentiformis	Quercetin 6,4′-dimethoxy-3-fructo rhamnoside, quercetin 4′-methoxy-3-fructo rhamnoside, kaempferol-4′-methoxy-rutinoside, kaempferol 7-rhamnoside, kaempferol 3,7-dirhamnoside, quercetin and kaempferol	Awaad et al. 2012
A. nummularia	Vit E, Vit A, saponins, polypodine, 20 hydroxyecdysone	Keckeis et al. 2000
A. hortensis	Kaempferol 3-*O*-sulphate-7-*O* arabinopyranoside quercetin 3-*O*-sulphate-7-*O*-arabinopyranoside	Bylka et al. 2001
A. littoralis	Patuletin 3-*O*-β-D-glucopyranoside, patuletin 3-*O*[5‴-*O*-feruloyl-β-D-apiofuranosyl (1‴→2″)-β-D-glucopyranoside	Bylka 2004
A. farinosa	Naringin, naringenin 7-O-glucoside, isorhamnetin 3-O-rhamnosyl (1-6) glucopyranoside and isorhamnetin 7-O-glucopyranoside	Al-Jaber et al. 1992
A. stocksii	Ursolic acid, oleanolic acid, β-amyrin, β-sitosterol, stigmasterol, atriplexinol	Siddiqui et al. 1994

regarded as a source of Vit A (Siddiqui et al. 1994). The arial parts of *A. hortensis* were used in flak medicine against diseases of respiratory tract, digestive and urinary systems, and due to their analgestic properties, in rheumatism (Bylka et al. 2001). *A. halimus* is effective in the treatment of type II diabetic patients (Bakhtiuary 2011) and it used in veterinary medicine to combat internal parasites. Extracts of *A.confertifolia* has significant bioactivity against human breast cancer cell lines; the bioactivity of *A. confertifolia* extract on these cells was compared to a FDA-approved cancer drug (Onxol®) and an industry-standard leukocyte control cell line. A dose-response curve of the extracts displayed significant cell death similar to Onxol® (Capua et al. 2010). Boughalleb et al. (2009) reported that many *Atriplex* species (*A. inflate* and *A. portulacoides*) may contain phytochemical compounds with fungicide properties.

Several studies attributed the anti-carcinogenic, anti-inflamatory, antifongique and antioxydants activities potential of plant extracts to their bioactive compounds compositions (Ksouri et al. 2011). Chemical investigation of the species of the genus *Atriplex* (Table 16.2) showed the presence of saponin glycosides, alkaloids, ascorbic acid and phytoecdysteroids (Keckeis et al. 2000). Benhammou et al. (2009) reported that *A. halimus* leaves and stems were characterized by the presence of the flavonoids, the tannins, the alkaloids and the sponins where the leaves exhibited the higher yields. Bylka et al. (2001) isolated from leaves of *A. hortensis* tow relatively rare sulphated flavonoids: kaempferol 3-*O*-sulphate-7-*O*-arabinopyranoside and quercetin 3-*O*-sulphate-7-*O*-arabinopyranoside (belong the group of compounds easily soluble in water) and a new acetylated flavonol glycoside from

Table 16.3 Genes isolated from some *Atriplex* species

Species	Gene	Gene Bank	Product	Reference
A. gmelini	*AgNHX1*	AB038492	Antiporter Na^+/H^+	Hamada et al. 2001
A. nummularia	*AnGAPDH*	U02886.1	Glyceraldehyde-3-phosphate dehydrogenase	Niu et al. 1994
	AnCMO	AB112481	Choline monooxygenase	Tabuchi et al. 2005
	AnPEAMT	AB196771	Phosphoethanolamine N-methyltransferase	Tabuchi et al. 2005
	AnSAMS	AB183565	S-adenosyl-L-methionine synthase 5	Tabuchi et al. 2005
	H^+-ATPase	–	PM H^+-ATPase	Niu et al. 1993
A. hortensis	*AhCMO*	AF270651	Choline monooxygenase	Zhang et al. 2009; Shen et al. 2002
	AhBADH	DQ497233	Betaine aldehyde dehydrogenase	
A. prostrata	*ApCMO*	AY082068	Choline monooxygenase	Wang et al. 2004
A. centralasiatica	*AcBADH*	AY093684	Betaine aldehyde dehydrogenase	Yin et al. 2002
A. halimus	*AsDBRE*	JF451138	DRE binding transcription factor	Khedr et al. 2011

A. littoralis (Bylka 2004). Other earlier works suggested the presence the naringin, naringenin 7-O-glucoside, isorhamnetin 3-O-rhamnosyl (1–6) glucopyranoside and isorhamnetin 7-O-glucopyranoside in *A. farinose* (Al-Jaber et al. 1992). More recently, two new flavonoids, quercetin 6,4′-dimethoxy-3-fructo-rhamnoside and quercetin 4′-methoxy-3-fructo-rhamnoside in addition to another five known compounds were isolated from *A. lentiformis* (Torr.) S. Wats (Awaad et al. 2012). All of the extracts and the isolated compounds were tested for their antioxidant activity, the two new compounds were found to have the highest antioxidant activity with no side effect.

Isolation and Characterization of Genes from *Atriplex* Species

Atriplex species are among the most salt tolerant higher plants. And the elucidation of its salt tolerance mechanisms is of significance for generating salt tolerant crops via selective breeding or genetic engineering. Studying the regulation of stress inducible genes can lead to understanding of the mechanisms by which halophytes maintain growth and thrive under abiotic stress. Several stress related genes have been isolated from these halophytes (Table 16.3). Both glycophytes and halophytes cannot tolerate large amounts of salt in the cytoplasm. Plants maintain a low concentration of Na^+ in the cytosol by active exclusion of Na^+ ions into the apoplast and vacuole by using specific plasma membrane and tonoplast Na^+/H^+ antiporter

(NHX1) (Shi and Zhu 2002). In particular, the vacuolar Na^+/H^+ antiporter had been demonstrated to play a key role in salt tolerance of plants (Blumwald et al. 2000). The greater salt tolerance in *Atriplex* species is related to the transport to shoots of high quantities of Na^+ concomitant to an efficient vacuolar compartmentation of this ion, which prevents the ionic damage to the cytoplasm. The vacuolar Na^+/H^+ antiporter genes has been characterized and identified from *A. gmelili* (*AgNHX1*) (Hamada et al. 2001). The analysis and comparison of these genes showed that they were highly homologous with similar structural and conserved domains. Ohta et al. (2002) demonstrated that transgenic rice plants overexpressing *AgNHX1* gene could survive after short period of high concentration salt exposure (300 mM NaCl for 3 days). Evacuation of Na^+ from the cytoplasm is energy-dependent. A partial sequence of an isoform of the plasma membrane PM-H^+-ATPase was been isolated from *A. nummularia*. Increased H^+-ATPase mRNA abundance was reported in *A. nummularia* when NaCl adapted (342 mM NaCl) cells were re-exposed to NaCl after having been grown in media without additional NaCl (Niu et al. 1993). Which provide evidence that enhanced H^+-transport activity by NaCl in *A. nummularia* is mediated at least in part by transcriptional or post-transcriptional processes that result in higher mRNA accumulation.

Exposure to saline and drought stress results in the accumulation in the cytosol of low-molecular mass compounds, termed as compatible solutes, which do not interfere with normal biochemical reactions. It has been frequently reported that GB acts as the main stress-induced agent involved in the osmotic adjustment and protection of cellular structure in plant species belonging to the Chenopodiaceae (Rhodes and Hanson 1993). GB facilitates osmotic adjustment by lowering the internal osmotic potential that contributes to the water stress tolerance ability. In addition, it stabilizes both PSII complex and RuBisCO during photosynthesis under stress conditions (Sakamoto and Murata 2000). Yang et al. (2007) reported that genetically engineered tobacco with the ability to accumulate GB showed a higher content of ascorbate and reduced glutathione as well as an increase in the activity of superoxide dismutase (SOD). The positive effect of exogenous glycine betaine application in plant growing under salinity stress has been proven. Plant cell could be protected from the adverse effect of salinity induced oxidative stress by the exogenous application of glycine betaine (Demiral and Türkan 2004). In *A. nummularia* GB play a major role in cytosol osmotic adjustment in both leaves and roots, regardless of NaCl presence (Silveira et al. 2009). In higher plants, the first and second steps in the biosynthesis of GB are catalyzed by a rate-limiting enzyme choline monooxygenase (CMO) and betaine aldehyde dehydrogenase (BADH), respectively (Sakamoto and Murata 2000). *CMO* gene from *A. hortensis* (*AhCMO*) has been isolated and used for GB production in tobacco (Shen et al. 2002) and cotton plants (Zhang et al. 2009) to improve its abiotic stress tolerance. CMO homologs have been also identified in *A. prostrate* (Wang and Showalter 2004) and *A. nummularia* (Tabuchi et al. 2005). The gene encoding the second enzyme, *BADH*, has been cloned from *A. hortensis* (*AhBADH*) and introduced into rice, wheat, and turf grass (Xiao et al. 1995; Guo et al. 1997, 2000) and improvement of salt tolerance in transgenic plants was observed during growth. Similar result was also achieved in transgenic trifoliate orange (Fu et al. 2011). The enhanced salt tolerance was correlated, at least in part, with reduced lipid peroxidation, greater abundance in photosynthetic proteins, stimulation of K^+ uptake, and low Na^+/K^+ ratios. The *BADH* gene that originated from *A. hortensis* was also transformed into the most important forage crop alfalfa with *Agrobacterium*-mediated transformation method. The transgenic plants grew vigorous in salt stress condition, whereas the wild type plants was retarded and did not survive. The expression of *BADH* gene in alfalfa genome enhanced its salt tolerance through improved membrane protection as measured by relative electrical conductivity and malondialdehyde (MDA) content, scavenge of free radicals by increase of peroxidase (POD) and SOD activities, and the osmotic adjustment (Liu et al. 2011).

Transcription factor genes play important roles in stress survival by serving as master regulators of sets of downstream stress-responsive genes via binding to specific elements (*cis*-elements) in target genes. Functional analysis of the promoter regions of some of stress-inducible genes has led to identification of the *cis*-element DRE (Dehydration-responsive element), which is responsible for dehydration-inducible transcription (Yamaguchi-Shinozaki and Shinozaki 1994). Full-length DRE-binding transcription factor (*AhDREB1*) gene has been isolated from *A. hortensis* (Shen et al. 2003). In transgenic tobacco, *AhDREB1* led to the accumulation of its putative downstream genes and these transgenic lines showed an increased stress tolerance, suggesting that the AhDREB1 protein functions as a DRE-binding transcription factor and play roles in the stress tolerant response of *A. hortensis*. *DREB* in *A. halimus* (*AsDBRE*) is regulated by the osmotic component but not by the ionic one of salt stress (Khedr et al. 2011). It seemed that *DREB* was not involved in the regulation of sodium manipulating genes like *NHX1*, *SOS1* or *H^+-PPase*. Moreover, *DREB* could be involved directly of indirectly in *CMO* regulation because of timing of induction. Also, *DREB* was the most up-regulated gene under salt (fivefold) and drought (twofold) conditions, which reinforced the importance of this gene in *A. halimus* tolerance to stress. Moreover, its constitutive expression under normal conditions also indicated its involvement in other growth and developmental programs (Khedr et al. 2011).

Microsatellites are widely used in population genetic studies and may prove to be useful in studies of closely related species to infer relationships when sequence variation is very low or there are few or no genome resources available. Ortíz-Dorda et al. 2005 has evaluated the genetic structure of 51 populations of *A. halimus* from the Mediterranean Basin using RAPD (random amplified polymorphic DNA)-PCR technique. The authors found that there are a clear intrapopulational diversity of *A. halimus*. Such heterogeneity could be exploited to select clones or develop synthetic populations with a combination of good traits such as high palatability, high edible biomass production, and good adaptability to environmental limiting factors in semi-arid Mediterranean environments. 12 polymorphic loci were isolated in *A. nummularia* (Byrne et al. 2008) which will be useful to describe levels of genetic variability across the range of the species and in a breeding programme.

Xu et al. (2011) investigate the physiological responses and differential gene expression caused by salinity exposure in *A. centralasiatica* plants grown from two different seed morphs. *A. centralasiatica* widely distributed in China produce tow type of seeds, yellow and brown seeds. Seedlings derived from yellow seeds showed a greater salt tolerance than those derived from brown seeds. By using suppression subtractive hybridization (SSH) and subsequent microarray and RT-PCR analysis to isolate and compare genes that were differentially expressed, the authors suggest a major contribution of gene regulation to the salt resistant phenotype of seedlings derived from yellow seeds. These genes encoded proteins related to osmotic and ionic homeostasis, redox equilibrium and signal transduction. This study clearly links physiological responses with differential gene expression in seedlings derived from dimorphic seeds. Such dimorphism offers the advantage to halophytic plants to survive in highly variable environments.

Conclusion and Future Perspective

The global distribution of the genus *Atriplex* in arid and semi-arid areas and its abiotic stress tolerance combined with the utility of *Atriplex* species for restoration, remediation and forage for livestock have helped these plants to rank among the most widely studied native halophytes species. The major limitation of use *Atriplex* in livestock production is its high salt concentration. *Atriplex* species are best considered as a supplement rather forage. The plant used for these purposes are primarily wild type and there are little information available on the nutritive value of *Atriplex* species growing in greenhouse and irrigated with different concentration of NaCl. Strategies need to be devised to minimize the salt contents in the *Atriplex* leaves.

Although the biochemistry of *Atriplex* species tends to establish that they may be a source of novel compounds along with providing a new source for many already know biologically active compounds. Data of chemical composition of *Atriplex* species is still not completed.

Atriplex species are well adapted to both salt and drought stress and can serve as model species to understand the mechanisms of tolerance in plant (Flowers and Colmer 2008). Very little research has been carried out to identify the molecular mechanisms directly responsible for the specific tolerance of *Atriplex* species to abiotic stress. In this way, *Atriplex* may serve as a particularly useful model plant for studies of regulatory mechanisms related to the activation of the GB biosynthetic pathway in response to environmental stress.

With over 400 species of this genus, a significant opportunity then exists to explore the potential of other locally adapted *Atriplex* species. Research is required to select and breed potentially useful plants and identify the best species combining nutritional, agronomic and environmental potential.

Acknowledgments This work was supported by the Tunisian Ministry of Higher Education and Scientific Research (LR10CBBC02).

References

Abu-Zanat MMW (2005) Voluntary intake and digestibility of saltbush by sheep. Asian Aust J Anim Sci 18:214–220

Al-Jaber NAA, Mujahid TG, Al-Hazmi HMG (1992) Secondary metabolites of chenopodiaceace species. J Chem Scoc Pak 14:76–83

Awaad AS, Maitland DJ, Donia AERM, Alqasoumi SI, Soliman GA (2012) Novel flavonoids with antioxidant activity from a Chenopodiaceous plant. Pharmaceutical Biol 50:99–104

Bakhtiuary Z (2011) Herbal Medicines in Diabetes. IJDO 3:88–95

Barrett-Lennard EG (2002) Restoration of saline land through revegetation. Agric Water Manag 53:213–226

Belkheiri O, Mulas M (2011) The effects of salt stress on growth, water relations and ion accumulation in two halophyte *Atriplex* species. Environ Exp Bot (in press). http://dx.doi.org/10.1016/j

Ben Hassine A, Ghanem ME, Bouzid S, Lutts S (2008) An inland and a coastal population of the Mediterranean xero-halophyte species *Atriplex halimus* L. differ in their ability to accumulate proline and glycinebetaine in response to salinity and water stress. J Exp Bot 59:1315–1326

Ben Salem H, Nefzaoui A, El-Mastouri A, Ben Salem L (2005) Nutritive value, behavior, and growth of Barbarine lambs fed on oldman saltbush (*Atriplex nummularia L.*) and supplemented or not with barley grains or spineless cactus (*Opuntia ficus-indica F. inermis*) pads. Small Rumin Res 59:229–237

Ben Salem H, Norman HC, Nefzaoui A, Mayberry DE, Pearce KL, Revell DK (2010) Potential use of oldman saltbush (*Atriplex nummularia* Lindl.) in sheep and goat feeding. Small Rumin Res 91:13–28

Benhammou N, Fawzia AB, Tatjana KP (2009) Antioxidant activity of methanolic extracts and some bioactive compounds of *Atriplex halimus*. Comptes Rendus Chimie 12:1259–1266

Benzarti M, Ben Rejeb K, Debez A, Messedi D, Abdelly C (2012) Photosynthetic activity and leaf antioxidative responses of *Atriplex portulacoides* subjected to extreme salinity. Acta Physiol Plant. doi:1007/s11738-012-0963-5

Blumwald E, Aharon GS, Apse MP (2000) Sodium transport in plant cells. Biochim Biophys Acta 1465:140–151

Boughalleb N, Trabelsi L, Harzallah-Skhiri F (2009) Antifungal activity from polar and non-polar extracts of some Chenopodiaceae wild species growing in Tunisia. Nat Prod Res 23:988–997

Brown JJ, Glen EP, Fitzsimmons KM, Smith S (1999) Halophytes for the treatment of saline aquaculture effluent. Aquaculture 175:255–268

Bylka W (2004) A new acylated flavonol diglycosides from *Atriplex littoralis*. Acta Physiol Plant 24:393–398

Bylka W, Stobiecki M, Franski R (2001) Sulphated flavonoid glycosides from leaves of *Atriplex hortensis*. Acta Physiol Plant 23:285–290

Byrne M, Hankinson M, Sampson JF, Stankowski S (2008) Microsatellite markers isolated from a polyploidy saltbush, *Atriplex nummularia* Lindl. (Chenopodiaceae). Mol Ecol Resour 8:1426–1428

Cambrollé J, Mancilla-Leytón JM, Muñoz-Vallés S, Luque T, Figueroa ME (2012a) Tolerance and accumulation of copper in the salt-marsh shrub *Halimione portulacoides*. Mar Pollut Bull 64:721–728

Cambrollé J, Mancilla-Leytón JM, Muñoz-Vallés S, Luque T, Figueroa ME (2012b). Zinc tolerance and accumulation in the salt-marsh shrub *Halimione portulacoides*. Chemosphere 86:867–874

Capua CJ, Hopson NP, Malcolm MGS, Johnston GR, KimL GB, Lee CM, Booth GM (2010). Cytotoxicity of *Atriplex confertifolia*. J Toxicol 1–7. doi:10.1155/2010/976548

Casas AM, Nelson DE, Raghothama KG, D'Urzo MP, Singh NK, Bressan RA, Hasegawa PM (1992) Expression of osmotin-like genes in the halophyte *Atriplex nummularia* L. Plant Physiol 99:329–337

Chisci GC, Bazzoffi P, Pagliai M, Papini R, Pellegrini S, Vignozzi N (2001) Association of Sulla and *Atriplex* shrub for the physical improvement of clay soils and environmental protection in central Italy. Agric Ecosyst Environ 84:45–53

Debez A, Huchzermeyer B, Abdelly C, Koyro HW (2011) Current challenges and future opportunities for a sustainable utilization of halophytes. In: Öztürk M et al (ed) Sabkha ecosystems, tasks for vegetation science 34. Vol 46, pp 59–77

Demiral T, Türkan I (2004) Does exogenous glycinebetaine affect antioxidative system of rice seedlings under NaCl treatment. J Plant Physiol 6:1089–1100

El Shaer HM (2010) Halophytes and salt-tolerant plants as potential forage for ruminants in the Near East region. Small Rumin Res 91:3–12

Fitzsimmons K, Lovely C, Glenn E (1998) Growth differences among widely separated geographic accessions of fourwing saltbush (*Atriplex canescens*) in the Great Basin Desert, New Mexico, USA. Arid Soil Res Reah 12:87–94

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

Fu X-Z, Khan EU, Hu S-S, Fan Qi-J, Liu Ji-H (2011) Overexpression of the betaine aldehyde dehydrogenase gene from *Atriple hortensis* enhances salt tolerance in the transgenic trifoliate orange (Poncirus trifoliate L. Raf.). Environ Exp Bot 74:106–113

Gardea-Torresdey JL, Peralta-Videab JR, de la Rosa G, Parsons JG (2005) Phytoremediation of heavy metals and study of the metal coordination by X-ray absorption spectroscopy. Coord Chem Rev 249:1797–1810

Gharaibeh MA, Eltaif NI, Albalasmeh AA (2011) Reclamation of highly calcareous saline sodic soil using *Atriplex halimus* and by-product gypsum. Int J Phytoremediation 13:873–883

Glenn EP, Brown JJ (1998) Effects of soil salt levels on the growth and water use efficiency of *Atriplex canescens* (Chenopodiaceae) varieties in drying soil. Am J Bot 85:10–16

Glenn EP, Nelson SG, Ambrose B, Martinez R, Soliz D, Pabendinskas V, Hultine K (2012) Comparison of salinity tolerance of three Atriplex spp. in well-watered and drying soils. Environ Exp Bot 83:62–72

Guo BH, Zhang YM, Li HJ, Du LQ (2000) Transformation of wheat with a gene encoding for the betaine aldehyde dehydrogenase (BADH). Acta Bot Sin 42:279–283

Guo Y, Zhang L, Xiao G, Chen SY (1997) Expression of the BADH gene and salinity tolerance in rice transgenic plants. Sci China 27:151–155

Hamada A, Shono M, Xia T, Ohta M, Hayashi Y, Tanaka A, Hayakawa T (2001) Isolation and characterization of a Na^+/H^+antiporter gene from the halophyte *Atriplex gmelini*. Plant Mol Biol 46:35–42

Hyder SZ (1981) Preliminary observations on the performance of some exotic species of *Atriplex* in Saudi Arabia. J Range Manage 34:208–210

Jacobs GA, Smith CJ (1977) Utilization of four *Atriplex* species by sheep. Agroanimalia 9:37–43

Kabata-Pendias A, Pendias H (2001) Trace elements in soils and plants. CRC Press, Florida

Kachout SS, Ben Mansoura A, Mechergui R, Leclerc JC, Rejeb MN, Ouerghi Z (2012) Accumulation of Cu, Pb, Ni and Zn in the halophyte plant *Atriplex* grown on polluted soil. J Sci Food Agric 92:336–342

Kadereit G, Mavrodiev EV, Zacharias EH, Sukhorukov AP (2010) Molecular phylogeny of Atripliceae (Chenopodioideae, Chenopodiaceae): implications for systematics, biogeography, flower and fruit evolution, and the origin of C4 photosynthesis. Am J Bot 97:1664–1687

Kandil HM, El-Shaer HM (1989) The utilization of *Atriplex nummularia* by goats and sheep in Sinai. Proceedings of international symposium on the constraints and possibilities of ruminant production in the dry tropics, Cairo, Egypt, pp 71–73

Keckeis K, Sarker SD, Dinan LN (2000) Phytoecdysteroids from *Atriplex nummularia*. Fitoterapia 71:456–458

Khan MA, Ungar IA, Showalter M (2000) Effects of salinity on growth, water relation and ion accumulation of the subtropical perennial Halophyte, *Atriplex griffithii var. stocksii*. Ann Bot 85:225–232

Khedr AHA, Serag MS, Nemat-Alla MM, Abo-Elnaga AZ, Nada RM, Quick WP, Abogadallah GM (2011) A DREB gene from the xero-halophyte *Atriplex halimus* is induced by osmotic but not ionic stress and shows distinct differences from glycophytic homologues. Plant Cell Tiss Organ Cult 106:191–206

Ksouri R, Ksouri WM, Jallali I, Debez A, Magné C, Hiroko I, Abdelly C (2011) Medicinal halophytes: potent source of health promoting biomolecules with medical, nutraceutical and food applications. Crit Rev Biotechnol. doi:10.3109/07388551.2011.630647

Le Houérou HN (1992) The role of saltbushes (*Atriplex* spp.) in arid land rehabilitation in the Mediterranean Basin: a review. Agrofor Syst 18:107–148

Lefèvre I, Marchal G, Meerts P, Corréal E, Lutts S (2009) Chloride salinity reduces cadmium accumulation by the Mediterranean halophyte species *Atriplex halimus* L. Environ Exp Bot 65:142–152

Liu Z-H, Zhang H-M, Li G-L, Guo X-L, Chen S-Y, Liu G-B, Zhang Y-M (2011) Enhancement of salt tolerance in alfalfa transformed with the gene encoding for betaine aldehyde dehydrogenase. Euphytica 178:363–372

Lomonte C, Sgherri C, Baker AJM, Kolev SD, Navari-Izzo F (2010) Antioxidative response of *Atriplex codonocarpa* to mercury. Environ Exp Bot 69:9–16

Luque CJ, Castellanos EM, Castillo JM, Gonzalez M, Gonzalez-Vilches MC, Figueroa ME (1999) Metals in halophytes of a contaminated estuary (odiel saltmarshes, SW Spain). Mar Pollut Bull 38:49–51

Lutts S, Lefèvre I, Delpérée C, Kivits S, Dechamps C, Robledo A et al (2004) Heavy metal accumulation by the halophyte species Mediterranean saltbush. J Environ Qual 33:1271–1279

Maganhotto de Souza Silva CM, Vieira RF, Oliveira PR (2008) Salinity, sodicity and microbiological properties of an Ultisol cultivated with saltbush and irrigated with saline effluents. Pesqui Agropecu Bras 43:1389–1396

Malcolm CV, Clarke AJ, D'Antuono MF, Swaan TC (1988) Effects of plant spacing and soil conditions on the growth of five *Atriplex* species. Agric Ecosyst Environ 21:265–279

Manousaki E, Kalogerakis N (2009) Phytoextraction of Pb and Cd by the Mediterranean saltbush (*Atriplex halimus* L.) metal uptake in relation to salinity. Environ Sci Poll Res 16:844–854

Martinez JP, Ledent JF, Bajji M, Kinet JM, Lutts S (2003) Effect of water stress on growth, Na and K accumulation and water use efficiency in relation to osmotic adjustment in two populations of *Atriplex halimus* L. Plant Growth Regul 41:63–73

Montgomery KR, Cheo PC (1969) Moisture and salt effects on fire retardance in plants. Am J Bot 56:1028–1032

Niu X, Wang W, Bressan RA, Hasegawa PM (1994) Molecular cloning and expression of a glyceraldehydes-3-phosphate dehydrogenase gene in a desert halophyte, *Atriplex nummularia* L. Plant Physiol 104:1105–1106

Niu X, Zhu JK, Narasimhan ML, Bressan RA, Hasegawa PM (1993) Plasma- membrane H^+-ATPase gene expression is regulated by NaCl in cells of the halophyte *Atriplex nummularia* L. Planta 190:433–438

Norman HC, Masters DG, Wilmot MG, Rintoul AJ (2008) Effect of supplementation with grain, hay or straw on the performance of weaner Merino sheep grazing old man (*Atriplex nummularia*) or river (*Atriplex amnicola*) saltbush. Grass Forage Sci 63:179–192

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

Ortíz-Dorda J, Martínez-Mora C, Correal E, Simón B, Cenis JL (2005) Genetic Structure of *Atriplex halimus* Populations in the Mediterranean Bassin. Ann Bot 95:827–834

Pitman MG, Lauchli A (2002) Global impact of salinity and agricultural ecosystems. In: Lauchli A, Luttge V (eds) Salinity: environment plants molecules. Kluwer, The Netherlands, pp 3–20

Reboreda R, Caçador I (2007) Halophyte vegetation influences in salt marsh retention capacity for heavy metals. Environ Pollut 146:147–154

Rhodes D, Hanson AD (1993) Quaternary ammonium and tertiary sulfonium compounds in higher plants. Annu Rev Plant Physiol Plant Mol Biol 44:357–384

Riasi A, Mesgaran MD, Stern MD, Moreno MJR (2008) Chemical composition, *in situ* ruminal degradability and post-ruminal disappearance of dry matter and crude protein from the halophytic plants *Kochia scoparia*, *Atriplex dimorphostegia*, *Suaeda arcuata* and *Gamanthus gamacarpus*. Anim Feed Sci Technol 141:209–219

Sakamoto A, Murata N (2000) Genetic engineering of glycinebetaine synthesis in plants: current status and implications for enhancement of stress tolerance. J Exp Bot 51:81–88

Salem AZM, Hassan AA, Khalil MS, Gado HM, Alsersy H, Simbaya J (2012) Effects of sun-drying and exogenous enzymes on nutrients intake, digestibility and nitrogen utilization in sheep fed *Atriplex halimus* foliages. Anim Feed Sci Tech 171:128–135

Sameni AM, Soleimani R (2007) Effect of salinity and some chemical properties of the under- and intercanopy soils on range plants in a dry region of Southern Iran. Commun Soil Sci Plan 38:15–33

Sampson JF, Byrne M (2012) Genetic diversity and multiple origins of polyploidy *Atriplex nummularia* Lindl. (Chenopodiaceae). Biol J Linn Soc 105:218–230

Sawalha MF, Peralta-Videa JR, Romeor-Gonzalez J, Gardea–Torresdey JL (2006) Biosorption of Cd(II), Cr(II), and Cr(VI) by Saltbush (*Atriplex Carnescens*) biomass: thermodynamic and isotherm studies. Colloid Interf Sci 300:100–104

Shen YG, Du BX, Zhang WK, Zhang JS, Chen SY (2002) *AhCMO*, regulated by stresses in *Atriplex hortensis*, can improve drought tolerance in transgenic tobacco. Theor Appl Genet 105:815–821.

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

Shi H, Zhu JK (2002) Regulation of expression of the vacuolar Na^+/H^+antiporter gene AtNHX1 by salt stress and abscisic acid. Plant Mol Biol 50:543–550

Siddiqui BS, Ahmed S, Ghiasuddin M, Khan AU (1994) Triterpenoids of *Atriplex stocksii*. Phytochemistry 37:1123–1125

Silveira JAG, Araújo SAM, Lima GPMS, Viégas RA (2009) Roots and leaves display contrasting osmotic adjustment mechanisms in response to NaCl-salinity in Atriplex nummularia. Environ Exp Bot 66:1–8

Slavich PG, Smith KS, Tyerman SD, Walker GR (1999) Water use of grazed saltbush plantations with saline watertable. Agricu Water Manag 39:169–185

Smaoui A, Barhoumi Z, Rabhi M, Abdelly C (2011) Localization of potential ion transport pathways in vesicular trichome cells of Atriplex halimus L. Protoplasma 48:363–372

Sousa AI, Caçador I, Lillebø, AI, Pardal MA (2008) Heavy metal accumulation in *Halimione portulacoides*: intra- and extra-cellular metal binding sites. Chemosphere 70:850–857

Tabuchi T, Kawaguchi Y, Azuma T, Nanmori T, Yasuda T (2005) Similar regulation patterns of choline monooxygenase, phosphoethanolamine N-methyltransferase and S-adenosyl-L-methionine synthetase in leaves of the halophyte *Atriplex nummularia* L. Plant Cell Physiol 46:505–513

van der Baan A, van Niekerk WA, Rethman NFG, Coertze RJ (2004) The determination of digestibility of *Atriplex nummularia* cv. De Kock (Oldman's Saltbush) using different in invitro techniques. South Afr J Anim Sci 34:95–97

Vickerman DB, Shannon MC, Banuelos GS, Grieve CM, Trumble JT (2002) Evaluation of *Atriplex* lines for selenium accumulation, salt tolerance and suitability for a key agricultural insect pest. Environ Poll 120:463–473

Vromman D, Flores-Bavestrello A, Šlejkovec Z, Lapaille S, Teixeira-Cardoso C, Briceño M, Kumar M, Martínez J-P, Lutts S (2011) Arsenic accumulation and distribution in relation to young seedling growth in *Atriplex atacamensis* Phil. Sci Total Environ 412–413:286–295

Wang LW, Showalter AM (2004) Cloning and salt-induced, ABA-independent expression of choline mono-oxygenase in *Atriplex prostrata*. Physiol Plant 120:405–412

Welch BL (1978) Relationships of soil salinity, ash, and crude protein in *Atriplex canescens*. J Range Manage 31:132–133

Xiao G, Zhang GY, Liu FH, Chen SY (1995) The study of the BADH gene in *Atriplex hortensis*. Chin Sci Bull 40:741–745

Xu J, Yin H, Yang L, Xie Z, Liu X (2011) Differential salt tolerance in seedlings derived from dimorphic seeds of Atriplex centralasiatica: from physiology to molecular analysis. Planta 233:859–871

Yamaguchi-Shinozaki K, Shinozaki K (1994) A novel *cis*-acting element in an *Arabidopsis* gene is involved in responsiveness to drought, low-temperature, or high-salt stress. The Plant Cell 6:251–264

Yang X, Wen X, Gong H, Lu Q, Yang Z, Tang Y, Liang Z, Lu C (2007) Genetic engineering of the biosynthesis of glycinebetaine enhances thermotolerance of photosystem II in tobacco plants. Planta 225:719–733

Yin X, Zhao Y, Luo D, Zhang H (2002) Isolating the promoter of a stress-induced gene encoding betaine aldehyde dehydrogenase from the halophyte *Atriplex centralasiatica* Iljin. Biochim Biophys Acta 1577:452–456

Zhang H, Dong H, Li W, Sun Y, Chen S, Kong X (2009) Increased glycine betaine synthesis and salinity tolerance in AhCMO transgenic cotton lines. Mol Breed 23:289–298

Zucca C, Julitta F, Previtali F (2011) Land restoration by fodder shrubs in a semi-arid agro-pastoral area of Morocco. Effects on soils. Catena 87:306–312