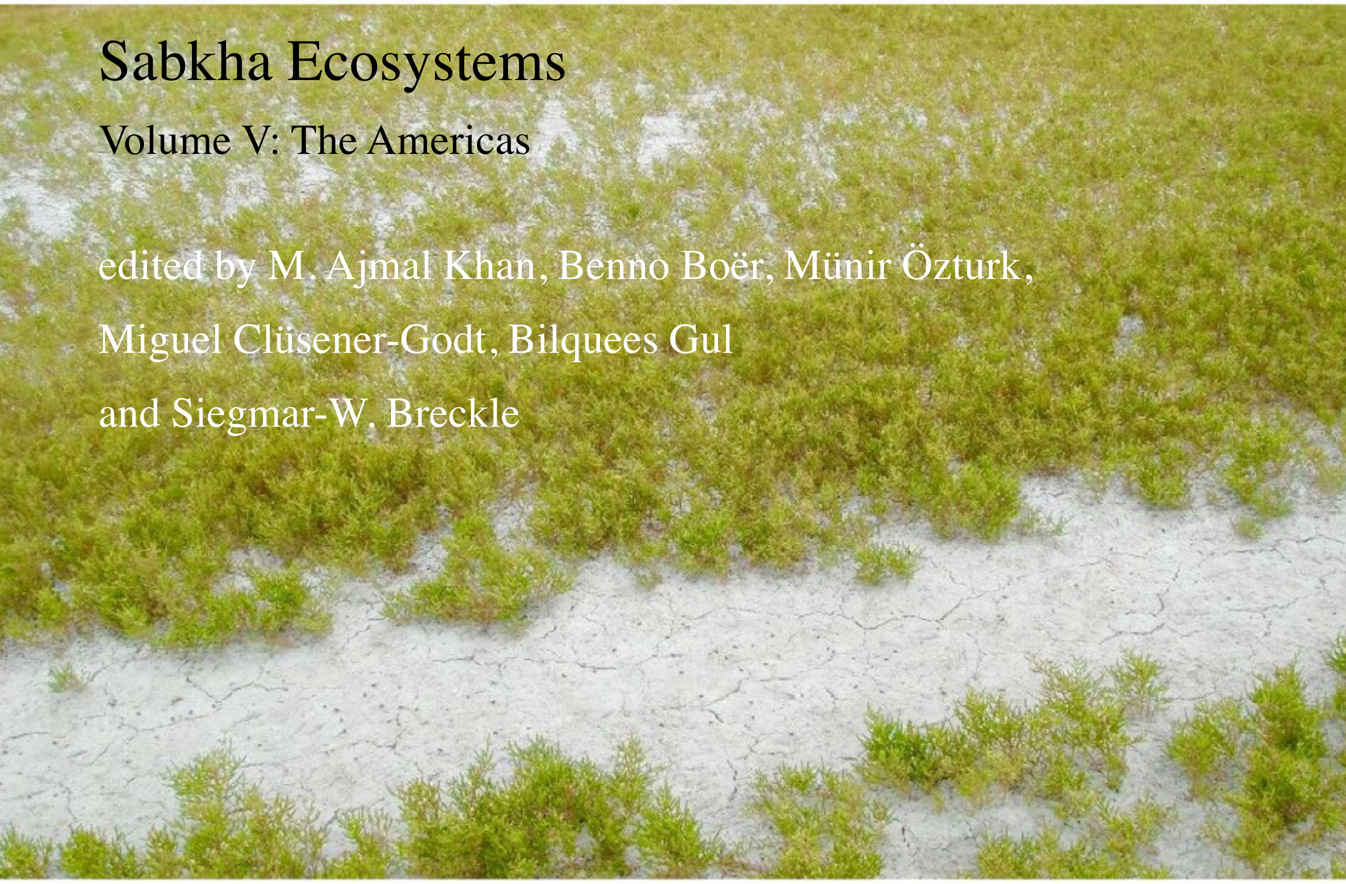
TASKS FOR VEGETATION SCIENCE – 48



Sabkha Ecosystems

Volume V: The Americas

edited by M. Ajmal Khan, Benno Boër, Münir Özturk,
Miguel Clüsener-Godt, Bilquees Gul
and Siegmar-W. Breckle

EXTRAS ONLINE

Springer

Tasks for Vegetation Science 48

Series editor

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More information about this series at http://www.springer.com/series/6613

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ISSN 0167-9406 ISSN 1875-130X (electronic)
Tasks for Vegetation Science
ISBN 978-3-319-27091-3 ISBN 978-3-319-27093-7 (eBook)
DOI 10.1007/978-3-319-27093-7

Library of Congress Control Number: 2002024322

Printed on acid-free paper

This Springer imprint is published by Springer Nature
The registered company is Springer International Publishing AG Switzerland

Foreword

The *Sabkha Ecosystems Series is the most comprehensive scientific documentation dealing with hypersaline coastal and inland ecosystems and with numerous scientific and development aspects. The series started in 2002 with Volume I, on the "Sabkha Ecosystems of the Arabian Peninsula and Adjacent Countries"; Volume II, on "West and Central Asia (2006)"; Volume III, on "Africa and Southern Europe (2011)"; and Volume IV, on "Biodiversity Conservation and Cash Crop Halophyte Development (2014)." Sabkha Ecosystems of the Americas* is the fifth volume of the series, and one additional volume on the *Sabkha of Asia – Pacific* is expected to conclude this global documentation in Springer's *Tasks for Vegetation Science*.

UNESCO is the only United Nations body with a specialized science sector and with the word *science* clearly stated in its name. UNESCO has the needed intellectual capacity and the leading role advancing the scientific bases for water management, ecosystem research, and biodiversity conservation, as well as education for sustainable development. The series was inspired and supported by UNESCO's Natural Sciences Sector.

Our planet's human life support system has reached and partly exceeded its limits, especially with a view to food and water security in the dry land areas.

Considering globally dwindling freshwater resources, increasing demand for freshwater for irrigation, considering the fact that we know approximately 2200 halophytic plant species, and considering that we have reached a total number exceeding 7.2 billion human beings living on Earth, it is surely in the best interest for mankind to continue the process of scientific research into halophyte development. There is an abundance of saline water resources available, including saline groundwater, saline wastewater, and full-strength seawater. The long process of scientific research and development needs to be accompanied with good ecosystem management practices, based on science and under consideration of ethics, biodiversity conservation, and numerous other aspects as required under the new United Nations Sustainable Development Goals.

It is also of importance for the scientific and development community to reach out to those who can provide the necessary financial resources to support halophyte research and development, until visible and profitable products become available for farmers and investors.

The current volume includes scientific contributions on biochemistry, biodiversity issues, biofuel production, botany, climate change, coastal ecosystem management, ecosystem restoration, ecophysiology, fodder production for sheep, genetics, germination strategies, grain production, halophyte-bacteria interaction, landscaping, morphophysiology, seed banks, soil-plant relationships, as well as halophyte farm development in hyper-ari coastal zones.

I wish to express my thanks and continuous support to the Springer Publishing House, as well as the editors and numerous authors of this important publication, who worked relentlessly to make this highly important book series a reality.

UNESCO Assistant Director-General for Natural Sciences Flavia Schlegel
Paris, France

Preface

This volume is devoted to the sabkha ecosystems of Americas. Sabkha is an Arabic word for salt flats, which occur on all continents. The largest area of true coastal sabkhas in Americas is along the Sonoran coast of the northern Gulf of California in Mexico. The Gulf of California acts as a tidal funnel, with tidal amplitude increasing as you proceed up the Gulf. At the head of the Gulf where the Colorado River enters the sea, mean tidal amplitudes of 5–10 m prevail. Although now dammed and diverted for human use, the Colorado River historically was known for its summer floods, depositing vast quantities of sediments into the northern Gulf over at least five million years. The Colorado River carved the Grand Canyon from the uplifting Colorado Plateau. The rock that was removed now resides as vast sediment beds in the northern Gulf of California. These sediments have created long, gently sloping shorelines on the eastern side of the northern Gulf. The combination of high tidal amplitudes and gently sloping shorelines has produced about 114,000 ha of coastal salt flats in Sonora with tides penetrating as much as 10 km inland.

On the Pacific coast of Baja California, the Vizcaino Desert supports large natural sabkhas as well as the world's largest salt-making facility at Guererro Negro, Mexico, with over 30,000 ha of evaporation and crystallization ponds where seven million tons of salt are produced from seawater each year. Coastal sabkhas also occur as salt pannes in the extensive coastal salt marshes of the Gulf of Mexico and Atlantic seaboard in the USA and Mexico. If the definition of sabkha is expanded to include inland salt flats, Americas supports a variety of other saline ecosystems. These include the salt flats and marshes along the shores of the Great Salt, Big Soda, Mono, Walker, and Pyramid Salt Lakes in the Great Basin Desert, the saline playas of the southwestern USA and northern Mexico, and the salt scalds of the Prairie Pothole region of the northern Great Plains in the USA and Canada.

If we extend the definition of sabkhas still further to include man-made saline ecosystems, they include the saline land and water bodies produced by irrigation districts in the western USA and northern Mexico. An example is the Salton Sea, California's largest inland lake, the salinity of which currently exceeds seawater. It is a below sea-level depression that receives brackish drain water from farms in the Imperial and Mexicali irrigation districts. It has no outlet to the sea, so it has become more saline with time. It has transitioned from a unique ecological asset for birds and marine life in its heyday in the 1950s to a looming environmental disaster for both wildlife and human health. Diversion of water from agriculture to cities in the region has caused the shoreline to contract, exposing decades of toxic chemicals to the atmosphere. Seasonal dust storms expose local residents to these chemicals, and the rotten egg odor of hydrogen sulfide from the exposed seabed triggers health alerts in Los Angeles 200 km away.

Like other volumes in the *Sabkha Ecosystems* series, this volume presents a wide-ranging treatment of the geology, hydrology, and ecology of Americas saline ecosystems. It also presents ideas on how to treat saline soils and water as assets rather than just problems, including using the unique halophytic flora of Americas sabkhas as potential crop plants. This volume also includes agriculture, biochemistry, biodiversity conservation, ecophysiology, genetics, livestock production, soil ecology, wastewater recycling, food waste recycling, and food security.

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Acknowledgement

The technical and financial support of UNESCO and ISHU (Institute of Sustainable Halophyte Utilization) is gratefully acknowledged for the publication of volume V of the global Sabkha Ecosystem series.

We also thank Dr. Abdul Hameed, Assistant Professor, Institute of Sustainable Halophyte Utilization, University of Karachi, for his help in coordinating the manuscripts.

Moreover, thanks are due to the Springer publishing house for their continuous cooperation and for their patience which is required in times, when authors merely wish to publish in 'index-rated journals' due to the pressure of employers, rather than for their real scientific interests and passion.

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Introduction

The world's population has increased even more and has reached a total of ca. 7.2 billion people since the publication of *Sabkha Ecosystems Vol IV* in 2014. We already warned that our planet's natural resources are limited. As a matter of fact, our planet's human life support system has reached and partly exceeded its limits, especially with a view to the dry land areas.

The amount of land needed to produce food has reached an alarming level. In addition, many regions of the world are suffering from scarcity or extreme scarcity of freshwater availability. Many regions have been degraded to water-scarce regions even with available natural water resources. Large freshwater lakes are drying up, due to overconsumption of water. Communities and civilizations are poised to new conflicts on water security and food-security, in several cases based on shared surface and groundwater resources. In addition due to increased sediment erosion and water pollution, many freshwater sources are becoming unsuitable for domestic consumption and agricultural production. Intense agriculture is also causing desertification and soil salinization rendering the productive agricultural land nonproductive and converting them into hypersaline sabkhat in arid regions. One of the solutions contributing to reversing the adverse situation could be the utilization of saline land and saline water for the production of salt-tolerant biomass which could be used as fodder, forage, edible oil, biofuel, biodiesel, medicine, and other economic usages by using nonconventional crops from the group of plants called halophytes. A number of research groups from different parts of the world have been trying to develop nonconventional cash crop halophytes. Significant progress has been made at various laboratories and experimental demonstration projects, but still the world at large is hesitant to test and apply this concept at productive commercial level and to make it cost-effective. We have proposed a model project here which can be used in any arid region of the world to begin a commercial scale sustainable production of halophyte biomass using saline resources and waste products. This volume of *Sabkha Ecosystems* in the Americas contains new information on saline ecosystems and their potential utilization from the American continent. This volume consists of chapters in the area of halophyte research and development, including agriculture, biochemistry, biodiversity conservation, biofuel production, botanical aspects, ecophysiology, genetics, habitat restoration, livestock production, sabkhat development with cash crop halophytes, soil ecology, wastewater recycling, food waste recycling, and food security.

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The original version of the Foreword and Preface was revised. An erratum can be found at http://dx.doi.org/10.1007/978-3-319-27093-7_25

1

Prospects of Environmentally Friendly Farms for Food Security in Hot and Dry Coastal Areas Based on Seawater Irrigation and Wasteproducts – An Inspirational Proposal

Benno Böer, M. Ajmal Khan, Hans-Werner Koyro, and Kenneth B. Marcum

Abstract

Salt-water-irrigated projects have been set-up in the 1980s and 1990s, with varying degrees of success, especially in Abu Dhabi, Khor Kalba, and Dubai in the United Arab Emirates, Ras as Zawr in Saudi Arabia, but also in Eritrea, Mexico, the Netherlands, Pakistan, Sudan and elsewhere, with the rational to develop productive agro-systems for food production under marginal soil-water conditions. The human population in coastal dry lands has significantly increased in the last 20–30 years, or so, and with it, their dependency on food-important, even more limited freshwater resources, and the increase of waste products. This manuscript is not another proposal to establish seawater experimental farms – it is a call to continue the overall process of the sustainable utilization of halophytes in hyper-saline ecosystems. In order to achieve meaningful progress, these projects need to find long-term support, with targeted scientific research, capacity augmentation, education, and the utilization of waste-products from human settlements.

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M.A. Khan et al. (eds.), *Sabkha Ecosystems Volume V: The Americas*,
Tasks for Vegetation Science 48, DOI 10.1007/978-3-319-27093-7_1

1 Introduction

The total number of humans living on Earth has grown from 370 million in the year 1350, rising to 1.6 billion in 1900 to over six billion in 2000, and has exceeded seven billion in 2011 or 2012. Even though the global population growth is difficult to predict, it is clear that it keeps growing. It is estimated to have reached by now a number of 7.5 billion. In the same time, the natural resources that form the basis of the food-production chain to supply this human population with enough food, have not grown and they cannot grow. Science and education-based technology innovations have assisted making agricultural land significantly more productive, towards more output of cash crops, livestock, poultry and fish, but, the needed energy for natural gas-derived fertilizers, as well as oil-derived pesticides, and hydrocarbon-fueled irrigation, and soil tillage and amelioration, is based on a finite source of energy: fossil fuel. Moreover, potentially productive land has been cleared from its natural ecosystems and converted into man-made agro-systems, leading to larger space-availability for food production. However, the blind believe in technology is not advisable because of frequently recurring technology accidents in the nuclear and fossil fuel energy sectors (i.e. the Tchernobyl (1986) and Fukushima Disasters (2011), the 1991 Gulf War Oil Spill). In addition the dangerous growth-associated release of green-house gas emissions (in particular CO_2 and CH_4) is highly questionable in view of ecosystems functioning, that is absolutely essential to keep the human life-support system of our planet intact. UNESCO warned about the unbridled exploitation of natural resources as early as the 1970s, and the pioneer ecologists Heinrich Walter summarized in his *Memoires of an ecologist* rapid population growth and blind believe in technology as the most threatening factors for ecosystem functioning (Walter 1989).

In order to try and guarantee food-security for all, we need to move into a new era of environmental and socio-economic ethics centered on responsibility and not merely on profit. We need to continuously and increasingly invest in scientific research, education, family planning, and professional environmental planning. Subsequently it is of paramount importance to find ways into seawater utilization for food-production, and the widespread utilization of environmentally friendly energy sources.

This manuscript provides a guideline into making hitherto non-productive ecosystems available for the environmentally friendly production of food for human consumption, based on the utilization of abundant seawater, wastewater, and halophytes and glycophytes for agricultural production in coastal dry lands. Our recommendations will most certainly not solve the massive and multi-dimensional issues of food-security, but, if taken seriously, they can play significant roles in food-security improvement in numerous coastal hot and dry desert countries in the world.

Hyper-arid hot coastal regions are mostly characterized by extremely low precipitation (<250 mm/year), high evapotranspiration (often exceeding 2500 mm/year), and low primary productivity of terrestrial zones. Due to lack of freshwater, there is obligate dependence on food import, and reliance on seawater desalinization as a freshwater source. However, intertidal marshes and coastal waters have high biological productivities through salt marsh halophytes, mangroves, seagrasses, and macro-algal supported fish, shrimp, and other marine organisms. Coastal cities in these hyper-arid regions produce large quantities of valuable resources, such as urban wastewater and foodwaste, which could be used in conjunction with seawater in saltwater agricultural production schemes to significantly enhance the food security of these regions. This paper provides a model for such a saltwater production system by using seawater, urban wastewater, and foodwaste resources in conjunction with salttolerant plants (halophytes).

Substantial achievements have been made in the development of halophytic ecosystems and the use of halophytes. Some of the efforts have been listed and explained in Böer and Lieth (1998, 1999), Böer (1999, 2002, 2004a, b), Clüsener-Godt and Böer (2002), and Baba et al. (2003).

UNESCO has supported science-based halophyte ecosystem studies for many years, utilizing its capacity in bringing together multi-disciplinary experts in halophyte research and development.

2 Rational

Hot and dry desert regions characterized by hyper-aridity, low precipitation, and extreme evaporation, including the riparian countries of the Gulf, the Arabian Peninsula, and the border countries of the red Sea, increasingly suffer from lack of freshwater sources, increased dependency on seawater desalinization, and dependency on foodimports, resulting from the rapid increase in human population and living standards.

Large quantities of seawater, saline groundwater, saline wastewater, and marine discharge waters are ready available. These facts lead to the corerationale of this paper:

There is a need to enhance food security, feed security, and biofuel production in environmental settings of freshwater limitation and saltwater abundance. The authors believe that a critical step to achieve these goals is the establishment of an "***Environmentally friendly farm for the sustainable production of cash crop halophytes and biodiversity conservation***". Though halophyte cash crop production is a difficult task, requiring inter-disciplinary expertise and rigorous research, much has been achieved in recent decades. Plants, including most halophytes, do grow better with lower than seawater salinities. Fertilizer is required, as well as soil amelioration, maintenance, and eventually profitability. How can this best be achieved in the socio-economic setting of hot, dry desert countries, considering their natural environment and economic systems? In this paper, authors have developed basic guidelines to enable establishment of farms, based on research knowledge to-date, as well as their experiences and vision.

Acceptance of halophyte farm systems continues to meet resistance among landowners, land users, and decision makers, though population pressures, food shortages, and widespread soil- and groundwater salinization urgently require solutions. Technologies now exist to make productive use of saline waters. Functioning pilot-systems need to be developed, tested, scientifically documented, and demonstrated in an understandable way, allowing farmers and landusers to understand and replicate halophyte production systems profitably.

3 A Concept to Enhance Food and Water Security in Hot Dry Deserts

Numerous researchers, developers and decision makers have attempted to develop bio-saline agricultural technologies, mainly at low- to medium-salinity levels. Based on their long-term experiences and published research, including the book series *Sabkha Ecosystems of the World* (Barth and Böer 2002; Khan et al. 2006, 2014; Öztürk et al. 2011), the authors believe that it is time to coordinate existing knowledge to develop integrated cash crop halophyte production systems. We believe that this can only be achieved given the political will and international support of UN agencies, governments, international development agencies, NGO's, and the private sector. It is currently feasible to establish environment friendly farms for cash crop halophyte production utilizing seawater as the main irrigation-water resource. These farms will function as a major international demonstration site for halophyte production technologies, a living collection of the world's halophyte biodiversity, as well as a place to build national and international capacity into halophyte R & D, including cash crop development, biodiversity conservation, education, scientific research, and public awareness. The farm will also develop environmentally friendly methods for water-, waste-, and energy-management, and explore the feasibility of utilizing heated marine-discharge water from power plants (cooling-water) for the irrigation of halophyte farms, ameliorating adverse impacts of large volumes of released anaerobic cooling water into coastal ocean environments.

Halophyte farms will enhance food and feed security, new biofuel sources which do not in compete with food crops, and that do not require freshwater resources for irrigation. This will result in new industries generating jobs and income, will contribute to the rational utilization of national water-, waste-, and energy resources applicable for farms; will assist developing methods for the enhancement of sustainable human living in hyper-arid hot desert regions; and will contribute to achieve the new UN Sustainable Development Goals, UN conventions, and national plans related to desertification, energy, food security, and biodiversity conservation.

Halophyte farms need to consider the land-sea salinity gradient, with the most saline area just landwards of the coastline, and a decrease of salinity away from the sea. Natural inter-tidal vegetation zones are ecologically determined on the tidal inundation regime, or, in other words, and the height above chart datum within the inter-tidal zone. The Fig. 1.1 of the Gulf coastal vegetation is self-explanatory.

Gradual decline in elevation from the most landward side of the farm to the most seaward will allow for inclusion of different natural vegetation zones, as well as allow accommodation of terrestrial and inter-tidal modules. The site will extend into the sea to include some suggested marine modules. This corridor should be located in coastal lowlands, and have a length of ca. 5 km, and a width of ca. 1000 m. It is feasible to locate it in an area of coastal alluvial plain (or coastal sabkha), with a combination of sabkha and higher sandy or gravelly surface available. The site should be located on the mainland to allow easy accessibility for staff and visitors, and good logistic supply of equipment and consumables. It should be located near a settlement of several thousand permanent inhabitants, as the facility will be dependent on use of recyclable waste products, especially greywater, blackwater, foodwaste, and compost.

A number of modules will be integrated into the farm, arranged in proximity to the waterfront based on their seawater inundation or dry-land requirements, respectively. The mangrove unit should be closest to the sea, consisting of two elements, one located in the marine coastal zone (floating mangroves), and the other located above the high-tide mark, in the coastal alluvial plain or sabkha (mangrove production unit). Floating mangroves should be developed in the coastal waters, consisting of those species naturally occurring in the region (Spalding et al. 2010). The floating mangrove unit will serve three purposes: cash crop halophyte development (mainly biofuel, and food), atmospheric carbon sequestration, and sequestration of marine pollutants. In addition, there should be a land-based mangrove production unit, consisting of two elements: an inter-tidal nursery for the germination of seeds, and a plantation of mangroves, utilizing the tidal regime to inundate and drain the mangrove plots. Mangrove units will produce wood-based biofuel (charcoal, wood-chips and pellets, and secondary processed products), fodder (seeds; leaves), as well as biomass for fishfeed, and honey.

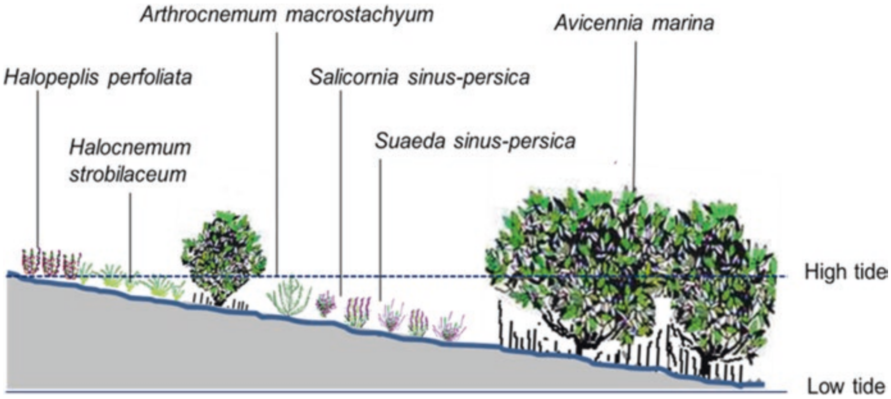

Fig. 1.1 Inter-tidal vegetation zones in Qatar (© ChanthyHuot & Benno Böer)

The next landward unit is a seagrass unit, using species of importance to the hot sub-tropics (Milchakova et al. 2014). Potential production from this unit include materials for mattresses, carpets, and insulation, livestock, and fish feed. The unit will also function for *ex situ* seagrass conservation, providing genotypes for commercial global seagrass restoration projects.

Moving landward, the next unit is annual halophytes, focusing on indigenous *Salicornia* species, and other annual and biennial halophytes. Research will be conducted to clarify the taxonomy of *Salicornia* species, and plant trials conducted to measure and improve productivity with special emphasis on vegetable oil, salad vegetable, and pickles. Taxonomy must be absolutely clear before conducting field trials, to avoid introduction of exotic species into open coastal environments. Objectives of the unit will be to clarify taxonomy of *Salicornia* species, and to test annual and biannual halophyte species for profitability.

The next unit is a salt-bush, salt-grass and groundcover unit, focusing on indigenous salt bushes, groundcovers, and grasses irrigated either with seawater, or mixed water of lower salinity levels. Salt bushes may include *Arthrocnemum macrostachyum, Atriplex* spp.*, Batis maritima, Halocnemum strobilaceum, Tetraena qatarensis, Tetraena simplex, Salsola imbricata, Halopeplis perfoliata,* and *Anabasis setifera. Batis maritima*, introduced to Abu Dhabi in the late 1980s, is known to be seawater tolerant, however, it is not currently being used for green areas. The groundcover *Sesuvium portulacastrum*, introduced into Abu Dhabi in the late 1980s, has replaced freshwater demanding Bermuda-grass in many green areas throughout Sinai Egypt to Oman. Though *S. portulacastrum* is known to be seawater tolerant (provided the soil can be readily leached), it is still being irrigated with freshwater in most places. There are two indigenous *Sesuvium* species in the Arabian Peninsula: *S. verrocosum* and *S. sesuvioides*, and we know little about their potential in green areas development. including coastal restoration projects, Moreover, there are a number of highly salt tolerant Middle East indigenous grasses (ex., *Sporobolus spicatus*, *Sprorobolus iocladus, Aeluropus littoralis*, *Aeluropus lagopoides*, *Halopyrum mucronatum*, and others), which have potential for development into cultivars for urban landscape turfgrasses. Though urban landscapes require huge water allocations in arid regions, there are currently no seawater tolerant turfgrass or grass fodder cultivars available on the market. Research is currently underway at United Arab Emirates University to collect and evaluate a broad collection of ecotypes of *Aeluropus lagopoides* and *Sporobolus spicatus* for potential use as turfgrasses under seawater irrigation. The purpose of this unit is investigate the economic value of these potential species, to develop plant material for coastal restoration projects, and urban landscape projects, and to research and document the most economically feasible irrigation and drainage methods for their utilization. Species will be evaluated for salinity tolerance, mowing tolerance and landscape aesthetic quality under seawater irrigation.

A unit on indigenous fodder plants will focus on the production of indigenous plants that are known to be good livestock fodder plants, such as *Cenchrus ciliaris*, *Panicum turgidum, Pennisetum divisum, Rhanterium epapposum*, *Sporobolus iocladus* (syn. *arabicus*) and others. Feeding experiments with livestock will be conducted, and analyzed for nutritional components in the laboratory. The purpose of this unit is to determine if these species have lower irrigation requirements, and higher salinity tolerance levels when compared with conventional alfalfa, Rhodes grass and other fodder plants. Production costs, yield potential, and fodder nutritional value of the plants irrigated with saline water will be studied and documented. An initial study is underway at United Arab Emirates University to evaluate UAE ecotypes of several native grass species for animal fodder use.

In conjunction with experimental fodder production, the farm will also have an animal production unit with livestock (camel, sheep, goat, gazelle, hare, and others) and poultry (ostrich, turkey, chicken, geese, ducks). The unit will function to produce livestock-based protein (meat and eggs), and other products based on high-salinity tolerant and / or indigenous, or mixed fodder. Costs, fresh water savings, and other relevant data will be collected and documented.

Finally, the farm will have a unit that functions as a World Halophyte Garden, with living collections of halophytes from the Arabian Peninsula, the Middle East & North Africa, and the world, with a multi-purpose nursery and a library. We will obtain and produce as many halophyte species and their ecotypes as possible from subtropic and tropic regions worldwide, with emphasis on the Middle East and North Africa. This will function as a biodiversity conservation contribution by *ex situ* conservation, but also for research, and as a biodiversity pool for halophyte ecosystem restoration globally.

4 Technical Units

In addition to plant and animal production units, technical units are needed, such as a water recycling and management unit. Based on specific, local climatic conditions, the project will utilize rainwater, urban greywater and secondary treated waste water, as irrigation water sources. As well as to function as decentralized treatment unit, including a grey-water reception unit, a raw sewage reception unit, a grey-water and black-water treatment (Neuschaefer system using septic tanks, geolined sand-pits with *Phragmites* reed-beds), a rainwater harvest system on roof-spaces of farm and associated buildings, a water from air-humidity, cool air, and electricity (Al Nuaimisystem), and condensed water from all air-condition units will be kept and stored. Mix-water batteries, seawater pumping-, storage-, and drainage facilities, seawater beach well supplies (Ron Daniel system), fresh and salt water storage tanks, fresh and salt water pumps, and fresh and recycled water pipe irrigation systems will be installed. The objective is to utilize all available water sources in environmentally friendly, low energy costfashion. Some native plant species considered for cash crop production may have salinity tolerance levels below seawater, requiring salinity level adjustment capability of the irrigation systems. Moreover, both personnel and farm livestock will have daily fresh waterdemands, which may be met, at least partially, via the various above-listed systems.

Other facilities include living accommodation for staff, labor, and short-term guests, offices for administration and strategic partners, dry and wet laboratories, a veterinary unit, shade houses and green houses, a visitors education and interpretation unit featuring a small restaurant serving farm produce, a water and electricity unit, staff facilities, such as, leisure/recreational, laundry, etc. Though facilities will be allocated to building space as efficiently as possible, sufficient land should be available for future expansion. As staff and livestock will be living on site, technological components will require continual maintenance, requiring permanent technical staff on site. It is therefore important to establish all necessary facilities for staff accommodation, administration, technicians, and also the required facilities for water, energy, and waste-management, as well as for animals and plants, prior to opening the facility. The buildings on the farm should be so designed, that external power supply, water supply, drainage, and waste-disposal is minimized as much as possible. One of the goals of the farm is to be as water, energy, and waste-management independent as possible. Water and energyconsumption, and wasteproduction will be monitored and minimized.

Food waste will be recycled for use as livestock and poultry feed, requiring facilities for sterilization and processing. This unit will be developed in conjunction with a fodder-production unit, where various livestock fodder compositions will be produced, analyzed and tested in the animal production units.

A compost production facility will test optimum compost compositions to enhance soil condition and crop productivity A Terra Save raw-sewage recycling facility will produce electricity based on solar energy, and it will produce high-quality irrigation freshwater based on reed-bed technology, under full consideration of hygienic issues. An Agri Green facility will produce drinking water based on de-humidifying air-humidity, utilizing solar-powered cooling elements.

A combined solar-wind system will be selected, based on cost-efficiency and longevity under conditions of extreme heat, humidity, and salinity.

The farm will offer options for testing and application of additional novel, environmentally friendly freshwater-, energy-, and waste-management technologies, the goal being to make the farm energy, water and waste-production independent.

It is advisable to have additional space available for future unit additions related to cash crop halophyte development, as well as other potentially profitable production units, for example cutor desert flowers, mushrooms, mari-culture phytoplankton and macro-algae production units, aquaculture, mesquite-charcoal and others. The farm will strive for innovation, adopting promising new unit technologies and production schemes which concur with farm objectives to develop sustainable, profitable salt water agriculture. Space and infrastructure flexibility should be considered in the planning phase to ensure future testing capabilities.

5 Educational, Economics, PR and Administration Units

It is important to establish a department that deals with education, socio-ethics, cultural acceptability of products and production systems, and the highly important aspect of profit. Administration should be done internally in order to avoid non-desired bureaucracy, dependency on remote Headquarters, and to allow for maximum flexibility. This, however, needs to be discussed.

6 Strategic Partnerships

Strategic partnerships are essential for success of the farm, in terms of research, sustainability, and productivity. Long-term partnerships with external organizations, such as UNESCO, other UN agencies (FAO, IFAD, UNDP, UNEP, WFP and others), university research groups at the Institute for Sustainable Halophyte Utilization (University of Karachi), the International Society for Mangrove Ecosystems (University of the Ryukyus), Centre for Sustainable Development (Qatar University), Arid land Agriculture (United Arab Emirates University), and others. Permanent and/or temporary office space may be needed for these, depending on level of involvement. In addition an international advisory committee needs to be established, in order to review progress made, and provide guidance based on international halophyte research and development capacities. Strategic partnerships are essential to obtain needed expertise and guidance, and to assist in research, training, information dissemination and commercialization.

7 Research Focus in Laboratories and External

Rigorous scientific research, including field and laboratory experimentation and publication of results, are absolutely essential for the success of the farm. This must be clear to everyone involved, including those providing financial support, and must be included in the budget for the establishment of the facility. It may take several years before one to several modules start generating profit; others may take 10 years or more. The proposed halophyte farm-project will not be successful or sustainable without solid, long-term funding commitment of at least 5–10 years. Research proposals will be made by head of departments and their staff, with focus decided by the Scientific Management Team. Research examples include primary productivity for food, feed, biofuel, ligno-cellulosic biomass, urban landscapes, environmental remediation, water requirements, growth, stress adaptations and evapotranspiration, propagation, nutritional analyses, soil analysis, medicinal and pharmaceutical value, industrial value, weather station and climate research, phyto-pathology, others. Research will focus on both ecological sustainability and economic profitability. Three major objectives will be pursued:(1) Development of profit-driven technologies for sustainable halophyte farm industries, (2) Generation of the critical scientific and practical knowledge-base to enable all aspects of a sustainable halophyte farm industry, and (3) Dissemination of practical knowledge and success stories to local industries. Research will be problem-driven and highly applicable to develop the basic operating system for high salinity agro-ecological productivity in hot, dry desert coastal ecosystems.

8 Benefits to the Farm Owner

Benefits to the farm owner include contribution to UN MDGs and UN SDGs, as well as UN conventions, and national human development plans. Participating farmowners will contribute to enhancing sustainable human living while reducing the environmental footprint in coastal hot and dry desert countries, while participating in an economically profitable industry. Major benefits include economic, capacity building, environmental, including improved methods for the handling of marine discharge waters, conservation of limited freshwater resources, agricultural and food security, educational and tourism, and societal.

9 Visits

External relations (PR) and units will jointly facilitate and coordinate visits of stakeholders to the farm, as well as staff visits to other stakeholder conferences and events. Educational unit will offer courses to agricultural producers and other stakeholders, focusing on important aspects of halophyte farm management. Expected visitors include regional schools, colleges, and university faculties, national and international educational bodies, visiting persons/delegates/VIP from NGOs, IGOs, farm and agricultural producers, other regional bodies from public and private sectors, et al.

10 Expected Products and Output

Expected products from research and development include new technologies for large-scale environmentally friendly cash crop halophyte production in coastal hot, dry environments, a living collection and production facility for cash crop halophytes and *ex situ* halophyte biodiversity conservation, involvement and training of young professionals, and education of farmers, land-owners, decision makers and investors about halophyte farm management aspects.

11 Human Resources and Technical Requirements

Space requirements are reasonable and land costs low: 5 × 1 km total size under hyper-saline conditions (ex. coastal alluvial plains or sabkha). Soil amendments may be needed, based on site conditions: it is likely that a certain amount of dune sand will be needed. The major required water sources include marine discharge water (power plant) and freshwater from urban waste-water. Necessary compost may be obtained from nearby urban food and landscape wastes.

Necessary equipment includes farm implements, preferably of non-corrosive materials, a weather station driven ETo based irrigation system (field), monitored by soil moisture/salinity sensors, greenhouse drip irrigation system, animal pens, feeding areas (land and marine based), laboratories with associated analytical equipment for soil and plant morphological, physical and chemical analyses, for instance psychrometers, conductivity meters, drying ovens, weighing scales, tissue digestion facility, DNA analysis (for genetic classifications), inorganic (AAs, IC etc.) and organic analysis (HPLC, etc.), composting facility, including capacity for recycling animal wastes, transport vehicles, consumables including soil amendments, fertilizers, petrol and vehicle servicing, office and other consumables.

The human resources include technical and scientific staff. The water and electricity requirements should be self-sufficient as much as possible. Though travel should be minimized based on budgetary considerations, it is an essential part of project development to visit relevant stakeholders in the world, and of importance for knowledge transfer and strategic partnerships.

12 Costs and Timing and Funding

Both 5 and 10 year plans, and a "50 Year Vision" should be developed in the document "Guidelines for the establishment of an environmentally friendly farm for cash crop halophytes and biodiversity conservation". A comprehensive budget including initial establishment and annual operation expenses should be should be included, specified in the subsequent Master Plan. Potential funding opportunities to consider include both national and external, government and private, obtained for four different project phases.

Work among in the four phases needs to be logically synchronized to allow for time optimization. Important elements must be established first, allowing coremanagement staff and laborers to commence work as soon as possible, while other units are still under development/construction. The Guidelines and Master Plan has to consider this aspect, providing clear guidance on technical and human resources development during the establishment of the farm. Therefore, identification of core staff, as well as the establishment of temporary buildings, may be useful.

Phase I: An International Advisory Committee Meeting will take place to produce the document "Guidelines for the establishment of an environmentally friendly farm for cash crop halophytes and biodiversity conservation", expected to be complete within three months of project inception.

Phase II: A Master Plan will be produced based on the outcome of Phase I. It will consider all aspects of the farm, including space, buildings, equipment, consumables, staff requirements, consumables, required supply of materials etc., investment and running costs, research budget, expected profit, and all other aspects.

Phase III: Site selection and establishment of the farm.

Phase IV: Inauguration and operational phase. The timing for the various phases of construction should be estimated in the document "Guidelines for the establishment of an environmentally friendly farm for cash crop halophytes and biodiversity conservation", and it must be clearly specified in the Master Plan. It is hoped that the farm could be inaugurated less than 2 years from start of project.

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Halophytic Life in Brazilian Salt Flats: Biodiversity, Uses and Threats

2

César Serra Bonifácio Costa
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Abstract

Brazil has over 8000 km of coastline and 1,085,187 km^2 of drought-affected areas where natural processes and land-use changes originated extensive salt flats. Brazilian coastal salt flats are found as transition zones of mangrove forests or salt marshes and dry upland areas, and they are located above the mean level of the spring tides, either in semiarid or in seasonally dry coasts. The salt flats' distributions are irregular, covering 1–24.4 % of the studied intertidal areas. Their sandy soils show salt contents near the seawater values and can increase to 150 ppt during the dry season. Dominant plants are widespread species more frequently found in tropical parts of South America. Halophytic forbs and grasses cover the mid-littoral and hypersaline gaps of the mangrove, whereas mixed stands with sedges occur when seasonal superficial fresh water drainages alleviate soil salinity. Although there are very few records of halophyte utilisation, intertidal crabs are important for the estuarine food web and exploited by indigenous peoples and fishermen for human consumption. Salt pans and shrimp farming are the most common anthropogenic activities that occur within salt flat areas. Inland salt flats are common in low annual rainfall (500–800 mm) areas of the northeast region of Brazil. The stony soils with sodium character promote natural formation of salt flats. Low rainfall, a high water deficit and careless irrigation management can establish very quickly secondary salinisation in these soils. Surface soil saturate extract of natural and manmade salt flats can average 8–40 dS m^{-1} CE values during the drought season. The dominant cover of inland salt flats includes few native halophytic forbs and exotic shrubs and grasses, intro-

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M.A. Khan et al. (eds.), *Sabkha Ecosystems Volume V: The Americas*,
Tasks for Vegetation Science 48, DOI 10.1007/978-3-319-27093-7_2

duced in NE Brazil for forage and fodder for domestic animals. Native Malvaceae species are common and also used for animal fodder. Several plants are traditionally used to treat influenza, urinary-renal problems and ulcers, as well as they shown anti-inflammatory and antioxidant properties. Coastal (*Sarcocornia ambigua*) and inland halophytes (*Atriplex nummularia*) has been cultivated in integrated multitrophic aquaculture systems and in salt flats resulting from secondary salinisation, as cash crops and phytoextraction techniques, removing salt from soil and waste nutrients from saline effluent.

1 Introduction

The Brazilian coast extends over 8,000 km, and salt flats occur widely in areas flooded only twice a month by spring tides, where relatively infrequent flooding creates conditions favouring the formation of hypersaline soils. In the past, human destruction of mangroves led to their conversion into coastal salt flats, which benefitted colonisation by herbaceous halophytes. More recently, the conversion of mangroves into salt pans for solar evaporation of salt from sea water, shrimp farms and new resorts has destroyed thousands of hectares of mangroves and their associated salt flats. Simultaneously, a relative sea level rise has been eroding mangrove banks but allowing mangrove propagules to colonise supratidal flats by alleviating salt stress. The impact of these land-use changes and natural perturbations on the biota of mangroves and associated salt flats has just begun to be understood. In northeast Brazil, salt-affected soils are common in drought-affected areas, which the Brazilian government estimated in 1989 to extend over 1,085,187 km^2 (PAN-Brasil 2004). Inland salt flats are present in this semiarid region either due to salinisation associated with natural pedogenic processes or human-induced soil salinisation as a result of inadequate irrigation with saline underground water (Tabosa et al. 2004; Costa et al. 2014a; Souza et al. 2014). Salt-adapted plant communities are established in these inland salt flats, but they remain poorly studied. Both the Brazilian coast and inland salt flats share similar genetic and ecosystemic traits with other salt flats of the world, such as the Middle Eastern “Sabkhas” and the French “tannes” (Albuquerque et al. 2014a).

2 Coastal Salt Flats

Brazilian coastal salt flats are categorised with different notations, such as “apicum”, “salgado” and “areal”. They are frequently found as transition zones of mangrove forests or salt marshes and dry upland areas, and they are located above the mean level of the spring tides, either in semi-arid or in seasonally dry coasts. Vascular plants are distributed increasingly sparsely as soil salinity rises at higher grounds to 2–3 times the concentration of seawater (Hadlich et al. 2008; Ucha et al. 2008; Costa et al. 2009; Hadlich and Ucha 2009; Chaves et al. 2010; Schmidt et al. 2013; Albuquerque et al. 2014a).

There are numerous reliable accounts in the literature of salt flats at individual locations along the Brazilian coast. The salt flats’ distributions are irregular, not occurring in all mangrove areas (Table 2.1). For example, along a ≈ 166-km stretch of the coastline of the Bragança coastal plain (northern state of Pará; 0–1° S) in 1997, mangroves covered 573 km^2 while salt flat coverage was only 5.6 km^2 (Cohen and Lara 2003). The flood fluvial-marine zone of the Apodi-Mossoró estuary, located in the coast of Rio Grande do Norte state (5° S), is subjected to seasonal flood tides up to 3.8 m, and the hypersaline salt flats have a remnant area of 58.4 km^2 because a great part of this plain including former mangrove areas (158.4 km^2) was occupied by solar salt pans (Costa 2010). Landsat 5 TM reflectance images of Itapessoca river estuary (PE; 7° S) taken in 2006 showed that mangrove vegetation occupied an area of 28.1 km^2 and salt flats covered 5.4 km^2 (Santana et al. 2011). Satellite images of São Francisco River estuary (NE

Table 2.1 Extension of salt flats associated with mangrove forests surveyed at different locations along the Brazilian coast

Location	State	Lat. (° S)	Mangrove	Salt flats	Salt flats (%)[a]	Ref.[b]
Bragança coastal plain	PA	1	573.0	5.6	1.0	1
Apodi-Mossoró estuary	RN	5	158.4	51.2	24.4	2
Itapessoca river estuary	PE	7	28.1	5.4	16.1	3
São Francisco river estuary	SE	10	30.1	1.4	4.4	4
Todos os Santos Bay	BA	17	177.6	10.2	5.4	5
Ratones mangrove	SC	27	8.4	0.2	2.3	6

Legend:
[a] Percentage of intertidal areas occupied by salt flats; Lat. = Latitude
[b] References: 1 = Cohen and Lara (2003); 2 = Costa (2010); 3 = Santana et al. (2011); 4 = Santos et al. (2014); 5 = Hadlich and Ucha (2009); 6 = Camargo et al. (2001)

Brazil; 10° S) taken in 2008 showed coverage estimates of 30.1 km^2 for mangroves and 1.4 km^2 for intertidal flats (Santos et al. 2014). At "Todos os Santos Bay" in NE Brazil (17° S), the mangroves and salt flats occupy 177.6 km^2 and 10.2 km^2, respectively (Hadlich and Ucha 2009). At Ratones River estuary in the southern state of Santa Catarina, mangrove forest covers 8.4 km^2 of intertidal areas but salt flats extend over only 0.2 km^2 (Camargo et al. 2001). Thus, hypersaline flats cover 1–24.4 % of the studied intertidal areas, which were distributed from equatorial to subtropical climates (Table 2.1).

2.1 Geomorphologic Features and Main Environmental Factors

There is a great knowledge gap concerning the formation and soil genesis of the Brazilian salt flats. According to Albuquerque et al. (2014a) coastal salt flats are formed primarily by the transport of sediments into the estuaries by water and (or) wind, promoting the formation of banks and the subsequent obstruction of tidal creeks, which locally limits the flow of seawater to tidal flooding during the spring tides. The excavation on salt flats has revealed the presence of a sedimentary pack of coarser granulometry resembling dark coloured and ancient mangrove sediments and the presence of roots in process of decomposition; some deeper levels with shells can also be found (Meireles et al. 2007; Hadlich and Ucha 2009). The frequently sandy constitution of surface- layer salt flat sediments is attributed to the dispersion of colloids by sodium in seawater (Bigarella 2001; Albuquerque et al. 2014a), combined with clay removal by the high energy of tides and rainfall events after the sediment deposition (Ucha et al. 2008; Hadlich and Ucha 2009; Hadlich et al. 2010). Data on pollen and pyrite distribution at these depths also support the hypothesis that coastal salt flats originated from the burial of ancient mangroves (Bigarella 2001; Meireles et al. 2007; Albuquerque et al. 2014a, b). Additionally, in Brazil, these ancient mangrove forests were located in upper physiographic positions (due to transgressive processes) and were probably displaced by the restriction of tidal flooding and lower sea levels that occurred during the last regression period, at ≈5000 years b.p (Marius et al. 1987; Hadlich et al. 2010; Albuquerque et al. 2014a).

The rainfall regimes with long and well-defined dry seasons also contribute to the development of hypersalinity in coastal salt flats. The seasonal variation in pore water salinity and the association of pore water hypersalinity with dry seasons were highlighted by authors across a large range of latitudes along the Brazilian coast (03–04° S, Santos 1989; Lara et al. 2010; 05° S, Costa et al. 2013; 2014b; 12–13° S, Hadlich et al. 2008, 2010; 20° S, Marius et al. 1987; 23° S, Chaves et al. 2010; 25° S, Angulo and Müller 1990). Salt contents are frequently near the seawater values and can increase to 150 ppt during the dry season. Soil salinity is directly related to the dissolved sodium content but may not be correlated with soil electrical conductivity (Hadlich et al. 2010; Costa et al. 2014b). This latter characteristic is strongly affected by the Ca, Mg and K present in pore water, which vary locally due to shell and mangrove debris deposition (Marius et al. 1987; Hadlich et al. 2010; Costa et al. 2014b). The Middle Eastern Sabkhas differ from the Brazilian coastal salt flats in the mineral composition of their sediments, which are composed of well-developed evaporite depositions dominated by carbonates or sulphates (Albuquerque et al. 2014a; Costa et al. 2014b).

The soil water regime is characterised by periodic water saturation, hypoxia conditions and the reduction of Fe (III) minerals (e.g., ferrihydrite, goethite, lepidocrocite; through the bacterial reduction of iron), which result in grey- or neutral-coloured subsurface soils (Marius et al. 1987; Albuquerque et al. 2014a, b). At deeper layers in salt flat soils and at the surface during higher water levels, iron sulphide formation (sulphidisation) may occur due to the combination of anoxic conditions with sulphate input by seawater, iron from the ground and the presence of existing organic matter (from ancient mangroves) (Albuquerque et al. 2014a). Sulphate reduction is an important microbial metabolic pathway in mangroves and other coastal wetland soils, and it controls trace metal biogeochemistry and bioavailability through the coprecipitation of metals with pyrite or via the formation of metallic sulphides (Albuquerque et al. 2014b). During the most common exposition period of salt flats, due to aerobic conditions, the oxidation of dissolved Fe (II) and of iron sulphides results in the accumulation of ferric compounds in the superficial sediment layers (*e.g.,* iron oxyhydroxides). The construction of burrows in the sediment by infauna (*e.g.*, polychaetes, molluscs) and crabs, as well as the penetration by halophyte roots containing aerenchyma tissues (with spaces or air channels that exchange gases in hypoxic soils), are conspicuous pedogenetic processes in coastal salt flats. Soil bioturbation causes the dispersion and (or) displacement of soil particles, and it allows water and airflow throughout the sediment, which affects nutrient biogeochemical cycles (*e.g.*, carbon, nitrogen, and phosphorus) (Pellegrini et al. 2000; Schmidt et al. 2013; Albuquerque et al. 2014a).

2.2 Plant Communities of Coastal Salt Flats

Most of the dominant plants of Brazilian coastal salt flats are widespread species more frequently found in tropical parts of South America but whose distributions extend a long way southward (Table 2.2). The succulent herbs *Batis maritima* and *Sesuvium portulacastrum* are essentially pan-tropical species, characteristic of salt flats flooded only by extreme tides, by they also occur on low sand flats, often extending into the mangrove fringes dominated by more salt-tolerant species of mangroves, such as *Avicennia* spp. (Santos 1989; Cohen and Lara 2003; Hadlich et al. 2008; Herrera et al. 2010; Lara et al. 2010; Schmidt et al. 2013). In equatorial climates, *B. maritima* also occurs in association with the grass *Sporobolus virginicus* and less abundant succulent species such as *Portulaca oleracea* and sedges (*Cyperus* sp.) in small areas of highly saline soils of abandoned salt pans or shrimp tanks (West 1977; Cohen and Lara 2003; Meireles et al. 2007). By contrast, Cohen and Lara (2003) and Cohen et al. (2004) found evident signs of an active progression of mangrove forest into an area previously dominated by herbs and grasses and flooded only during the highest spring tides, with coexistence of *S. portulacastrum*, *S. virginicus* and small (0.5–2 m height) *Avicennia* trees. This progression may be associated with a local relative rise in sea level. It is important to highlight that, along the Atlantic coast, *A. germinans* trees occur from the Caribbean region to the state of Rio de Janeiro (22–23° S), whereas *A. schaueriana* extends over the intertidal zone from 5° S to the southern limit of mangroves at Santa Catarina state (29° S) (Pellegrini et al. 2000; Meireles et al. 2007; Costa 2010; Herrera et al. 2010). When sympatric, *A. germinans* shows larger abundances in hypersaline flats than *A. schaueriana* (Pellegrini et al. 2000; Costa 2010).

Table 2.2 Occurrence of the dominant halophytic species of the salt flats along the Brazilian coast

		Latitude/Brazilian state									
		01 S	3–4 S	5 S	12–17 S	20 S	22–23 S	23–25 S	25 S	27–29 S	30–33 S
Species	Family	PA	MA	CE	BA	ES	RJ	SP	PR	SC	RS
Sporobolus virginicus	Poaceae	+	+	+	+	(+)	+	+	+	+	
Sesuvium portulacastrum	Aizoaceae	+	+	+	+	+	+	+		+	(+)
Batis maritima	Batidaceae		+	+	+	(+)	+			+	
Eleocharis geniculata	Cyperaceae	+		+	+	+	+				
Fimbristylis spadicea	Cyperaceae	+			+				+	+	+
Blutaparon vermiculare	Amaranthaceae			+	+	+	+	+			
Sarcocornia ambigua	Amaranthaceae				+	(+)	+	+	+	+	+
Jaumea linearifolia	Asteraceae										+
Avicennia germinans	Avicenniaceae	+	+	+	+	+	+				
Avicennia schaueriana	Avicenniaceae			+	+	+	+	+	+	+	
References		1	2	3–5	6–8	9–10	11–14	15–16	17–18	19–22	23–24

Legend:
1 = Cohen and Lara (2003); 2 = Santos (1989); 3 = Meireles et al. (2007); 4 = Herrera et al. (2010); 5 = Herrera et al. (2010); 6 = Pinto et al. (1984); 7 = Hadlich et al. (2008); 8 = Schmidt et al. (2013); 9 = Carmo (1987); 10 = Marius et al. (1987); 11 = Dansereau (1947); 12 = Lacerda and Hay (1982); 13 = Pellegrini et al. (2000)); 14 = Chaves et al. (2010); 15 = Rawitscher (1944); 16 = Coelho et al. (2010); 17 = Bigarella (2001); 18 = Angulo and Müller (1990); 19 = Reitz (1961); 20 = Souza Sobrinho et al. (1969); 21 = Santos and Araujo (1987); 22 = Soriano-Sierra (1990); 23 = Marangoni (2003); 24 = Cordazzo et al. (2007)
(+) Pers.comm. C.S.B. Costa

S. virginicus is a cosmopolitan species and an important component of the lower and upper mid-littoral zones in gaps of the mangrove canopy or mid-tidal flats (Santos 1989; Cohen and Lara 2003). Along tropical coasts of NE (Soares et al. 2008) and SE Brazil (Lacerda and Hay 1982; Meireles et al. 2007; Angulo and Müller 1990) with marked rainfall seasonality, *S. virginicus* is frequently associated with the perennial glasswort *Sarcocornia ambigua*, forming sparse coverage of salt flats in hypersaline lagoons.

Sarcocornia ambigua (synonymous with *Salicornia gaudichaudiana*, *Salicornia ambigua* and *Salicornia virginica*; Reitz 1961; Alonso and Crespo 2008) occurs along the Atlantic coast of Central and South Americas, down to Buenos Aires province in Argentina. Monospecific stands of *S. ambigua* were found in salt flats with soil salinities between 40 and 100 ppt neighbouring mangrove areas in the NE (Schmidt et al. 2013), SE (Pellegrini et al. 2000; Chaves et al. 2010) and southern Brazil (Freitas and Costa 2014). Mixed stands with the sedge *Eleocharis geniculata* (formerly: *Eleocharis caribaea*) and *Triglochin striata* can occur when superficial fresh water drainages alleviate soil salinity (Schmidt et al. 2013). The occurrence of *E. geniculata* in hypersaline (40 ppt) areas of equatorial mangroves may reflect a salt-induced annual or deciduous perennial habit of this species because it produces live aerial shoots only during the rainy season (Santos 1989).

Blutaparon vermiculare occurs in the Caribbean region, from Florida to Guiana, and along the Brazilian coast (Hadlich et al. 2008; Herrera et al. 2010; Schmidt et al. 2013); it has also been recorded near Guayaquil in Ecuador (Mears 1982). Marius et al. (1987) highlighted the dominance of salt flats in the state of Espirito Santo by *B. vermicularis*, *S. portulacastrum* and *E. geniculata*. Soils of these salt flats had near neutral pH (6.9–7.3), and EC ranged from 21 to 120 dS m^{-1}. According to Lacerda and Hay (1982), *B. vermiculare* associated with *S. portulacastrum* forms very dense herbaceous communities that may permanently occupy disturbed mangrove areas subjected to soil salinisation.

The plant community, the evolution of coastal salt flats and their relationship with mangroves are determined by the flat topography (*e.g.*, slopes up to 0.4 % according Hadlich et al. 2008), coastal dynamics, a pronounced hydric deficit, the movement of the tides and fresh water input (rain water) (Lacerda and Marins 2002; Cohen et al. 2004; Lara et al. 2010; Albuquerque et al. 2014a). For instance, Schmidt et al. (2013) considered sparsely vegetated salt flats as the herbaceous face of Brazilian mangroves, which together with the unvegetated salt flat, arboreal mangrove and the shrubby landward ecotone form the mangrove ecosystem. On places located above the neap tide, small height differences can produce marked changes in flooding frequency that affect soil salinity and the sediment colonisation by plants. For example, in the northern Brazilian state of Pará, the coast is subject to a macrotidal regime, and there is an 80-cm increase in topographical height between salt flat areas inundated at high tide only during neap tides and areas reached only by spring tides (Cohen et al. 2004; Lara et al. 2010); however, this height difference results in a decrease of landwards flooding frequency of approx. 85 % (Fig. 2.1). At the same site, a longitudinal transect across the salt flat-mangrove profile made during the dry season (June-November) showed pore water salinities reaching 90 and 100 ppt at the "elevated flats" that were inundated only during the highest spring tides (<28 days year^{-1}) (Cohen and Lara 2003; Lara et al. 2010). Vegetation in these hypersaline flats was dominated in the dry season by *S. virginicus* and *S. portulacastrum*, but in the wet season the vegetation is dominated by Cyperaceae (*E. geniculata* and *F. spadicea*; Cohen and Lara 2003). Down in the intertidal zone, "upper mudflats" were inundated only during normal spring tides (28–78 days year^{-1}), and they had pore water salinities between 90 and 50 ppt. These habitats were covered mainly by dwarf trees of *A. germinans*. At about mid-tide level, a slope break occurred and an area of relatively steep, frequently flooded (~233 days year^{-1}) mudflats with pore water salinity of approximately 36 ppt and mixed mangrove forest led down to *Rhizophora*-dominated sectors fringing the estuary (Fig. 2.1). Although this equatorial coast is subject to an annual precipitation averaging 3000 mm and a relative humidity of 80–90 % (Spalding et al. 2010), the marked rainfall seasonality of this region creates appropriate conditions for hypersaline salt flat formation. Much more commonly, hypersaline flats appear along dry tropical coasts. In the Rio Grande do Norte

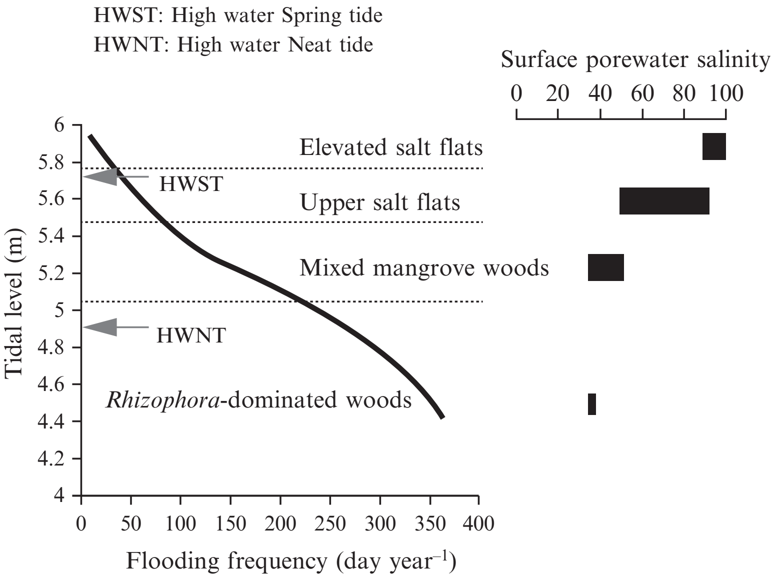

Fig. 2.1 Topographic distribution of salt flat habitats and pore water salinities (ppt) observed during the dry season (June–November) on the coast of the northern Brazilian state of Pará (Modified from Cohen and Lara 2003; Cohen et al. 2004)

state (5° S), high temperatures (>28 °C), low rainfall (<800 mm/year) and high evaporation rates (Costa 2010) result in the surface waters of Apodi-Mossoró estuary becoming hypersaline during the dry season (April to December), reaching salinity values above 45 ppt (Costa et al. 2013). The surface sediment of salt flats showed high electric conductivity values between 77.2 and 150 dS m^{-1}. This reflects the high concentration of sodium in the samples. All the sediment samples presented a high concentration of salts, with surface crusts of crystallised salts (mainly NaCl) (Costa et al. 2014b).

2.3 Ecological and Social Significance of Coastal Salt Flats

Salt flats perform important functions in terms of biodiversity maintenance of flora and fauna in coastal environments, and they provide supplemental food and cash to traditional populations. Giarrizzo et al. (2011), analysing surface soil samples from a northern Brazil salt flat, found a significant abundance of filamentous green algae and microphytobenthos communities. Both producers have small size, fast digestibility, high primary production and spatial closeness. The benthic microalgae were dominated by three diatom species (*Navicula* sp., *Cylinderutheca closterium* and *Pleurosigma angulatum*), and they were isotopically distinct from other primary producers; they were enriched in d13C (−21.5 ± 0.8) and the most depleted in d15N (3.0 ± 1.1). Meireles et al. (2007), Schmidt et al. (2013) and Albuquerque et al. (2014a) reported the occurrence of carpets or mats of filamentous cyanophytes in the mud of salt flats, and they highlighted the important contribution of carbon and fixed nitrogen by these producers to neighbouring mangroves and water bodies.

Brazilian salt flats support large populations of intertidal crabs. Populations of fiddler crabs (*Uca* spp.) are very common, and these deposit feeders form important connections in the estuarine food web (Giarrizzo et al. 2011). It was observed that recruitment of the burrowing crab *Ucides cordatus* occurs at the boundary of mangroves and vegetated salt flats (Spalding et al. 2010; Giarrizzo et al. 2011; Schmidt et al. 2013). This crab is distributed from Florida (USA) to southern Brazil and is the second largest crustacean found in the Brazilian mangroves, and it is the most exploited species for human consumption (Schmidt et al. 2013; Amaral et al. 2014). Albuquerque et al. (2014a) highlighted that the land crab *Cardisoma guanhumi* is also an important food source for traditional populations, and their burrows are mostly built in elevated sites where flooding is less frequent, specifically in salt flats. Salt flats are important feeding grounds for resident and migratory birds. They are also grazed by domestic animals (goats) and provide hunting grounds for crab and mussel collectors (Meireles et al. 2007; Albuquerque et al. 2014a). Aside from the spaced plant cover of coastal salt flats, they have a high potential for C sequestration because their formation frequently occurs via mangrove burial processes (Albuquerque et al. 2014a, b).

Due to their location and topography, coastal salt flats are described as ambient landscapes that can be colonised by mangrove vegetation due to the sea level elevation (Schmidt et al. 2013). Indeed, in sites subjected to relative sea level rise (Cohen and Lara 2003; Souza Filho et al. 2006; Lara et al. 2010) or where rainwater drainage removes the excess of salts (Hadlich and Ucha 2009), the herbaceous vegetation advances over bare salt flats and even mangrove trees start to colonise vegetated salt flat areas.

2.4 Threats and Conservation

Over the last thirty years of the 20th century, Brazil witnessed rapid economic growth, leading to increasing conversion of intertidal lands for agricultural, livestock, port, residential, and industrial development purposes. As opposed to mangroves, which have always been explicitly protected by Brazilian laws, coastal salt flats were poorly protected (Hadlich et al. 2008; Ucha et al. 2008). Since 1965, mangrove forests have been protected by Federal Law and considered permanent preservation areas. Only after the publication of the new Brazilian Forest Code in 2012 did salt marshes and salt flats become protected. However, the new law still allowed an occupancy rate of 10 to 35 % of the salt flats by shrimp farms and salt pans, and the salt flat areas lost to these activities prior to 22 July 2008 were legalised (Albuquerque et al. 2014a).

Salt pans and shrimp farming (exotic species *Litopenaeus vannamei*) are the most common anthropogenic activities that occur within salt flat areas. Along the NE coast of Brazil, salt production was a major economic activity in the region during most of the 20th century (Parente et al. 2006; Costa et al. 2014b; Santos et al. 2014), and large extensions of salt flats and mangroves were converted to ponds for salt extraction. For example, between 1976 and 2008, approximately 20 km^2 of salt flats and 40 km^2 of mangroves of the Apodi-Mossoró estuary were converted to salt pans (Costa 2010). These values represent 30 % and 95 % of the year 1976 total areas of salt flats and mangroves of the estuary, respectively. However, overall throughout the NE Brazil region, salt pans were abandoned between the 1970s and 1990s due to the establishment of local regulation of the land use, and a rapid mangrove expansion occurred in this disturbed areas. Parente et al. (2006) estimated that mangrove areas expanded steadily approximately 37 % (or approximately 166 km^2) from 1978 to 2003. Additionally, along the last three decades, salt pans and other intertidal areas were converted to shrimp farming (Spalding et al. 2010). Only in the estuary of the São Francisco River (state of Sergipe) from 2004 to 2008 did such activity show an expressive growth of 70 % in area (1.84 km^2; Santos et al. 2014).

Mangrove conversion to salt pans or shrimp farms could contribute to later development of salt flats because both activities promote changes in water flow in intertidal areas because of pond construction (Costa et al. 2009). After abandonment, the regions affected by ponds construction may develop hypersaline soils (Meireles et al. 2010; Albuquerque et al. 2014a). Furthermore, the construction of dams in semiarid inland river basins would reduce freshwater delivery to estuaries, therefore increasing the salt intrusion into freshwater regions (Lacerda and Marins 2002; Hadlich and Ucha 2009). In many estuaries of NE Ceará state, the opening of access roads and abduction canals for shrimp farms resulted in a loss of salt flats and mangrove forests. Urbanisation and tourism development have also caused salt flat area reduction in specific locations (Lacerda and Marins 2002; Parente et al. 2006).

2.5 Ethnobotany and Potential Utilisation of Halophytes as Cash Crop

Although indigenous peoples and fishermen collect crustaceans and shellfish for their diets from salt flats and associated mangrove areas, there are very few records of halophyte utilisation by these traditional populations on the Brazilian coast. *S. portulacastrum*, *B. maritima* and *S. virginicus* stands are used for goat and cattle forage (Sousa 2010; Albuquerque et al. 2014a). The human consumption and medicinal use of these plants are not common in Brazil, although in Central America shoots of *S. portulacastrum* and *B. maritima* are used for vegetables, salads and pickles (Duke 2009). Additionally, both species show antiscorbutic and anti-inflammatory properties, and cold compresses or hot crushed plants of *S. portulacastrum* are applied against bacterial and fungal skin infection (Duke 2009). Much more common is the harvest and burn of *Avicennia* trees as fuel wood (Carneiro et al. 2010; Sousa 2010; Albuquerque et al. 2014a), the use of its smoke to dispel mosquitoes (Sousa 2010) and the application of the astringent bark decoction for diarrhoea, haemorrhoids and wounds (Duke 2009).

The most advanced research on the biotechnological and biomass production potentials of coastal salt flat halophytes in Brazil has been performed with *S. ambigua*. This species has high concentrations of sodium, chlorine, magnesium, calcium and potassium in its shoots (EPAGRI 2008; Medina et al. 2008; Bertin et al. 2014). Fresh shoots of *S. ambigua* have a high protein content (8–18 %) and an ash content of 27–32 % (expressed in dry matter; Costa 2011; Bertin et al. 2014). Additionally, the bioactive phytosterols β-sitosterol and stigmasterol were found in shoots of *S. ambigua* (EPAGRI 2008), as well as 15 phenolic compounds, including five flavonoids and eight phenolic acids (Bertin et al. 2014). Their seeds have a 10–15 % oil content, mostly (≈70 %) polyunsaturated fatty acids such as the linoleic-ω6 acid, which has medical significance (D'oca et al. 2012). *S. ambigua* shoot meal showed a quantitative fatty acid composition very similar to the seed oil of this species; however, it has a higher percentage of saturated lipids (56 %) than that of vegetable oils with a MUFA nutritional profile. Thus, shoot meal of *S. ambigua* may be used as biosalt and/or food supplement for animal/human diets. On the basis of the composition of esterified fatty acids, its vegetable oil could be recommended for animal consumption or biofuel production (D'Oca et al. 2012; Costa et al. 2014c). Field trials showed that *S. ambigua* can achieve a shoot yield of 23 t ha^{-1} fresh weight under irrigation with saline shrimp farm effluent after 3–4 months of cultivation (Costa et al. 2014c). The development of cultivation of *S. ambigua* plants in integrated multitrophic aquaculture systems to remove waste nutrients from shrimp farm effluents can potentially reduce contamination of estuarine and coastal waters (Costa 2011).

3 Inland Salt Flats

Salt flats are common in drought-affected areas of the northeast region of Brazil, which extend over 1,085,187 km^2 (PAN-Brazil, 2004) and enclose nine of Brazil's 26 states (Fig. 2.2). Eighty percent of NE Brazil territory possesses a

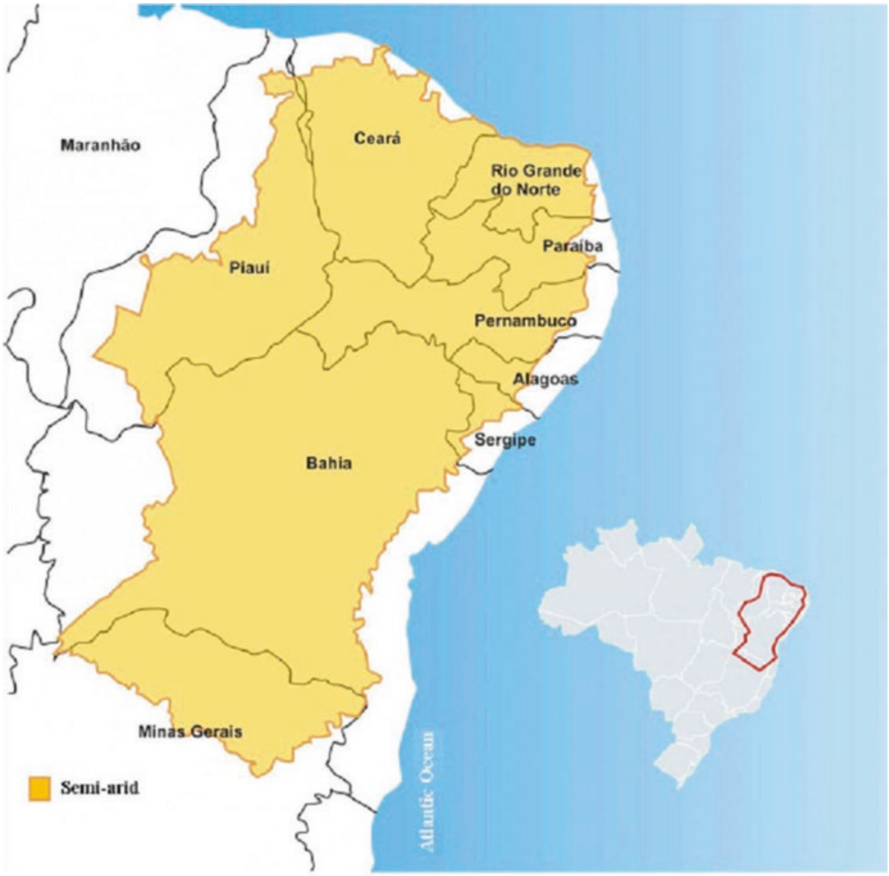

Fig. 2.2 Map of the tropical semiarid region in northeast Brazil (Source: National Water Agency-Brazil – ANA)

tropical semiarid climate, and 34 million hectares are covered by Caatinga vegetation. The term "Caatinga" is of indigenous origin and means "white forest" or "whitish forest". The name reflects the observation that during the dry season the dominant cover, composed of thorny trees and shrubs, sheds its leaves and takes on a white or shiny look. The Caatinga is associated with areas 50–100 km away from the Atlantic coast subject to frequent droughts or low rainfall (annual averages between 500 and 800 mm). Almost all of this semiarid region is situated in a crystalline basement, where the occurrence of very stony soils with sodium character and solodic soils are common and associated with Precambrian source materials such as gneiss and granite; these promote natural or primary salinisation (Oliveira 1997) and the formation of salt flats. Surface and groundwater are frequently very rich in minerals and unsuitable for human and animal consumption due to the high salt content (PAN-Brazil 2004). Secondary salinisation and the resulting salt flats can be established very quickly in this soil due to the effects of low rainfall, a high water deficit and careless irrigation management (Costa et al. 2010).

3.1 Geomorphologic Features, Inland Salt Flat Formation and Main Environmental Factors

The soils of the semiarid region of Brazil are frequently stony and shallow with the rock-mother scarcely decomposed to small depths and much blooming of the solid rocks. Geologically, the region is subordinated into two great structural domains: the Precambrian and that of the sedimentary basins of the Parnaíba (states of Maranhão and Piauí) and São Francisco Rivers (states of Pernambuco and Bahia). The Precambrian occupies an area from the state of Bahia to the state of Ceará, extending westwards to the state of Piauí (Fig. 2.2). Moderate epeirogenesis exposed crystalline rocks (gneisses and granites) by erosion and these structures are isolated from youngest surfaces of the Caatingas (Moreira 1977). These crystalline rocky outcrops (inselbergs) are frequently surrounded by soils with shallow depths (up to few metres) and large amounts of stone and gravel (Fig. 2.3). The granite-type bedrocks are rich in plagioclase feldspars, particularly an aluminium-oxysilicate

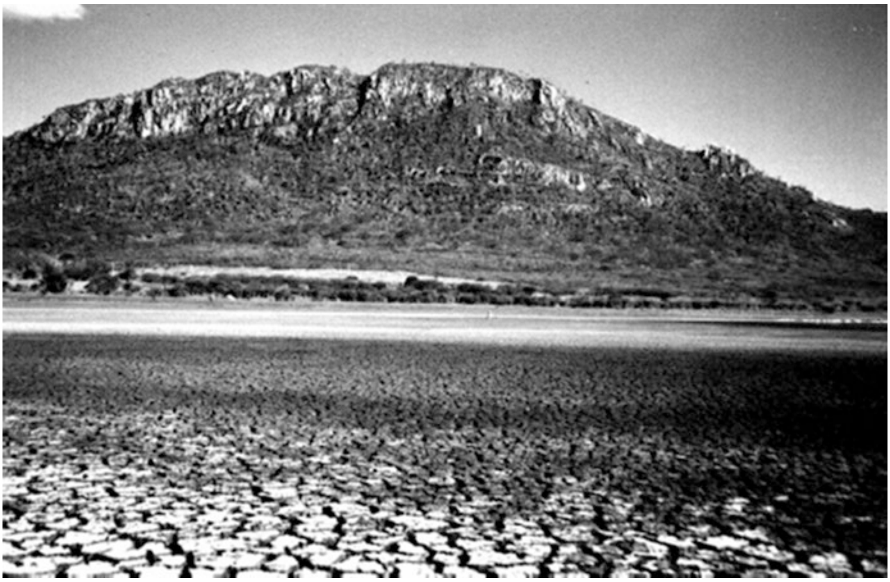

Fig. 2.3 Salt flat near a crystalline rocky outcrop (inselberg) in the municipality of Serra Talhada (Pernambuco state, NE Brazil) (Source: Oriel Herrera Bonilla)

of sodium composition (Na_2O. Al_2O_3. $6SiO_2$). During the bedrock chemical weathering, "free" sodium ions accumulate in the soil and cause primary salinisation. The underground water accessed by drilled wells in the crystalline is also rich in minerals and frequently inappropriate for drinking by people and animals. Additionally, the capillary rise from shallow water tables in the alluvial valleys can contribute to a salinity build-up in the root zone (Souza et al. 2014). In many places, traditional surface irrigation practices and the reduced depth of percolation failed to provide adequate leaching of salts that formed due to intense evaporation, leading to a secondary salinisation process (Tabosa et al. 2004).

Semi-arid characteristics of NE Brazil prevailed during most of the Quaternary period (Ab'Saber 1977; Clapperton 1993). Currently, rains are extremely irregular from year to year, varying from 300 to 1600 mm. Annually, approximately 50 % of the semiarid NE receives less than 750 mm concentrated within a 3-month period. When rains happen, they are often very intense and thus promote inundation with great superficial drainage, little infiltration, and accentuated erosion of soil. Most of the rivers in the drought-affected areas turn sporadic or ephemeral. Temperatures are high, with annual averages between 23 and 28 °C and a maximum of approximately 40 °C. The evaporation is 2000 to 2500 mm per year, and the annual water deficit values are greater than 1.000 mm, which is a primary limiting factor for vegetation growth (Fig. 2.4). Under these climatic conditions, secondary salinisation is a major threat to soils when irrigated.

The irrigated agricultural area in northeast Brazil is approximately 500,000 hectares. In the São Francisco River watershed alone (between Pernambuco and Bahia states), there are at least 50,000 hectares characterised as suffering from high salinisation (Heinze 2002). For example, the sodium (associated with bicarbonates) and chloride concentration averages in the surface soil saturate extract of an irrigated area at Serra Talhada (Pernambuco state) during the drought season were 23.3 and 36.0 g L^{-1}, respectively (Santos et al. 2013). In the irrigated area of Sousa (Paraiba state), Sá et al. (2013) found saturated extracts in the soil to average 6.7 g L^{-1} in sodium content and 39.9 dS m^{-1} in CE. Smaller CE values (20.9–23.8 dS m^{-1}) were found between 0 and 80 cm soil depths in the alluvial valley of the Ipanema River (Pesqueira, Pernambuco state), where the extractable sodium content ranged between 0.79 and 1.01 g kg^{-1}, and pH was between 8 and 9 (Souza et al. 2014). Since the year 1950, when the irrigation programs began in the NE region, the soil began to turn saline, and many areas were abandoned or underutilised (Tabosa et al. 2004; Bezerra 2002). Shallow soils, when irrigated with low efficiency, frequently become saline in the first 5 years of use, which undoubtedly reflects the expected framework for the northeastern areas of low rainfall and poor drainability (Fig. 2.5). In the state of Ceará, irrigated areas particularly in the perimeters in Fluvisols (alluvium) show relatively high percentages of salt-affected soils with varying degrees of degradation. These areas also have flooding problems as a result of poorly draining

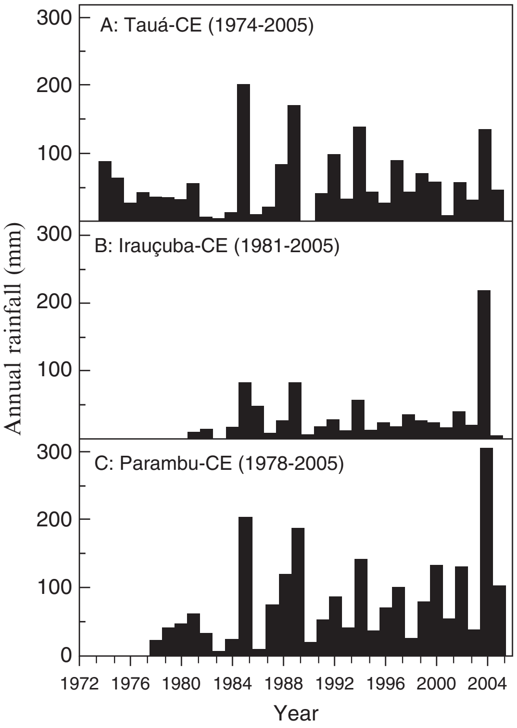

Fig. 2.4 Annual rainfall in the municipalities of Tauá, Irauçuba and Parambu, located in the state of Ceará in the semiarid region of NE Brazil

Fig. 2.5 Secondary salinisation in an irrigation area in the municipality of Petrolina (Pernambuco state, NE Brazil) (Source: Nilton de Brito Cavalcanti)

soils. According to Bezerra (2002), there are twelve irrigation schemes operating in Ceará, and seven of them have soil salinity problems, namely: Morada Nova, Icó-Lima Campos, Jaguaruana, Ayres de Souza, Forquilha, Varzea do Boi and Curu-Recuperação. Approximately 4350 ha of the irrigated lands have salinity or sodicity problems; 1472 ha (34 %) have been replaced by salt flats and are considered irrecoverable (in technical and economic regards; Costa et al. 2010).

The Ministry of Environment (MMA 2004) determined that in Brazil 1.3 million km^2 (15.7 % of the national territory) are in process of desertification. About half of this area lies in eight northeastern states (665,543 km^2; Ferreira and Rodrigues 1994; Drumond et al. 2000). This problem has been aggravated by the increasing number of irrigated areas abandoned due to salinisation, leaving them susceptible to desertification. Furthermore, intensive cattle and/or sheep grazing is incompatible with the environmental fragility, accentuating the degradation of the soils of Caatinga and in many areas of the state of Ceará, as in other neighbouring states. The environmental degradation has already reached practically irreversible conditions and clear marks of desertification can be observed on over-grazed areas.

3.2 Biodiversity and Plant Communities

Salt-adapted plant communities are established in the inland salt flats, but they remain poorly studied. Herrera and Veste (2005) showed an increasing average of electrical conductivity with soil depth on salt flats (from 9.5 to 25.6 dS m^{-1}) in irrigated areas of Pernambuco and Ceará states. Freire et al. (2014) reported similar soil values for abandoned salinised farms (averages pH = 10.3 and CE = 8.7 dS m^{-1}). The dominant cover of these salt flats includes 16 species of halophytes from 7 different families (Table 2.3). Three species are succulent species (*Sesuvium portulacastrum*, *Blutaparon vermiculare* and *Portulaca pilosa*; later sin. *Portulaca lanata* Rich.) also found in coastal salt flats and wetland areas fringing mangrove forests. The Australian shrub *Atriplex nummularia* was introduced in NE Brazil during the 1930s for forage and fodder for domestic animals, and currently it is widely spread on salt flats formed by primary and secondary salinisation. *Brachiaria mutica* and *Cynodon dactylon* are exotic grasses well adapted to the Caatinga environment, and they have a history of high-yield productivity (10–20 t ha^{-1}) on highly alkali soil (*i.e.*, pH 9–10) at high salinity (EC = 10 dS m^{-1}) (Dagar and Singh 2007). *Digitaria insularis* is also an exotic species, and its tussocks are rarely eaten by sheep and goats (Guimarães and Soares 2000; Sousa 2010). The native grass *Paspalum plicatulum* is locally abundant on salt flats. Previously, Harding (1972) stated that this tufted perennial with short rhizomes was suited to infertile coastal soils, which are flooded in the wet season and then dry out rapidly. The Malvaceae family has a higher number of species (5) in the salt flats, and Nunes et al. (2015) highlighted that *Herissantia crispa*, *Sida galheirensis* and *Melochia tomentosa* are used for animal fodder in rural communities in northeastern Brazil. These three species were also the most frequently visited plants by bee species in a Caatinga area of Itatim in the state of Bahia (Aguiar 2003).

At least three salt flat species are toxic to animals or have allelopathic compounds. The consumption of *Amaranthus spinosus* (Melo et al. 2014), *Froelichia lanata* (Pimentel et al. 2007) and *Senna obstusifolia* (Queiroz et al. 2012) are major causes of poisoning of domestic animals. Leaf extracts of *Senna obstusifolia* affect the germinability and germination speed rate of seeds from the native tomato *Lycopersicum esculentum* (Silva and Santos 2010). Consequently, negative plant-plant and plant-herbivores interactions may foster the occurrence and abundance of some of the plant species in the inland salt flats.

3.3 Ethnobotany and Potential Utilisation of Halophytes as Cash Crop

The dominant plants of the inland salt flats of northeastern Brazil have been used to treat a variety of illnesses, including influenza (*Heliotropium indicum*, *Herissantia tiubae* and *Melochia tomentosa*), urinary-renal problems (*Sesuvium portulacastrum*, *Sida cordifolia*, *Heliotropium indicum*) and ulcers (*Senna obstusifolia*). Several of them have shown anti-inflammatory and antioxidant properties (Table 2.3). Salt flat plants can be used to address the issue of emergency food to combat hunger in northeast Brazil, particularly during drought years. Ethnobotanical studies noted that *Blutaparon vermiculare* and *Portulaca pilosa* are edible and can be eaten after being cooked (Sousa 2010; Medeiros and Albuquerque 2014).

Due to the poor quality of the water in existing wells in the northeastern semi-arid regions, reverse osmosis membranes are employed for desalination to remove a significant portion of the salt present in the water (Cirilo 2008). As for the destination of refuse, the use of tanks with slim water blades are designated to accommodate the increase in evaporation speed and consequently depositing of salt, as well as the accumulation in tanks for the breeding of fish such as the pink tilapia and salt-water shrimp. *Atriplex nummularia* is also cultivated, a plant with a great capacity for salt absorption offering excellent forage, which contains between 16 and 20 % protein and has a life span of up to 20 years (Cirilo 2008). *Atriplex nummularia* was also planted in salt flats resulting from secondary salinisation due to bad irrigation practices, such as a phytoextraction technique, wherein plants absorb and accumulate salts in their shoots, allowing the contaminant to be removed from soil via harvesting the foliage and stems (Souza et al. 2014). Recently, the coastal halophyte *S. ambigua*, which is edible and a potential oil seed producer (Costa et al. 2014c), has been cultivated inland under saline irrigation, and it produced average shoot yields of 14.7–21.7 t ha^{-1} after 24–29 weeks of growth (Costa et al. 2014a). Despite the high soil salinities ($EC_{1:2} > 20$ dS m^{-1}), *S. ambigua* grew vigorously, showing its potential use as forage-fodder production on inland salt flats of NE Brazil.

Table 2.3 List of plant species found in inland salt flats in the states of Pernambuco and Ceará (NE Brazil)

Species	Family	Uses/Observations	Ref.
Sesuvium portulacastrum L.	Aizoaceae	Against urinary afflictions, blenorrhea, emmolient, laxative; forage	1, 12
Amaranthus spinosus L.	Amaranthaceae	Nephrosis on poisoned cows	2
Blutaparon vermiculare (L.) Mears	Amaranthaceae	Forage; eaten cooked and seasoned	12, 13
Froelichia lanata Moq.	Amaranthaceae	Cattle feeding and improve milk production; causes photosensitization in domestic animals	3
Atriplex nummularia Lindl.	Amaranthaceae	Forage; used as fodder by domestic animals	14
Heliotropium indicum (L.) DC	Boraginaceae	Against foot swelling, influenza, cough, inflammations in general, hepatic problems, conjunctivitis, renal problems, diuretic	1
Senna obstusifolia (L.) Irwin & Bernaby	Fabaceaae	Against ulcer; negative allelopathic effects; miotoxic and hepatotoxic effects on poisoned cows	1, 4, 5, 12
Herissantia crispa (L.) Brizicky	Malvaceae	Important bee plant	8
Herissantia tiubae (K. Schum) Brizicky	Malvaceae	Against influenza, fever	1
Melochia tomentosa L.	Malvaceae	Against influenza, colds, bronchitis, lung inflammation; important bee plant	1, 8
Sida galheirensis Ulbr	Malvaceae	Against acne, coughs and leucorrhea; antioxidant activities; important bee plant	6, 7, 8
Sida cordifolia L.	Malvaceae	Against renal inflammation, acne, cough, leucorrhea	1
Brachiaria mutica (Forsk.) Stapf	Poaceae	Used as fodder by sheep and goats	9, 12
Cynodon dactylon L.	Poaceae	Used as fodder by sheep and goats	9, 12
Digitaria insularis (L.) Fedde	Poaceae	Rejected by sheep	10, 12
Paspalum plicatulum Michx.	Poaceae	Used as fodder by sheep and goats	11
Portulaca pilosa L.	Portulaceae	Eaten cooked	13

References: 1 = Albuquerque et al. (2007); 2 = Melo et al. (2014); 3 = Pimentel et al. (2007); 4 = Silva and Santos (2010); 5 = Queiroz et al. (2012); 6 = Trentin et al. (2011); 7 = Silva et al. (2006); 8 = Aguiar (2003); 9 = Dagar and Singh (2007); 10 = Guimarães and Soares (2000); 11 = Norton (1985); 12 = Souza (2010); 13 = Medeiros and Albuquerque (2014); 14 = Souza et al. (2014)

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3

Physiological Ecology of Psammophytic and Halophytic Plant Species from Coastal Plains in Northern South America

Ernesto Medina

Abstract

Coastal plains of all tropical and subtropical latitudes are the habitat for a number of highly specialized plants able to establish in a range of sandy to clayey soils, submitted to periodical flooding from rainfall and tides, tolerant to large variations of salinity of soils interstitial water, withstanding coastal winds and sea-salt spray, and submitted to yearlong high solar irradiation and day temperatures. In northern South America semi-arid climates predominate in the southern Caribbean coasts from 10 to 15° N, an area that includes from the Goajira peninsula in Colombia to the Paria Peninsula in eastern Venezuela, and most southern Caribbean islands. The functional properties of mangroves (*Laguncularia racemosa, Avicennia germinans*) and associated halophytes (*Conocarpus erectus, Sesuvium portulacastrum* and *Batis maritima*) in seasonal arid coasts reveal the impact of highly seasonal distribution of rainfall affecting photosynthesis and leaf osmotic relations. The soil-plant nutritional relationships of a number of commonly occurring coastal species allowed the characterization of psammophytes and halophytes, based on the Na/K, and Ca/Mg ratios, and their preferential absorption of K over Na. Carbon 13 isotopic analyses showed the C_4 species were well represented within the selected species (*Sporobolus virginicus, Atriplex oestophora, Euphorbia mesembryathemifolia*) but this photosynthetic metabolism is not the most common. Natural abundance of ^{15}N indicates that sources of N are enriched in the heavier isotope suggesting that these coastal systems are limited by P but not by N. Mycorrhizal associations were common in most species but intensity of colonization was generally low. The occurrence of mycorrhizal associations in true halophytes remains to be assessed.

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Electronic supplementary material The online version of this chapter (doi:10.1007/978-3-319-27093-7_3) contains supplementary material, which is available to authorized users.

M.A. Khan et al. (eds.), *Sabkha Ecosystems Volume V: The Americas*,
Tasks for Vegetation Science 48, DOI 10.1007/978-3-319-27093-7_3

1 Introduction

The Caribbean coastal region of Venezuela and Colombia includes a large diversity of geoforms related to local geology and topography and to the rainfall and surface run-off regimes (Ellenberg 1978). The largest extension of the coastline is constituted by sandy shores with low cliffs. Areas where mountain ranges surround the coast line, are characterized by high cliffs and steep slopes interspersed with narrow sandy beaches and sedimentary platforms (Wilhelmy 1954; Rieger 1976; Ellenberg 1985). Along the coasts with sandy beaches, strongly influenced by sea water salinity and with permanent incidence of marine salt spray, sandy soils occur with usually low or very low plant nutrient availability, and little water retention capacity. These areas harbor a variety of vegetation types that include: (a) mangrove tree communities, in the intertidal region of areas protected against energetic waves, and (b) psammophytic and halophytic communities constituted by shrubs, subshrubs, dicot herbs and grasses, both annuals and perennial, and creeping vines. The actual composition and extension of these communities is associated with the availability of continental freshwater run-off and actual rainfall at each specific site.

The ecophysiological analysis of the plants integrating coastal vegetation requires the measurement of functional properties such as photosynthesis and transpiration, structural characterization of the photosynthetically active surface, and assimilate allocation for development of photosynthetic surfaces and root development. Additionally, considering the complex interactions of environmental factors determining their rates of growth, reproduction, and mortality, it is necessary to determine the physico-chemical characteristics of the soils on which they establish and develop, and the relationships with the mineral composition of their photosynthetic and nutrient absorbing organs.

This chapter will be restricted to the vegetation of the arid and semiarid coastal regions in northern South America, comprising the continental coast from the Goajira peninsula in Colombia to the Araya peninsula in eastern Venezuela, and including some of the larger Caribbean islands near the coast of Venezuela (Fig. 3.1 indicates localities mentioned in the text). The study describes and discusses ecophysiological properties mostly related to the nutrient relations and the water and salt stress endured by these coastal vegetation types. The plant names are written in full the first time they are mentioned in the text. Thereafter the genus name will be contracted to the first two letter, to reduce confusion because there are several genera with the same initial letter. Species authors are given in Tables 3.1, 3.7, and 3.15.

Fig. 3.1 Caribbean coastline of Colombia and Venezuela including the names of localities mentioned in the text

2 Climate and Soils

The dry belt in northern South America stretches from the Paria Peninsula, approximately 62° W, to Cartagena in Colombia, nearly 75° 30′ W. The southern boundary runs approximately at 10° 30′ N, although pronounced local variations are found due to topography (Lahey 1973). The aridity of northern South America is caused by topography, relative cool waters of the Caribbean sea, and the oblique incidence of trade winds (Lahey 1973). Climatic anomaly in this region is not only represented by reduced rainfall, but also by its seasonal distribution. Reduced rainfall is observed during periods of high solar angle, i.e. during June-August, and of reduced frequency of afternoon rains (Herrman 1970; Lahey 1973).

Typical arid climates in the northern coast of Venezuela are depicted in Fig. 3.2. The graphs show the seasonal variations of temperature, nearly constant through the year, rainfall and evaporation from Tank A corrected according to García-Benavides and López-Díaz (1970). Expanding on the concept of climate diagrams (Walter and Medina 1971) the addition of evaporation curve identify wet and dry periods, when the evaporation curve runs above or below the rainfall curve, respectively, and humid and very dry periods when the rainfall curve runs above or below the temperature curve (represented in a scale of 2:1), respectively. The climates depicted in Fig. 3.2 represent the whole spectra of dry climates in northern South America ranging from semi-arid, strongly seasonal climate (Barcelona)

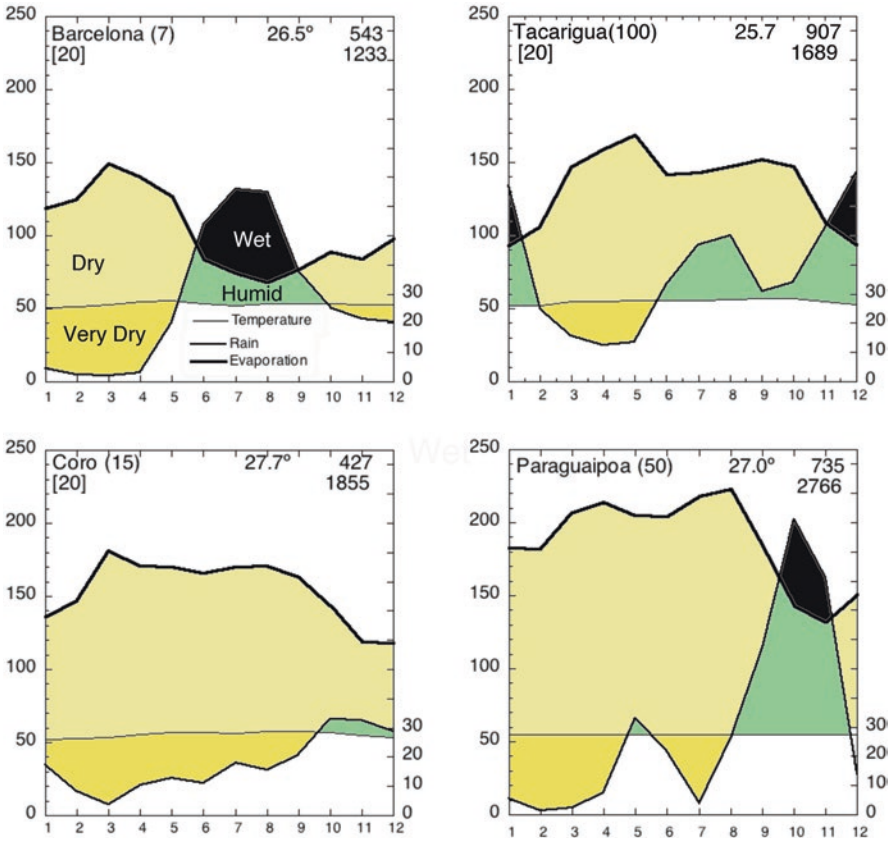
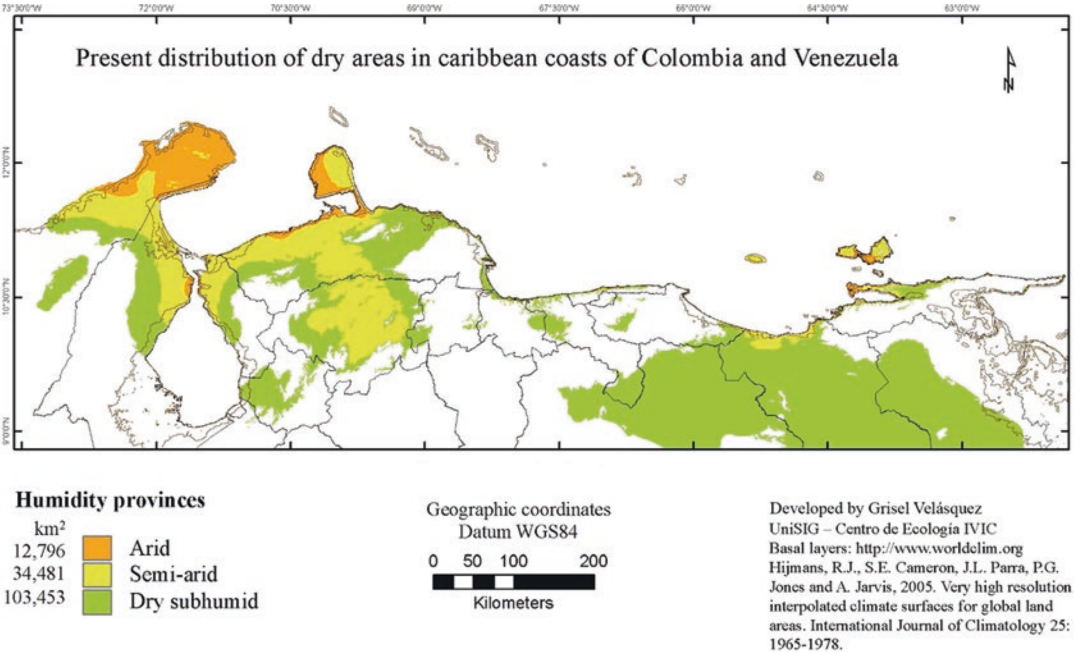


Fig. 3.2 Arid and semiarid climates in the caribbean coast of Venezuela. *Left* ordinate rainfall and evaporation (Tank A×0.812, García-Benavides and López-Díaz 1970), and temperature on the *left* ordinate. In the abscisa months from January to December. Rainfall:temperature scales 2:1. The *upper* text line indicate station name, altitude, annual averages of temperature and rainfall. The second line indicates number of years averaged and average evaporation



Developed by Grisel Velásquez
UniSIG – Centro de Ecología IVIC
Basal layers: http://www.worldclim.org
Hijmans, R.J., S.E. Cameron, J.L. Parra, P.G. Jones and A. Jarvis, 2005. Very high resolution interpolated climate surfaces for global land areas. International Journal of Climatology 25: 1965-1978.

Fig. 3.3 Delimitation of dry climates in northern Venezuela and Colombia using the S index of Bayley (1979) with average annual rainfall and temperature data. Conceptual development in Nassar et al. (2013)

to locations with bimodal rainfall pattern recording the relative path of the sun through zenital positions (Paraguaipoa and Tacarigua), and the extreme arid location of Coro.

The combination of high temperatures and high radiation loads leads to elevated values of potential evapotranspiration that cannot be compensated by rainfall. Variations in the degree of water stress to which the coastal vegetation is subjected may be quantitatively depicted using a simple moisture availability index calculated on the basis of average temperature and rainfall (Bailey 1979) (Fig. 3.3). This index gives a similar distribution of seasonal tropical dry climates as that described by the Holdridges index (Holdridge 1959) without making assumptions on biothermal limits (Nassar et al. 2013). The map shows that arid and semiarid coastal areas are concentrated in the western side (Goajira and Paraguaná peninsulas) and the eastern Araya peninsula.

Soils are highly variable, depending on the hydrological setup of the site, ranging from clay soils in coastal areas surrounded by mountains supplying sediments in superficial run-off, to sandy soils in areas predominantly influenced by waves and marine currents (Ellenberg 1978). Under semiarid climates, for a given amount of fresh water available from rain or superficial run-off, clay soils are less favourable for plant establishment and development due to their higher water retention capacity, whereas sandy soils allow rapid percolation of rain water, leading to the formation of underground water reserves. Furthermore, sandy soils reduce salinization of upper soils layers caused by evaporation because the lack of capillar connections usual in clay soils.

3 Vegetation Types and Floristics of the Coastal Regions and Islands of the Caribbean Coast of Colombia and Venezuela

A schematic depiction of the vegetation types occurring along the semi-arid coasts of northern South America emphasizes the role of salt water intrusion and the potential effect of salt spray car-

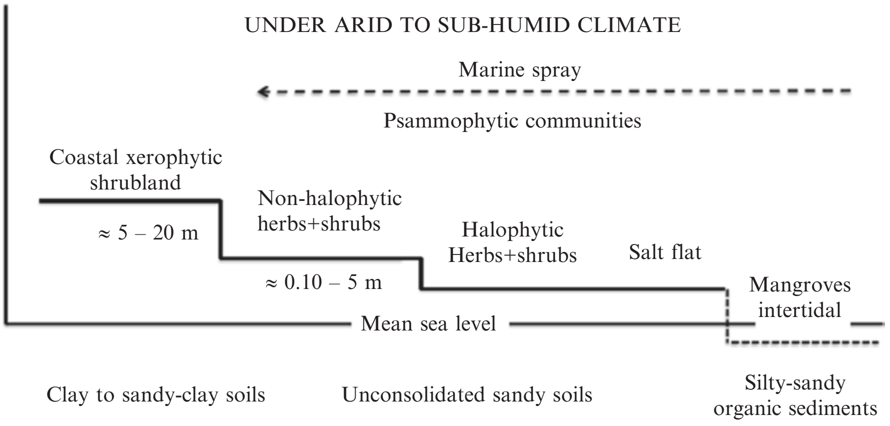


Fig. 3.4 Schematic representation of coastal vegetation types in a transect from intertidal zone to *upper* coastal xerophytic shrubland

ried by strong sea-continent coastal winds (Fig. 3.4). The land-sea sequence can be represented simply as a series of types going from coastal xeric shrublands and woodlands, dominated by evergreen sclerophyll, and deciduous woody plants, frequently including a variety of columnar, shrubby, and globular cacti, growing on clay or clay sandy soils, followed by strand psammophytic vegetation on sandy soils, including coastal dunes. Psammophytes include a reduced number of plants characterized by their capability of rooting in sandy, unconsolidated soils, which frequenly contain high amounts of sea salt, due to water intrusion during high tides or by salt spary blown by strong coastal winds (Plate I). These psammophytic plants are physiologically halophytes or halotolerant. The last component of this transect are mangrove communities, consisting of true halophytes tolerant to high salinity of coastal salt flats, or subjected to periodical inundation by sea water in the intertidal zone. Mangrove communities show usually a clear-cut zonation, particularly in low rainfall coasts, where species of the genus *Rhizophora* occupy the more exposed positions towards the sea, and are therefore flooded by diurnal or semi-diurnal tides. In these locations the mangroves roots are permanently in contact with liquid water, and salinity conditions tend to be maintained within narrow limits around the mean sea water value (≈35 ‰). Further inland, other species dominate the vegetation. The landward limit of the intertidal zone is usually dominated by species of the genus *Avicennia*. In these areas flooding occurs usually during “live tides” (syzygial tides), when sea water penetrates farthest inland. The salt remains in place as the water evaporates during the following days, creating salt flats. In these areas it is frequent to find extreme terrestrial halophytes and scrubby *Avicennia* trees.

The vegetation of the Guajira peninsula was described in great detail by Rieger (1976). Most of this area is dominated by plant communities consisting of dry deciduous trees and shrubs, or thorny trees and arborescent and shrubby cacti. In addition Riegel described two widely distributed coastal halophytic associations dominated by *Heterostachys ritteriana* and *Batis maritima*. The former occurs in strongly saline or silty fine sediments, with high lime content. The other dominant species of this association are *Philoxerus (Blutaparon) vermicularis, Lycium tweedianum* and *Sesuvium edmondstonei*. The *Ba. maritima* association includes also *Sesuvium portulacastrum* and *He. ritteriana.* This association occupies also strongly saline, sandy, silty and even clayey fine sediments. It develops succesfully only in those habitats with almost continuous water availability throughout the year (Plate II).

The Caribbean coasts of Venezuela “Tierra Firme” extends for more than 2000 km, from the

Cocinetas lagoon in the west to the tip of the Paria Peninsula in the east (Fig. 3.1). The coast lines of several islands, such as Margarita, Coche, Cubagua, La Tortuga, La Blanquilla, Archipiélago Los Roques, and La Orchila, harbor beach vegetation similar to that described for the West Indies by Stoffers (1993). The area of interest for the present analysis of psammophytic and halophytic vegetation is located below the 20 m isoline, influenced by coastal wind and salt spray and submitted to sea water intrusions. Under subhumid to arid climatic conditions the general type of vegetation in this area includes xerophytic forests and shrublands (without edaphic salinity), and coastal shrubby and herbaceous communities of varying canopy density, occurring on sandy soils or sandy-saline depressions (Huber and Alarcón 1988; Huber and Riina 1997). Mangroves are an integral part of the coastal vegetation in the Caribbean that occupy intertidal zones, in coastal areas protected from direct wave impact (Plate III).

The floristic and ecological characteristics of such gradients have been described by Medina et al. (1989) for the area of Chichiriviche (Falcón), Cumana-Campos (1999), and Cumana-Campos et al. (2000), for the Araya peninsula, Lemus-Jiménez and Ramírez (2002) for the Paraguaná peninsula. Vegetation composition and ecological relationships have been described also for the Archipélago Los Roques and the islands of La Orchila (Aristeguieta 1956), Los Testigos (Fernández del Valle and Ortega 1984), La Blanquilla (Colonnello 1986), Margarita (González 2007; Sanz et al. 2011), and the most recent report by Véliz (2012) on the vegetation of La Tortuga Island (locations in Fig. 3.1). Beyond the Caribbean coasts of northern South America similar dry coastal ecosystems have been described in the West Indies (Stoffers 1993), Trinidad (St. Omer and Barclay 2002), and the Gulf of Mexico (Castillo et al. 1991; Moreno-Casasola 1988). These coastal vegetation types extend well beyond the tropical latitudes thanks to the warming Atlantic currents up to the Bermuda islands in the Atlantic where many tropical species are found established in the strand vegetation (Harshberger 1908).

Several of the vegetation studies (see Cumana-Campos 1999) cited above identify physiognomic communities (derived from definitions by Huber and Alarcón 1988) and plants habits in the dry coastal areas in both the islands and the continent. Table 3.1 gives a summarized version of the communities described by Cumana-Campos

Table 3.1 Examples of common species in vegetation along semi-arid coasts in the Araya península (Edo. Sucre, Venezuela)

Shrubby or Herbaceous Psammophytes	Shrubby or Herbaceous Halophytes
Allionia incarnata L.	*Ammannia latifolia* L.
Atriplex pentandra (Jacq.) Stand.	*Batis maritima* L.
Altemanthera lanceolata (Bth.) Schz.	*Fimbristylis ferruginea* (L.) Vahl
Alternanthera canescens Kunth	*Fimbristylis spathacea* Roth.
Calotropis procera (Ait.) Aiton	*Heliotropium curassavicum* L.
Euphorbia buxifolia (Lam.) Sm.	*Ipomoea pes-caprae* (L.) R. Br.
Ditaxis rubricaulis Pax. & Hoffm.	*Argusia gnaphalodes* (L.) Heine
Egletes prostrata (Sw.) Kuntze	*Senna italica* Mill.
Heliotropium curassavicum L.	*Sesuvium portulacastrum* (L.) L.
Ipomoea pes-caprae (L.) R. Br.	*Sporobolus pyramidatus* (Lam.) Hitch.
Argusia gnaphalodes (L.) Heine	*Sporobolus virginicus* (L.) Kunth.
Mollugo verticillata L.	
Senna italica Mill.	
Sesuvium portulacastrum (L.) L.	
Tephrosia cinerea (L.) Pers.	
Trianthema portulacastrum L.	

Modified from Cumana-Campos (1999)

(1999) for the Araya peninsula in eastern Venezuela including some of most common species characterizing these communities. Descriptions of quite similar communities for the Paraguaná peninsula were reported by Lemus-Jiménez and Ramírez (2002).

4 Functional Characterization of Halophytic Vegetation

4.1 Mangroves

Mangrove in arid coasts in the Caribbean have been described by several authors (Cintron et al. 1978; Lugo et al. 2007) and the general picture is a sequence of fringe mangroves mainly constituted by *Rhizophora mangle* followed by different proportions of *Laguncularia racemosa* and *Avicennia germinans*. The latter species usually occurs in the innermost border of the mangrove community, bordering vegetationless salt flats. Salinity of interstitial water increases landward reaching saturation in the salt flats. Further inland the influence of sea-salt disappears giving place to the development of coastal xerophytic vegetation. This vegetation sequence on arid coasts was described in detail for African mangroves, and the salinity gradient was documented measuring the osmotic potential of leaf cell sap (Walter 1973). A similar profile was documented in Puerto Rico (Lugo et al. 2007), showing clearly the variations in vegetation structure and composition in association with pore water salinity (Fig. 3.5 and Table 3.2).

Arid coasts have a strong seasonal distribution of their scarce rainfall. Frequently, heavy show-

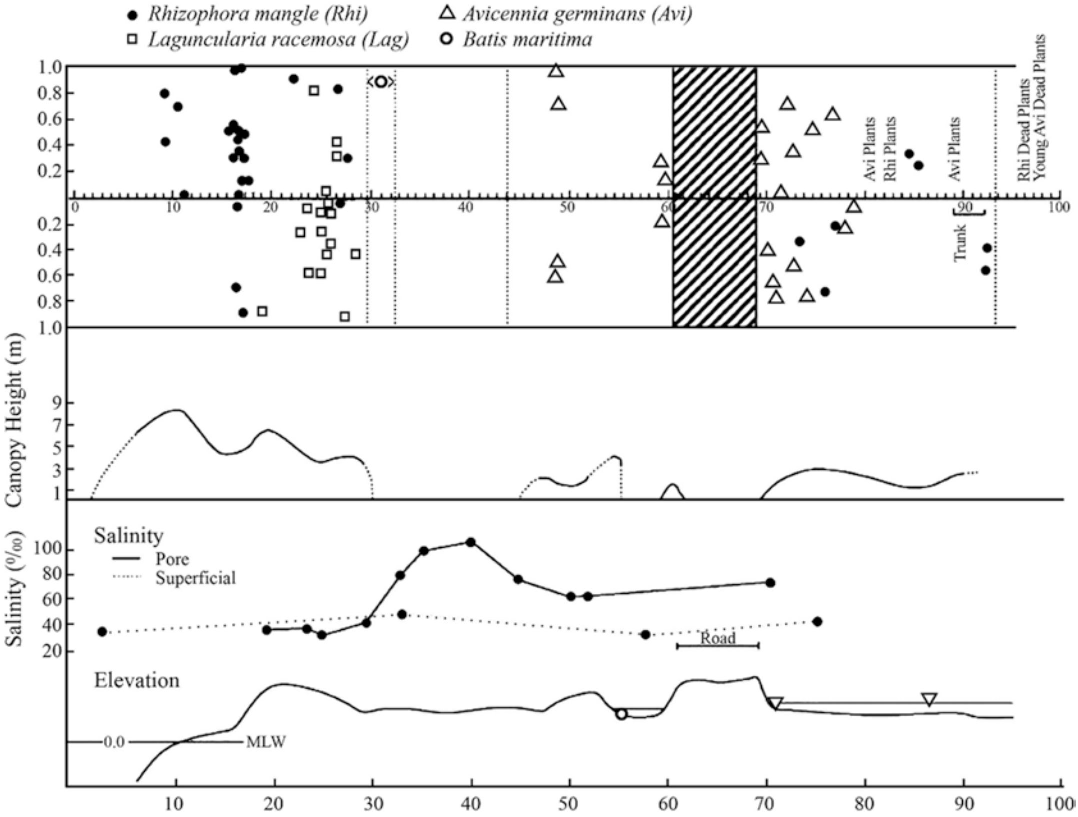


Fig. 3.5 Vegetation profile, topography, and pore salinity in an ocean fringe forest in Jobos, Puerto Rico. The *upper* panel shows the location of the 100 m × 2 m transect from the ocean (*left*) towards inland (*right*). The road is shown in the *upper* panel with dashed oblique lines. In this gradient the correlation between soils salinity and plant osmotic values is quite clear. The salinity gradient is also observable in the species distribution

Table 3.2 Paired osmolality values of soil water and leaf sap, and mid-day xylem tension of mangrove species

	Pore water		Cell sap		Xylem tension
Species	mmol kg^{-1}	πMPa	mmol kg^{-1}	πMPa	MPa
Rhizophora mangle					
Fringe	860	2.1	1305	3.2	–
Basin	1025	2.5	1489	3.7	3.6 (0.6)
Laguncularia racemosa					
Fringe	860	2.1	988	2.4	–
Basin	1025	2.5	1178	2.9	3.4 (0.6)
Avicennia germinans					
Basin	1633	4.0	1799	4.4	5.1 (1.0)

Osmotic pressure calculate from osmolality for 25 °C. Cell sap osmolalities are averages of three replicates sampled in the morning. Xylem tension is the average of 12 measurements per species taken between 0900 and 1500 h at Jobos Bay, Puerto Rico. Standard deviation in parenthesis
From Lugo et al (2007)

Table 3.3 Seasonal changes in cell-sap osmolality and ion concentrations of leaves of *Avicennia germinans* and *Conocarpus erectus* in Chichiriviche, Venezuela

	Cell-sap Osmolality	Ion concentration (mol m^{-3})					Total cations
Species	(mmol kg^{-1})	Cl	K	Na	Ca	Mg	mol equival. m^{-3}
Avicennia germinans							
Rainy season	1300	744	130	261	–	271	≈933
Dry season	2650	935	107	891	–	259	≈1516
Conocarpus erectus							
Rainy season	760	431	49	154	4	201	613
Dry season	1640	600	35	504	1	130	801

Modified from Smith et al. (1989)

ers of short duration occur during the rainy season that are capable of washing out salt accumulated in the upper soil surface. In northern Venezuela (Ciénaga El Ostional, Chichiriviche, Venezuela) salt flats are covered by fresh water during several weeks during the rainy season, to the point that salt intolerant dicots and aquatic plants are able to grow and reproduce (Medina et al. 1989). This seasonality in water availability is reflected also in the osmotic properties of the mangroves bordering the salt flats in Chichiriviche (Smith et al. 1989). Cell sap osmolality increases by a factor of two from the rainy to the dry season in both *Av. germinans* and *Co. erectus*, while total concentrations of cations increased by only by 1.3 to 1.6 (Table 3.3). Sodium is the cation responsible for most of this increase, whereas K and Mg decreases, and Ca is either absent or at very low concentrations in both species.

The osmotic variations are also expressed in leaf xylem tension as measured with the Scholander pressure bomb. Maximum tensions during clear days increase markedly from the rainy to the dry season (Fig. 3.6) in the order of 4.5 MPa in *Co. erectus* and 5 MPa in *Av. germinans*. The range of variation in xylem tension during rainy and dry seasons between predawn and noon decrease from 1.6 MPa to 0.7 in *Co. erectus,* and from 2.6 MPa to nearly 2 in *Av. germinans*.

Both integrated photosynthetic gain and total water loss through transpiration during the light period changed drastically from the rainy to the dry season in both species (Table 3.4). However, the effect of drought was more pronounced in *Co. erectus* where photosynthesis near saturation decreased by 50 % and total CO_2 uptake by 70 % in the dry season. Total water losses during the light period decreased by 95 % in *Co. erectus* and only by 70 % in *Av. germinans*. Correspondingly, the increase in water use efficiency during the dry period was much higher in the former species.

The integrated results of variations in cell sap composition, xylem tension, and gas exchange indicate that *Av. germinans* is markedly more tolerant to saline and possibly drought stress than *Co. erectus*. These physiological properties explain the distribution of these species in arid coasts.

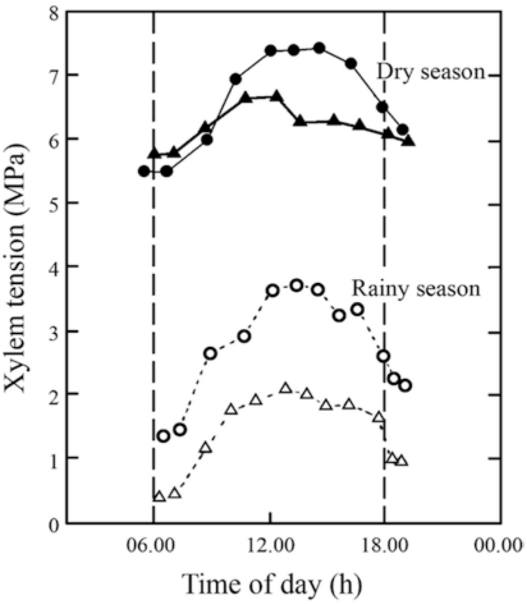


Fig. 3.6 Diurnal course of xylem tension measured with a pressure bomb during rainy and dry season in *Avicennia germinans* (*circles*) and *Conocarpus erectus* (*triangles*) (From Smith et al. 1989)

4.2 Terrestrial Halophytes Associated with Inland Mangroves

Dense populations of two extreme succulent halophytes, *Se. portulacastrum* and *Ba. maritima,* border the salt flats. Both species produce creeping succulent stems, rooting at the nodes, but *Ba. maritima* may also develop as a sub-shrub with upright stems. In addition, they have a superficial root system able to resist the extreme variations in salt concentration of salts in the upper soil layers of these habitats, that range from fresh-water conditions in the rainy season and solid salt in the dry season (Lüttge et al. 1989). Also, leaf succulence is similar in both species and increases strongly in the dry season (Table 3.5). However, they have quite different strategies to counteract the effect of salinity. *Ba. maritima* has a higher range osmolalities during both seasons and accumulates more Cl than Na, whereas *Se. portulacastrum* accumulates more Na than Cl (Table 3.5). In the case of *Ba. maritima* excess Na may be compensated by accumulation of SO_4, while in *Se. portulacastrum* the Na excess is probably compensated by oxalate. In this species accumulation of compatible solutes proline and pinitol was measured.

In *Ba. maritima* photosynthetic gas exchange is not much affected by drought and salinity in the dry season, compared to *Se. portulacastrum* (Table 3.6). During the dry season diurnal photosynthetic carbon gains and transpirational losses

Table 3.4 Gas-exchange and photosynthetic characteristics of *Avicennia germinans* and *Conocarpus erectus* on the vegetation islands of the Cienega el Ostional, Chichiriviche, during the rainy season and the dry season

	Rainy season		Dry season	
	A. germinans	*C. erectus*	*A. germinans*	*C. erectus*
Photosynthetic rate near light saturation[a] (µmol CO_2 m^{-2} s^{-})	5.61	4.67	3.87	2.07
Total net CO_2 uptake per light period [mmol CO_2 m^{-2} $(12\ h)^{-1}$]	173	133	105	40
Total transpiration per light period [mol H_2O m^{-2} $(12\ h)^{-1}$]	101	154	31	8
Water-use efficiency during light period (mmol CO_2: mol H_2O)	1.71	1.27	3.33	4.28

Modified from Smith et al. (1989)

[a] Average rates at PAR > 1 mmol m^{-2} s^{-1}

Table 3.5 Leaf succulence, leaf sap osmolality, and ion contents of *Batis maritima*, and *Sesuvium portulacastrum,* succulent halophytes in the alluvial plain of the Cienega el Ostional

	Succulence	Osmolality	Total N	Inorganic ions (mol m^3)		
	(kg m^{-2})	(osmol kg^{-1})	(% d. wt)	Cl$^-$	Na$^+$	K$^+$
Sesuvium portulacastrum						
Rainy season	0.711	0.89–1.43	1.65	263–450	373–723	18–29
Dry season	1.530	1.83–2.34	1.81	540–812	1118–1585	32–70
Batis maritima						
Rainy season	1.073	1.69–1.76	1.54	662–1080	509–661	26–57
Dry Season	1.589	2.42–2.95	1.70	1060–1409	922–1253	7–45

Modified from Lüttge et al. (1989)

Table 3.6 Photosynthesis and gas-exchange characteristics of *Batis maritima* and *Sesuvium portulacastrum*

Photosynthesis	Rainy season	Dry season
at ≥1 mmol m^{-2} s^{-1}		
Batis maritima	4.08	2.41
Sesuvium portulacastrum	9.16	2.47
Photosynthesis per light period [mmol CO$_2$ kg^{-1} (12 h)$^{-1}$]		
Batis maritima	n.d	82.1
Sesuvium portulacastrum	n.d.	78.9
Transpiration per light period [mol H$_2$0 kg^{-1} (12 h)$^{-1}$]		
Batis maritima	n.d.	47.5
Sesuvium portulacastrum	n.d	40.8
WUE [(C0$_2$:H$_2$O) × 10^{-3}		
Batis maritima	2.97	1.73
Sesuvium portulacastrum	1.43	1.93

Modified from Lüttge et al. (1989)

are higher in *Ba. maritima*, leading to smaller water use efficiency compared to *Se. portulacastrum*.

5 Nutritional Characterization of Psammophytic and Halophytic Species Based on Their Elemental Composition

The halophytic characteristics can be assessed on the basis of total and soluble cation concentrations and elemental ratios in photosynthetic tissues, compared with the availability of cations in the soil on which they grow. Such analysis was conducted in the east coast of the isthmus of the Paraguaná Peninsula in northern Venezuela (Falcón State) documenting these relationships in several widely distributed psammophytic species (Medina et al. 2008). This coast is exposed to the perpendicular incidence of the trade winds, and receives the impact of energetic waves. In this region the National Park "Los Medanos de Coro" is located, an area with highly active dunes that cross the southern extreme of the isthmus in the east–west direction (Fig. 3.7). The sites selected for soil and plant collections are indicated in the map as COVE (east of the city of Coro), TAC (Tacuato bay), and COP (peninsula eastern coast).

The dune activity may be observed throughout the whole east coast at least to the town of Adicora in the north. The origin of these dunes is still a matter of discussion, but there is evidence suggesting that the massive movement of sands is derived in part from coastal hills deforested during the XVI and XVII centuries. Their nearly perpendicular exposure to the trade winds (NE-SW), and the dry climate of this region facilitated erosion (Camacho et al. 2011; Tamayo 1941; Walter 1973). Studies on the vegetation of this area emphasize the habitat diversity and floristic composition of the northern section of the State and the Paraguaná peninsula (Tamayo 1941; Lasser and Vareschi 1957; Mateucci 1987), and describe the phenological and polinization characteristics of the shrubby-herbaceous, psammophytic, and halophytic coastal vegetation and mangroves (Lemus-Jiménez and Ramírez 2002, 2003). In those studies the halophytic character of the vegetation is inferred from observation of their occurrence along the land-sea gradient.

Eighteen species distributed among 12 families were systematically sampled for analysis

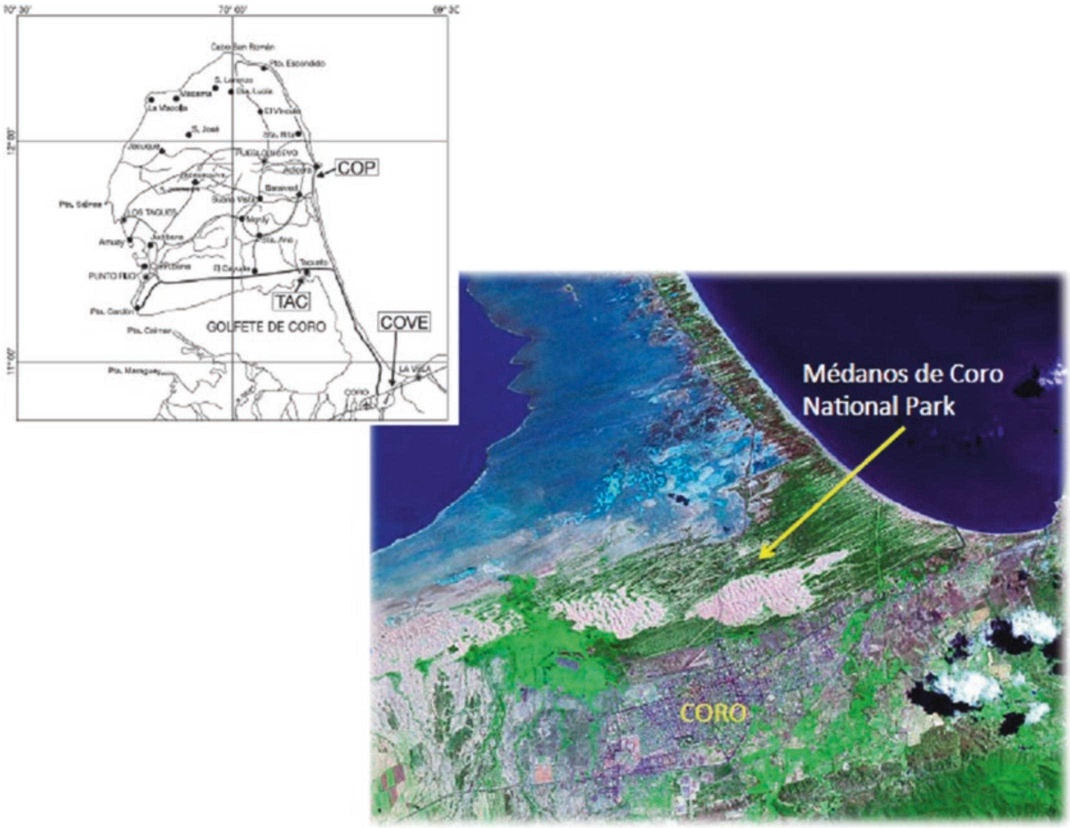


Fig. 3.7 Collection sites of psammophytes in the Paraguana peninsula in Venezuela, in north-east Coro (COVE), Tacuato bay (TAC) and eastern coast south of Adicora (COP). The Land Sat image (LANDSAT VENEZUELA/N-19-10_2000/) shows the extensive dune fields north of the city of Coro where many studies on psammophytes plant communities have been carried out

(Table 3.7). Species such as *Se. portulacastrum* (Plate VI)*, Ba. maritima* (Plate III)*, Heliotropium curassavicum, Ipomoea pes-caprae* (Plate I) and *Sporobolus virginicus* are widely distributed in saline coastal areas, covering from southern United States to Argentina. Other widely distributed species are the Amaranthaceae *Sarcocornia ambigua* (Plate III) reaching from Argentina to Belize, and *Alternanthera halimifolia* (Plate IX) found from the Caribbean coasts to Chile. *Sesuvium edmondstonei* (Plate VI) and the Amaranthaceae *He. ritteriana* (Plate VII) *Atriplex oestophora* (Plates IV, IX) and *Gomphrena albiflora* (Plate VII) stand out because they have been recorded only for northeastern Venezuela and the neighboring Colombian coast. *Atriplex oestophora* belongs to a genus with numerous well studied halophytic species, mainly from subtropical latitudes (Albert 1982). In Venezuela only two species have been recorded. *Melochia crenata* (Plate V) is recorded only for the southern Caribbean coast including Jamaica and Puerto Rico. The Euphorbiaceae *Croton punctatus* (Plate VIII) is frequently associated with the latter species and *Euphorbia (= Chamaesyce) mesembryanthemifolia* (Plate VII) occurs throughout the Caribbean from Venezuela to Florida. *Egletes prostrata* (Asteraceae) (Plate VIII) belongs to family with many halophytic species well described in temperate climates (Albert 1982), but little is known in the tropics. *Suriana maritima* (Plate V) and *Argusia gnaphalodes* (Plate IV) are distributed throughout the Caribbean islands where they develop vigorous

Table 3.7 Species selected for studies of elemental composition and stable isotopes including their habit and distribution in the American continent

Aizoaceae	
Sesuvium edmondstonei Hook. f.	Sub-shrub, succulent
Sesuvium portulacastrum (L.) L.	Creeping herb
Amaranthaceae	
Alternanthera halimifolia (Lam.) Standl. ex Pittier	Procumbent herb
Atriplex oestophora S.F. Blake	Sub-shrub
Gomphrena albiflora Moq.	Procumbent herb
Heterostachys ritteriana (Moq.) Ung.-Sternb.	Sub-shrub, succulent
Sarcocornia ambigua (Michx.) Alonso & Crespo	Herb, succulent
Asteraceae	
Egletes prostrata (Sw.) Kuntze	Herb
Bataceae	
Batis maritima L.	Sub-shrub, succulent
Boraginaceae	
Argusia gnaphalodes (L.) Heine	Shrub, succulent leaves
Heliotropium curassavicum L.	Sub-shrub, succulent
Convolvulaceae	
Ipomoea pes-caprae (L.) R.Br.	Creeping vine, latex
Euphorbiaceae	
Euphorbia mesembrianthemifolia Jacq.	Herb, latex
Croton punctatus Jacq.	Subshrub, latex
Goodeniaceae	
Scaevola plumieri (L.) Vahl	Sub-shrub
Poaceae	
Sporobolus virginicus (L.) Kunth	Grass
Surianaceae	
Suriana maritima L.	Shrub
Sterculiaceae	
Melochia crenata Vahl	Prostrate subshrub

Families according to Stevens (2006)

populations on sandy soils and mobile dunes. *Scaevola plumieri* (Plate IX) belongs to one genus of Goodeniaceae found outside Australia, the species is widely distributed in African and South American Atlantic coasts.

5.1 Soils

Soils from COP are sandy, with significant lower concentrations of N, P, K, and Na than the clay-sandy soils from TAC and clay soils from COVE (Table 3.8). Soils from TAC show higher concentrations of Na, Mg, and Ca, whereas the samples from COVE have the higher values for N, P, and K.

Hot-water soluble ions show a similar, although more variable pattern (Table 3.9). TAC soils have in average higher specific conductivity and sum of cations. Sandy soils from COP have again smaller amounts of extractable ions. Specific conductivity is highly correlated with the sum of cations ($r^2 = 0.966$) and the concentration of Na ($r^2 = 0.922$). Notice that in the case of total cations, Ca and Mg are the predominant elements. In the case of extractable cations Ca and Mg predominate in COP, while Na is the dominant ion in COVE. In TAC soils cation concentrations are variable, but concentrations of Mg, Ca, and Na are well above all that of the other soils. In absolute terms the species whose roots are exposed to higher salinity (expressed by Na

Table 3.8 Total element concentration (mmol kg^{-1}) in superficial soils (0–10 cm) from Coro and the Paraguaná peninsula

Sample and site	N	P	Na	K	Mg	Ca
Península eastern coast (COP)						
Argusia gnaphalodes	62	10	21	9	106	2266
Euphorbia mesembrianthemifolia	65	9	36	7	149	3237
Egletes prostrata	66	14	20	12	155	2298
Scaevola ambigua	68	10	35	8	173	3365
Suriana maritima	58	14	17	12	144	2036
Average	64	11	26	10	145	2640
Tacuato Lagoon (TAC)						
Alternanthera halimifolia	226	22	38	87	680	5077
Batis maritima	95	16	167	71	626	6879
Gomphrena albiflora	110	17	399	185	1253	3105
Heterostachys ritteriana	127	14	220	229	1485	2830
Sarcocornia ambigua	104	18	206	114	748	4224
Sesuvium edmondstonei	117	14	166	204	1228	3205
Sesuvium portulacastrum	92	15	97	67	544	6647
Average	124	17	185	137	938	4567
Road Coro-La Vela (COVE)						
Atriplex oestophora	182	24	29	238	144	948
Heliotropium curassavicum	118	20	48	208	157	1347
Average	150	22	39	223	150	1147

Table 3.9 Specific conductivity (mmhos kg^{-1}), bulk density (g cm^{-3}and concentration of hot-water soluble ions (mmol kg^{-1}) in soils from Coro and the Paraguana peninsula, collected around the species indicated. Conductiviy was measured deionized water extract of soils dried at 40 °C (1 g in 25 mL water)

Specie and site	Specific conductivity	Bulk density	Na	K	Mg	Ca	∑
Península eastern coast (COP)							
Argusia gnaphalodes	916	1.06	0.3	0.4	0.8	1.1	2.4
Egletes prostrata	911	1.37	0.1	0.5	0.7	1.8	3.1
Euphorbia mesembrianthemifolia	957	1.46	0.7	0.4	1.5	1.2	3.8
Scaevola plumieri	951	1.38	0.3	0.4	0.9	1.6	3.1
Suriana maritima	851	1.43	0.3	0.4	0.9	1.2	2.7
Average	917	1.61	0.3	0.4	1	1.4	3
Tacuato LagOON (TAC)							
Alternanthera halimifolia	3248	1.35	2.2	5.8	5	6.7	19.7
Batis maritima	11,670	1.19	65.2	7.1	7.8	3.6	83.8
Gomphrena albiflora	90,737	1.54	365.1	20.1	64.4	272.2	721.9
Heterostachys ritteriana	62,661	1.6	190.7	15.6	16.1	216.7	439.1
Sarcocornia ambigua	19,448	1.43	107.9	10.5	7.8	4.4	130.6
Sesuvium edmondstonei	62,222	1.64	140.2	15.3	11.1	288	454.5
Sesuvium portulacastrum	2463	1.45	5.6	6.5	2.1	1.4	15.6
Average	36,064	1.45	125.3	11.6	16.3	113.3	266.5
Road Coro-La Vela (COVE)							
Atriplex oestophora	5758	1.54	21.6	11	1	6.5	40.1
Heliotropium curassavicum	6777	1.68	17	5.4	3.9	10.2	36.6
Average	6267	1.61	19.3	8.2	2.4	8.3	38.4

concentration and ∑ions) are *Go. albiflora, He. ritteriana, Se. edmonstonei, Sa. ambigua* and *Ba. maritima*, all of them in the TAC site.

5.2 Plants

5.2.1 Succulence and Ash Content

The degree of succulence (water content per unit fresh weight or area) of photosynthetic tissues is a highly variable character in coastal plants (Table 3.10). Typical succulents such as *Ba. maritima* and *Se. portulacastrum* reach values around 90 %. Grasses such as *Sp. virginicus* never reach values above 50 %. Dicots develop leaves with variable degree of succulence usually increasing with leaf age. In these species exposure to marine salt spray deposited on the leaves induces succulence. This development is associated with the amount of salt accumulated in the photosynthetic tissue, and that is the reason for the higher %ash in succulent tissues (Table 3.10).

Table 3.10 Degree of succulence expressed as % water [fresh mass – dry mass/fresh mass] and ash content (%) estimated by mass loss on ignition

Species	Succulence %	Ash %
Sporobolus virginicus	40.7	10.1
Alternanthera halimifolia	57.5	16.0
Melochia crenata	58.4	11.8
Heterostachys ritteriana	72.4	24.7
Euphorbia mesembrianthemifolia	75.2	8.3
Suriana maritima	75.6	12.7
Croton punctatus	76.6	17.6
Average-non succulents	65.2*	14.5*
Atriplex oestophora	81.7	29.4
Sarcocornia ambigua	84.5	29.6
Gomphrena albiflora	85.5	27.0
Egletes prostrata	86.3	23.4
Argusia gnaphalodes	86.6	23.5
Sesuvium edmonstonei	87.2	36.2
Heliotropium curassavicum	87.6	31.6
Scaevola plumieri	87.8	18.1
Ipomoea pes-caprae	87.9	–
Batis maritima	89.7	43.5
Sesuvium portulacastrum	90.7	45.2
Average succulents	86.9	30.8
Overall average	78.2	23.9

*Indicates significant differences between groups at $p \leq 0.01$

5.2.2 Total Element Concentrations

The concentration of total elements in photosynthetic tissues shows a pattern associated with soil texture and salinity (Table 3.11). The COP site, with the lowest soil salinity, includes the species with lower Na concentration in photosynthetic tissues, although several Na accumulators occur such as *Sc. plumieri*, *Eg. prostrata*, and *Ar. gnaphalodes*. TAC species have higher Na concentrations and are also more succulents. The species from COP and COVE stand out due to their P concentrations compared to TAC species. Notably the two species from COVE have very high N concentrations. Ca concentrations varied widely ranging from 42 in *Se. portulacastrum* to more than 1000 mmol kg^{-1} in *Ba. maritima* and *He. curassavicum*.

Only three species have more K than Na, *Me. crenata, Eu. mesembryanthemifolia,* and *Cr. punctatus* (Fig. 3.8a). Sodium concentrations vary in these species by almost two orders of magnitude, whereas K remains around the 400 mmol kg^{-1}. Ordering the species by their K/Na molar ratios allows the separation of halophytes *sensu stricto* with ratios ≤0.1, salt tolerant species with K/Na ratios between 0.1 and 1, and non-halophytes with ratios >1 (Fig. 3.8b). This type of analysis to assess halophytism can be made with total or soluble concentrations of Na and K as these elements do not constitute part of any insoluble structure in the plant. The halophyte category includes the species with the most succulent photosynthetic tissues. This analysis shows that the Euphorbiaceae, *Cr. punctatus* and *Eu. mesembrianthemifolia*, and the Sterculiaceae *Me. crenata* are not halophytes, and should be considered as salt resistant. The grass *Sp. virginicus*, the only monocot species in this group, departs in several aspects from the behavior the of rest of the species. It behaves as a salt tolerant plant that restrict Ca uptake into the photosynthetic tissues. It has salt secreting glands that are active throughout the leaf life time and contribute to regulate Na content in leaf tissues (Naidoo and Naidoo 1998; Bell and O′Leary 2003).

The distribution of total Ca and Mg concentrations shows the predominance of Ca/Mg molar ratios below 1, revealing the influence of sea

Table 3.11 Total element concentration (mmol kg^{-1}) in photosynthetic tissues of plants collected at the indicated coastal sites

Species	P	N	Na	K	Mg	Ca	K/Na	Ca/Mg	N/P
Península eastern coast (COP)									
Argusia gnaphalodes	41	1059	1613	293	786	467	0.18	0.6	26
Euphorbia mesembrianthemifolia	74	1085	204	408	236	265	2.00	1.1	15
Croton punctatus	75	1651	229	634	419	455	2.76	1.1	22
Egletes prostrata	75	1444	2055	421	365	427	0.21	1.2	19
Ipomoea pes-caprae	47	1154	1223	380	137	95	0.31	0.7	25
Melochia crenata	103	1373	105	326	360	602	3.11	1.7	13
Scaevola plumieri	47	1220	2289	640	426	101	0.28	0.2	26
Sporobolus virginicus	42	1031	293	144	394	197	0.49	0.5	25
Suriana maritima	92	1023	763	90	366	350	0.12	1.0	11
Average (COP)	66	1227	975	371	388	329	–	–	–
Tacuato Lagoon (TAC)									
Alternanthera halimifolia	30	1345	804	434	1082	812	0.54	0.8	45
Batis maritima	30	907	5687	178	593	1040	0.03	1.8	30
Gomphrena albiflora	23	931	1883	624	1424	620	0.33	0.4	41
Heterostachys ritteriana	28	1473	4442	353	335	108	0.08	0.3	52
Sarcocornia ambigua	31	1099	4435	249	283	61	0.06	0.2	36
Sesuvium edmonstonei	18	990	7758	332	382	216	0.04	0.6	56
Sesuvium portulacastrum	22	600	6122	184	77	42	0.03	0.5	28
Average (TAC)	26	1049	4447	336	597	414	–	–	–
Road Coro-La Vela (COVE)									
Atriplex oestophora	67	2444	4103	853	578	549	0.21	1.0	36
Heliotropium curassavicum	68	2039	2465	254	257	1483	0.10	5.8	30
Average (COVE)	68	2242	3284	554	418	1016	–	–	–

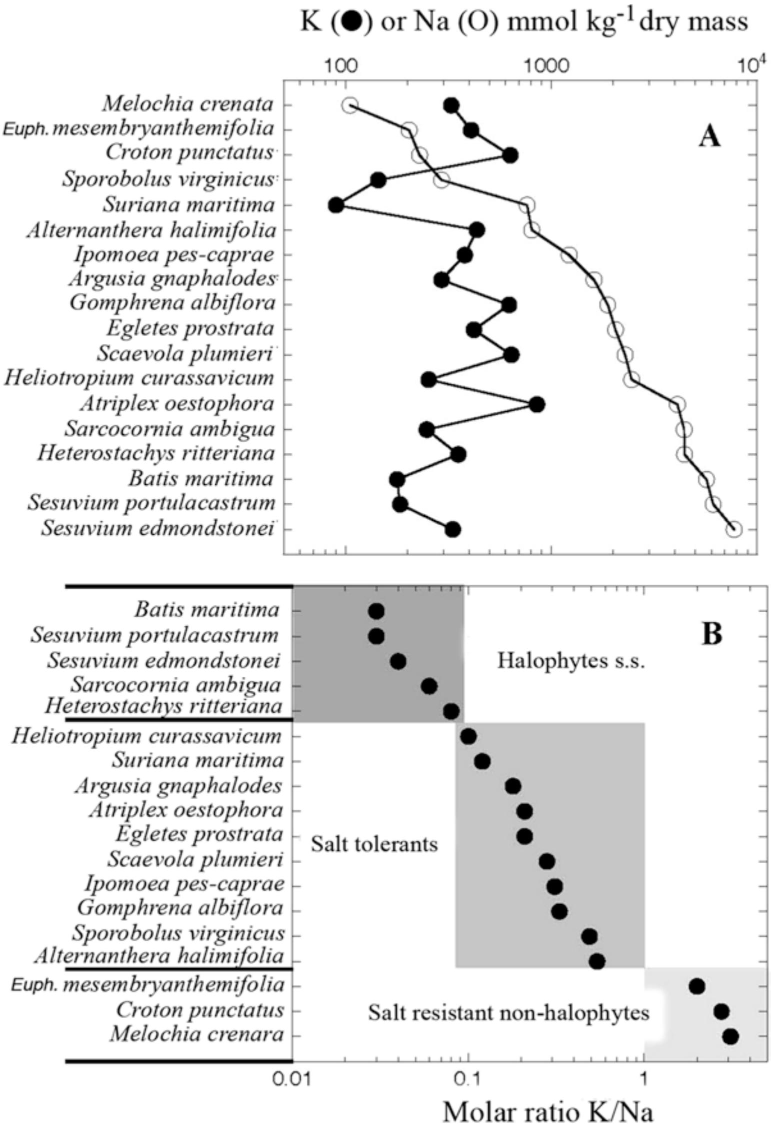
From Medina et al. (2008)

water intrusions and/or salt spray (Table 3.11). Concentration of total Ca range from less than 50 mmol kg^{-1} in the succulents *Se. portulacastrum* and *Su. maritima* up to concentrations above 800 mmol kg^{-1} in the Amaranthaceae *Go. albiflora* and *Al. halimifolia*, and the succulents *Ba. maritima* and *He. curassavicum*. The lowest Ca/Mg ratios (<0.5) ratios are those of *Sc.plumieri* and the Amaranthaceae *Sa. perennis, He. ritteriana* and *Go. albiflora*, whereas the largest ratios (>1.5) are those of *Me. crenata, Ba. maritima*, and *He. curassavicum*. The same ratio analysis will be conducted later on with soluble concentrations of Ca and Mg as this elements can be rendered insoluble, and therefore physiological irrelevant, when precipitated within cells as oxalate salts.

5.2.3 Concentration of Soluble Elements

Concentration of soluble elements has a general pattern similar to that observed by the total element concentrations. Plants from TAC have in average larger Na concentrations followed by those of COVE and COP (Table 3.12). Sodium concentrations >4000 mmol kg^{-1} are found in the succulents *He. ritteriana, Ba. maritima, Sa. ambigua* and the *Sesuvium* species. Concentrations of K and Mg are less variable among species and sites, while those of Ca can be separated into a group of plants with concentrations of <100 mmol kg^{-1}, a second group with concentrations between 100 and 150 mmol kg^{-1}, and a third group with two strong accumulator species, *Ba. maritima* and *He. curassavicum*,

Fig. 3.8 (**a**) Distribution of the total Na and K concentrations in plant leaves; (**b**) Ordination of the species according to their halophytic character based on their K/Na ratios



with concentrations >1300 mmol kg^{-1}. The soluble K/Ca ratio can be used as a measure of the preference of Ca uptake under natural conditions. In the group of plants under study there are only 4 species with soluble K/Ca ratios equal or lower than one, and could be considered calciotrophs in the sense of Kinzel (1989) (Fig. 3.9). At the other extreme there are 4 species with K/Ca ratios well above 100, and they may probably be considered as calciophobs. Sodium cannot be considered a factor influencing those ratios because in both extremes there are extreme halophytes. Confirmation of these relationships under experimental conditions could help to get a deeper insight into the mineral metabolism of halophytic plants. An additional confirmation of the Ca relationships of these plants is revealed by the soluble Ca/Mg ratios. The Ca/Mg ratios were well below one in most of the species under study (Fig. 3.10). The species *Su. maritima, Ba. maritima* and *He. curassavicum* have a Ca/Mg ratio above 1, confirming the calciotrophic character detected in Fig. 3.9. The calciophob species in Fig. 3.10 (Ca/Mg ratios <0.01) are again the Amaranthaceae *He. ritteriana, Go. albiflora,* and *Al. halimifolia.*

Table 3.12 Concentration of solubles cations (mmol kg^{-1}) in photosynthetic tissues of plants collected at the indicated coastal sites

Species and site	Na	K	Mg	Ca	K/Na	Ca/K
Península eastern coast (COP)						
Euphorbia mesembrianthemifolia	262	433	49	106	1.65	0.24
Suriana maritima	649	118	170	248	0.18	2.10
Argusia gnaphalodes	1411	299	421	133	0.21	0.44
Egletes prostrata	1789	393	80	67	0.22	0.17
Scaevola plumieri	2082	635	296	73	0.30	0.11
Average	1239	375	203	125	–	–
Tacuato Lagoon (TAC)						
Alternanthera halimifolia	722	430	648	36	0.60	0.08
Gomphrena albida	2064	691	910	35	0.33	0.05
Heterostachys ritteriana	4287	409	256	12	0.10	0.03
Batis maritima	4312	232	467	1431	0.05	6.17
Sarcocornia ambigua (green)	4405	276	218	58	0.06	0.21
Sarcocornia ambigua (red)	5068	275	283	50	0.05	0.18
Sesuvium portulacastrum	5666	261	129	18	0.05	0.07
Sesuvium edmonstonei	7354	363	317	14	0.05	0.04
Average						
Road Coro-La Vela (COVE)						
Atriplex oestophora	4037	881	344	40	0.22	0.05
Heliotropium curassavicum	2189	254	135	1358	0.12	5.34
Average	3113	568	240	699	–	–

From Medina et al. (2008)

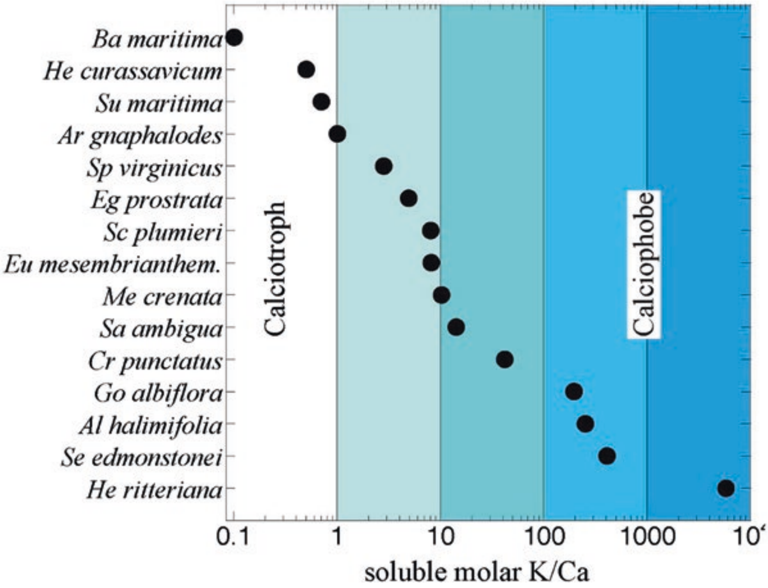


Fig. 3.9 Separation of calciotroph and calciophobs species according to soluble K/Ca ratios

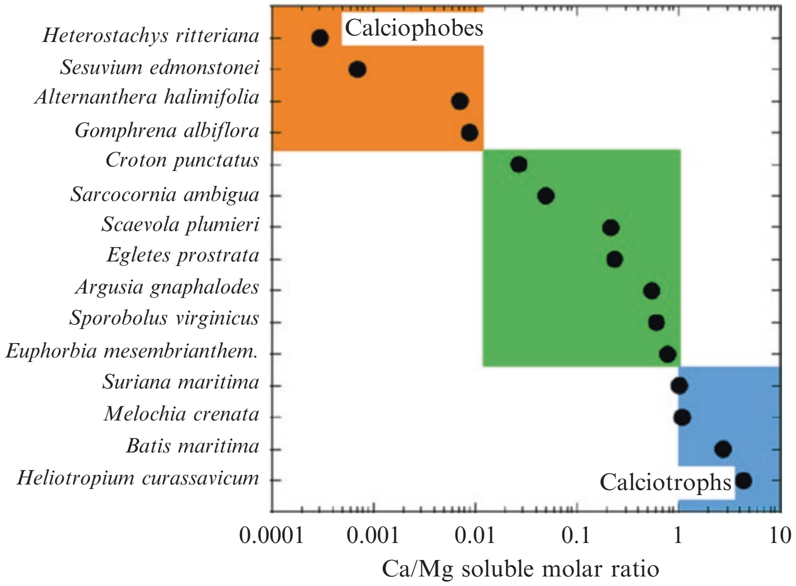


Fig. 3.10 Soluble Ca/Mg ratios as indicator of degree of calciophylly

The capacity for extracting K from soil, in the presence of high concentrations of other ions, particularly Na, varies between species, and is an indication of the physiological tolerance to salinity (Breckle 2002). The distribution of the soluble K/Na ratio of the photosynthetic tissue plotted against the molar ratio of the soil soluble K/Na ratio where the plant grows gives a distinct pattern of K accumulators (Fig. 3.11). The K accumulating species are ordered as follows: *Eu. mesembrianthemifolia* and *Sc.plumieri* by a factor between 10 and 100, *Ar. gnaphalodes, Eg. prostrata*, *Su. maritima* y *Go. albiflora* by a factor between 1 and 10. The species with lower relative capacity of K accumulation were *Sa. ambigua, Ba. maritima, He. ritteriana, He. curassavicum* and *At. oestophora* (factor below 1 and >0.1), and the two *Sesuvium* species with a factor <0.01.

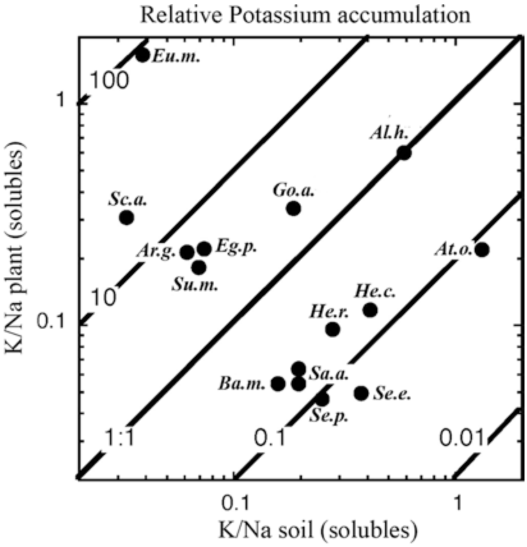


Fig. 3.11 Variation in the soluble molar K/Na ratios in photosynthetic tissues plotted agains the same ratio of the soils where the plants are growing following to Breckle (2002). The central diagonal indicates the values where relative concentrations of K related to Na are identical in plants and soils. Diagonal above represent accumulation factors of 10 and 100, whereas those below indicate reductions in the relative K concentration by factor of 0.1 and 0.01. Abbreviations: Ar.g. *Argusia gnaphalodes*, Al.h. *Alternanthera halimifolia*, At.o. *Atriplex oestophora*, Ba.m. *Batis maritima*, E.m. *Euphorbia mesembryanthemifolia*, Eg.p. *Egletes prostrata*, Go.a. *Gomphrena albiflora*, He.c. *Heliotropium curassavicum*, He.r. *Heterostachys ritteriana*, Sa.a. *Sarcocornia ambigua*, Sc.p. *Scaevola plumieri*, Se.p. *Sesuvium portulacastrum*, Se.e. *Sesuvium edmondstonei*, Su.m. *Suriana maritima*

5.2.4 Fractionation of Ca from Photosynthetic Tissues

The absolute concentration of Ca in photosynthetic organs and its distribution among different fractions such as soluble, associated to membranes and cell wall, and insoluble, characterizes physiological types. Those "physiotypes" differ in their tolerance to soil acidity, and the Ca requirements for the stability of ion selecting mechanisms of the plasma membrane (plasmalemma) and vacuole membrane (tono-

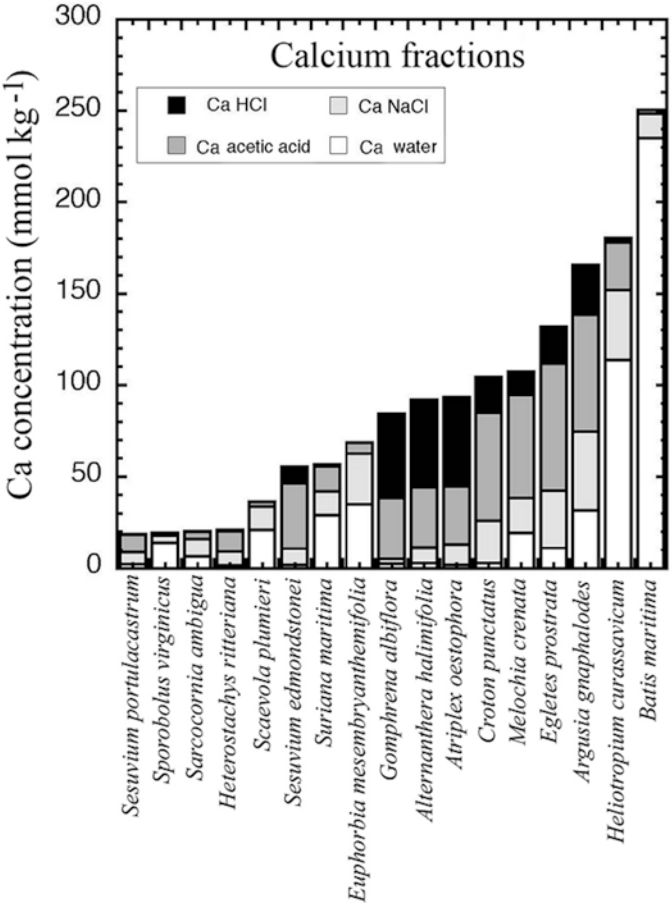


Fig. 3.12 Fractionation of Ca extracted from photosynthetic tissues of the species under analysis following the procedure described by Kinzel (1989)

plast) (Kinzel 1989). As might be expected from the concentration of total Ca in photosynthetic tissues, the species under analysis constitute a heterogeneous group regarding the distribution of Ca into different fractions within the leaf tissues. The fractionation of Ca included sequential extractions with hot water (soluble Ca), NaCl 10 % (adsorbed Ca), 2 N acetic acid (phosphates and carbonates), and 2 N HCl (oxalate). Addition of all fractions gives the total Ca content of the tissue analyzed. The largest concentrations of total Ca correspond to the same species already discussed when dealing with the total Ca measured by acid digestion; those are *Ba. maritima*, *He. curassavicum,* and *Ar. gnaphalodes* (Fig. 3.12). The former two species stand out because their water soluble fraction represent from 60 to 90% of the total Ca. In contrast, in the species *Cr. punctatus, Me. crenata, Eg. prostrata*, and *Ar. gnaphalodes*, more than 50 % of their total Ca is found in the acetic acid soluble fraction. In the Amaranthaceae *Go. albiflora, Al. halimifolia*, and *At. oestophora*, the predominant fraction is HCl soluble, presumably representing Ca oxalate. The most succulent species have total Ca concentration below 60 mmol kg^{-1}. The exception within this group is represented by *He. curassavicum* and *Ba. maritima*, strict calciotrophic species as indicated by their large Ca/K ratios (see Table 3.12).

6 Natural Abundance of ^{13}C and ^{15}N in Photosynthetic Tissues

The natural abundance of ^{13}C expressed as δ^{13}C (‰) is frequently used to determine the photosynthetic types of higher plants (Farquhar et al.

1982). High values (between ≈ −10 and −15‰) indicate the presence of C_4 or CAM, whereas lower values (below −25‰) usually indicate the presence of C_3 photosynthetic metabolism. The most practical way to accurately separate C_4 from CAM plants is the anatomy of the photosynthetic tissues. The presence of a well-developed vascular bundle sheath with chloroplasts ("kranz"-anatomy) indicates C_4 metabolism (Medina et al. 1976). Several species under analysis have C_4 photosynthesis according to their $\delta^{13}C$ values (Table 3.13) and anatomical characteristics (García et al. 2008). Those are the grass *Sp. virginicus*, the Amaranthaceae *Go. albiflora*, *Al. halimifolia,* and *At. oestophora*, and the Euphorbiaceae *Eu. mesembrianthemifolia*. Within the Amaranthaceae *sensu stricto* the C_4 metabolism has evolved independently several times (Sage et al. 2007). In the monophyletic genus *Alternanthera* C_4 metabolism appears in a terminal lineage of procumbent herbs. On the other hand, within the genus *Gomphrena* the C_4 and C_3 species are distributed in different clades. The genus *Atriplex* is now subsumed within the Amaranthaceae. It belongs to the group Atripliceae within the earlier Chenopodiaceae, and it contains both C_3 and C_4 plants (Kadereit et al. 2010). The C_4 plants of the genus have been quite succesful in occupying dry and saline environments throughout the world. The other species have a carbon isotopic signature corresponding to C_3 photosynthesis. Within this group there are large variations in $\delta^{13}C$ probably derived from differences in water use efficiency caused by drought or salinity (Farquhar et al. 1982). The C_3 species *Ar. gnaphalodes, Su. maritima, Se. portulacastrum, Se. edmondstonei* have higher water use efficiency as evaluated with $\delta^{13}C$ ($\delta^{13}C > -27‰$), and the least efficient *Eg. prostrata, Cr. punctatus*, and *He. curassavicum* ($\delta^{13}C \leq 30‰$).

The ^{15}N iotopic signatures are quite positive varying from 3.5 in *Eu. mesembrianthemifolia* and 14.5 in *Al. halimifolia*. These values are difficult to interpret without a detailed analysis of the potential sources of N in the soil, but in this case they suggest high N availability probably in the form of nitrate enriched in ^{15}N in the upper

Table 3.13 Natural abundance of stable isotopes in photosynthetic tissues of the plants collected at the study sites

Species and site	$\delta^{13}C$ ‰	$\delta^{15}N$ ‰
Península eastern coast (COP)		
Egletes prostrata	-31.2	7.4
Croton punctatus	-30.3	6.1
Scaevola plumieri	-27.9	6.6
Melochia crenata	-27.3	4.4
Argusia gnaphalodes	-26.5	6.0
Suriana maritima	-26.1	4.3
Sporobolus virginicus	-14.6	4.8
Euphorbia mesembrianthemifolia	-14.2	3.4
Tacuato Lagoon (TAC)		
Heterostachys ritteriana	-28.7	10.6
Sarcocornia ambigua	-27.8	8.6
Batis maritima	-27.2	10.6
Sesuvium portulacastrum	-26.2	8.3
Sesuvium edmondstonei	-24.0	7.6
Alternanthera halimifolia	-14.2	14.5
Gomphrena albiflora	-13.9	8.5
Road La Vela – Coro (COVE)		
Heliotropium curassavicum	-30.0	8.8
Atriplex oestophora		
(shade)	-17.4	9.2
(sun)	-16.1	10.2

Shaded names correspond to C_4 plants

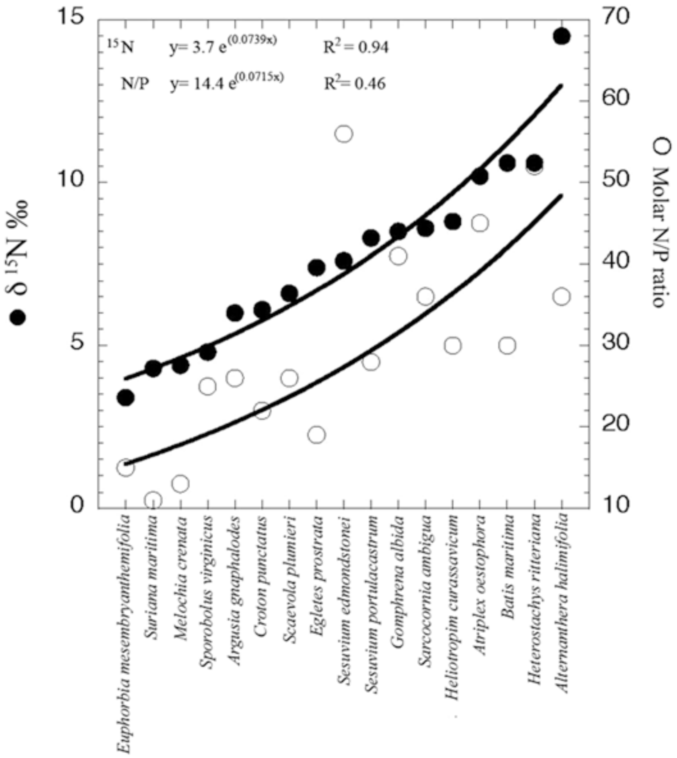


Fig. 3.13 Relationship between the natural abundance of ^{15}N (δ^{15}N) and the N/P molar ratio in photosynthetic tissues

soil layers through denitrification. The lowest values of average δ^{15}N were recorded in samples from the COP site, in correspondence with the lower N and P availability in these soils. The pattern of ^{15}N isotopic signatures is approximated by that of the N/P molar ratio, considered an indicator of potential availability of N determined by the availability of P in the same site (Fig. 3.13).

7 Mycorrhiza and Nutrition of Psammophytes

Sandy soils under the influence of marine spray are frequently infertile, mainly because of their texture, and usually high concentrations of Na of marine origin (Medina et al. 1989; Alarcón and Cuenca 2005). The successful establishment of plants on these soils depends on the rate of development of fine roots systems characteristics of many herbaceous plants, leading to efficient stabilization of the substrate. Fine roots are also important for an efficient exploration and absorption of nutrients from the soil environment. Alarcón and Cuenca (2005) showed that several of the shrubby and herbaceous species colonizing coastal dunes in the eastern coast of the Paraguaná penísula (Venezuela) conform vesicular-arbuscular mycorrhizas (Table 3.14). Colonization frequency was always above 60 % but the intensity seldom reaches values above 10 %, revealing a comparatively low role of mycorrhiza in the shrubby-herbaceous componentes of these communities. The study included three halophytes, *Se. portulacastrum, Ipomoea pes-caprae* and *Euphorbia dioica* for which no data on mycorrhizal symbiosis was reported.

8 Halophytes and Psammophytes of the Caribbean Coast of Venezuela

Robert Winfield (Herbario CORO, Instituto Tecnológico de Coro, Falcón, Venezuela) compiled a comprehensive list of plant species occurring in the Caribbean coast of Venezuela and

Table 3.14 Ranges of frequency (%F) and intensity (%M) of arbuscular mycorrhizal (AM) colonization of plant species in different topographic positions of the coastal sand dunes on Paraguana Peninsula

Topographic positions on the dunary landscape				
Plant species	Plain	Slope	Crest	Hollow
	Sporobolus virginicus	*S. virginicus*	*S. virginicus*	*S. virginicus*
	Paspalum vaginatum	*A. gnaphalodes*	*P. vaginatum*	*P. vaginatum*
	Argusia gnaphalodes	*Suriana maritima*	*A. gnaphalodes*	*A. gnaphalodes*
	Scaevola plumieri	*Croton punctatus*	*S. maritima*	*C. punctatus*
		Egletes prostrata,	*C. punctatus,*	*E. prostrata*
		Melochia tomentosa	*C. rhamnifolius*	*M. tomentosa*
		Fimbrystilis cymosa	*A. tortuosa*	*F. cymosa*
		Acacia tortuosa		*L. rigidum*
(%F)	74.9	69.4	82.0	63.5
(%M)	9.0	5.4	8.8	5.0

Modified from Alarcón and Cuenca (2005)

Colombia, and several large islands in the Caribbean based on his own long-term research and a thorough review of the available literature (Table 3.15). Species names included in the list have been updated, and their status regarding ecological behavior as psammophytic and halophytic character has been evaluated. Information on introduced and naturalized species was also included.

9 Concluding Remarks

The common coastal species described in this review constitute a heterogeneous group in regards of photosynthetic tissue succulence, element concentration, ionic relationships, and concentration of stable isotopes (^{13}C and ^{15}N). This eco-physiological heterogeneity is related to the diversity of environments on which those species grow and their phylogenetic relationships. Soils were sandier and less saline in COP site on the isthmus of Paraguaná, those of TAC were clayey and more saline, and COVE soils had intermediate salinity and higher concentrations of N and P. Those differences are related to their position in the Peninsula. COP and COVE located on the eastern side, receive constant supply of sand carried out by the trade winds, while the TAC site, located in the isthmus west coast in the Tacuato bay, still has clay sediments on the surface scarcely covered by sand. Differences in texture are related to the penetration of rain water, quickly in sandy soils, and remaining for longer periods at the surface in clay soils. In general, the environmental conditions for plant development in the TAC site are more stressful.

It is also eco-physiologically significant that Ca and Mg are the dominant soluble cations in COP soils, because both ions counteract partially the toxic effect of Na in plant tissues (Cramer 2002).

Species from the COP site may be ranked as typical psammophytes, for their capacity to establish in sandy, unstable soils, under the permanent influence of north-easterly winds. Several species within this group are of low stature, cushion- or rosette- forming, prostrate, creeping or stoloniferous. Reduced stature and prostrate habits favor establishment in sandy soils avoiding the impact of strong winds. However, they should be quick-growers to avoid being covered by wind-blown sand. Within this group three species (*Sc. plumieri, Su. maritima* and *Ar. gnaphalodes*) are erect growing subshrubs, up to 1 m tall, that grow more frequently in wind protected sites in the small coastal dunes characteristic of the isthmus.

The analysis of the total or the water soluble cations allows to rank the species according to their degree of halophytism, related to the Na/K ratios, and calciophylly, related to soluble K/Ca ratios. Strict halophytic species documented in this paper are those with a molar ratio K/Na <0.1.

Table 3.15 Robert Winfield′s list of halophytes and psammophytes of the Caribbean coast of Venezuela (Herbario Instituto Tecnológico de Coro)

FAMILY-Species	Status
Acanthaceae	
Avicennia germinans (L.) L	H, M
A. schaueriana Moldenke	H, M
Aizoaceae	
Sesuvium edmonstonei Hook f.	H, P
Sesuvium portulacastrum (L.) L.	H, P
Amaranthaceae	
Alternanthera halimifolia (Lam.) Standl. ex Pittier	Ht
Atriplex oestophora S.F. Blake	H
Atriplex cristata Willd (= *A. pentandra* Standley)	H
Gomphrena albiflora Moq.	Ht
Blutaparon vermicularis (L.) Mears	H, MA
Heterostachys ritteriana (Moq.) Ung.-Sternb.	H, P
Sarcocornia ambigua (Michx.) Alonso & Crespo	H
Amaryllidaceae	
Crinum erubescens Ait.	Ht, MA
Apocynaceae	
Calotropis procera (Aiton) W.T. Aiton	x, P *
Rhabdadenia biflora (Jacq.) Muell. Arg	H, MA
Asteraceae	
Egletes florida Shinners	x
E. prostrata (Sw.) Kuntze var. *glabrata* (DC.) Kuntze	Ht, P
Gundlachia corymbosa (Urb.) Boldingh	H
Oxycarpha suaedifolia S.F. Blake	H
Bataceae	
Batis maritima L.	H, P
Boraginaceae	
Argusia gnaphalodes (L.) Heine (*Mallotonia/Tournefortia)*	H, P
Bourreria succulenta Jacq.	Ht
Heliotropium curassavicum L.	Ht
H. ternatum Vahl	x, P
Lennoa madreporoides Lex.	x, P, parasite
Combretaceae	
Conocarpus erectus L.	H, MA
Laguncularia racemosa L.	H, M
Convolvulaceae	
Ipomoea imperati (Vahl) Griseb (= *I. stolonifera*)	H, P
I. pes-caprae (L.) R.Br.	H, P
Cruciferae	
Cakile lanceolata (Willd.) O.E. Schulz	H, P
Cymodoceaceae	
Halodule wrightii Asch.	H, submerse
Syringodium filiforme Kütz.	H, submerse
Cyperaceae	
Cyperus articulatus L.	Ht, swamps

(continued)

Table 3.15 (continued)

FAMILY-Species	Status
C. laevigatus L.	Ht
C. oxylepis Steud.	Ht, P
C. planifolius Rich.	H
Eleocharis geniculata (L.) Roem. & Schult.	Ht
E. mutata (L.) Roem. & Schult.	Ht, swamps
Fimbristylis cymosa R.Br.	H, P
F. ferruginea (L.) Vahl	Ht
F. spadicea (L.) Vahl	x
Schoenoplectus americanus (Pers.) Schinz & Keller	x
S. tabernaemontani (C.C. Gmel.) Palla	Ht
Euphorbiaceae	
Euphorbia bombensis Jacq.	H, P
E. mesembrianthemifolia Jacq.	Ht, P
E. thymifolia (L.) Millsp.	Ht, P
Croton punctatus Jacq.	Ht, P
Hippomane mancinella L.	H, P
Fabaceae	
Caesalpinia bonduc (L.) Roxb,	Ht, P
Canavalia rosea (Sw.) DC (= *C. maritima)*	Ht, P
Dalbergia ecastaphyllum (L.) Taub.	Ht, P
Senna italica Mill.	x, P*
Tephrosia cinerea (L.) Pers.	x, P
T. littoralis (Jacq.) Benth.	x, P
T. senna Kunth	x, P
Vigna marina (Burm.) Merr.	Ht
Goodeniaceae	
Scaevola plumieri Vahl	H, P
Hydrocharitaceae	
Halophila baillonii Asch.	H, submerse
H. decipiens Ostenf.	H, submerse
Thalassia testudinum K.D. Koenig	H, submerse
Malvaceae	
Corchorus hirsutus L.	Ht, P
Melochia crenata Vahl	Ht, P
Pavonia paludicola Nicolson	Ht, MA
Talipariti tiliaceum (L.) Fryxell var *pernambucense* (Arruda) Fryxell	Ht
Thespesia populnea (L.) Correa	Ht, MA*
Molluginaceae	
Mollugo verticillata L.	Ht
Poaceae	
Aristida venesuelae Henrard	Ht, P
*Cenchrus ciliaris*L.	Ht, P *
C. echinatus L.	Ht, P
C. spinifex Cav (= *C. incertus*)	Ht, P
Chloris barbata Sw (= *C. inflata* Link.)	x, P
Leptochloa fusca (L.) Kunth ssp. *fascicularis* (Lam.) N. Snow	x, P

(continued)

Table 3.15 (continued)

FAMILY-Species		Status
L. fusca ssp. *uninervia* (Presl) N. Snow		Ht, P
Leptophrium rigidum Kunth		x, P
Pappophorum krapovickasii Rosengrutttl		x, P
Paspalum vaginatum Sw.		H
Spartina patens (Ait.) Muhl.		H
S. spartinae (Trin.) Hitchc.		H, P
Sporobolus pyramidatus (Lam.) Hitchc.		Ht, P
S. virginicus (L.) Kunth		H, P
Uniola pittieri Hack.		H, P
Polygonaceae		
Coccoloba uvifera (L.) L.		Ht, P
Portulacaceae		
Portulaca halimoides L.		H, P
P. elatior Rohrb.		Ht, P
Pteridaceae		
Acrostichum aureum L.		H, MA
Rhamnaceae		
Condalia henriquezii Bold.		Ht, P
Rhizophoraceae		
Rhizophora mangle L.		H, M
Rubiaceae		
Erithalis fruticosa L.		Ht
Strumpfia maritima Jacq.		Ht
Ruppiaceae		
Ruppia maritima L.		H, submerse
Sapindaceae		
Dodonaea viscosa var. *viscosa* Jacq.		Ht, P
Scrophulariaceae		
Bontia daphnoides L.		Ht, P
Surianaceae		
Suriana maritima L.		Ht, P
Tetrachondraceae		
Polypremum procumbens L.		Ht, P
Typhaceae		
Typha domingensis Pers.		Ht, swamp
Verbenaceae		
Phyla nodiflora (L.) Greene		x
Zygophyllaceae		
Kallstroemia maxima (L.) Hook. & Arn.		x, P
Tribulus zeyheri Sond. ssp. *macranthus (*Hassk.) Hadidi		Ht, P*
Totals		
34 Families	73 genera	97 species

H halophyte, *Ht* salt tolerant and salt resistant, *P* psammophyte, *M* mangrove species, *MA* mangrove associated species, * introduced species, *x* possible halophytic species according to its coastal distribution, no information on its physiology

This group includes the most succulent species (*Ba. maritima, Se. portulacastrum, Se. edmondstonei*, and *He. ritteriana*). Development of succulent tissues is caused by increased water uptake leading to larger vacuolar volume. To a certain extent this process regulates effective intracellular ionic concentration, as suggested by Biebl and Kinzel (1965) for the succulent leaves in the mangrove *Laguncularia racemosa*. The group of salt resistant, non-halophytes, have K/Na ratios >1, and include *Eu. mesembrianthemifolia, Cr. punctatus*, and *Me. crenata.* The capacity of taking up K in ionic environments with high concentration of Na counteracts effectively the plasmatic toxicity of this cation (Albert 1982; Breckle 2002). The species with intermediate K/Na ratios from 0.1 to 1 are denominated salt tolerants. The mechanisms operating in this group resulting in salt tolerance are not fully understood, but probably include restrictions in salt uptake through the roots, relocation of absorbed salt in different tissues, and accumulation of compatible solutes.

Comparison of the K/Na ratios from the photosynthetic tissues and that of the soil water soluble ions provides an effective way to visualize the K absorption capacity in an environment with high Na availability. This approach applied to the species set described here revealed that the succulents identified as strict halophytes are less capable of restricting Na uptake, or favor Na uptake against K by a factor of 10. The same occurs in the case of *He. curassavicum* and *At. oestophora*, species that can be considered Na accumulating species in the sense of Collander (1941). This author cultivated a number of species under identical conditions of cation availability and found that cation composition of photosynthetic tissue may be associated to taxonomic groups. The *Atriplex* species in Collander experiment showed the largest Na accumulation values within the whole group studied. To the contrary, the species *Ar. gnaphalodes, Eg. prostrata, Su. maritima*, and *Go. albiflora* tend to accumulate K, or are more efficient restricting Na uptake. The most effective K accumulators compared to Na described here are *Sc. plumieri* by a factor of 30 and *Eu. mesembrianthemifolia*by a factor of 100. The species *Al. halimifolia* has a neutral behavior showing a leaf K/Na identical to that of the soluble soil fraction.

Molar ratios of water soluble Ca and K allows the identification of physiological types, and species may be categorized as calciophobes (K/Ca > 1) and calciotrophs (K/Ca < 1) (Kinzel 1989). Application of this criteria to the species studied in the Paraguaná peninsula clearly delineates three groups of relative Ca accumulation: calciophobes, K/C > 10 (*He. ritteriama, Se. edmonstonei, Al. halimifolia, Go. albiflora, Cr. punctatus, Sa. ambigua*; intermediate calciophobes, K/Ca between 1 and 10 (*Me. crenata, C. mesembryanthemifolia,Sc. plumieri, Eg. prostrata, Sp. virginicus*); and calciotrophs, K/Ca <1.0 (*Su. maritima, He. curassavicum*, and *Ba. maritima*). These differences are determined essentially by variations in water soluble Ca associated with the production of oxalate in those species intolerant to high levels of this cation.

Fractionation of total Ca confirms the calciophobe character of *At. oestophora*, *Al. halimifolia*, and *Go. albiflora*, because more than 50 % of total Ca in these species is in the form of insoluble oxalate. The other calciophobic species according to their K/Ca ratio are those in which more than 50 % of the total Ca is in the acetic acid fraction, that is, in form of phosphates, pectates, and other similar compounds of the cell wall (*Ar. gnaphalodes*, *Eg. prostrata*, *Cr. punctatus*, and *Me. crenata*). The physiology of these species is little known, and they deserve as a group an experimental analysis of their mineral metabolism, focusing on determining the exact composition of the acetic acid fraction. A remarkable fact is the difference in the calciophobic behavior within the Amaranthaceae. One subgroup precipitates most of the total Ca in photosynthetic tissue through the production of oxalic acid (*At. oestophora, Al. halimifolia, and Go. albiflora*), while the succulent species of this family (*Sa. ambigua* and *He. ritteriana*) restrict Ca transport to the photosynthetic tissues. The latter two species are within the former family Chenopodiaceae, characterized by very low levels of soluble Ca (Wiebe and Walter 1972).

Unexpectedly δ^{15}N values have a range of variation up to 11 ‰. Within the group of species studied there were no N_2-fixers, therefore the variation in ^{15}N enrichment can be attributed only to differences in the isotopic signatures of the mineral source of N (NO_3 or NH_4) and the actual N availability in the soil. Positive values suggest the uptake of ^{15}N enriched NO_3 from the upper soil layers occurring in plants with shallow root systems. It appears that P availability does not limits N utilization, which would partially explain the positive correlation between $\delta^{15}N$ values and the N/P of photosynthetic tissues.

Acknowledgements To Mag. Grisel Velasquez of UniSIG at the Center of Ecology of the IVIC for producing the map of humidity provinces of northern Venezuela and Colombia.

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4

Morphophysiology and Biochemistry of *Prosopis strombulifera* Under Salinity. Are Halophytes Tolerant to All Salts?

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and M. Virginia Luna

Abstract

Prosopis genus is an important member of semiarid, arid and saline environments around the world. This genus includes shrubs and trees that exhibit a high economic and ecological potential in different American regions. These plants are considered to be unique terrestrial species due to their combined ability to fix nitrogen and grow under high-salinity conditions. The South American halophyte, *Prosopis strombulifera* (Lam) Benth, is distributed from the Arizona desert (U.S.A.) to Patagonia (Argentina) and is especially abundant in the salinized areas of central Argentina. The soil of these areas is characterized by similar proportions of NaCl and Na_2SO_4. *P. strombulifera* species showed a halophytic response to NaCl surviving up to 1 M NaCl in *in-vitro* experiments, but in contrast, a strong growth inhibition at lower Na_2SO_4 concentrations was observed. These differential responses to the most abundant salts present in salinized soils of Argentina make this species an excellent model to study salt-tolerance mechanisms in halophytic plants. This chapter provides an overview of different salt tolerance mechanisms in the American halophyte *Prosopis strombulifera*, especially phytohormone pattern, oxidative responses and production of biomolecules. This halophyte may be considered as a new useful genetic source to improve crop salt tolerance and a promising plant as source of natural products for pharmaceutical industry.

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M.A. Khan et al. (eds.), *Sabkha Ecosystems Volume V: The Americas*,
Tasks for Vegetation Science 48, DOI 10.1007/978-3-319-27093-7_4

1 Introduction

Plants actually are more and more affected by environmental stresses, especially by the negative consequences of desertification, water scarcity and salinization, which can be seen and felt all over the world. This problem is catalyzed by global climate change which exacerbates desertification and salinization. About 3.6 billion of the world's 5.2 billion hectares of dry land used for agriculture have already suffered a negative impact, resulting in erosion, soil degradation and salinization.

Particularly, soil salinity is a severe problem in some parts of the world, and actually is affecting more and more lands. Some of the most serious examples of salinity occur in the arid and semiarid regions. For example, in Iran, Pakistan, Egypt, and Argentina, out of the total land area of 162.2, 77.1, 99.5, and 237.7 million hectares, about 23.8, 10, 8.7, and 33.1 million hectares are salt-affected, respectively (FAO 2008). As the world population has expanded, an increase in the area of land under cultivation as well as land productivity as yields per hectare is required (Flowers and Flowers 2005). For this reason, genetic improvement of salt tolerance has become an urgent need for the future of agriculture (Owens 2001; Munns 2007). This requires a detailed knowledge about tolerance mechanisms in plants, which comprise a wide range of responses on molecular, cellular, and whole plant levels.

During the last years, it has been proposed that improving our knowledge about the specialized physiology and biochemistry of halophytic plants, which impart their exceptional degree of salt tolerance, would give us new insides on plant salt tolerance and still represents a challenge for scientists. For this purpose, *Thellungiella* (the tolerant relative of *Arabidopsis*) has been considered the alternative halophytic genetic model system that incorporates the most important features of the *Arabidopsis* model (Inan et al. 2004). Nevertheless, others halophytic species with higher levels of salt tolerance must be taken into account to deep our knowledge on halophytic salt tolerance mechanisms.

American native plants have had diverse ecological and social impacts on ecosystems and are advantageous for regions affected by salinity. Successful management demands an understanding of the ecology and physiology of native taxa, which are documented for *Prosopis* populations in America. Therefore, *Prosopis* genus includes many important arboreal and shrub-like species that are present in saline zones of the Americas and some of them are considered to be unique terrestrial species due to their combined ability to fix nitrogen and grow under high-salinity conditions.

This chapter provides an overview of different salt tolerance mechanisms in the American halophyte *Prosopis strombulifera*, especially focused on phytohormone pattern, oxidative responses and production of biomolecules. This halophyte may be considered as a new useful source to improve our knowledge on halophytic salt tolerance mechanisms, for crop salt tolerance and as a promising plant as source of different natural products and biomolecules for cancer research and treatment, and possibly others pharmacological issues.

2 Soil Salinization

The distinguishing characteristic of saline soils from the agricultural standpoint is that they have accumulated sufficient neutral soluble salts to adversely affect growth of most crop plants. According to FAO (1997) saline soils are generally those which have an electrical conductivity of the saturation soil extract (EC_e) of 4 dS m^{-1} at 25 °C or more, and soils exceeding 15 dS m^{-1} are considered strongly saline.

It is well known, according to the water and salt movement theory, that two conditions are needed for soil salinization to occur. First, soil must be in contact with a salt source and, second, salt accumulation processes must prevail either permanently or periodically over salt removal processes (Darab 1981). Salt concentration in a specific soil volume and at a certain time is due to a complex process of addition, transportation and accumulation of water and salt flows (Sokolenko

1984). This balance is structurally governed by topographic position, climatic condition, water table depth (WTD) and hydrophysical characteristics of the soil. Functionally, vegetation is a crucial factor because the presence or absence of vegetation regulates the accumulation sites, the velocities and direction of the salt flows (Cisneros et al. 1999).

The most common cations in saline soils are Na^+, Ca^{2+}, and Mg^{2+} while the common anions are Cl^-, SO_4^{2-} and HCO_3^-. Saline soil types can be characterised by the ratio of the principal anions present (e.g. Cl^- and SO_4^{2-}) (Mao et al. 2002):

- 'Cl-type' soils, in which Cl^- anion is dominant ($Cl^-: SO_4^{2-} > 8$)
- 'SO_4^{2-} -Cl-type' soil, in which SO_4^{2-} anion is dominant ($Cl^-: SO_4^{2-} < 2$)
- 'Mixed anions', in which there are roughly equal amounts of Cl^- and SO_4^{2-}.

Generally, plant growth inhibition in saline soils can result from: (1) toxicity due to high concentrations of ions, such as Cl^-, SO_4^{2-}, Na^+ and Mg^{2+}; (2) diminished absorption of nutrients because of poor ion balance; (3) decreased water absorption by roots because high ion concentrations lead to water stress; and (4) a decline in soil structure, particularly where Na^+ is the dominant cation (as occur in saline sodic soils) to generate soils with high exchangeable sodium percentages (ESPs) (Mao et al. 2002).

However, most studies concerning salt tolerance of plant species have been based on experiments in which NaCl is the predominant salt, and injury symptoms are often ascribed to the toxicity of Na^+ and Cl^- ions. Nevertheless, NaCl is not the only salt present in salinized soils; Na_2SO_4 is another abundant salt, as mentioned above, and is present at higher concentrations than NaCl in the soils and groundwater in many areas of the world including several countries as Argentina, Pakistán, India, Egypt, China, Tunisia and California (Manchanda and Sharma 1989; Bañuelos et al. 1993; Iqbal 2003; Bie et al. 2004; Manivannan et al. 2008; Naeem and Quereshi 2005; Shi and Sheng 2005; Sosa et al. 2005; Tarchoune et al. 2010).

For that reason it is important to analyze and compare the effects of these two abundant salts on plant growth to have a better knowledge of the physiological responses of plants in natural environments.

3 Introducing the Genus *Prosopis*

The genus *Prosopis* L. (Fabaceae) has 44 species, 40 of which are native from America, three from Asia and one from Africa, which are considered as important members of adverse environmental conditions. This genus belongs to the family Leguminosae (Fabaceae), sub-family Mimosoideae. *Prosopis* species are distinguished from other sub-family of Mimosoideae by their indehiscent fleshy pods and the release of pollen in single grains (Folliott and Thames 1983). In America, Argentina has 28 native species, 13 of which are endemic, six species are autochthonous of the tropical Andean region and eight species are found in the Texas area, seven of them being endemic. Within *Prosopis* spp. there are trees and shrubs of varying size, mainly characterized by the presence of thorns and prickles (Burkart 1976). The ability of *Prosopis* species to tolerate adverse environmental conditions is the reason for their dominant position in the woody vegetation of the arid and semiarid zones of America. Therefore, Pasiecznik et al. (2001) reported the natural distribution of *Prosopis* genus, where *Prosopis tamarugo* is one of the few tree species capable of surviving in the extremely arid climate of the Atacama desert in Northern Chile (Figs. 4.1 and 4.2). Other species are distinctive from the large deserts of North America and from the arid and semiarid regions of South America. However, only a few representatives of the genus, such as *Prosopis africana* are partially distributed in subhumid tropical or subtropical regions.

The genus *Prosopis* is thought to be a primitive one within Mimosoideae (Burkart 1976) with a base chromosome number of 14 (Burkart and Simpson 1977). The taxonomical classification of the genus *Prosopis* by the Argentine bota-

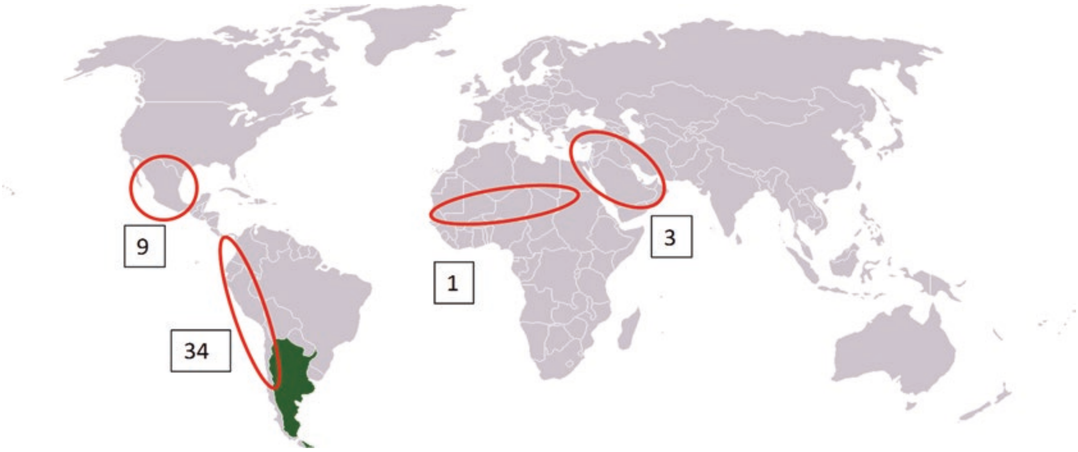

Fig. 4.1 Natural distribution of genus *Prosopis*. Numbers indicate the native species for each region

Fig. 4.2 Natural habit of *Prosopis strombulifera* on the salinized areas of Central Argentina

nist Arturo Burkart (1976) is widely accepted as the most complete. The presence and type of frame and shoot structure of these species allows to divide this genus into five sections (Burkart 1976). These sections are based on morphological differences. The main sections, called Algarobia and Strombocarpa, are native from North and South America. Both sections include approximately 90 % of all the species of the genus. The Monilicarpa section comprises only one endemic species to central Argentina and Anonychium and Prosopis sections belong exclusively to Africa (Pasiecznik et al. 2001).

Biochemical and molecular techniques have also been employed to infer the relationship between different species in the genus (Bessega et al. 2005; Landeras et al. 2006). RAPD analysis and isozyme markers have been utilized to determine the population structure of Algarobia section (Juárez-Muños et al. 2002, Ferreyra et al. 2007; Hamza 2010). Studies based on the genetic data derived from isozyme and RAPD analysis of 17 populations of 5 species from Algarobia suggest a reduction in the classification of many species and varieties determinated by Burkart (1976). Moreover, the molecular phylogeny and diversification history of *Prosopis* was studied by Catalano et al. (2008), who suggested that *Prosopis* section is not a natural group. Molecular dating analysis indicates that the divergence between Strombocarpa and Algarobia plus Monilicarpa sections occurred in the Oligocene, contrasting with a much recent diversification within each of these groups. The diversification within the major lineages of *Prosopis* American species is coincident with the spreading of arid areas in America, suggesting a climatic control for diversification of the group. The optimization of habitat parameters suggests an ancient occupation of arid environments by *Prosopis* species.

Regardless of its origin, *Prosopis* species have been introduced in many countries such as India, Pakistan, Brazil, Hawaii, South Africa, Egypt, Kuwait, and Australia as a source of fuel, firewood, timber, charcoal, gum, honey production, for erosion control and other raw materials (De Loach 1985). In recent decades, *Prosopis* species are extensively planted as wood producers. The wood is an excellent fuel, and the use and trade of firewood and charcoal is an important part of the rural economy. Trees harvested for fuel are coppiced and resprout vigorously after cutting, leading to increased productivity. The wood is also used for tool handles and other household items. In fact, *Prosopis* technically ranks with the world's best furniture species (Felker and Guevara 2003). When this stability is combined with the reddish-brown color wood and above average specific gravity (ca. 0.75) and hardness (770 kg cm^{-2} *P. alba* and 1010 kg cm^{-2} *P. glandulosa*), *Prosopis* lumber meets all the requisites to be included in the class of the world finest indoor furniture species. In the southwestern United States, despite the lack of availability of long clear logs on the 22 million hectares where *Prosopis* grows, it has being increasingly used for very high value custom furniture manufacture (Rogers and Ken 2000).

In Argentina the growth of different *Prosopis* populations has been studied in several regions: Chaco, Espinal and Monte. The environmental conditions, relative humidity and temperature, soils, the water table depth, biological disturbances and interactions, for example, predation and seed dispersal, herbivory and competence have been pointed out by diverse authors as the factors determining the structure and dynamics of the *Prosopis* populations. Villagra (2000) reported that the genus *Prosopis* has an adaptive mechanism in Chaco region to more arid and cold areas of west and south of Argentina. This process has occurred by the acquisition of morphological and physiological adaptations, such as a shrubby tree, leaf reduction, osmotic adjustment, etc. Therefore, the *Prosopis* distribution covers a variety of environmental conditions, including two clear gradients: one latitudinal temperature (warm cold at north and south) and one longitudinal moisture (wet at east and dry at west). These variations on environmental conditions lead to different *Prosopis* populations within each region and environmental condition. However, the higher *Prosopis* population is in the Chaco Province which yearly harvests 100,000 t of logs for furniture manufacture, meanwhile in Santiago del Estero Province, the majority of doors, windows and home furniture are made from *P. alba*. Government from both provinces are raising more than one million of *P. alba* seedlings (albeit from wild trees) per year for new plantations (Felker et al. 2001). Probably, due to this economic utility, the vast majority of the physiological and genetic studies have been done on members of the Papilionoideae subfamily with the implicit assumption that the physiology of the other genera would not be radically different.

Other economic utility is related to the production of abundant quantities of sweet fruit pods, readily consumed by livestock and wild animals. This behavior results in widespread dispersal of seeds. Mature trees produce 20–100 kg of nutritious pods every year. The pods are used for foods and drinks, some 'rustic' foods and delicacies, and these are important in local nutrition and trade. Industrial processing of the pods can produce seed gums used as a thickening agent in food preparation, dietary fibre and ethanol as a biofuel (Pasiecznik et al. 2004). The honey produced from the trees, which have long and abundant flowering, is of the highest quality. The exudate gum produced from wounds in the bark is comparable to commercial gum arabic (from *Acacia senegal*) and can be found in large quantities. The leaves of most introduced species are rarely browsed by livestock, an advantage in establishment, with only native Indian, African and a few American species valued for leaf fodder. Leaves are occasionally gathered and used as a mulch or compost on agricultural fields, with some fungicidal and insecticidal qualities. The bark is a source of tannins, dyes and fibres, and the plants are used in the preparation of medicines, mostly for eye, skin and stomach problems. *Prosopis* can survive on inhospitable sites where little else can grow, tolerating some of the hottest temperatures ever recorded, and some very saline or alkaline soils. Because they are nitrogen-fixing trees, it have also been demonstrated that *Prosopis* is able to improve the fertility and physical characters of soils in which they grow. They are deep-rooted, allowing trees to reach water tables, and they can grow and fruit even in the driest of years providing an invaluable buffer during droughts. Many species appear to require access to a water table to survive, and some people believe they are responsible for the depletion of ground water reserves.

3.1 *Prosopis strombulifera*

The halophytic shrub *Prosopis strombulifera* (Lam.) Benth. grows in areas that spread from the Arizona desert to Patagonia and is particularly abundant in the salinized areas of Central Argentina (Burkart 1976; Cantero et al. 1996). In these areas, proportions of NaCl and Na_2SO_4 are generally similar, although Na_2SO_4 was as much as three times more abundant in some samples (Sosa et al. 2005). In previous studies we observed considerable variability in the response of *Prosopis strombulifera* to salinity depending on the type of salt(s) used and osmotic potential (Ψ_o) in the culture medium. Therefore, *P. strombulifera* showed a halophytic response to NaCl surviving up to 1 M NaCl in vitro experiments, but a strong growth inhibition at lower Na_2SO_4 concentrations. Moreover, a stimulation of shoot growth at Ψo values up to −1.9 MPa (500 mM) NaCl is an interesting response of this halophyte, distinct from findings in other woody *Prosopis* species (Felker 2007). Several studies indicate that the NaCl tolerance of *P. strombulifera* exceeds the limits described for most halophytic plants (Catalán et al. 1994). However, *P. strombulifera* is much less tolerant to Na_2SO_4 than to NaCl. Plants grown in the presence of Na_2SO_4 showed immediate and sustained reduction of shoot height and leaf number per plant accompanied by senescence symptoms, such as chlorosis, necrosis, and leaf abscission (Reinoso et al. 2005; Reginato et al. 2012). Furthermore, treatment of *P. strombulifera* seedlings with Na_2SO_4 induced structural alterations in cells and tissues and modification of growth patterns. These alterations included anatomical and histological differences in roots, stems, and leaves of plants grown under high NaCl concentrations as compared to control plants (Reinoso et al. 2004, 2005). We demonstrated that *P. strombulifera* responds to progressive salt stress by different salts changing the leaf development, particularly in Na_2SO_4-treated plants, leading to structural modifications in leaf size and micro-morphology of leaf cells (increase in stomatal density (SD) and epidermal cell density (ECD) with smaller stomata) (Reginato et al. 2013). These anatomical modifications are consistent with our previous physiological studies which demonstrate that the adaptive success of *P. strombulifera* grown under high NaCl salinity would imply: (i) a delicate balance among Na^+ accumulation (and its use for osmotic adjustment) and efficient compartmentation in vacuoles (Reginato et al. 2014a); (ii) the ability of the whole plant to ensure a sufficient K^+ supply by maintaining a high degree of K^+/Na^+ discrimination; (iii) maintenance of normal Ca^{2+} levels in leaves (Reginato et al. 2014a); and (iv) osmotic balance and protection by compatible solutes such as proline, polyols (Llanes et al. 2013) and polycations such as polyamines under salt stress (Reginato et al. 2012).

4 Endogenous Hormonal Responses of *P. strombulifera*

Phytohormones have been reported to play important roles in stress responses and adaptation (Peleg and Blumwald 2011; Kohli et al. 2013). The fluctuations of stress-responsive hormones alter the cellular dynamics and hence play a central role in the coordinated regulation of growth responses under stress. Thereby, a small variation in the endogenous levels of each phytohormone, changes its physiological activity, although their specific roles in different biological processes still remain to be elucidated (Pieterse et al. 2009). Additionally, the roles of phytohormones in halophytes under salinity conditions remain relatively obscure. However, studies from our laboratory revealed important information on possible roles of different phytohormones in the halophyte *P. strombulifera*.

The analysis of the endogenous levels of ABA and metabolites in leaves and roots of *P. strombulifera* demonstrated that ABA levels varied depending on type of salt in the medium, NaCl or Na_2SO_4, salt concentration, organ analyzed and age of plants. ABA levels in leaves were much higher than in roots because of rapid biosynthesis in leaves and transport from roots. Leaves of Na_2SO_4-treated plants showed the highest ABA levels, which were related with sulfate toxicity symptoms. In this halophyte, ABA metabolism occurred mainly through conjugation. Therefore, a significant content of ABA-glucose ester (ABA-GE) was accumulated in both roots and leaves in all treatments, whereas phaseic acid (PA) and dihydrophaseic acid (DPA) levels were low. The highest levels of free ABA in leaves were correlated with high ABA-GE glucosidase activity in these organs, demonstrating ABA-GE transport from roots to leaves. Plants treated with Na_2SO_4 showed the highest levels of ABA-GE and free ABA in roots and leaves. Therefore, both compounds work together to create and intensify the salt-specific stress signal (Llanes et al. 2014a). It is interesting to point out that in these plants stomata remained opened allowing high transpiration, suggesting that sulfate toxicity interfered at some point with ABA signaling.

Recent studies suggested that salicilyc acid (SA) participate in the signaling of abiotic stresses (Hao et al. 2011). In the case of osmotic and salt stress, the role of SA is ambiguous considering different plant species, intensity and duration of stress, as well as application of SA doses (Horvath et al. 2007). The synthesis of salicylic acid by *P. strombulifera* seedlings in response to NaCl and Na_2SO_4 was analyzed at both 30 % and 70 % relative humidity conditions. The high SA levels observed in Na_2SO_4-treated plants at 48 days of culture were correlated with a failure in ion compartmentalization by these plants when compared with NaCl-treated plants. This response was accentuated at low relative humidity (30 % RH). In fact, NaCl-treated plants accumulated similar levels of Na^+ than Na_2SO_4-treated plants in their leaves, but they succeeded in ion compartmentalization and osmoregulation with direct consequences on their growth; these plants showed the lowest levels of SA. This response suggests that SA production is not a protective hormonal signal like ABA but a signal of injury in *P. strombulifera* under these adverse conditions (Devinar et al. 2013). Besides, SA is produced from phenylalanine by the action of the enzyme phenylalanine ammonia lyase (PAL). This enzyme is known to be induced by different types of abiotic and biotic stresses and is a key regulator of the phenylpropanoid pathway, which gives rise to various types of phenolics with multiple functions (Yalpani et al. 1994). Treatment with NaCl did not affect polyphenol content in *P. strombulifera*; instead, Na_2SO_4 sharply induced an increase in flavonoid compounds, mainly total flavan-3-ols, as well as increased levels of malondialdehyde (MDA) (Reginato et al. 2014b), indicating a role for these compounds in counteracting the damage induced by severe salt stress, and providing additional evidence that PAL pathway was induced when SO_4^{-2} was present in the medium.

Cytokinins and auxins act as endogenous regulators whose levels are environmentally modulated to regulate the formation of roots and shoots and their relative growth. The response to both hormones is often expressed in complementary patterns to impart distinct fates on neighboring cells (Schaller et al. 2015). This is achieved through interactions at the level of signaling and biosynthesis, though it is clear that there remains much to learn. For example, no studies have described all aspects of the interaction between these hormones (i.e., biosynthesis, transport, signaling, and degradation); indeed, additional points of regulation are known, such as the induction of several LOG and CKX genes by auxin, that have not as yet been linked to a particular developmental process (Bhargava et al. 2013). Accordingly, cytokinins and auxins could also act as stress hormones directly or indirectly, altering the expression of several stress-responsive genes, altering the growth and development as part of a general acclimation strategy, although validation of this assumption requires further experimentation.

Studies in the halophyte *P. strombulifera* showed that the high level of auxin (measured as indole acetic acid, IAA) in roots of Na_2SO_4-treated plants is in relation with increased lateral root formation previously observed in these plants (Llanes et al. 2014b). However, the roots of NaCl treated plants showed low IAA levels, no lateral roots formation and no anatomical and histological differences when compared to controls (Reinoso et al. 2004). Therefore, these results suggest the involvement of IAA signaling in the physiological responses of *P. strombulifera* roots to salt stress, related to the induction of lateral roots by ionic stress caused by the presence of sulfate anion in the medium. Accordingly, the results about zeatina (Z) content showed that in roots of *P. strombulifera* plants, this hormone is negatively correlated with IAA content. The lowest Z content was observed in roots of Na_2SO_4 treated plants where the highest IAA levels and increased lateral root formation were observed as mentioned above. Inversely, roots of NaCl treated plant showed highest Z levels at moderate salinity associated with an enlarged root system. Therefore, these results suggested that in this halophyte Z participates with IAA in the induction or inhibition of lateral roots formation. Moreover, several studies have confirmed the cytokinins action as antagonist of ABA on stomatal regulation. Higher levels of leaf cytokinins can be correlated with stomatal opening in some plants (Vysotskaya et al. 2004). In *P. strombulifera*, the accumulation of Z in leaves of Na_2SO_4 treated plants at high salinity (−2.6 MPa) may explain the high transpiration previously observed in these plants, in spite of the high ABA levels (Llanes et al. 2014a). Therefore, this influence of cytokinin on stimulating stomatal opening could be facilitating the transpiration and magnifying the effect of salt stress. On the contrary, the low transpiration in leaves of NaCl treated plants correlated with their low Z levels may be as a result of less synthesis or decreased transport of Z from the roots (Llanes et al. 2014b)

Several studies have shown that modifications in the growth-promoting hormones, such as gibberellins (GAs) levels or signal, affects the plant response to drought, salinity and other environmental stresses (Shan et al. 2007; Li et al. 2012). Under abiotic stress specific changes in GAs content can be beneficial for the physiology and metabolism modulating several metabolic processes (Iqbal et al. 2011). In *P. strombulifera*, the concentration and chemical composition of the salts present in the medium modify the GA biosynthesis. Notably, GA_4 is the predominant active form found in this halophyte mainly in roots, where GA_4 accumulation in NaCl- treated plants was the highest. In leaves, a 5 fold increase respect to controls (non-salt treated plants) was determined at −1.9 MPa in correlation with optimum growth for this species. High GA_4 levels were maintained at −2.6 MPa. In these organs, also GA1 levels were significantly increased in relation to controls (3.5 fold at −1.9 MPa) indicating that both gibberellins play a role in controlling shoot growth in this species under NaCl treatment (Llanes et al. 2014b). The high levels of active GAs in *P. strombulifera* NaCl treated plants are correlated with their low ABA levels compared with Na_2SO_4 treated plants, probably due to competition for the common intermediate for the synthesis of both carotenoids and GA from the precursor geranyl-geranyl diphosphate (Lefsrud et al. 2006). In Na_2SO_4 treated plants at high salinity (−2.6 MPa) the lowest levels of GA_4 and GA_1 were detected, in coincidence with the maximum growth inhibition related to sulfate toxic effect which was accentuated with increasing salinity. Furthermore, bisaline-treated plants showed intermediate levels of GA_4 and GA_1 in concordance with an intermediate shoot length, showing a partial reversion of sulfate toxicity when both anions (chloride and sulfate) are present in the medium. Therefore, these results suggest that differential growth responses to both salts would be mediated, at least in part, by GA_1 and GA_4. This pattern was correlated with the inactive GAs profile observed in our experiments. In fact, in roots of NaCl-treated plants the diminution of GA_{34} levels at −2.6 MPa corresponds to an increment in GA_4 levels, probably due to the need of maintaining growth rate under high salt concentration; as mentioned above, under 500 mM NaCl *P. strombulifera* plants showed growth stimulation. Inversely, Na_2SO_4 treated plants had much lower levels of GA_4 together with high levels of its metabolite GA_{34} suggesting that GA_4 inactivation may be a consequence of sulfate toxicity; the highest concentration of this salt causes very low levels of all GAs, in their active or inactive forms. Lower levels of GA_8 in relation to GA_{34} in most salt treatments would indicate that, for some reason, there was less GA_1 oxidation in our experiments. Recently, it has been demonstrated that GA_1 has a role in cell expansion of the endodermis in the elongation zone of the primary root of Arabidopsis thaliana (Uehara et al. 2008). In our study, less content of GA_1 in roots of Na_2SO_4 treated plants might be related with their scarce root development as compared to controls.

5 Oxidative Stress and Antioxidant Defense

The deleterious effects of salinity on plant growth are associated with (1) low water potential of the root medium which causes a water deficit within the plant; (2) toxic effects of major ions present in the soil solution as Na^+, Cl^- and SO_4^{-2}; and (3) nutritional imbalance caused by reduced nutrient uptake and/or transport to the shoot (Ashraf and Ahmad 2000; Hasegawa et al. 2000; Parida and Das 2005; Munns and Tester 2008; Hariadi et al. 2011; Reginato et al. 2014a). In addition, salt stress can induce oxidative stress by generation and/or accumulation of reactive oxygen species, including hydrogen peroxide (H_2O_2), superoxide anion, and hydroxyl radicals (Kovtun et al. 2000; Miller et al. 2010). For that, salt tolerance is a complex trait involving responses to cellular osmotic and ionic stresses, subsequent secondary stresses (*e.g.* oxidative stress), and whole plant coordination of these responses.

Reactive oxygen species are extremely reactive and undergo uncontrollable and damaging reactions with all cellular components including DNA, lipids and proteins, which can aggravate the detrimental effects of the initial stress and even lead to cell death (Halliwell 2006; Van Breusegem and Dat 2006). Oxidative stress occurs when there is a serious imbalance in any cell compartment between ROS production and antioxidant defence leading to dramatic physiological challenges (Foyer and Noctor 2003). During salinity-induced oxidative stress, availability of atmospheric CO_2 is reduced because of increased stomatal closure and consumption of NADPH by the Calvin Cycle is decreased. When ferrodoxine is over-reduced during photosynthetic electron transfer, electrons may be transferred from PS-I to oxygen to form superoxide radicals ($O^{2\bullet-}$) by the process called Mehler Reaction, which initiates chain reactions that produce more harmful oxygen radicals (Hsu and Kao 2003). It was considered that ROS concentration needs to be maintained as low as possible, although actually this concept is changing because of the multiple functions that are currently being discovered for these molecules (Mittler and Blumwald 2010). Thus, it is important for cells to keep a tight control of ROS concentration, but not to eliminate them completely (Schützendübel and Polle 2002).

Halophytic species are known for their ability to withstand unfavourable conditions by quenching these toxic ROS, since they are equipped with powerful antioxidant systems, which include specific ROS-scavenging antioxidative enzymes and small non-enzymatic molecules that act as ROS scavenger such as ascorbate, glutathione, α-tocopherol, flavonoids, anthocyanines, polyphenolic compounds and carotenoids.

Salt-induced damage to cellular membranes due to lipid peroxidation was studied in the halophyte *P. strombulifera.* In agreement with our previous results (Reginato et al. 2014a), this halophyte showed a greater sensitivity to Na_2SO_4 than to NaCl, as indicated by the important oxidative damage induced in tissues when the SO_4^{-2} anion was present in the medium. This significant increase in malondialdehyde (MDA) concentration under Na_2SO_4 treatment was correlated with the growth inhibition and metabolic disorders induced by this salt (Llanes et al. 2013). Also, H_2O_2 concentration was significantly increased in roots of Na_2SO_4 and Na_2SO_4 + NaCl-treated plants at moderate salinity (−1.9 MPa) in correlation with increased lipid peroxidation in the former.

An interesting observation is that when SO_4^{-2} and Cl^- are both present in the culture medium, ionic interactions between the two anions occur, possibly at the membrane level, causing a partial reversion of the oxidative damage caused by SO_4^{-2} in roots. This response is in agreement with the observation that NaCl + Na_2SO_4-treated plants showed intermediate values in growth parameters, compatible solute synthesis and ion content between those obtained with monosaline treatments, as previously demonstrated (Llanes et al. 2013; Reginato et al. 2014a).

Several studies showed that halophytes have higher constitutive antioxidant defense activity as compared with glycophytes. Some authors argued that antioxidant enzymes in halophytes increase their activity with increasing salt concentrations at which plants are exposed (Bose et al. 2014). In relation to antioxidant enzymes, results obtained on the activities of catalase (CAT) and superoxide dismutase (SOD) in *P. strombulifera* showed that CAT and SOD exhibited differential responses to different salts and in different organs. NaCl-treated plants showed an increase in CAT activity in roots under moderate and high salinity (−1.9 MPa, −2.6 MPa). Nevertheless, leaves showed an increased in CAT activity at moderate salinity followed by a marked decrease at high salinity. In Na_2SO_4-treated plants, a gradual decrease in CAT activity in roots was observed, while in leaves showed a marked increase at high salinity. In contrast, a strong SOD activity was observed, with increases in both leaves and roots, with activity levels much higher than in NaCl-treated plants. In Na_2SO_4 + NaCl-treated plants enzyme activity changed. While the CAT activity in roots and leaves decreased with salinity, SOD activity decreased in roots and increased in leaves. From these result it seems that CAT plays an important role in early detoxification of H_2O_2 in roots, while SOD would have a predominant role in leaves, reflecting its important role in the anion superoxide detoxification. At higher salt concentrations, the enzymatic activity allows the H_2O_2 to act as a stress signal to trigger other physiological responses, like early suberification and lignification. Thus, the intense activity principally of SOD in Na_2SO_4–treated plants indicates an effort of plants to counteract the severe oxidative stress caused by this salt.

6 Synthesis of Polyphenols – An Expensive Cost to Survive

To counteract oxidative stress induced by salinity, plants have developed different strategies among which the stimulation of secondary metabolites synthesis may be involved in cell protective roles such as ROS scavenging (Simic and Jovanovich 1994). Natural antioxidants occur in all plant organs, and the typical compounds with high antioxidant activities include polyphenols, carotenoids and vitamins (Chanwitheesuk et al. 2005).

It is well established that the accumulation of secondary metabolites strongly depends on the growing conditions, such as temperature, light regime, nutrient supply etc. (Gleadow and Woodrow 2002; Falk et al. 2007; Ballhorn et al. 2011). In addition, more severe environmental influences, such as stress conditions, will also impact on the metabolic pathways responsible for the accumulation of secondary metabolites. The enhanced synthesis of particular secondary metabolites under stressful conditions is also believed to protect the cellular structures from oxidative effects (Jaleel et al. 2007). Among these compounds, polyphenols (mainly flavonoids) play an important role in the defence against ROS, and their synthesis and accumulation has been proposed to be stimulated in plants under salt stress (Navarro et al. 2006).

In the halophyte *P. strombulifera* salt treatments increased the accumulation of several polyphenols in both leaves and roots. Na_2SO_4 treatment sharply induced an accumulation of flavonoids and flavan-3-ols. Bisaline treated plants also accumulated high levels of polyphenols. HPLC analysis in these plants showed high levels of rutin, catechin, epicatechin and proanthocyanidine in these plants. The increase in total flavonoids and flavan-3-ols when SO_4^{2-} anion is present in the growth solution may indicate a role for these compounds in counteracting the strong oxidative damage induced by severe salt stress (Reginato et al. 2014b). When other ROS-detoxifying systems such as the xanthophyll cycle are not effective enough, as could be the case of Na_2SO_4-treated plants, polyphenols production is increased as an alternative detoxifying system. Agati et al. (2012) reported that antioxidant mesophyll flavonoids, at micromolar range, may effectively avoid reactive oxygen forms generation (e.g. by chelating transition metal ions).

Nevertheless, despite their protective functions, stress-induced increase of secondary metabolites was often counteracted by a corresponding decrease in biomass in several species (Selmar and Kleinwächter 2013). Accordingly, in *P. strombulifera* the large increase in total polyphenols found in Na_2SO_4-treated plants was accompanied by strong growth inhibition. In contrast, in NaCl-treated plants, polyphenols did not increase as much and growth was not affected, with healthy plants without toxicity symptoms. It might be thought that under NaCl treatment more efficient energy dissipation mechanisms such as xanthophyll cycle or detoxification of the oxygen radicals by SOD would render unnecessary investment of resources in flavonoid synthesis (Reginato et al. 2014b).

These observations lead to the proposal of a fundamental role of polyphenols in the protection of the photosynthetic apparatus under severe stress when other ROS-detoxifying systems are not sufficient, at the expense of growth.

7 *P. strombulifera* as a Natural Source of Biomolecules

As mentioned above, to cope with different abiotic stresses, and particularly to overcome oxidative stress generated by severe habitat conditions, plants produce a higher number of naturally occurring secondary metabolites which help them to grow under these conditions. These metabolites are bioactive molecules that can be a rich source of medicinally important compounds such as flavonoids, terpenoids, tannins, saponins, alkaloids etc (Qasim et al. 2011). Many of them have unique pharmacologic activities (Calis et al. 1997; Quiroga et al. 2001; Podolak et al. 2007; Kappel et al. 2008). Particularly, phenolic compounds possess diverse biological activities such as anti-inflammatory, anti-carcinogenic and anti-atherosclerotic activities. These activities might be related to their antioxidant activity (Chung et al. 1998).

In the past, herbs often represented the original sources of most drugs and herbal remedies, but nowadays, alternative medicines are used widely in all over the world. With increasing recognition of herbal medicine as an alternative form of health care, the interest in finding naturally occurring antioxidants for use in foods or medicine to replace synthetic antioxidants has been increased considerably.

Plants growing in severe environments are mostly halophytes and xerophytes which are well adapted to survive under extreme conditions. Several halophyte species are actually used in folklore medicine, since the extracts proved to have activity against human, animal, and plant pathogens (Ksouri et al. 2012).

In Argentina, the study of compounds obtained from regional plants is emerging. There are a lot of species for which “folkloric medicine” has described several uses to preserve and aid health (Roig 2002). Only a small number of them have recently been studied to confirm their phytopharmaceutical properties.

The fruits of *P. strombulifera* have been used in folk medicine as an astringent, anti-inflammatory and odontalgic agent and anti-diarrheic (Ariza Espinar et al. 2006; Ratera and Ratera 1980; Toursarkissian 1980). Recent scientific studies have confirmed part of its ethnopharmacological uses, describing the molecular mechanism involved in the analgesic effect of this plant (Saragusti et al. 2012) and its biological activity against several microorganisms such as

Escherichia coli, *Staphylococcus aureus* and *Salmonella typhi* (Anesini and Perez 1993; Pérez and Anesini 1994a, b). These data support, at least in part, the ethnomedical use of *P. strombulifera* fruits. Moreover, recently Hapon et al. (2014) reported by first time the *P. strombulifera* cytotoxic activity against human tumoral cell lines. Also, in this study it was demonstrated that the crude aqueous extract obtained from leaves of this halophyte can be used without risking the unexpected effects observed as a consequence of DNA injuries. These interesting results make *P. strombulifera* as a promising native plant to obtain natural products and biomolecules with different purposes, as for cancer research and treatment and other pharmacological uses.

8 Conclusions and Future Prospects

Salt tolerance research traditionally was being conducted using NaCl as the sole salt agent. Only relatively few studies have considered other salts in their experimental design; when other salts were taken into account very different tolerance responses in different species were obtained, principally between NaCl and Na_2SO_4 (Manchanda and Sharma 1989; Bañuelos et al. 1993; Iqbal 2003; Bie et al. 2004; Shi and Sheng 2005; Naeem and Quereshi 2005; Manivannan et al. 2008; Tarchoune et al. 2010).

In our studies in the halophyte *P. strombulifera* we have clearly demonstrated that ionic interactions between different salts in salinized soils can modify the biochemical and morphophysiological responses of plants to salinity. These resulted in a halophytic response of these species only to NaCl. This observation implies that halophytes may vary in their response to different salts, and in some cases plants can be tolerant and have a halophytic response to one specific salt only.

The phytohormone patterns in this halophyte confirm that the primary signaling pathways are modified by the chemical composition of the salts in the medium. The understanding of the interplay between hormonal changes and stress tolerance is crucial for identifying key steps involved in stress signaling and plant stress adaptation. However, differences in the hormonal, metabolic and oxidative status caused by chloride and sulfate sodium salts are complex and this interplay requires further experimentation.

Moreover, halophytes are an important source of bioactive compounds and need immediate consideration for carrying out detailed chemical and pharmacological evaluations. Such investigations may lead to the discovery of novel bioactive compounds that will help to assess the efficacy of herbal remedies. The results obtained about biomolecules present in the leaves make *P. strombulifera* a promising plant as source of natural products for cancer research and treatment, and possibly other pharmacological issues.

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A Review of the North American Halophyte *Suaeda linearis* (Ell.) Moq.

5

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Abstract

Suaeda linearis (Ell.) Moq. is a New World temperate, subtropical, and tropical maritime species that typically occurs 1.0–1.5 m above the mean high tide mark. It is a facultative annual that occurs on saturated substrates consisting of unconsolidated sand, shell fragments, and slightly elevated saline clays and sandy clays. Also known as sea blite, it is found in salinity conditions ranging from 10 to 50 parts per thousand. Sexual reproduction is the only mechanism of reproduction. Seed production is prolific and seed banks are well-supplied with this species. Seeds are dimorphic, and germination is high in both full sun and in shaded conditions.

1 Introduction

Suaeda, in the family Amaranthaceae (formerly Chenopodiaceae), is a temperate-, subtropical, and tropical genus of 90–100 species that has a cosmopolitan distribution (Correll and Correll 1972; Fisher et al. 1997; Schenk and Ferren 2001). *Suaeda linearis* (Fig. 5.1) is a common halophyte species in salt marshes, in the ecotone between the low and high salt marsh, and in brackish marshes (Stalter 1968; Eleuterius and McDaniel 1978; Dunlop and Crow 1985; Klotz 1986; Judd and Lonard 2002; Heinsch et al. 2004; Alexander and Dunton 2006; Forbes and Dunton 2006). *Suaeda linearis* is an annual in the temperate zone, but is a long-lived annual or weak perennial on subtropical or tropical shorelines (Ferren and Schenk 2004). It is morphologi-

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M.A. Khan et al. (eds.), *Sabkha Ecosystems Volume V: The Americas*,
Tasks for Vegetation Science 48, DOI 10.1007/978-3-319-27093-7_5

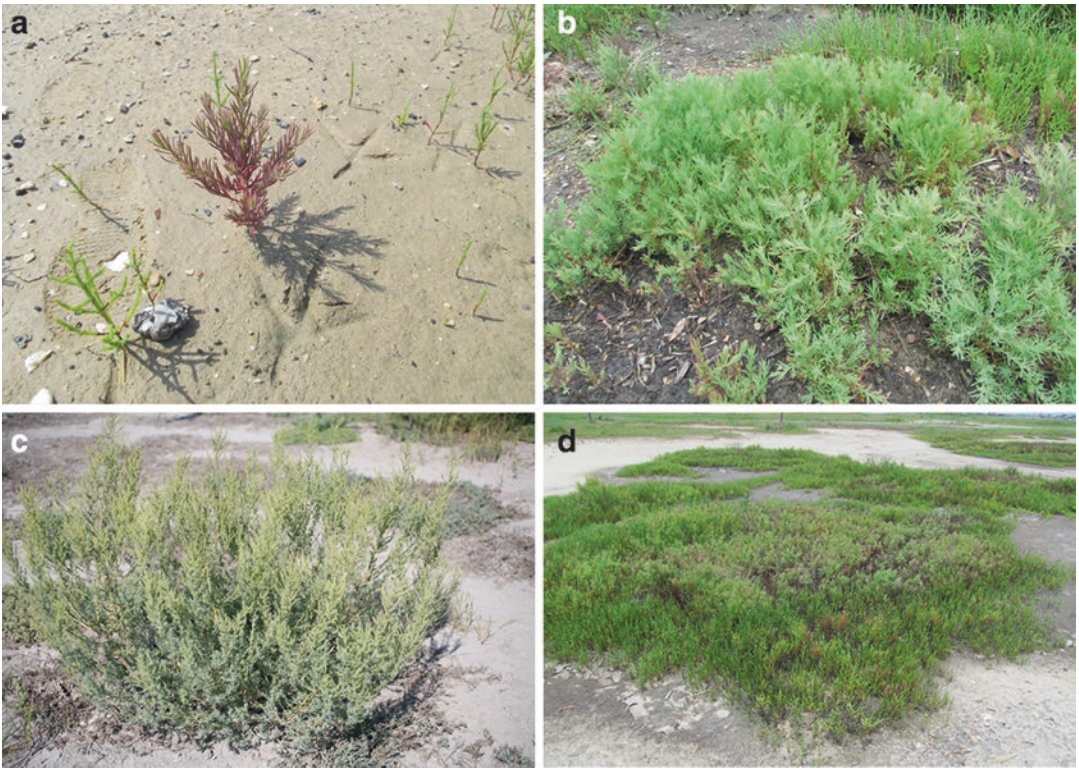

Fig. 5.1 *Suaeda linearis*. (**a**) Seedling with *Salicornia bigelovii*; (**b**) Large colony of immature plants; (**c**) Mature, flowering plant; (**d**) Habitat with *Salicornia bigelovii*

cally variable, and it occurs over a broad salinity gradient ranging from 10 to 50 ppt (Ungar 1962; Stalter 1968). Herein, we review the biology of this halophytic species.

2 Taxonomy and Variation

Suaeda linearis (S. Elliott) C. Moquin-Tandon is a member of the family Amaranthaceae, and is included in the subfamily *Suaedoideae*, tribe Suaedeae, subgenus *Brezia* and Section *Brezia* (Schütze et al. 2003) The section, as delineated by Schütze et al. (2003), is comprised of approximately 31 species, most of which are annuals. Other North American species in this section include *S. calceoliformis*, *S. esteroa*, *S. mexicana*, *S. occidentalis*, *S. puertopenascoa* and *S. rolandii*. Species in this section have a common *Brezia* type leaf with C_3 anatomy (Schütze et al. 2003). The genus *Suaeda* was proposed by Forsskål in 1775 (Schenk and Ferren 2001). Synonyms or rejected names are included in Table 5.1. Common names include sea blite, southern sea blite, annual seepweed, and linear-leaf seepweed.

Table 5.1 Synonyms or rejected names for *Suaeda linearis* (after Hopkins and Blackwell 1977)

Chenopodium maritima Pursh
Salsola linearis (Ell.) Sk.
Suaeda maritima Torr.
Chenopodium linearis (Ell.) Moq.
Chenopodium maritima Gray
Suaeda linearis (Ell.) Wats.
Suaeda linearis (Ell.) Wats. var. *ramosa* Wats.
Dondia linearis (Ell.) Heller
Dondia carinata Millsp.

2.1 Taxonomy

The following taxonomic description has been derived from Correll and Correll (1972), Ferren and Schenk (2004); Lonard personal observations, and Radford et al. (1968).

2.2 Seed Morphology

Seeds are dimorphic. Lenticular seeds are 1–1.8 mm in diameter and have a black, shiny, finely reticulate seed coat. Flat seeds are 1.5–2.6 mm in diameter, and have a dull brown seed coat. The embryo is coiled.

2.3 Root Morphology

A tap root system, characteristic of dicots, was noted for this species. Stalter (1974) found the root system 7.6–12.7 cm below the soil surface, but some taproots were 35.6 cm below the surface.

2.4 Shoot Morphology

Suaeda linearis is an annual in the temperate zone, but is a long-lived annual or a weak perennial on subtropical and tropical shorelines. Stems are 50–90 cm tall. Stems are erect and glabrous and are green to reddish purple, and are slightly woody at the base. Branches are numerous, slender, and are ascending or spreading. Plants usually turn black after drying. Leaves are succulent, simple, alternate, 1.5–5.0 cm long, linear, and the margins are entire. Leaves on branches are usually much shorter. Schütze et al. (2003) note a common leaf type for the members of the *Brezia* section—succulent, flattened to semiterete, usually concave on the adaxial side and slightly attenuated at the base.

2.5 Inflorescence

The inflorescence consists of densely-flowered compound spikes or cymules. Flowers are clustered in glomes or glomerules. Spikes are 1–12 cm long and are ascending. Bracts in the inflorescence are usually shorter than the cauline leaves. Flowers are bisexual, and the perianth is 1.2–2.5 mm in diameter. The corolla is absent. The calyx is 5-lobed. Calyx segments are slightly unequal, and are rounded or keeled-crested. Five stamens are present. The ovary is superior, and the stigmas are 2 or 3, and are often purplish-pink.

2.6 Fruits

The fruit is a utricle which is enclosed by the calyx.

2.7 Variability

No taxonomic varieties are recognized. Northern populations are annuals and have green shoots. Southern populations are often short-lived, glaucous perennials, and have reddish-purple shoots (Lehman 2013). Succulence and leaf diameter increase with increasing salinity (Hopkins and Blackwell 1977).

2.8 Chromosome Number

The chromosome number of *S. linearis* is $2n = 54$ (Ferren and Schenk 2004).

3 Geographic Distribution

Suaeda linearis occurs on temperate-, subtropical, and tropical shorelines in the New World. In the United States, it ranges from New Hampshire to Florida along the Atlantic coast, and on the Gulf Coast from Florida to Texas (Fig. 5.2) (Eleuterius 1972; Dunlop and Crow 1985; Klotz 1986; Perry and Atkinson 1997; Bruno 2000; McAvoy and Bennett 2001; Goldenheim et al. 2008; Guo and Pennings 2012). Bassett and Crompton (1978) did not report it from the Canadian Maritime Provinces.

Sea blite is distributed from Campeche and Yucatán in Mexico (Sauer 1967; Hopkins and Blackwell 1977; Moreno-Casasola and Espejel

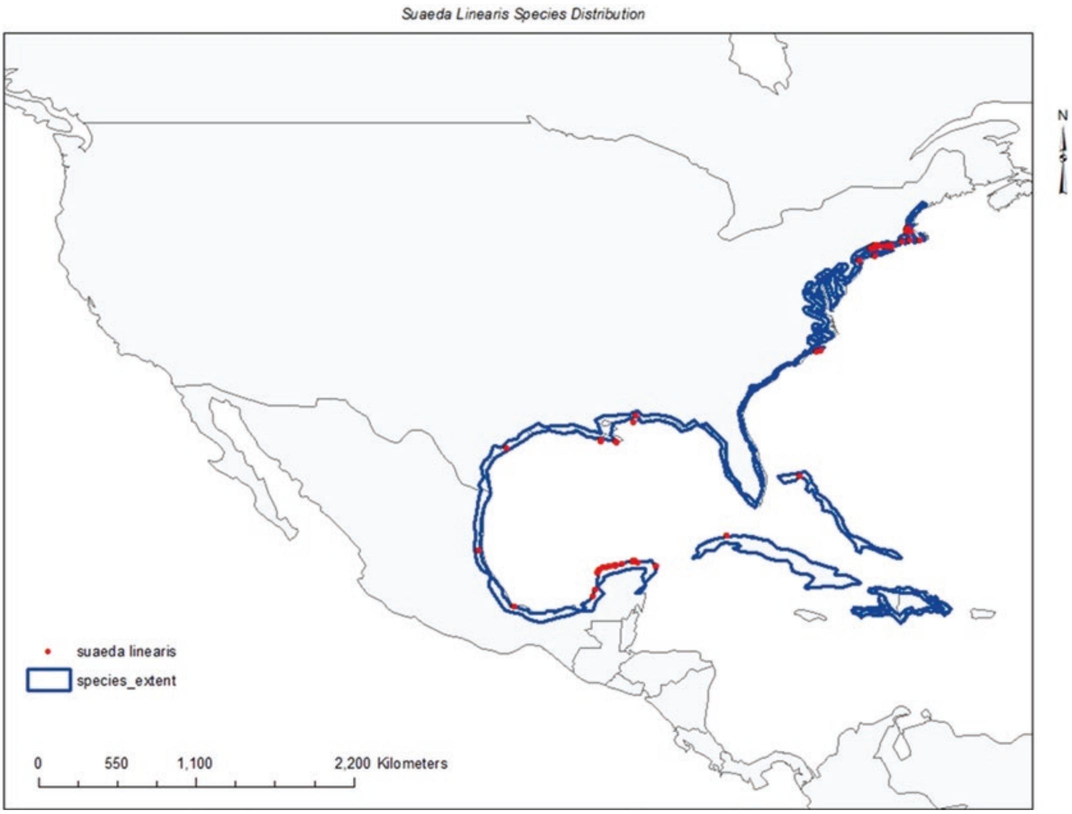

Fig. 5.2 Distribution of *Suaeda linearis* in North America and the Caribbean. *Red* dots indicate localities reported from the GBIF database (www.gbif.org)

1986; Britton and Morton 1989). It also occurs in the Caribbean in the Bahamas, Cuba, and Haiti (Correll and Correll 1972; Hopkins and Blackwell 1977).

4 Range of Habitats

Suaeda linearis is a pioneer species in coastal ecosystems where it occurs in a wide variety of topographic facets. The most common habitats are the high salt marsh, the ecotone between the high and low marsh, and brackish marshes. These sites are characterized by moist soils, and are in a zone flooded infrequently by high tides (Radford et al. 1968). In Rhode Island, sea blite is abundant in higher elevation salt marshes on cobblestone beaches (Bruno 2000; Bruno and Kennedy 2000; van de Koppel et al. 2006; Goldenheim et al. 2008; Irving and Bertness 2009). In Georgia, this species is rare in salt marshes and has a patchy distribution on oyster shell deposits (Guo and Pennings 2012). Sea blite also occurs on salt flats, in estuarine marshes, in tidal basins, on the margins of wind-tidal flats and hurricane washover channels, and along roadsides (Gillespie 1976; Lonard et al. 1978, 1991, 2003; Feagin and Wu 2006; Forbes and Dunton 2006).

4.1 Substrate Characteristics

Sea blite usually occurs on saturated substrates which consist of unconsolidated sand, shell fragments, and slightly elevated, wet saline clays, and sandy clays (Sauer 1967; Stutzenbaker 1999; Lonard et al. 2004). Judd et al. (1977) reported that 77.4–95 % of sand particles were 0.125–0.18 mm in diameter on the margins of the wind-tidal flats on South Padre Island, Texas. Stalter

(1968) found that salinity in *S. linearis* habitats in South Carolina ranged from 10 to 50 ppt, and the pH ranged from 6.0 to 7.5. In Louisiana, Courtemanche et al. (1999) noted that the pH ranged from 7.5 to 8.5 in the high marsh.

4.2 Climatic Requirements

The geographical distribution of *S. linearis* extends from about 43° N latitude in New Hampshire in the temperate zone to about 18° N latitude in Haiti in the tropics (Dunlop and Crow 1985; Hopkins and Blackwell 1977). Ferren and Schenk (2004) suggested that the northern distribution is limited because of the duration and severity of freezing temperatures. No freeze-tolerance data have been reported.

4.3 Response to Water Levels

Suaeda linearis is usually limited to a belt 1–1.5 m above the mean high tide mark (Kennedy and Bruno 2000). Therefore, the zone is occasionally flooded by high tides or less frequently by storm surges. Flooding may lead to burial, and scouring may result in removal of plants.

5 Plant Communities

Plant communities on coastlines where *S. linearis* occurs are often referred to by terminology used to describe habitats and topographic zones. Communities are designated as salt marshes, brackish marshes, or as other coastal habitat designations. On South Padre Island, Texas, Judd et al. (1977) listed plant communities with topographic designations. Sea blite occurs on the margins of wind-tidal flats, on the margins of hurricane wash over channels, and along island roadsides (Judd et al. 1977).

In Rhode Island, *S. linearis* occurs in a cobble beach community behind protective stands of emergent *Spartina alterniflora. Suaeda linearis* is associated with halophytes including *Limonium carolinianum*, *Salicornia europaea* (probably *Salicornia bigelovii*),*Sarcocornia ambigua* (formerly *Salicornia virginica*), and *Spergularia marina* (Bruno 2000; Bruno and Kennedy 2000; Kennedy and Bruno 2000; van de Koppel et al. 2006).

Oyster shell deposits provide a unique niche for *S. linearis* in Georgia. Guo and Pennings (2012) found that oyster shells alter the substrate and provide conditions that exclude the usual dominant species *S. alterniflora*, *Borrichia frutescens*, and *Juncus roemerianus*. In South Carolina, Stalter and Lamont (1993) described a high salt marsh community. Species associated with sea blite include *Spartina patens, Distichlis spicata, B. frutescens, Symphyotrichum tenuifolium*, and *Sabatia stellaris* (Stalter and Lamont 1993).

Thompson and Slack (1982), Moreno-Casasola and Espejel (1986) and Britton and Morton (1989) assigned plant communities in coastal wetland with species specific nomenclature. *Suaeda linearis* is common to all community types, but it is usually not a dominant species in any of the communities. Thompson and Slack (1982) referred to a *Borrichia* community of the Texas coastline that extends from the Laguna Madre near Corpus Christi to Louisiana. Species associated with the dominant *B. frutescens* are *Sesuvium portulacastrum, Salicornia bigelovii, Amaranthus greggii, Distichlis littoralis, Suaeda conferta*, and *S. linearis*.

In the Rio Grande Delta near the mouth of the Rio Grande, Britton and Morton (1989) described a Texas mangal (*Avicennia germinans*) community. *Suaeda linearis* occurs with *D. spicata, L. carolinianum, B. frutescens, D. littoralis, S. patens*, and *Blutaparon vermiculare* (Britton and Morton 1989).

Moreno-Casasola and Espejel (1986) listed plant communities on the Yucatán peninsula of southern Mexico with species specific nomenclature. Community dominants and associated taxa are listed as follows:

- *Cakile edentula-Cakile lanceolata* community. Common species: *Ambrosia hispida, Sporobolus virginicus*, *Atriplex pentandra, S. linearis.*
- *Suaeda linearis* community. Common species: *Euphorbia buxifolia, C. edentula,*

C. lanceolata; mangroves may be present adjacent to the community.

- *Sesuvium portulcastrum – Euphorbia buxifolia* community. Common species: *S. virginicus, Cenchrus* spp., *S. linearis.*
- *Euphorbia buxifolia – Sporobolus virginicus* community. Common species: *S. portulacastrum, S. linearis.*

Table 5.2 contains representative species associated with *S. linearis* in the United States and Mexico.

6 Physiological Ecology

The epidermis of *S. linearis* leaves has thin cuticles and stomata on both the upper and lower surfaces (Fisher et al. 1997). Sea blite has "austrobassioid" leaf anatomy (Fisher et al. 1997). Water storage tissue surrounds vascular bundles. However, a chlorenchyma –bearing sheath is absent around the vascular bundles. Small vascular bundles are supported by non-uniform, unspecialized, parenchyma tissue.

Table 5.2 Representative species associated with *Suaeda linearis* in the United States and Mexico

Species	RI	VA	GA	FL	MS	TX	YU
Agalinus maritima				X			
Amaranthus greggii						X	X
Ambrosia hispida							X
Atriplex arenaria				X			
Atriplex patula	X						
Atriplex pentandra						X	X
Batis maritima				X		X	
Blutaparon vermiculare						X	
Borrichia frutescens		X	X	X			X
Cakile lanceolata							X
Cakile edentula							X
Cassia sp.							X
Cenchrus spp.							X
Croton punctatus							X
Coreopsis tinctoria						X	
Cuscuta indecora						X	
Distichlis littoralis						X	
Distichlis spicata	X	X			X	X	
Fimbristylis spadicea				X			
Iva frutescens				X			
Iva texensis						X	
Jacquinia aurantiaca							X
Juncus gerardii	X						
Juncus roemerianus			X		X		
Limonium carolinianum	X	X		X	X		
Lycium carolinianum						X	X
Machaeranthera phyllocephala						X	
Polypogon monspeliensis						X	
Rhizophora mangle				X			
Sabatia stellaris					X		
Salicornia bigelovii					X	X	
Salicornia europaea[a]	X						

(continued)

Table 5.2 (continued)

Species	RI	VA	GA	FL	MS	TX	YU
Sarcocornia ambigua[b]	X	X		X		X	
Scaevola plumieri							X
Sesuvium portulacastrum				X		X	X
Solidago sempervirens	X						
Spartina alterniflora	X	X	X			X	
Spartina patens	X			X		X	
Spartina spartinae				X			
Spergularia marina	X					X	
Sporobolus pyramidatus						X	
Sporobolus virginicus						X	X
Suaeda conferta						X	
Suriana maritima							X
Symphyotrichum tenuifolium	X	X			X		
Tournefortia gnaphalodes							X

[a](probably *Salicornia bigelovii*—*S. europaea* is a European species)

[b]formerly *Salicornia viriginica*

RI Rhode Island (Bruno and Kennedy 2000; Shumway and Bertness 1992); *VA* Virginia (Perry and Atkinson 1997); *GA* Georgia (Guo and Pennings 2012); *FL* Florida (Stalter, personal observations; Wheeler and Hoebeke 1982); *MS* Mississippi (Eleuterius 1972); *TX* Texas (Alexander and Dunton 2006; Britton and Morton 1989; Feagin and Wu 2006; Forbes and Dunton 2006; Heinsch et al. 2004; Lonard and Judd 2002; Lonard et al. 2003; Marquardt and Pennings 2010, 2011; Thompson and Slack 1982); *YU* Yucatán (Britton and Morton 1989; Moreno-Casasola and Espejel 1986)

Austrobassioid leaf anatomy accounts for water storage capacity (Fisher et al. 1997).

Suaeda linearis is a C_3 plant in its mode of carbon metabolism in the light dependent reactions of photosynthesis (Fisher et al. 1997; Schenk and Ferren 2001). The absence of a double vascular bundle sheath is an indication of non Kranz anatomy and C_3 metabolism.

Infrequent flooding in the high salt marsh and evaporation results in concentration of salts. Sea blite tolerates substrate salinities ranging from 10 ppt (brackish) to 50 ppt (hypersaline) conditions in South Carolina (Stalter 1968). High salinities promote increased succulence of shoots and leaves (Hopkins and Blackwell 1977). High rainfall reduces substrate salinity and increases root:shoot ratios (Dunton et al. 2001).

Betacyanin replaces anthocyanin photo-accessory pigments in some species of the Amaranthaceae (Song and Wang 2015). Shoots are usually green in northern populations. However, in the subtropics and tropics, *S. linearis* shoots turn red or purple late in the growing season (Lehman 2013).

Sitostanol, a steroid alcohol and other ethyl sterols, occurs in sea blite leaves. Sterols of differing structures may influence cell membrane functions in response to variable saline conditions (Salt and Adler 1985).

6.1 Phenology

In Rhode Island, *S. linearis* seedlings emerge in May (Bruno 2000). In Maryland, Virginia, and Mississippi, flowering and fruiting phenophases occur from August to October (Eleuterius and Caldwell 1984; Hill 1986). Flowering and fruiting of *S. linearis* in northern Florida is from July to August (Anderson and Alexander 1985). Lonard and Judd (1989) noted flowering and fruiting stages from June to November on South Padre Island, Texas.

7 Population Biology

Suaeda linearis is a facultative annual in the subtropics and tropics (Fisher et al. 1997; Forbes and Dunton 2006). Therefore, it may be a perennial in warmer areas of its distribution (Ferren and Schenk 2004). Germination typically occurs after senescence and release of seeds in late autumn on South Padre Island. Therefore, plants are present throughout the year in the southern portion of the range.

7.1 Population Dynamics

Seedling emergence is the life-history stage controlling population dynamics of *S. linearis*. Bruno (2000) found that sea blite seedlings emerge and survive only behind emergent stands of *S. alterniflora* on cobblestone beaches in Rhode Island. Neither substrate quality nor herbivores limited seedling emergence (Kennedy and Bruno 2000). Goldenheim et al. (2008) also found that positioning on cobblestone beaches influences biomass production, length and number of shoots, and levels of seed production.

8 Reproduction

Sexual reproduction is the only method of reproduction in *S. linearis*. Sea blite does not produce rhizomes or stolons. Flowers are wind pollinated and inconspicuous. Seed production is prolific, but no data are available for per capita seed production.

8.1 Dispersal

Seeds are dispersed by water in fall and winter and remain buoyant for weeks or months (Bruno 2000; Bruno and Kennedy 2000). Lonard and Judd (1980) suggested that seeds may be dispersed by birds.

8.2 Seed Bank and Seed Size

Bruno and Kennedy (2000) estimated a seed bank of 253 seeds/m^2 for *S. linearis* between stands of *S. alterniflora* on the Rhode Island coastline. Ferren and Schenk (2004) indicated that seeds are dimorphic, and are 1–2.6 mm in diameter.

8.3 Germination Ecology

Suaeda linearis has dimorphic seeds. Dimorphic seeds may provide adaptive advantages in a saline environment that allows seedlings to avoid sibling competition and for a species to tolerate harsh environmental fluctuations (Wang et al. 2012). In China, Song et al. (2008) found that the Eurasian *Suaeda salsa* produces brown and black seeds at maturity. Higher germination rates occurred in black seeds under high salinity conditions than brown seeds, but brown seeds had higher germination rates than black seeds in all temperature and light conditions tested. They concluded that dimorphic seeds are advantageous to a halophytic species in harsh environmental conditions (Song and Wang 2015). Similar experiments have not been reported for *S. linearis*.

Mature sea blite plants are usually found in a zone 1–1.5 m above mean low water levels in a salt marsh (Kennedy and Bruno 2000). Seeds buried in the substrate may germinate, but seedlings may fail to emerge (Kennedy and Bruno 2000). Seed germination is restricted by high soil salinity. Bruno (2000) reported 10 % seedling emergence and survival in sites between stands of *S. alterniflora*.

Shumway and Bertness (1992) found 99 % germination in freshwater and full sun and shaded conditions, but only 48 % germination at 30 ppt salinity. Ungar (1962) reported that germination was enhanced when the seed coat was ruptured. He found that *S. linearis* maintained a relatively high germination rate up to 10 ppt salinity. However, germination did not occur at 50 ppt. Seeds washed with distilled water germinated after high salinity treatments. Ungar (1962) indicated that the limiting factor for germination success was an osmotic one.

9 Geomorphological Interactions

Suaeda linearis does not play a major role in geomorphology. The annual life-history and patchy distribution pattern are not conducive to shoreline stabilization. Plant mortality was due to burial or to removal during storm surges (Bruno 2000).

10 Interactions with Other Species

Annual plants are rare in many salt marshes and tend to be distributed in small patches. A wide range of interactions occurs between *S. linearis* and other species including competition, facilitation, predation, and parasitism.

In Georgia, Guo and Pennings (2012) found that *S. linearis* occurs on small, slightly elevated islands of oyster shell remains. Those small niches exclude salt marsh perennial dominants; namely *B. frutescens, J. roemerianus*,and *S. alterniflora*. In sites where oyster shell deposits are absent, the dominants exclude *S. linearis* (Guo and Pennings 2012).

10.1 Competition and Facilitation

In Rhode Island, Bruno (2000) and Bruno and Kennedy (2000) reported that the emergent salt marsh dominant, *S. alterniflora*, facilitates the establishment of *S. linearis* populations. *Spartina alterniflora* stabilizes the substrate by reducing wave-related disturbance. *Spartina alterniflora* stands also facilitate the establishment and persistence of other halophytes including *S. utahensis* and *L. carolinianum* (Irving and Bertness 2009). Competition is also an important parameter influencing populations of halophytes in a salt marsh. *Spartina alterniflora* limits the establishment of *S. linearis, Salicornia europaea* (probably *Salicornia bigelovii*), and *L. carolinianum* in the lower elevations of the salt marsh subjected to high tides in Rhode Island (van de Koppel et al. 2006).

Competition and facilitation play an important role in vegetation dynamics on the margins of the wind-tidal flats of Padre Island National Seashore, Texas. A wild fire removed much of the vegetation of this topographic site in December 1999 (Lonard et al. 2003). In March 2000, dominant species on an unburned site included *Sporobolus virginicus* (53 % cover), *Distichlis littoralis* (25 % cover), and *Blutaparon vermiculare* (5.0 % cover). Total cover for the unburned site was 85 %. *Suaeda linearis* ranked 4th in importance with a cover value of 1.5 %. In March 2000, dominant species in the burned site included *S. virginicus* (8.2 % cover), *S. linearis* (1.4 % cover), and *D. littoralis* (0.6 % cover). Total cover was 10.7 %. At the completion of the study in February 2002, dominant species in the unburned site were *S. virginicus* (25 % cover), *D. littoralis* (12 % cover), and the seasonal annual *Coreopsis tinctoria* (10 % cover). *Suaeda linearis* ranked 9th in importance (0.15 % cover). Total cover for the unburned site was 85.6 %. At the burned site at the conclusion of the study, *S. virginicus* (41 % cover), *D. littoralis* (11 % cover), and *C. tinctoria* (5 % cover) were the dominant species. Total plant cover was 57 %. *Suaeda linearis* (0.85 % cover) was ranked 4th in importance. In June 2000, *S. linearis* had its greatest cover value of 4.8 % and was ranked 2nd in importance during a peak growth period for the species (Lonard et al. 2003). Initially fire removes competing perennial grasses, namely *S. virginicus* and the mat-forming *D. littorialis*, and temporarily facilitates the establishment of *S. linearis*.

10.2 Predation

Insect predators play a minor role in *S. linearis* populations. Aphids are commonly found on green shoots. However, they do not appear to cause extensive damage (Lonard, personal observation). Wheeler and Hoebeke (1982) found that sea blite and other halophytes are hosts to nymphal stages of *Acanalonia pumila* and *Cynarda* spp (plant hoppers). *Suaeda linearis* is also reported as a host for *Creontiades signatus* (verde plant bugs) (Brewer et al. 2012).

10.3 Parasitism

Sea blite is occasionally parasitized by *Cuscuta indecora* (dodder) (Marquardt and Pennings 2010, 2011). Dodder overwinters in *B. frutescens* and *Iva frutescens* on the Texas coastline. The infection spreads from those species to *S. linearis* and other halophytes later in the growing season (Marquardt and Pennings 2011).

11 Economic Importance

Several species of *Suaeda* and other salt tolerant, succulent halophytes have potential use in saline agriculture. *Suaeda salsa*, distributed in Eurasia, may be used as a vegetable, and as a source of seed oil that is rich in unsaturated fatty acids (Song and Wang 2015). Other North American members of Section *Brezia* are used as food. *Suaeda edulis* is a Mexican species commonly known as romerito, which is consumed as a vegetable, particularly in Lent, Easter and Christmas celebrations (Noguez-Hernández et al. 2013). Brown and Glenn (1999) found that another member of the Section *Brezia*, *S. esteroa* (perhaps *S. puertopenascoa*) was effective as a biofilter to remove nutrients from saline aquaculture effluent.

However, *S. linearis* has limited economic importance. Leaf tips can be cooked and used as a food additive, and seeds are occasionally ground and added to cereals and bread dough (Anonymous 2015a).

11.1 Wildlife Value

Some wildlife values are attributed to *S. linearis*. On the Texas Gulf coast, seaside sparrows (*Ammodramus maritimus*) feed on leaves, fruits, and seeds (Bartosik 2010), and least terns (*Sterna antillarum*) and laughing gulls (*Larus atricilla*) nest in halophytic vegetation that includes *S. linearis* (Thebeau and Chapman 1984; Thompson and Slack 1982).

11.2 Medical Uses

No data are available about medical uses of this species. However, wind-borne pollen has been reported as a mild respiratory allergen (Anonymous 2015b).

Other members of Section *Brezia*, particularly *Suaeda maritima*, have been investigated extensively for medicinal compounds with divergent results. For example, Singh et al. (2013) mentions the use of *S. maritima* for treating hepatitis, and noted that it reportedly possesses antiviral, antibacterial activity and antioxidant activity, while Sudjaroen (2014) found no evidence of anti-cancer or anti-bacterial properties in this species. Nevertheless, given the paucity of data on the phytochemical composition of *S. linearis*, further studies are warranted, especially since it is known that halophytes are super-producers of anti-oxidants (e.g. Jithesh et al. 2006).

11.3 Potential Biological Control Agents

No biological control compounds have been isolated from *S. linearis*.

Acknowledgments We thank Glennis and David Lonard for providing assistance in preparation of this manuscript. Alfred Richardson and Ken King kindly provided the digital image. We thank Dr. Sumith Pathirana of Qatar University for his kind assistance in drafting the distribution map.

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6

Assessing Seed Germination Responses of Great Basin Halophytes to Various Exogenous Chemical Treatments Under Saline Conditions

Bilquees Gul, Abdul Hameed, Darrell J. Weber, and M. Ajmal Khan

Abstract

Salinity causes imbalances in endogenous level of different dormancy regulating chemicals (DRCs) of seeds, resulting in germination inhibition and/or viability loss. Exogenous application of DRCs could therefore be an effective means to mitigate salinity effects on seed germination. In this study, we compared (1) salt tolerance and (2) variability and efficacy of various DRCs on seed germination of Great Basin halophytes under controlled laboratory conditions. Optimal seed germination of all test species was observed in distilled water and increases in salinity generally decreased seed germination. Exogenous application of all DRCs enhanced seed germination at all salinities, with more alleviations under high salinity. Ethephon, fusicoccin and kinetin treatments were generally most effective than others. While, *Salicornia rubra* and *Sarcocornia utahensis* responded to nearly all DRCs in comparison to other species. Our results thus indicate that effectiveness of DRC treatments could be salinity, species and chemical specific.

1 Introduction

Soil salinity is the key factor that determines both the timing and the magnitude of seed germination, thereby population establishment of most halophytes in temperate saline habitats (Ungar 1978; Gul et al. 2013). Salinity tolerance of halophyte seeds from temperate dry cold habitats varies considerably among species (Khan and Gul. 2006; Easton and Kleindorfer 2008). For instance, seeds of some succulent halophytes such as

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M.A. Khan et al. (eds.), *Sabkha Ecosystems Volume V: The Americas*,
Tasks for Vegetation Science 48, DOI 10.1007/978-3-319-27093-7_6

Salicornia herbacea (1700 mM NaCl, Chapman 1960), *Suaeda aralocapsica* (1.5 M NaCl, Wang et al. 2008), *Sarcocornia perennis* (1.3 M NaCl, Redondo et al. 2004) and *Haloxylon ammodendron* (1.3 M NaCl, Huang et al. 2003) could germinate in about twice the salinity as in seawater. While, seed germination of many dicot forbs such as *Tanacetum cinerariifolium* (260 mM NaCl; Li et al. 2011), *Limonium iconicum* (300 mM NaCl, Yildiz et al. 2008), *Limonium lilacinum* (300 mM NaCl, Yildiz et al. 2008) and *Chenopodium album* (300 mM NaCl; Yao et al. 2010) reduced substantially (≤10 %) even under moderately (≤300 mM NaCl) saline conditions.

Seed germination responses of halophytes to salinity can generally be divided into three types, i.e. (1) delayed seed germination under salinity (Ahmed and Khan 2010; Hameed et al. 2013, 2014), (2) prevention of seed germination due to osmotic constraint (Zia and Khan 2004; Liu et al. 2006) and (3) loss of seed viability due to ionic toxicity under (Khan and Gul 2006; Khan et al. 2006; Rasheed et al. 2015). Exposure of seeds to 300 mM NaCl for example led to marginal inhibition of seed germination in *Haloxylon salicornicum* (El-Keblawy and Al-Shamsi 2008), substantial germination inhibition in *Panicum turgidum* (El-Keblawy 2004), while high seeds mortality in *Suaeda heterophylla* (Hameed et al. 2013). Hence, it appears that the seed germination responses of halophytes to increasing salinity are quite complex.

A growing body of evidence suggests that the salinity upsets the balances of various chemical regulators such as phyto-hormones and protective compounds in the seeds, which leads to germination inhibition and/or viability loss of the seeds (Atia et al. 2009; Gul et al. 2013; Li et al. 2015). For instance, decline in endogenous gibberellic acid (GA_3) levels is often ascribed to the seed germination inhibition under saline conditions (Kabar and Baltepe 1989; Bewley and Black 1994; Khan and Gul. 2006), which is further supported by the ameliorative effects of exogenous GA on seed germination of halophytes (Atia et al. 2009). Similarly exogenous supply of many other chemicals such as kinetin (Ahmed et al. 2014; El-Keblawy et al. 2011), ethylene (Khan et al. 2009), fusicoccin (El-Keblawy et al. 2011; Rasheed et al. 2015) and nitrogenous compounds (Gul and Weber 1998; Khan and Ungar 2001a, b, Li et al. 2005; Atia et al. 2009) is also known to have positive effects on seed germination of halophytes under saline conditions. However, germination responses to these chemicals may vary among species and habitats (Ahmed et al. 2014; Gulzar and Khan 2002; Khan and Gul. 2006; El-Keblawy et al. 2011).

Seed germination inhibition under saline conditions is generally associated with changes in seeds' chemical environment (Khan and Gul 2006; Debez et al. 2001; Atia et al. 2009). The understanding of the action of various dormancy regulating chemicals (DRCs) on seed germination thus appears important. The aim of this research work was therefore to investigate the role of different DRCs in improving seed germination of some Great Basin halophytes under increasing salinity. Specifically, we addressed following questions:

(a) How variable are the seed germination responses of halophytes to increasing salinity?
(b) Can exogenous application of different DRCs enhance seed germination of halophytes in both non-saline and saline conditions?
(c) Whether the effects of different DRCs to alleviate seed germination under saline are similar?

2 Materials and Methods

2.1 Seed Collection and Study Site

Seeds of eight halophytes *Atriplex rosea*, *Suaeda nigra*, *Sarcobatus vermiculatus*, *Sarcocornia utahensis*, *Salicornia rubra*, *Bassia scoparia*, *Halogeton glomeratus* and *Krascheninnikovia ceratoides* were collected from their healthy populations growing in vicinity and inland sabkhas around Great Salt Lake, Utah, United State of America (Table 6.1). More specifically, seed collection sites were situated at the area which

Table 6.1 Common name(s), life cycle, habit, distribution and habitat (seed collection site) of the test species

Species	Common name	Life cycle	Habit	Distribution	Habitat
Atriplex rosea L.	Tumbling saltbush, red orach	Annual	Herb	Disturbed sites, often in riparian habitats and barnyards in Eurasia and North America (Billings 1945; Welsh et al. 1987)	Salt marsh near Faust, Utah, USA
Bassia scoparia (L.) A.J.Scott (Syn. *Kochia scoparia* (L.) Schrader)	Mexican fireweed, Summer cypress	Annual	Herb	Saline areas in Southern and Eastern Russia, Europe, and North America	Salt marsh near Faust, Utah, USA
Halogeton glomeratus (Bieb.) C.A. Mey	Saltlover, Aral barilla	Annual	Herb	Saline -alkaline soils in Russia, China, Pakistan and western United States	Salt flats 2.5 miles northwest of Faust, Utah, USA
Krascheninnikovia ceratoides (L.) Gueldenst. (Syn. *Ceratoides lanata* (Pursh) J.T. Howell)	Winterfat, White-sage	Annual	Shrub	Central and southern Europe, northern Africa, and parts of Asia and western North America	Salt marsh near Faust, Utah, USA
Salicornia rubra A. Nelson	Red Glasswort, red swampfire	Annual	Herb	Central North America specially Manitoba to British Columbia and southwards.	Salt playas near Goshen, Utah, USA
Sarcobatus vermiculatus (Hook.) Torr.	Greasewood, seepwood, and saltbush	Perennial	Leaf Succulent Shrub	Medium to heavy textured soils in the Western USA (Richards, 1982; Welsh et al. 1987)	Salt flats in Utah, USA
Sarcocornia utahensis (Tidestrom) A.J. Scott (Syn. *Salicornia utahensis*)	Utah glasswort, Utah swampfire	Perennial	Stem succulent herbaceous	Southwestern United States	Salt playas 1–2 km east of Goshen, Utah, USA
Suaeda nigra (Raf.) J.F.Macbr. (Previously *Suaeda moquinii* (Torr.) Greene)	Mojave seablite	Perennial	Leaf Succulent Shrub	Western North America (from central Canada through the Western United States and Great Basin to the Mojave Desert in California) and northern Mexico	Salt marsh near Faust, Utah, USA

was once part of Lake Bonneville, a prehistoric pluvial ice-age lake that covered much of western Utah in past (Fisher 1974). Soil salinity of the area may range from 27 to 145 dS m^{-1} and water table varies from 1 to 3 m below the surface (Gul et al. 2001). It was a temperate area, where precipitation mainly occurs in the winter months. Seeds of test species were collected randomly from large number (>100) of plants, to ensure adequate representation of population's genetic diversity. Seeds were separated from inflorescence husk manually and dry-stored at 4 °C after surface sterilization with fungicide Phygon (2, 3 dichloro-1, 4-naphthoquinone) prior to use.

2.2 Experiment 01: Determining Salt Tolerance of Halophyte Seeds During Germination

Salt tolerance limits of halophyte seeds during germination were determined in growth chamber set at alternating temperature regimes (See Table 6.2), where the higher temperature coin-

Table 6.2 Salinity and temperature treatments used in germination experiments, based on preliminary trials

Species	NaCl (mM)				Temperature (°C)
	CK	Low	Medium	High	
*Atriplex rosea*L. – Black Seeds	0	200	400	600	20/30
*Atriplex rosea*L. – Brown Seeds	0	300	600	900	20/30
Bassia scoparia (L.) A.J.Scott	0	300	600	900	25/35
Halogeton glomeratus (Bieb.) C.A. Mey	0	300	600	900	25/35
Krascheninnikovia ceratoides (L.) Gueldenst.	0	300	600	900	25/35
Salicornia rubra A. Nelson	0	300	600	900	25/35
Sarcobatus vermiculatus (Hook.) Torr.	0	300	600	900	20/30
Sarcocornia utahensis (Tidestrom) A.J. Scott	0	300	600	900	25/35
Suaeda nigra (Raf.) J.F.Macbr.	0	400	800	1200	5/15

cided with the 12-h light period (Sylvania cool white fluorescent lamps, 25 µmol photons m^{-2} s^{-1}, PAR 400–750 nm) and the lower temperature coincided with the 12-h dark period. Germination was carried out in clear-lid plastic Petri-plates (50 × 9 mm; Gelman No. 7232) with 5 mL of test solution (0–1200 mM NaCl; Table 6.2). Each Petri-plate was placed in another 10-cm diameter plastic Petri-plate as an added precaution against loss of water by evaporation. There were four replicates of 25 seeds each per treatment. Seeds were considered to be germinated with emergence of the radicle (Bewley and Black 1994). Percent germination was recorded on alternate day for 20 days. The rate of seed germination was calculated with the help of a modified Timson's index of germination velocity, which is given below:

$$\begin{array}{c}\text{Germination rate}\\ \text{(Timson Index)}\end{array} = \frac{\Sigma G}{t}$$

Where, G is the percentage of seed germination at 2-day intervals and t is the total germination period (Timson 1965; Khan and Ungar 1984). Maximum value possible for this index with our data was 50 (i.e., 1000/20). The higher the value, the more rapid was the germination.

2.3 Experiment 02: Examining Efficacy of Different DRC Treatments in Improving Salt Tolerance of Halophyte Seeds

Seeds were germinated in different salinity treatments (Table 6.2) under optimal thermoperiod (Table 6.2) and 12-h light/12-h dark photoperiod in presence and absence of different dormancy regulating chemicals (DRCs). Ethephon (10 mM), fusicoccin (5 µM), gibberellic acid (GA_3; 3 mM), glycine-betain (1 mM), kinetin (0.05 Mm), nitrate (KNO_3; 20 mM), Proline (0.1 mM) and thiourea (10 mM) were used. Germination data were noted, as described above. Effects of these DRCs were expressed as change (in folds) in seed germination as compared to no-DRC treatment, as shown below:

$$\text{Change (folds)} = \frac{(\text{Germination with DRC} - \text{Germination without DRC})}{\text{Germination without DRC}}$$

A positive value indicted promotion in seed germination, while negative value was indicator of germination inhibition by a DRC.

2.4 Statistical Analyses

Germination data were arcsine transformed before statistical analysis. Analyses of variance (ANOVAs) were used to determine if treatments (salinity and DRCs) had significant effect on seed germination. While, a Bonferroni test was carried out to compare mean values for significant ($P < 0.05$) differences. Software SPSS Version 11.0 (SPSS 2011) was used for data analysis.

3 Results

3.1 Salt Tolerance of Halophyte Seeds During Germination

Seed germination of all test species, irrespective of their habit and life cycle traits, decreased ($P < 0.05$) with increases in salinity (Fig. 6.1). However, some (<20 %) seeds of *Suaeda nigra* could germinate in up to 1200 mM NaCl treatment (Fig. 6.1i), those of *Atriplex rosea* (brown seeds; Fig. 6.1a), *Bassia scoparia* (Fig. 6.1c), *Halogeton glomeratus* (Fig. 6.1d), *Krascheninnikovia ceratoides* (Fig. 6.1e), *Salicornia rubra* (Fig. 6.1f), *Sarcobatus vermiculatus* (Fig. 6.1g) and *Sarcocornia utahensis* (Fig. 6.1h) in up to 600 mM NaCl, while of *Atriplex rosea* (black seeds Fig. 6.1b) in up to 400 mM NaCl. Seed germination rate (Timson's index) of all test species also decreased with increases in salinity, with highest value (≥40) in absence of salinity and lowest (≤10) under high NaCl treatments (Fig. 6.1a–e).

3.2 Efficacy of DRC Treatments in Improving Salt Tolerance of Halophyte Seeds

All DRC treatments improved seeds germination of halophytes but response varied among seeds from different species and with the differential effect of NaCl concentrations. Higher seed germination was recorded by the DRC applications at NaCl concentrations where it was inhibited substantially. Exogenous application of ethephon could improve seed germination of *Salicornia rubra, Krascheninnikovia ceratoides* and *Sarcocornia utahensis* more than other species under high salinity (Fig. 6.2). Fusicoccin ameliorated seed germination of *Sarcocornia utahensis, Krascheninnikovia ceratoides* and *Bassia scoparia* more than other species under high salinity (Fig. 6.3). Gibberellic acid (GA_3) alleviated inhibitory effects of high salinity in *Salicornia rubra, Sarcocornia utahensis* and *Bassia scoparia* more in comparison to other species (Fig. 6.4). Glycinebetaine (GB) enhanced seed germination of *Sarcocornia utahensis, Salicornia rubra* and *Bassia scoparia* under high salinity stress more than other species tested (Fig. 6.5). Kinetin showed more pronounced ameliorative effects on seed germination of *Sarcocornia utahensis, Salicornia rubra* and *Sarcobatus vermiculatus* under high salinity as compared to other species (Fig. 6.6). Nitrate treatment could improve seed germination in *Sarcocornia utahensis* and *Salicornia rubra* under high salinity in comparison to other species (Fig. 6.7). Proline had more pronounced ameliorative effects on seed germination of in *Sarcocornia utahensis, Salicornia rubra* and *Halogeton glomeratus* than other species (Fig. 6.8). While, thiourea alleviated high salinity effects in *Sarcocornia utahensis* and *Salicornia rubra* more as compared to other species (Fig. 6.9).

4 Discussion

Seeds of Great Basin halophytes used in this study were non-dormant and germinated maximally in distilled water; however increases in salinity decreased their germination which is in agreement with the general trend of halophyte seeds reviewed by Ungar (1978) and Gul et al. (2013). Similar results have been reported for the seeds of *Halocnemum strobilaceum* (Pujol et al. 2001), *Arthrocnemum macrostachyum* (Vicente

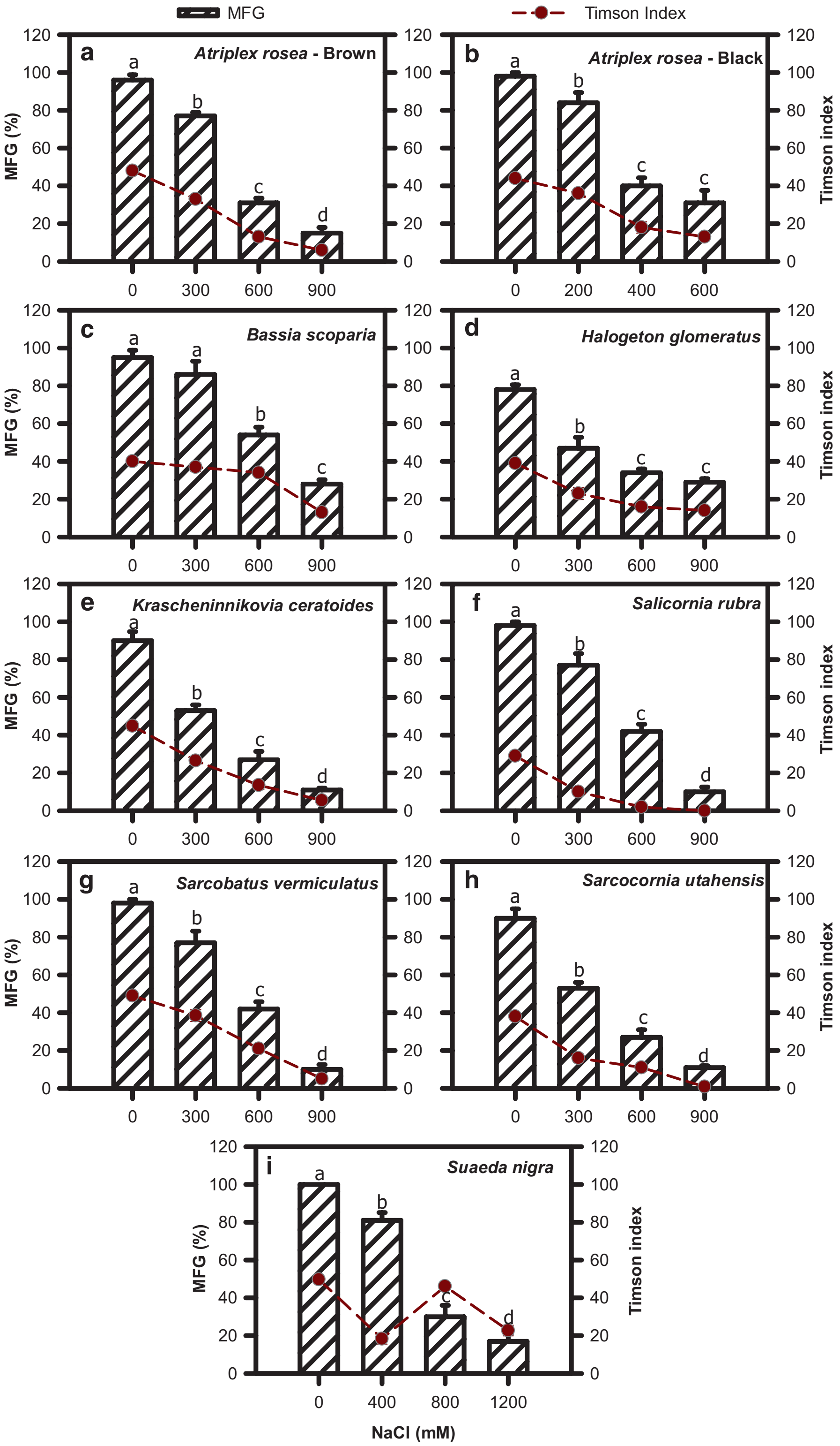

Fig. 6.1 Effect of salinity on mean final (MFG) and rate of seed germination (Timson's index) of Great Basin halophytes. Data is given as mean ± standard error. Bars with different alphabets are significantly different from each other (Bonferroni test, $P < 0.05$)

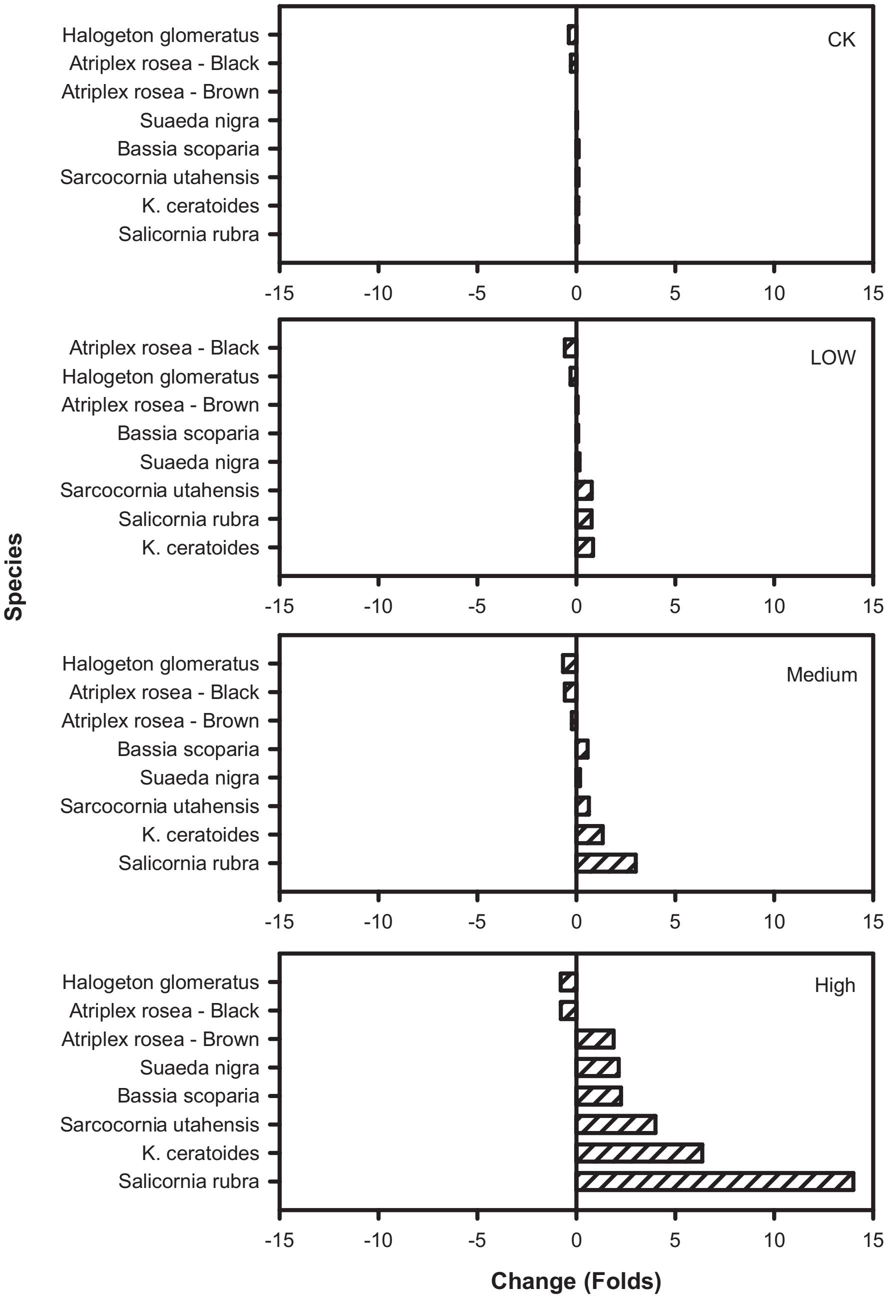

Fig. 6.2 Effects of Ethephon on seed germination Great Basin halophytes in present of different NaCl treatments (mentioned in Table 6.2). Values are change (in folds) in seed germination with and without Ethephon

et al. 2007) and *Sarcocornia* spp (Redondo et al. 2004). This reduction in seed germination could be a result of decreasing osmotic potential of the solution caused by salinity that impedes adequate seed hydration essential for radicle protrusion (Ramoliya and Pandey 2002; Hameed et al. 2014). Furthermore, a substantial inhibition of seed germination was observed, when seeds of all test species were exposed to hyper-salinity (>600 mM NaCl). Such high germination inhibi-

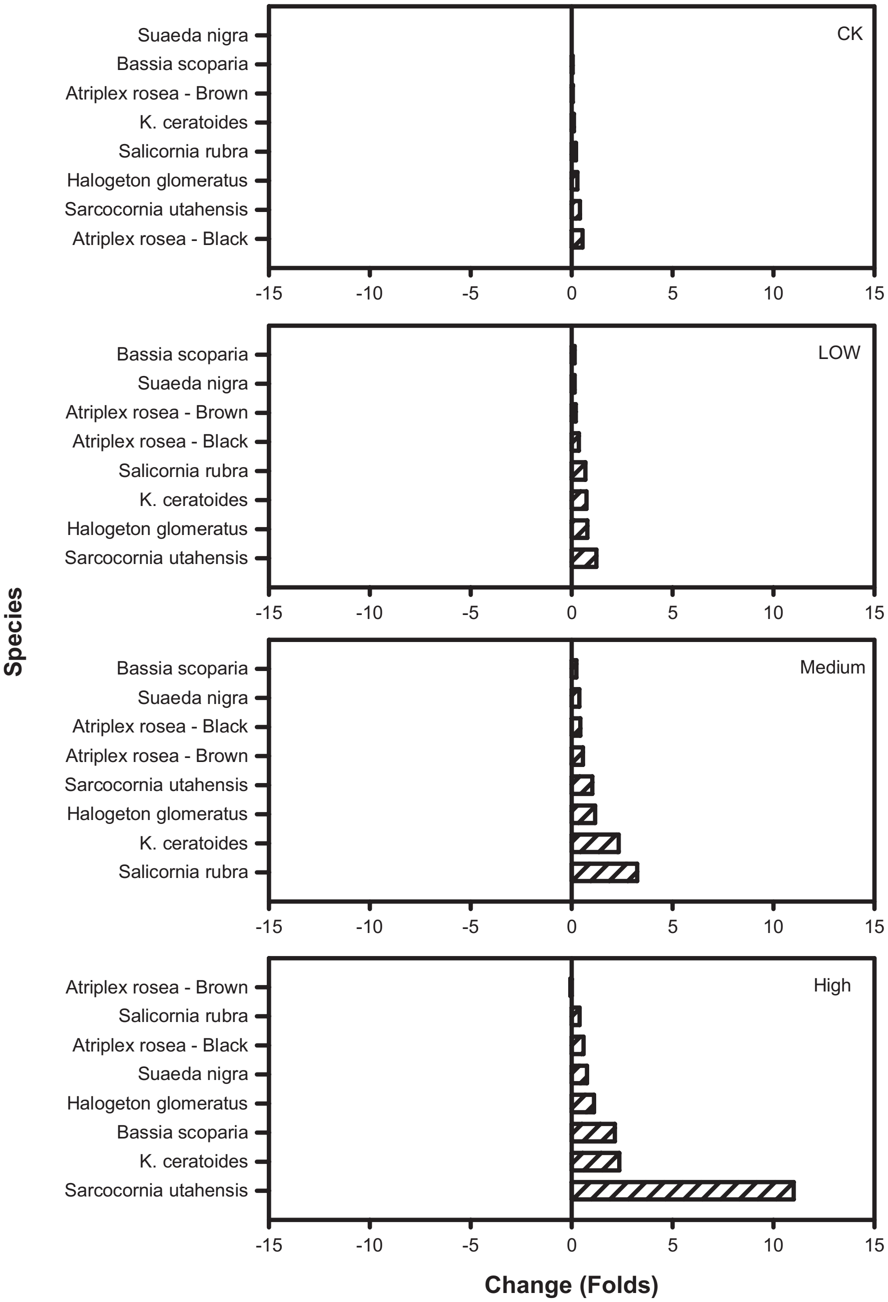

Fig. 6.3 Effects of Fusicoccin on seed germination Great Basin halophytes in present of different NaCl treatments (mentioned in Table 6.2). Values are change (in folds) in seed germination with and without Fusicoccin

tion under hyper-salinity could be a general strategy of Great Basin halophytes to circumvent summer drought accompanying high soil salinity, which is not conducive for seedling survival. While, high seed germination of Great Basin halophytes in distilled water and low (300 mM NaCl) salinity indicates that they would germinate only after winter rains, which create “window of germination” (Noe and Zedler 2001) or “window of opportunity” (Eriksson and Fröborg

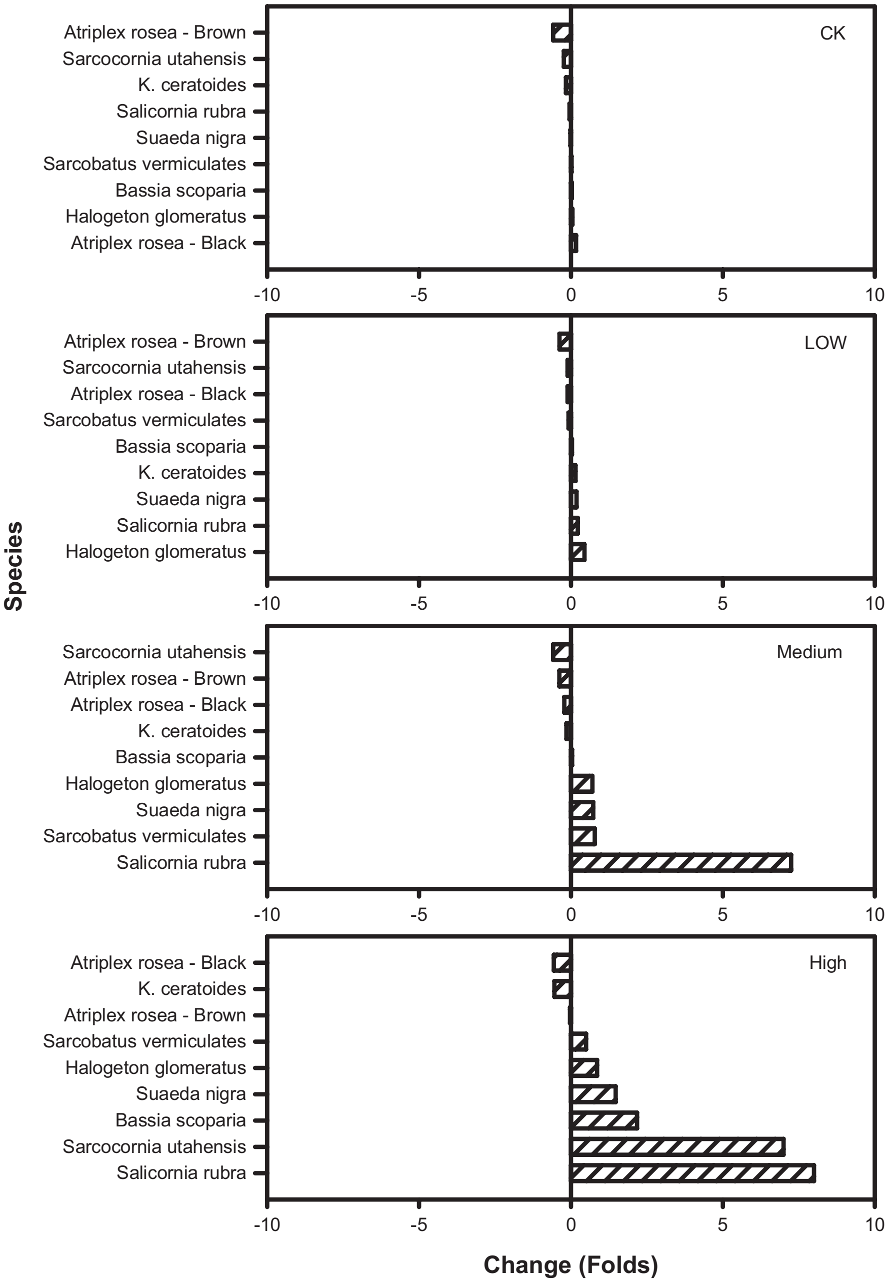

Fig. 6.4 Effects of GA_3 on seed germination Great Basin halophytes in present of different NaCl treatments (mentioned in Table 6.2). Values are change (in folds) in seed germination with and without GA_3

1996) by diluting soil salinity and providing moisture.

Salt tolerance of Great Basin halophytes during their seed germination varied considerably among species. Seeds of *Suaeda nigra* could germinate in up to 1200 mM NaCl solution, those of *Atriplex rosea* (brown seeds), *Bassia scoparia, Halogeton glomeratus, Krascheninnikovia ceratoides, Salicornia rubra, Sarcobatus vermiculatus* and *Sarcocornia utahensis* in up to 600 mM NaCl, while black seeds of *Atriplex rosea* germinated in up to 400 mM NaCl treatment. Gul

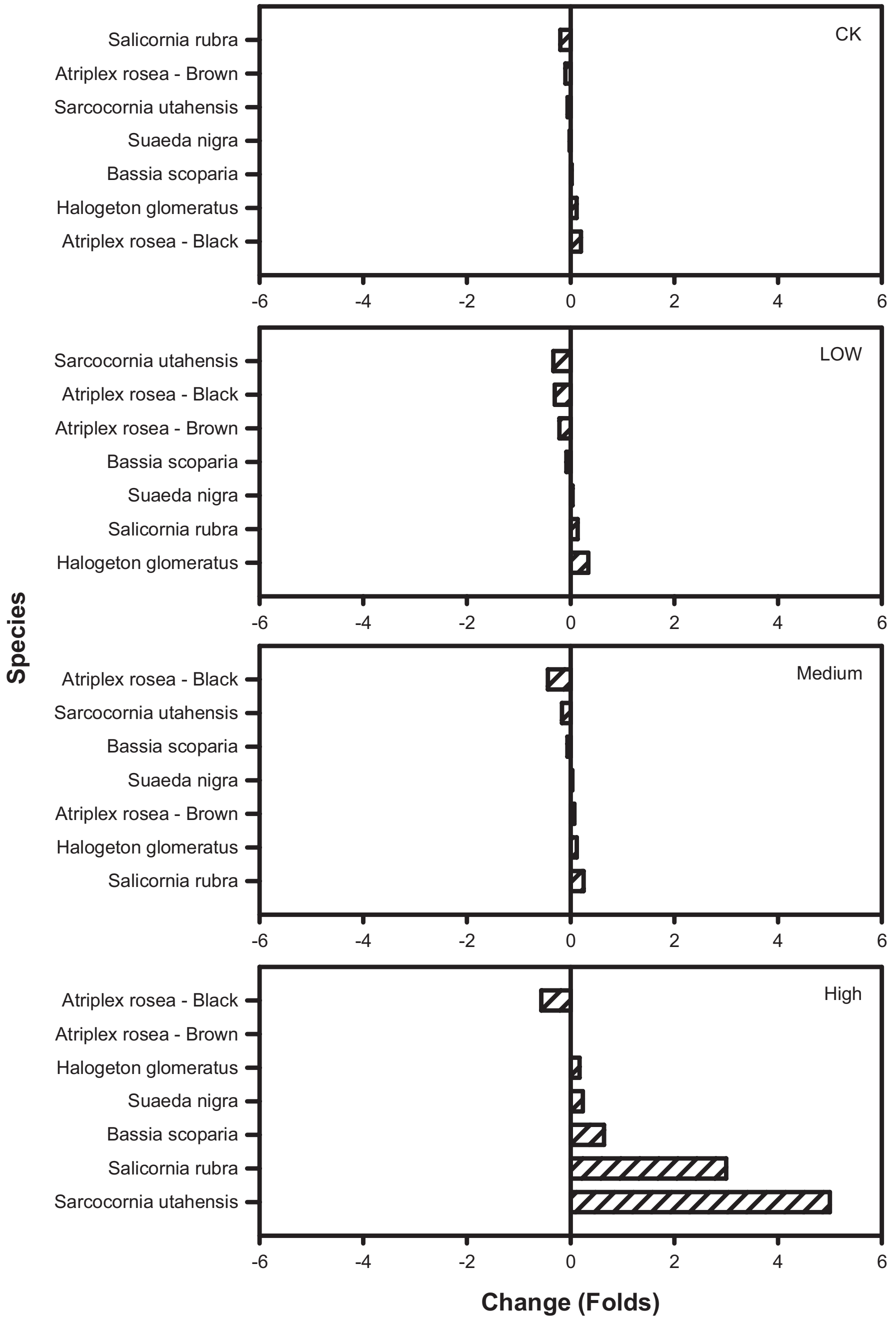

Fig. 6.5 Effects of GB on seed germination Great Basin halophytes in present of different NaCl treatments (mentioned in Table 6.2). Values are change (in folds) in seed germination with and without GB

et al. (2013) recently reviewed that the salt tolerance of halophyte seeds ranges from 1700 mM NaCl (*Salicornia herbacea*, Chapman 1960) to ≤ 300 mM NaCl (*Chenopodium album*, Yao et al. 2010; *Tanacetum cinerariifolium*, Li et al. 2011). This variability in salt tolerance is often related to the habitat conditions of the species (Khan and Gul 2006; Easton and Kleindorfer

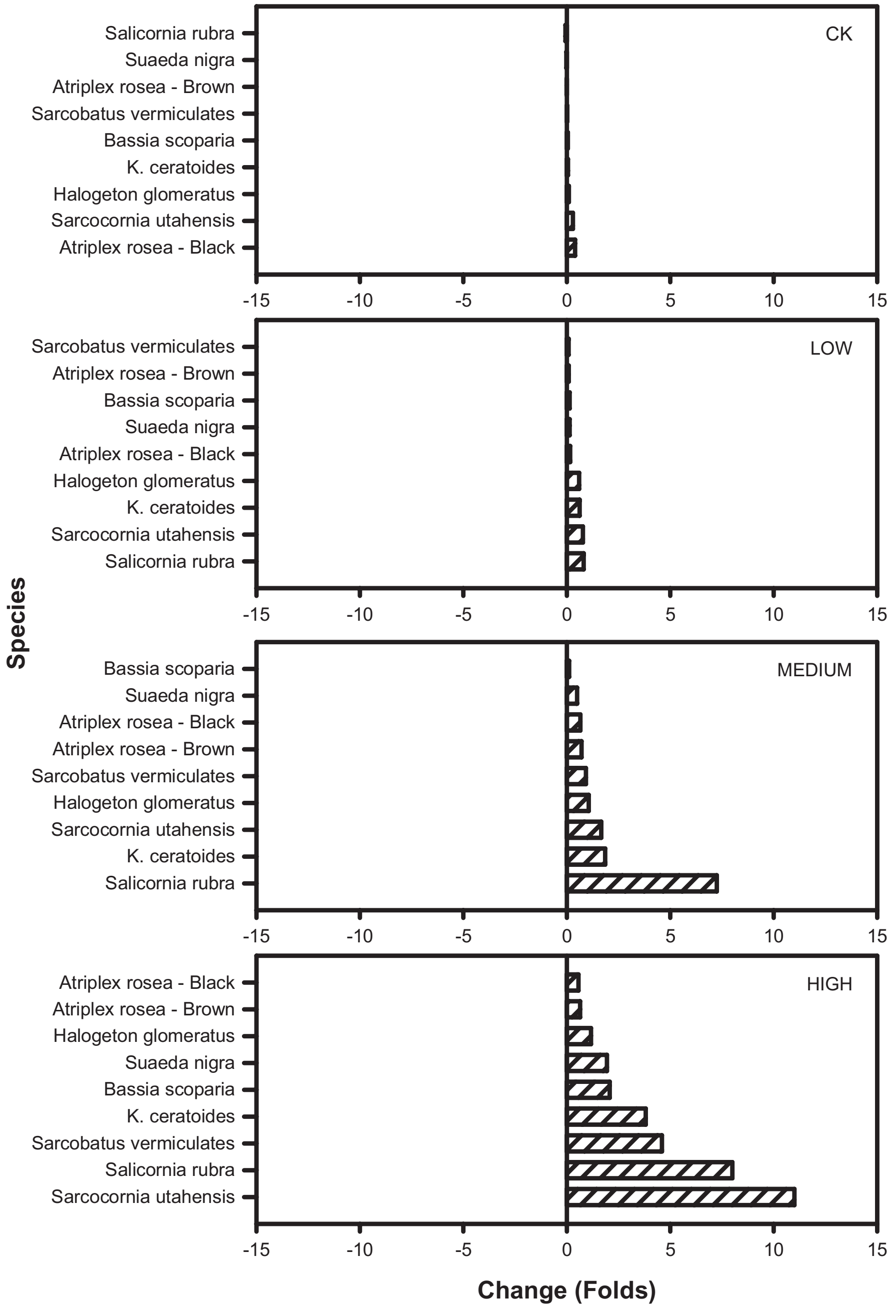

Fig. 6.6 Effects of Kinetin on seed germination Great Basin halophytes in present of different NaCl treatments (mentioned in Table 6.2). Values are change (in folds) in seed germination with and without Kinetin

2008). Populations found in habitats with high soil salinity generally have higher salt tolerance than those found in less saline habitats (Debez et al. 2001; Ghars et al. 2009; Gul et al. 2013). However, salt tolerance of plants during their seed germination is generally 10–100 times lesser than during mature vegetative phase (Mayer and Poljakoff-Mayber 1975; Hameed and Khan 2011).

Salinity exposure disturbs the endogenous levels of various dormancy regulating chemicals

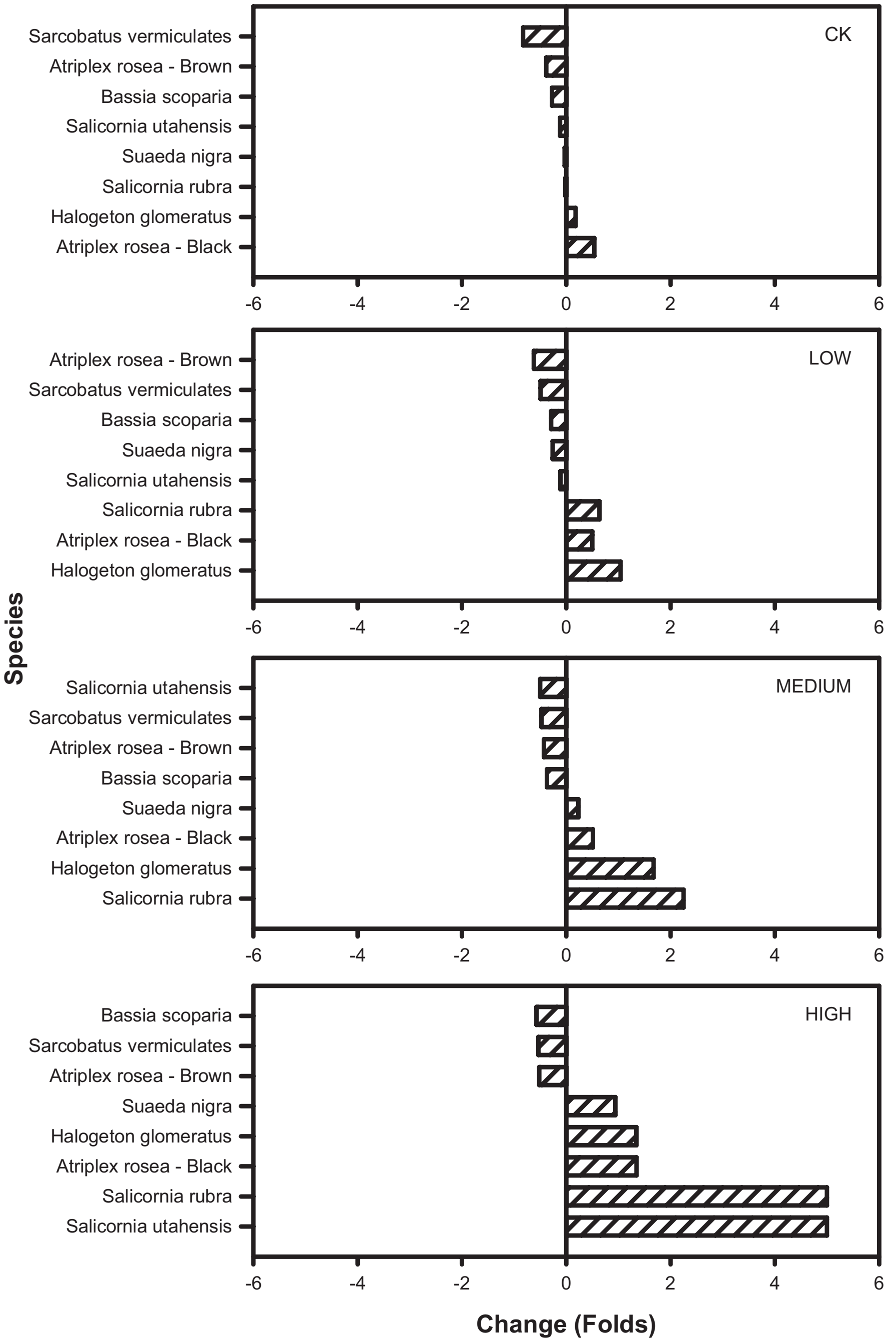

Fig. 6.7 Effects of KNO_3 on seed germination Great Basin halophytes in present of different NaCl treatments (mentioned in Table 6.2). Values are change (in folds) in seed germination with and without KNO_3

(DRCs) in seeds, which leads to germination inhibition or even loss of seed viability (Atia et al. 2009; Gul et al. 2013; Ahmed et al. 2014; Li et al. 2015). Therefore, exogenous application of different DRCs such as phyto-hormones and protective compounds is often reported to enhance seed germination under salinity stress (Khan and Gul 2006; El-Keblawy 2013; Li et al. 2005; Khan

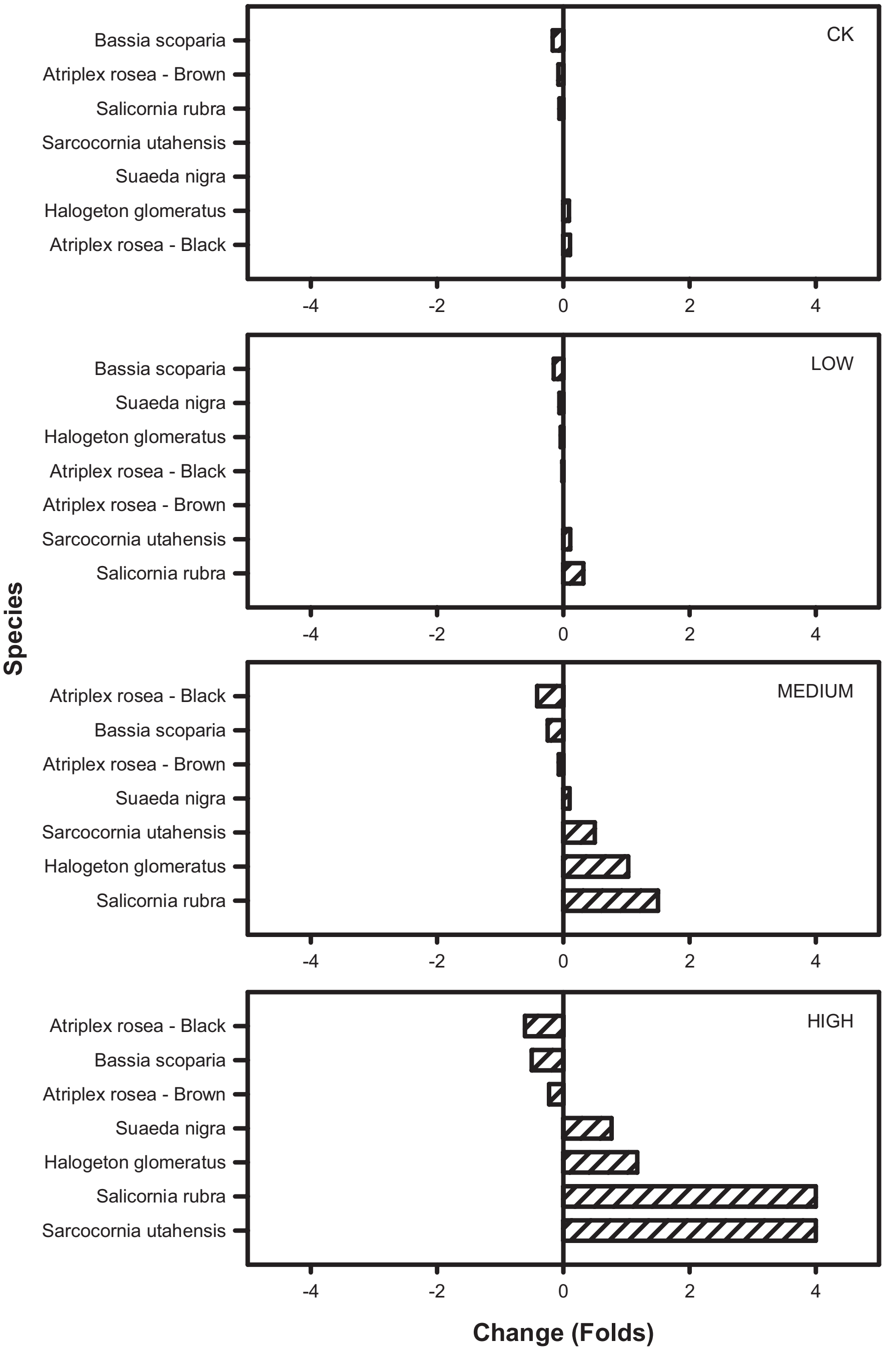

Fig. 6.8 Effects of Proline on seed germination Great Basin halophytes in present of different NaCl treatments (mentioned in Table 6.2). Values are change (in folds) in seed germination with and without Proline

and Ungar 2001a, b). However, success of chemical treatments applied to seeds depends on multiple factors (Khan and Gul 2006; Cohn 2002). In this study, we observed improvement in seed germination of Great Basin halophytes by different DRCs, but ameliorative effects were chemical, salinity and species specific. Ahmed et al. (2014) also reported that the ameliorative

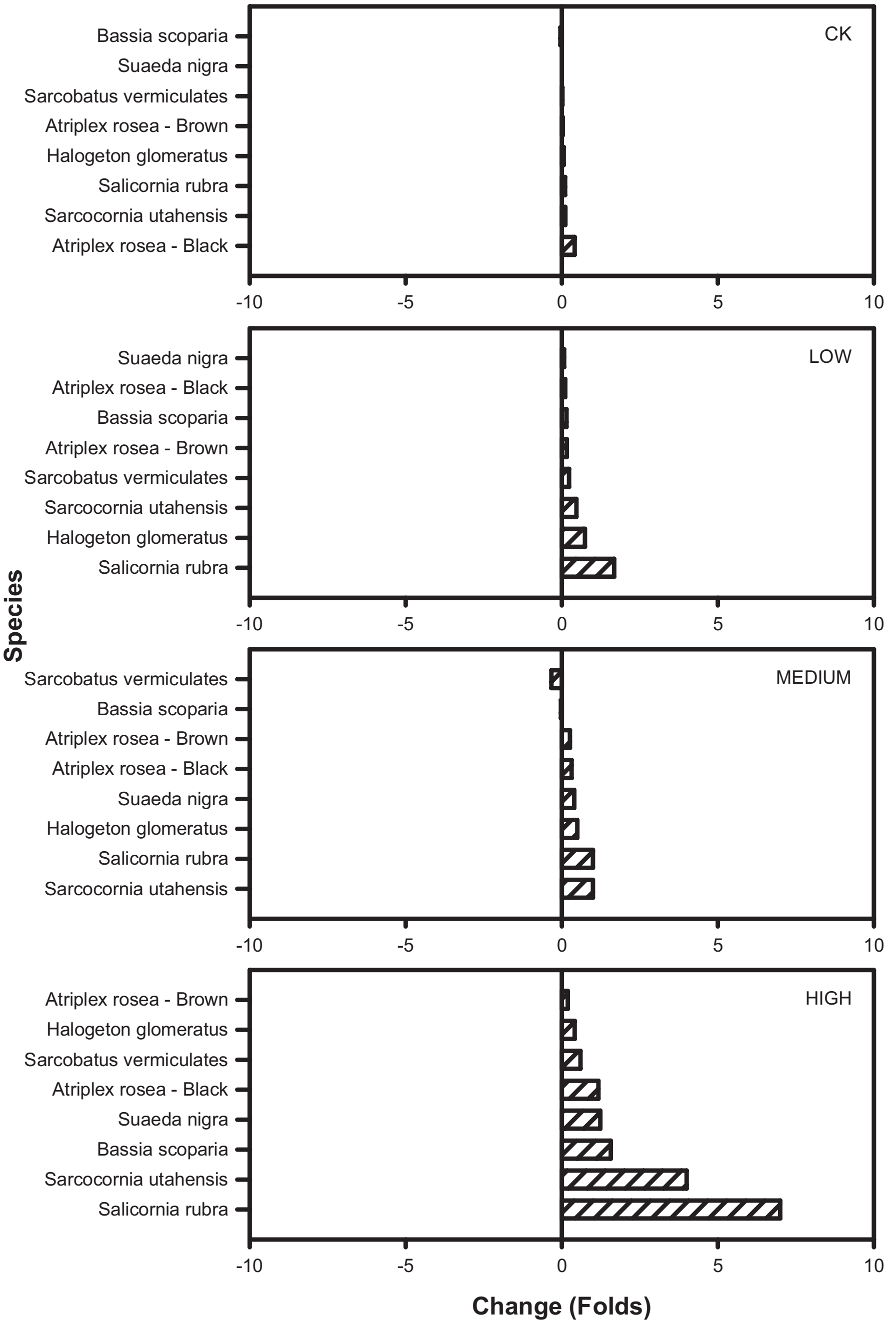

Fig. 6.9 Effects of Thiourea on seed germination Great Basin halophytes in present of different NaCl treatments (mentioned in Table 6.2). Values are change (in folds) in seed germination with and without Thiourea

effects of DRC treatments for the seeds of salt-playa halophytes of Pakistan *Halogeton glomeratus, Lepidium latifolium* and *Peganum harmala* were both species and environment-dependant.

Plant hormone gibberellic acid (GA_3) is a key positive regulator of seed germination owing to its signaling in endosperm cap weakening, expansion of embryo cells, expression of α-amylase genes, antagonizing effects of ABA and opposing the activities of DELLA proteins (Peng and Harberd 2002; Miransari and Smith 2014). A decline in endogenous GA_3 levels is often reportedly linked to the seed germination inhibition under saline conditions (Kabar and Baltepe 1989; Bewley and Black 1994; Khan and Gul 2006). Exogenous application of GA_3 is thus often used to enhance seed germination of plants under saline conditions (Khan and Gul 2006). In this study, exogenous application of GA_3 could alleviate inhibitory effects of high salinity in nearly all species, but its ameliorative effects were more pronounced in *Salicornia rubra, Sarcocornia utahensis* and *Bassia scoparia* as compared to other species. GA_3 application could also mitigate salinity effects on seed germination of *Allenrolfea occidentalis* (Gul and Khan 2008), *Crithmum maritimum* (Atia et al. 2009), *Lepidium latifolium* (Ahmed et al. 2014), *Phragmites karka* (Zehra et al. 2013), *Zygophyllum simplex* (Syn. *Tetraena simplex*) (Khan and Gul 2006) and *Halopyrum mucorantum* (Khan and Ungar 2001a, b) and *Panicum turgidum* (El-Keblawy et al. 2011).

Cytokinins are also plant hormones, which are implicated in a number of plant activities including seed germination (Chiwocha et al. 2005; Riefler et al. 2006; Nikolić et al. 2007). They are also involved in mitigating stresses such as salinity and drought (Khan and Ungar 1997; Atici et al. 2005; Khan and Gul 2006). Kinetin mitigated salinity effects on seed germination of *Sarcocornia utahensis, Salicornia rubra* and *Sarcobatus vermiculatus* to higher extent than other test species in this study. A similar effect of kinetin was reported for *Allenrolfea occidentalis* (Gul and Khan 2008), *Atriplex halimus* (Debez et al. 2001) and *Zygophyllum simplex* (Khan and Ungar 1997), but not in *Zygophyllum qatarense* (Ismail 1990), *Sporobolus arabicus* (Khan and Ungar 2001b). These findings thus indicate that responses to kinetin are highly variable. However, Debez et al. (2001) indicated that salinity decreased levels of many endogenous chemical regulators in *Atriplex halimus* during seed germination and exogenous kinetin could improve seed germination probably by overcoming its dwindling endogenous contents.

Ethylene, which is a gaseous plant hormone, is also involved in promoting seed germination particularly under stress conditions (Khan and Gul 2006; Khan et al. 2009). For instance, it alleviated salinity effects on seed germination of many halophytes such as *Triglochin maritima* (Khan et al. 2009) and *Zygophyllum simplex* (Khan et al. 2009). Similarly, in this study, ethephon (a common source of ethylene) treatment also improved germination of salinity-stressed seeds of many halophytes particularly of *Salicornia rubra, Krascheninnikovia ceratoides* and *Sarcocornia utahensis*. Ethylene production in salinity-stressed seeds of *Cucumis sativus* decreased with concomitant reduction in their germination (Chang et al. 2010). Similarly, seed germination inhibition in *Stylosanthes* spp. under saline condition was linked to salinity-induced reduction in ethylene production (Silva et al. 2014). However, mechanisms underlying ethylene action in improving seed germination and salt tolerance are yet inconclusive (Khan et al. 2009; Petruzzelli et al. 2000; Rinaldi 2000). A literature search indicates that ethylene might control germination of salt-stressed seeds by interacting with other hormones such as abscisic acid (Linkies et al. 2009; Linkies and Leubner-Metzger 2012), brassinosteroids (Wang et al. 2011) and polyamines (Zapata et al. 2004). While, ethylene alleviated salinity effects on seed germination of model plant *Arabidopsis thaliana* by decreasing reactive oxygen species (Lin et al. 2013).

Fusicoccin, which is a diterpene glycoside initially isolated as a toxin from fungus *Fusicoccum amygdali* (Ballio et al. 1976), is also widely reported to promote seed germination of halophytes (Gul and Weber 1998; Gul et al. 2000; Khan and Gul 2006; El-Keblawy and Al-Shamsi 2008). For example, fusicoccin mitigated salinity effects on seed germination of *Zygophyllum simplex* (Khan and Ungar 2002), *Salsola drummondii* (Rasheed et al. 2015), *Panicum turgidum* and *Lasiurus scindicus* (El-Keblawy et al. 2011). It also improved seed germination of Great Basin halophytes particularly of *Sarcocornia utahensis, Krascheninnikovia ceratoides* and *Bassia scoparia* under salinity. It may promote seed germination probably by enhancing cell elongation growth through ATPase mediated proton extrusion (Galli et al. 1979; Marre 1979). According to Cocucci et al. (1990) fusicoccin reversed the inhibitory effects of salinity in *Raphanus sativus* seeds by enhancing H^+ extrusion and malic acid synthesis. While, Lutsenko et al. (2005) suggested that fusicoccin affects the ionic balance particularly the K^+/Na^+ ratio.

Seeds use nitrate (NO_3^-) as "spatial signal" for the dormancy loss and germination promotion (Alboresi et al. 2005; Huang et al. 2015). Nitrate levels could be a good indicator for seeds to detect gaps, as competing plants deplete soil nitrates (Pons 1989). It can also mitigate effects of various stresses such as of salinity on seed germination of plants. For instance, exogenous NO_3^- could mitigate salinity-induced germination inhibition in *Crithmum maritimum* (Atia et al. 2009) and *Sporobolus arabicus* (Khan and Ungar 2001b). Similarly, seed germination of our test species especially of *Sarcocornia utahensis* and *Salicornia rubra* was also improved under saline conditions. Action of NO_3^- in modulating seed germination and dormancy could be ascribed to its role in decreasing seeds' ABA level probably by inducing expression of *CYP707A2* gene (Ali-Rachedi et al. 2004; Matakiadis et al. 2009).

Thiourea is another nitrogenous compounds that also contains a redox active thiol (–SH) group and is known to improve germination and salinity tolerance of halophytes seeds (Khan and Gul 2006; El-Keblawy 2013). For example, it could alleviate salinity induced germination inhibition in *Triglochin maritima* (Khan and Ungar 2001a) and *Distichlis spicata var. stricta* (Shahba et al. 2008). In this study, thiourea application alleviated salinity-induced germination inhibition of *Salicornia rubra* and *Sarcocornia utahensis* seeds to greater extent than in other species. Action of thiourea in mitigating salinity effects on seed germination could be ascribed to its roles in enhancing the antioxidant defense system (Srivastava et al. 2010), altering the cell's redox status (Srivastava et al. 2010), controlling membrane kinetics for ion uptake (Aldasoro et al. 1981) and/or regulating activity and turnover of many enzymes (Srivastava et al. 2010).

Exogenous application of glycine betaine (GB) and proline is often reported to enhance salt tolerance of halophyte seeds. For example, exogenously applied GB and proline improved seed germination of a Great Basin halophyte *Allenrolfea occidentalis* (Gul and Khan 2008) and two subtropical halophytes *Zygophyllum simplex* and in *Arthrocnemum macrostachyum* (Khan and Gul 2006). Similarly, these chemicals could also improve germination of salt-stressed seeds of Great Basin halophytes especially of *Sarcocornia utahensis* and *Salicornia rubra*. Ameliorative effects of these chemical could be linked to their multiple roles in plant stress tolerance. For example, GB and proline are two important osmoprotectants/compatible solutes, which are involved in osmotic adjustment in halophytes in response to salinity (Flowers and Colmer 2008; Hameed and Khan 2011). They might also act as antioxidants to eliminate toxic reactive oxygen species, which are known to accumulate under stress conditions (Chen and Murata 2008, 2011; Szabados and Savouré 2010). Poljakoff-Mayber et al. (1994) reported that *Kosteletzkya virginica* seeds contain significant amounts of GB and proline. GB contents increased during seed germination of *Suaeda japonica* under saline conditions (Yokoishi and Tanimoto 1994).

Efficacy of DRC treatments in this study was generally dependent on magnitude of salinity imposed. Under non-saline conditions nearly all DRCs were ineffective in improve seed germination of halophytes, however their ameliorative effects increased with increases in salinity. Likewise, most DRC treatments were ineffective in enhancing seed germination of *Panicum turgidum, Lasiurus scindicus* (El-Keblawy et al. 2011), *Coelachyrum brevifolium, Pennisetum divisum* (El-Keblawy 2013) and *Limonium stocksii* (Khan and Gul 2006) under non-saline conditions. Furthermore, in some species such as in *Salsola imbricata* (Mehrun-Nisa and Weber 2007) DRC treatments inhibited the seed germination under non-saline condition. These findings could be explained by the fact that the unstressed seeds contain adequate levels of various DRCs (Miransari and Smith 2014; Khan and Gul 2006; Li et al. 2015), thereby exogenous supply is ineffective or may cause feedback inhibition (Khan and Gul 2006). Extent of amelioration in seed germination under saline conditions was also dependent on nature of chemicals used. Ethephon, fusicoccin and kinetin were generally more effective than other DRCs used. Aforementioned DRCs were also most effective in alleviating salinity effects on seed germination of most sub-tropical halophytes (Khan and Gul 2006). Likewise, DRC treatments had varying effects on the seed germination of *Crithmum maritimum* (Meot-Duros and Magné 2008), and three salt playa halophytes (Ahmed et al. 2014).

5 Conclusions

Great Basin halophytes used in this study lacked innate dormancy and germinated maximally in distilled water. Increases in salinity generally decreased their seed germination; however some (≥20 %) seeds of nearly all species could germinate in/above 600 mM NaCl (equivalent to seawater salinity). Exogenous application of all DRCs improved seed germination of test species, especially under high salinity. Ethephon, fusicoccin and kinetin treatments were generally most effective. While, *Salicornia rubra* and *Sarcocornia utahensis* responded to nearly all DRCs than other species (Table 6.3). These findings indicate that the efficacy of DRC treatments could be salinity, species and chemical specific. However, detailed biochemical and/or molecular studies are recommended to understand the basis of variability in ameliorative effects of various DRC treatments on seed germination.

Table 6.3 Top species, in order of magnitude, showing positive effects of DRCs on seed germination

DRC	Species
Ethephon	*Salicornia rubra, Krascheninnikovia ceratoides, Sarcocornia utahensis*
Fusicoccin	*Sarcocornia utahensis, Krascheninnikovia ceratoides, Bassia scoparia*
Gibberellic acid	*Salicornia rubra, Sarcocornia utahensis, Bassia scoparia*
Glycine betaine	*Sarcocornia utahensis, Salicornia rubra, Bassia scoparia*
Kinetin	*Sarcocornia utahensis, Salicornia rubra, Sarcobatus vermiculatus*
Nitrate	*Sarcocornia utahensis, Salicornia rubra*
Proline	*Sarcocornia utahensis, Salicornia rubra, Halogeton glomeratus*
Thiourea	*Salicornia rubra, Sarcocornia utahensis*

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Genetic Variability of Three Annual Halophyte Species in an Inland Salt Marsh Through Time

7

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Abstract

Soil seed banks have been proposed to be a repository of genetic information and reported to be more genetically diverse than a single population at any given point in time. Genetic diversity of three annual autogamous halophytic species (*Atriplex prostrata*, *Salicornia depressa*, and *Spergularia salina*) from an inland salt marsh community was compared within and among three cohorts representing populations from 1981, 1998, and the persistent seed bank of 2000 using Inter-Simple Sequence Repeat (ISSR) analysis. Genetic variation was assayed using three primers on 30 samples (individuals) for each cohort of each species. Analysis of Molecular Variance (AMOVA) showed that cohorts were significantly different for each species. Principal Coordinates Analysis (PCoA) indicated a high degree of separation for the three cohorts of each species, indicating a turnover in genetic composition over the 17-year period and between above- and belowground cohorts. Percent polymorphic loci indicated the 2000 seed bank of *S. salina* and *S. depressa* were less diverse than either cohort representing 1981 or 1998 (the seed bank of *S. salina* was monomorphic), but the persistent seed bank from 2000 of *A. prostrata* was more diverse than either the 1981 or 1998 aboveground cohorts. Overall diversity increased from 1981 to 1998 for *S. salina* and *A. prostrata*, but decreased for *S. depressa*. Our findings show that seed banks are not always a long-term repository of genetic information and can be less genetically diverse than any one population. Genetic diversity may increase or decrease for a given population over time. More multi-year or cross-decade investigations on seed banks and aboveground vegetation in wetland species, especially those found in extreme habitats such as inland salt marshes, are needed.

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M.A. Khan et al. (eds.), *Sabkha Ecosystems Volume V: The Americas*,
Tasks for Vegetation Science 48, DOI 10.1007/978-3-319-27093-7_7

1 Introduction

Seed banks are a collection of seeds representing the production of offspring from many years past (Templeton and Levin 1979; Baker 1989). Over time, the number of overlapping generations increases, providing a pool that can give rise to future populations. This pool, therefore, has the capacity to function as a repository of genetic diversity and should be more genetically diverse than the aboveground vegetation during any one year (Templeton and Levin 1979).

Previous investigations elucidating genetic diversity of populations and their respective seed banks have focused overwhelmingly on species within terrestrial habitats. These studies compared genetic diversity of seed banks to aboveground vegetation of a single population at a single point in time or have assessed diversity among populations of the same species across a geographic region (Cabin 1996; Cabin et al. 1998; McCue and Holtsford 1998). Some have focused on the seed banks of common outcrossing species, such as *Plantago lanceolata* and *Cardamine amara* (Tonsor et al. 1993; Koch et al. 2003). Additionally, many investigations have focused primarily on the diversity within and/or among populations of endangered or rare species at a given point in time (Allphin et al. 1998; Gemmill et al. 1998; Martinez-Palacios et al. 1999). For those studies comparing the seed bank to aboveground vegetation, the genetic diversity of the persistent seed bank was found to be greater than the aboveground vegetation (Cabin et al. 1998; McCue and Holtsford 1998). One investigation in a wetland habitat also found the genetic diversity of the seed bank of a wetland perennial to be highly genetically diverse when compared to the aboveground vegetation (Liu et al. 2014). Previous investigations have not assessed genetic diversity of salt marsh annuals and their seed banks from multiple specieswithin a palustrine community over time.

It is widely known that the genetic variability of populations and seed banks is affected by type of reproduction for a given species, variations in population size, longevity of seeds in the seed bank, and dispersal distance from the parent plant. We hypothesize that genetic variability will be low for all three species in this investigation for both the aboveground populations and the seed bank. This can be attributed to several factors inherent to these three species. The first is that all three species reproduce autogamously. It is generally accepted that self-fertilizing species are primarily homozygous with regards to their genetic composition. Autogamy minimizes genetic variability in a population, both in the aboveground vegetation and the soil seed bank, thereby preserving genetic constancy from one generation to the next. Additionally, population sizes for these three species at this site are also small and their fruits and/or seeds fall by gravity near the parent plant. Even though some fruits and seeds may float at the surface of the water when the marsh floods during the winter and the spring, this marsh system is closed and seeds would remain within the same population. Because of these conditions, we also assert that little or no changes in overall diversity will have occurred over a 17-year period for these species' populations.

In order to address Templeton and Levin's (1979) hypothesis, individuals representing three annual halophytic species that reproduce autogamously were used for this investigation and were collected from an abandoned salt mine well field on the property of the Morton Salt Company in Rittman, Ohio, USA (40° 57′ 30″ N; 81° 47′ 30″ W). Aboveground genetic diversity from 1998 was compared with a cohort from 1981 derived from seeds collected from plants for three mainly autogamously reproducing salt marsh species. Diversity of these populations was then compared with the diversity of the persistent seed bank from 2000. We chose to present findings from three dominant annual species in this inland zonal salt marsh community in order to compare whether they would demonstrate similar responses with respect to seed bank diversity and to changes in diversity over time. Even though the entire inland salt marsh approximates two hectares, the annuals were established over an area approximating 30 m × 100 m in this site from 1998 to 2000. In this zonal community, the unvegetated salt pan maintains the highest salinity levels and is flanked by *Salicornia depressa*, *Spergularia salina* and *Atriplex prostrata*, ranging from highest to lowest salinity, respectively. At the time of sampling, a significant portion of the inland marsh was occupied by *Phragmites australis* (Cav.) Trin. Ex Steud, a perennial grass, that had established on the site in a lower-salinity area near the rear of the marsh some 15 years prior. *P. australis* forms dense stands and a thick litter layer, but it had also begun to encroach into the more saline sections of the marsh and replace the three dominant halophytic annuals in the aboveground vegetation. It is reasonable to anticipate that the shorter annual halophytes could be completely replaced in the aboveground vegetation by *P. australis* given the aggressive nature of this species. Understanding the genetic diversity present within the seed bank may also assist with future restoration efforts on this site if these species are completely displaced.

The following questions were asked in this investigation: (1) Is the seed bank more genetically diverse than either of the aboveground population cohorts from 1981 or 1998 for each of the three species?; (2) Are the cohorts of each species genetically similar or do they differ?; and (3) Has genetic diversity for each of these species increased or decreased over time?

2 Materials and Methods

2.1 Description of the Species

Atriplex prostrata Bouchér ex DC. (Chenopodiaceae) is a halophytic annual with a cosmopolitan distribution. It is found in beaches and coastal and inland salt marshes with soil salinities ranging from 0.003 to 3.62 % (Ungar 1965, 1973; Osmond et al. 1980; Gleason and Cronquist 1991). A diploid population is found at the Rittman study site (Katembe et al. 1998). Plants grow to 1.0 m tall, flower in the summer, and produce dimorphic seeds in the autumn (Gleason and Cronquist 1991); seed rain on this site typically occurs in late October and early November. Autogamy seems to be the prevailing method of reproduction (Van-der Meijden 1970). Large brown seeds are 1.5–3.0 mm in diameter while small black seeds have harder seed coats and are 1.0–2.0 mm in diameter (Gleason and Cronquist 1991).

Salicornia depressa Standley (Chenopodiaceae) is a succulent halophytic annual that has widespread, primarily-coastal distribution in North America but has been reported at a few inland marshes as an apparent introduction. The species noted above was formerly included in a broader circumscription of *S. depressa* L. (Gleason and Cronquist 1991), but recent studies have demonstrated that European populations of the latter are strictly diploid. The current taxonomy tentatively recognizes two diploid and two tetraploid species in North America, with *S. depressa* occasionally found in the interior (Welsh et al. 2003). The tetraploid status and morphological features of the population at the Rittman study site match those of *S. depressa* (Wolff and Jefferies 1987). Plants reach heights between 0.1 and 0.5 m, flower in the summer, and produce dimorphic seeds in the autumn (Gleason and Cronquist 1991); seed rain for this species also occurs in late October and early November. Reproduction is primarily cleistogamous in nature (Jensen and Jefferies 1984). Large seeds, produced in central flowers at each node, are greater than 1.5 mm in length while small seeds, produced in smaller lateral flowers at each node, are less than 1.4 mm in length (Dalby 1962; Ungar 1979).

Spergularia salina J. Presl & C. Presl (Caryophyllaceae) is a halophytic annual found in coastal brackish and saline habitats of North America and inland along salted highways, salt marshes, and alkaline areas (Gleason and Cronquist 1991; Ungar 1991). It has often passed under the name of *S. marina* (L.) Griseb (Gleason and Cronquist 1991) but recent taxonomic studies have resurrected *S. salina* as the correct name (Hartman and Rabeler 2005). It grows to 35 cm tall and flowers from June to September, producing capsules each containing approximately 55 seeds (Gleason and Cronquist 1991). Like *A. prostrata* and *S. depressa*, reproduction occurs mainly through autogamy (Mazer et al. 1999).

2.2 Determination of Sample Size

Preliminary analyses were performed to determine sample size for each species based initially on 30 individuals from a single cohort. For each species, the most genetically variable cohort was used so that minimum sample sizes would be based on the greatest amount of genetic variation possible. Percent of polymorphic loci (means ± SD) was determined for each sample size up to 30 individuals based on 500 permutations without replacement. Minimum sample size was determined as the point at which percent polymorphic loci became repetitive and the standard deviation was zero. Sample size calculations were performed in SAS v. 8.2 (SAS Institute 2001).

2.3 Plant Tissue Collection

Plant samples were obtained for three separate cohorts of *Spergularia salina*, *Atriplex prostrata*, and *Salicornia depressa*. Cohorts included plant samples representing populations in 1981, 1998, and the persistent seed bank of 2000 for the three species.

For the 1998 cohort, 30 leaf samples were collected from plants that were derived from seed produced in October, 1998, for *S. salina*, *A. prostrata*, and *S. depressa*. Seeds were collected from multiple plants spread across the site and widely separated to obtain high genetic diversity among individuals. Seeds from individual plants were exposed to an alternating 5/25 °C temperature regime and a 12 h night/12 h day photoperiod (20 µmol m^{-2} s^{-1}) in a Percival incubator to promote seed germination (Ungar 1978). Even though a high proportion of seeds germinated for all species and individuals, only 30 samples were collected for analysis from the many individuals for each of the three species.

Samples from the persistent soil seed bank were derived from 100 soil cores randomly collected with a bulb planter across the salt marsh in September, 2000, because seed rain for *Atriplex prostrata* and *Salicornia depressa* does not occur until late October at this site. Care was taken to collect soils widely separated to obtain high genetic diversity among seeds. Soil cores were stored individually in polyethylene containers and returned to the lab where they were exposed to an alternating 5/25 °C temperature regime and a 12 h night/12 h day photoperiod (20 µmol m^{-2} s^{-1}) in a Percival incubator to promote seed germination (Ungar 1978).

With respect to seed set for *Spergularia salina*, it was assumed that seeds produced by *S. salina* during this growing season would not germinate or would represent an insignificant portion of the samples from the soil cores subjected to this germination treatment because *S. salina* has a physiological dormancy and requires cold stratification in order to germinate. Because we collected soil cores at the end of the summer, the seeds of *S. salina* that would have matured and fallen to the soil would not yet have been exposed to wet and cold conditions. According to Ungar (1988b), unstratified seeds collected in the field in 1981 and then exposed to a 5/15 °C temperature regime with a 12 h night/12 h day photoperiod, conditions optimal for *S. salina* seed germination, showed less than 6 % germination. At most, only one or two, if any, of the 30 total samples could have reasonably come from *S. salina* seed produced during the same growing season. Additionally, because soil seed banks tend to be patchy in their distribution, the number of individuals of a particular species present in each soil core ranged from zero to over 100. Only one representative from each species, however, was sampled from 30 randomly selected cores of the original 100 cores containing a particular species to avoid any potential sib relationship.

Finally, for samples of an older cohort, seeds of *S. salina*, *A. prostrata*, and *S. depressa*, randomly collected from plants in the Rittman salt marsh in 1981 and stored at 5 °C in the dark in polyethylene containers, were germinated using methods outlined in Ungar (1978). At this time, plant distributions for *A. prostrata* and *S. depressa* approximated 0.5 hectare–a larger area than what was found for these populations in 1998 (Ungar and Riehl 1980). Seeds collected for *S. salina* in 1981 were from a much smaller population that covered approximately 600 cm^2 with densities that ranged from 5 to 15 plants per 100 cm^2 plot. The restricted size of this population is attributed to the species first being introduced on this site in 1978 (Riehl and Ungar 1980). A large proportion of seeds germinated for *A. prostrata* (both large and small) and *S. salina* under laboratory conditions. Plant tissue from 30 randomly selected individuals was stored for both species, when necessary, in individually labeled 1.5 ml microcentrifuge tubes with silica gel at 5 °C until extractions were performed. Nine samples from the 1981 *S. depressa* cohort were used because only nine seeds germinated after multiple attempts were made to promote seed germination for this cohort. It is important to note that it is unknown as to exactly how seeds of the species representing the 1981 cohorts were collected. We assert that it is not necessary, however, that the aboveground cohorts from 1998 to 1981 be sampled in an identical manner because this is a "site level" investigation where the focus is on genetic turnover of this particular site through a period of time.

2.4 DNA Extraction and ISSR Amplification

Extraction of DNA was conducted on tissue samples using a Promega Wizard® Genomic DNA Purification Kit and a protocol designed for the isolation of genomic DNA from plant tissue (Promega 1998). Extracts of genomic DNA were stored in 1.5 ml microcentrifuge tubes at −20 °C until PCR amplification. Eleven ISSR primers based on sequences provided by Wolfe et al. (1998) and H. Ballard (unpubl.) and produced by Qiagen Operon (Valencia, California) were screened in preliminary analyses to determine which would result in the amplification of band fragments. Even though each primer produced band fragments, three were ultimately selected for each species based on the greatest variation, number of bands, and band sharpness produced (Table 7.1). The ISSR technique was selected given that it is easy to use, it is relatively inexpensive as compared to other molecular techniques, produces high levels of polymorphism, produces consistent results among samples, and is appropriately applied to population level questions (Wolfe and Liston 1998).

Table 7.1 ISSR primer sequences used for genetic variation analyses for *Spergularia salina*, *Atriplex prostrata*, and *Salicornia depressa*. The number of loci and range of fragments refers to the actual number of bands generated between 250 and 2000 bp, and the size of fragments found for each species in this study

Species	Primer sequence	Number of bands	Range of fragments (bp)
Spergularia salina	$(GA)_6CC$	12	300–1800
	$(CAC)_3GC$	13	600–1900
	$(GTG)_3GC$	16	300–1900
Atriplex prostrata	$(CAC)_3GC$	16	500–1800
	$(GTG)_3GC$	16	350–1850
	$(CA)_6GG$	19	400–1800
Salicornia depressa	$(CAC)_3GC$	18	550–1800
	$(GTG)_3GC$	17	400–1750
	$(CA)_6GG$	25	400–1700

ISSR amplifications were conducted in 25 μl sample reactions. A master mix was created with 16 μl autoclaved distilled water, 3 μl of 10× PCR buffer (Invitrogen), 5 μl of 50 mM $MgCl_2$ (Invitrogen), 4 μl of 10 mM dNTP mix (Promega), 2.5 μl of 4 mg/ml bovine serum albumin (BSA) (Fisher), 0.5 μl of, 20 mM primer, 0.25 μl of 5U/μl Taq (Invitrogen), and 1.5 μl DNA sample in a Stratagene Robocycler Gradient 96 v 4.2 thermocycler (La Jolla, California). The following thermocycler program was used: an initial 2 min. denaturing stage at 94 °C was followed with 42 cycles which included a 30 s denaturation stage at 94 °C, a 45 s annealing stage at 44 °C, and a 1 min. 30 s amplification stage at 72 °C, followed by, 20 min. extension at 72 °C.

2.5 Visualization and Scoring of Bands

DNA fragments produced from PCR were separated on 1.3 % agarose gels with ethidium bromide using electrophoresis in 0.5×TBE buffer. Each well was loaded with 10 μl of sample with each gel containing three wells with 250 bp ladder (Gibco; Carlsbad, California) to function as a standard against which ISSR fragments could be sized for molecular weight in base pairs. Band images for nucleic acid gels stained with ethidium bromide were captured with a digital camera with a selected 160 mm scan dimension using Fluor-S MAX MultiImager Gel Doc in Quantity One v 4.3.1 software (Bio-Rad; Hercules, California). Images were exposed for approximately 10 s. Image analysis for the scoring of bands was performed with Quantity One v 4.3.1 software (Bio-Rad; Hercules, California). A final binary matrix (1 = presence of band, 0 = absence of band) was used to identify all bands and for statistical analyses.

3 Statistical Analyses

For each species, measures of genetic diversity were calculated among and within cohorts (1998, persistent seed bank of 2000, and 1981) using percent polymorphic loci, F-statistics adapted for dominant genetic markers, and an analysis of molecular variance (AMOVA). A principal coordinates analysis (PCoA) and unweighted pair group mean method cluster analysis (UPGMA) were used to effectively portray and interpret findings in population genetic variation above and below ground through time.

3.1 Genetic Diversity Within and Among Cohorts

Percent polymorphic loci, used to determine genetic diversity within and among cohorts (1998, persistent seed bank of 2000, and 1981) for each species, was calculated using Tools for Population Genetic Analysis (TFPGA) 1.3 (Miller 1997). Because ISSR's are a dominant marker system, the frequency of recessive alleles was estimated based on the square root of the frequency of the recessive genotype (Weir 1990). Cohorts were assumed to be in Hardy-Weinberg equilibrium.

3.2 Genetic Differentiation

An analysis of molecular variance (AMOVA) was used to calculate genetic differentiation among cohorts with binary data for each species in GenAlEx (Peakell and Smouse 2001). Statistical significance among cohorts was affirmed in GenAlEx by comparing the frequency distribution of observed Φpt values to permuted Φpt values at 1000 permutations. If observed Φpt values were within the distribution of permuted Φpt values, then differences were not significant. If observed Φpt values were outside the distribution of permuted Φpt values, then differences among cohorts were found to be significant.

The Bartlett statistic was calculated to determine homogeneity of molecular variance (Stewart and Excoffier 1996) in WINAMOVA v 1.55 (Excoffier 1993). Data were modified using Euclidean distance (Excoffier et al. 1992) in AMOVA-PREP v 1.01 (Miller 1998) since AMOVA was designed for codominant data.

3.3 Relationships Among Cohorts

Principal coordinates analysis (PCoA) and unweighted pair group mean method cluster analysis (UPGMA) were used to display relationships among cohorts for each species. Principal coordinates analysis was performed in Numerical Taxonomy and Multivariate Analysis Systems (NTSYS) pc v 2.10 t (Applied Biostatistics, Inc. 2000). Calculation of eigenvectors in this analysis was based on Dice's coefficient for binary data (Dice 1945). A dendrogram produced from a UPGMA was created using Tools for Population Genetic Analysis (TFPGA) (Miller 1997). Clusters among cohorts were based on Nei's (1978) unbiased distance measure and allele frequencies were based on the square root of the frequency of the recessive genotype (Weir 1990). Bootstrapping was performed with 1000 replications.

4 Results

4.1 Determination of Sample Size

Given that percent polymorphic loci reached an asymptote at 24, 29, and 22 individuals for *S. salina*, *A. prostrata*, and *S. depressa*, respectively, 30 individuals were determined to adequately capture the genetic variability for these species (Fig. 7.1). Even though nine individuals were available for analysis for the 1981 cohort for *S. depressa*, 98.5 % of the variation was still captured for this particular cohort.

4.2 Genetic Diversity Within and Among Cohorts

Amounts of diversity differed for cohorts across species. For *S. salina* and *A. prostrata*, the percent of loci that were polymorphic increased between 1981 and 1998, but decreased for *S. depressa* (Table 7.2). The persistent seed bank from 2000 of *A. prostrata* had more percent polymorphic loci than the other two cohorts, but the persistent seed banks from 2000 of *S. salina* and *S. depressa* had less percent polymorphic loci than either of the cohorts representing a given year. The persistent seed bank from 2000 of *S. salina* was found to be monomorphic. Overall percent polymorphic loci for *S. salina*, *A. prostrata*, and *S. depressa* was 39.02 %, 60.78 %, and 73.3 %, respectively (Table 7.2).

4.3 Genetic Differentiation

AMOVA showed that for *S. salina*, *A. prostrata*, and *S. depressa*, variance among cohorts was greater than variance within cohorts, and differences among cohorts were statistically significant (Table 7.3). The percent variation explained among cohorts for each of the species (*S. salina*, 93.2 %; *A. prostrata*, 70.2 %; and *S. depressa*, 91.3 %) indicated a high degree of population differentiation (as represented by the 1981 and 1998 cohorts) over 17 years and with the persistent seed bank of 2000. These findings were supported by the Φpt and Bartlett's statistics (Table 7.3). The Φpt values approximated values for percent variance among cohorts, indicating little commonality of loci among cohorts across

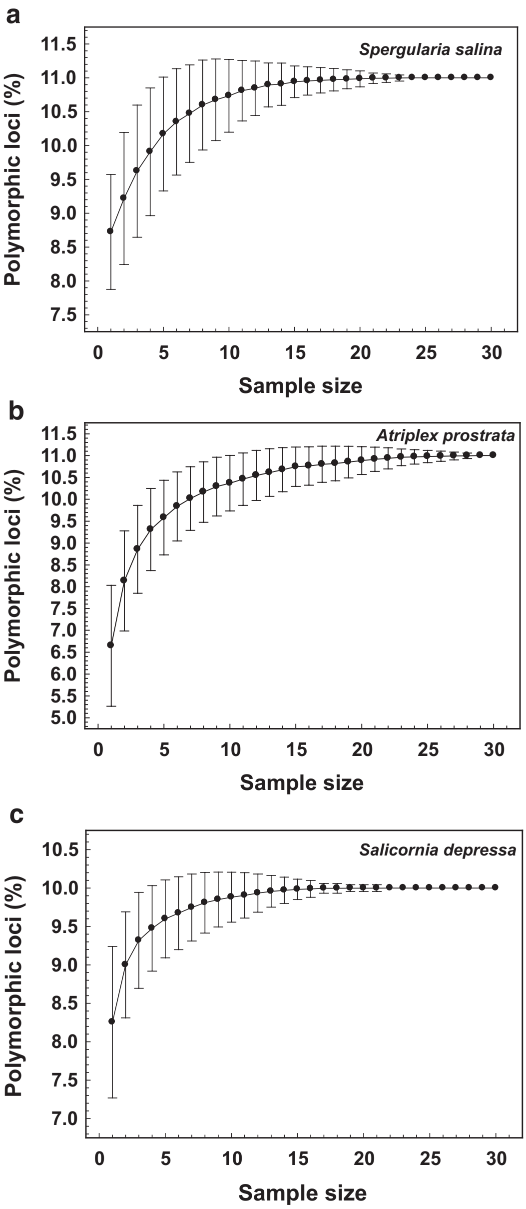

Fig. 7.1 Percent polymorphic loci (mean ± SD) as a function of sample size for *Spergularia salina* (**a**), *Atriplex prostrata* (**b**), and *Salicornia depressa* (**c**). Means were calculated based on 500 permutations (without replacement) per sample size. Percent polymorphic loci reached an asymptote at 24, 29, and 22 individuals for *S. salina*, *A. prostrata*, and *S. depressa*, respectively

17 years. Significant differences among cohorts for each species were also supported with Bartlett's statistic (Table 7.3).

4.4 Relationships Among Cohorts

For each species, principal coordinates analysis (PCoA) formed distinct groups of cohorts, indicating that cohorts were highly differentiated (Figs. 7.2, 7.3, and 7.4). For *A. prostrata*, Axes 1 and 2 accounted for 37.2 % and 23.8 % of the variation, respectively, for a total of 61 % (Fig. 7.2). When comparing the persistent seed bank cohort with the 1981 cohort, 18 of the 51 loci differed with 9 being specific to the seed bank and 9 to the 1981 cohort. Fifteen of 51 loci differed between the persistent seed bank and the 1998 cohort. Five loci were specific to the 1998 cohort and 10 were specific to the seed bank. Of the 12 loci that differed between the 1981 and 1998 cohorts, 4 were specific to 1998 and 8 were specific to 1981. Eleven genotypes were found for the 1981 cohort, supporting findings of percent polymorphic loci that genetic diversity was least for this cohort for *A. prostrata* (Fig. 7.2).

Table 7.2 Percent polymorphic loci within and among cohorts from *Spergularia salina*, *Atriplex prostrata* and *Salicornia depressa*

Species	Cohort	n	# marker bands	% poly loci
Spergularia salina	1981	30	19	2.44
	1998	30	39	14.63
	Seed bank	30	35	0.00
	Overall	90	41	39.02
Atriplex prostrata	1981	30	40	11.76
	1998	30	37	25.49
	Seed bank	30	39	39.21
	Overall	90	51	60.78
Salicornia depressa	1981	9	34	25
	1998	30	33	15
	Seed bank	30	38	6.7
	Overall	69	60	73.3

For *S. depressa*, Axes 1 and 2 accounted for 73.0 % and 13.3 % of the variation, respectively, for a total of 86.3 % (Fig. 7.3). When comparing the persistent seed bank of 2000 with the 1981 cohort, 30 of 60 loci differed among the two groups. Seventeen of the loci were specific to the seed bank and 13 were specific to the 1981 cohort. Forty loci differed among the persistent seed bank and the 1998 cohorts. Twenty-three were specific to the seed bank and 17 were specific to the 1998 group. Of the 20 loci that differed between the 1981 and 1998 cohorts, 11 were specific to 1981 and 9 were specific to 1998. Four genotypes representing 30 individuals were found for the seed bank cohort, supporting the

Table 7.3 Analysis of Molecular Variance (AMOVA) for three cohorts of *Spergularia salina*, *Atriplex prostrata* and *Salicornia depressa*

Species	Source of variation	df	Variance component	% Variance	P-value[a]	Φ statistic	Bartlett's statistic
Spergularia salina	Among cohort	2	3.93	93.2	<0.001	0.93	[b]
	Within cohort	87	0.29	6.8	–	–	–
Atriplex prostrata	Among cohort	2	5.07	70.2	<0.001	0.70	13.23*
	Within cohort	87	2.15	29.8	–	–	–
Salicornia depressa	Among cohort	2	13.2	91.3	<0.001	0.91	16.25*
	Within cohort	66	1.3	8.7	–	–	–

[a] randomization test at 1000 permutations

[b] value not able to be calculated since one cohort is monomorphic

* significant at $p<0.005$

finding that the persistent seed bank was the least diverse of the three cohorts (Fig. 7.3).

For *S. salina*, Axes 1 and 2 accounted for 74.8 % and 16.5 % of the variation, respectively, for a total of 91.3 % (Fig. 7.4). When comparing the persistent seed bank of 2000 with the 1981 cohort, 10 of 41 loci differed between the two groups. Eight loci were specific to the seed bank and 2 were specific to the 1981 samples. Six loci differed among the persistent seed bank and 1998 cohorts where one locus was specific to the seed bank and 5 were specific to the 1998 cohort. Of the 12 loci that differed between the 1981 and 1998 cohorts, one was specific to the 1981 group and 11 were specific to the 1998 group. Plots of the 30 individuals for each cohort further supported the lack of genetic diversity within cohorts as the seed bank was found to be monomorphic and the 1981 and 1998 cohorts were found to have 4 and 8 genotypes, respectively (Fig. 7.4).

UPGMA cluster analyses showed that clusters formed among cohorts differed between species (Figs. 7.5, 7.6, and 7.7). For *A. prostrata* and *S. salina*, the seed bank and 1998 cohorts were more closely related, with the 1981 cohort being the most distant (Figs. 7.5 and 7.7). The persistent seed bank was the most distant cohort for *S. depressa* (Fig. 7.6).

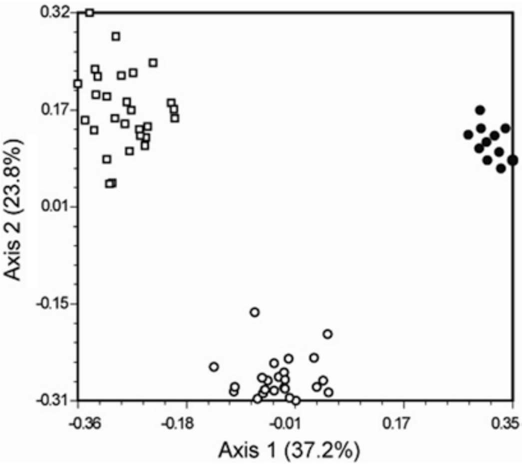

Fig. 7.2 Principal Coordinates Analysis for three cohorts of *Atriplex prostrata*: □ = seed bank, ○ = 1998, and ● = 1981

5 Discussion

Spergularia salina was first found at this location in the Rittman salt marsh in 1978 (Riehl and Ungar 1980), and it is reasonable to assume that this population began from a single seed or small group of seeds introduced by migratory birds. The percent polymorphic loci found in the 1981 cohort could be explained by its recent introduction 3 years prior, having an autogamous form of reproduction, and having few individuals in the

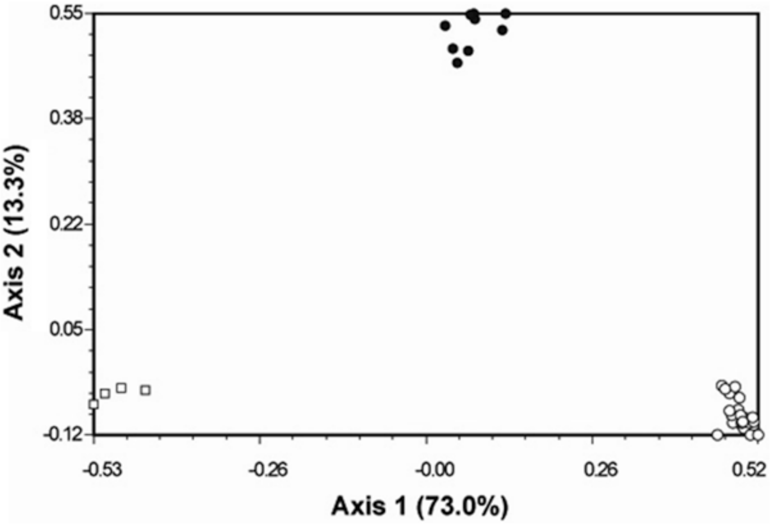

Fig. 7.3 Principal Coordinates Analysis for three cohorts of *Salicornia depressa*: □ = seed bank, ○ = 1998, and ● = 1981

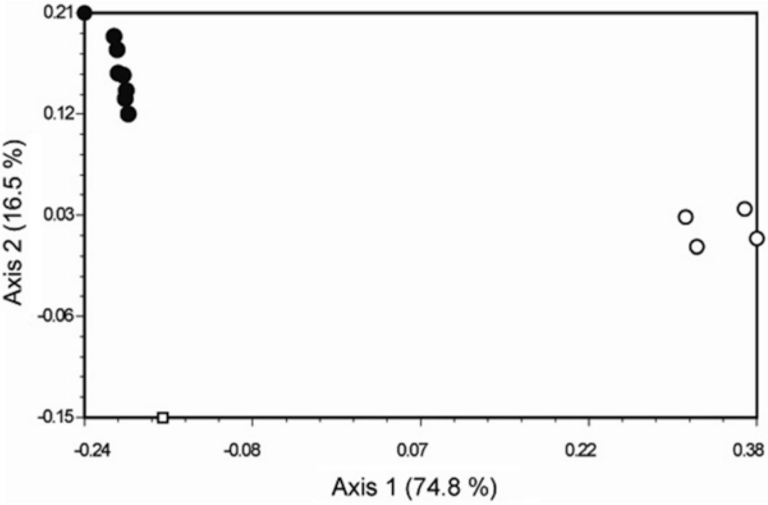

Fig. 7.4 Principal Coordinates Analysis for three cohorts of *Spergularia salina*: □ = seed bank, ○ = 1998, and ● = 1981

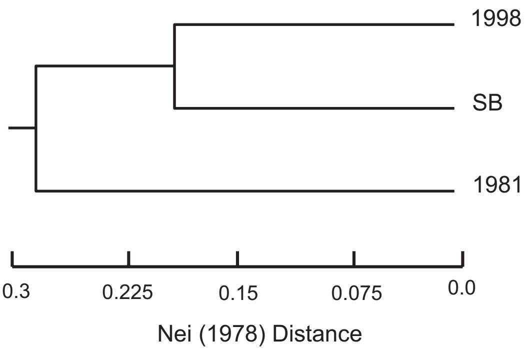

Fig. 7.5 UPGMA cluster analysis of three cohorts of *Atriplex prostrata* using Nei's (1978) distance measure. SB = persistent seed bank from 2000

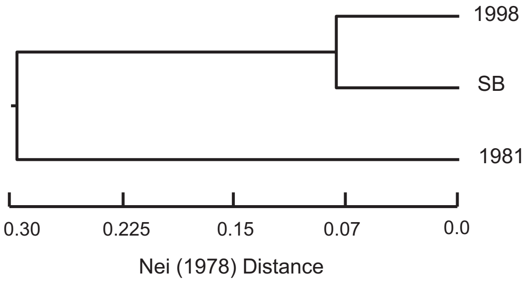

Fig. 7.7 UPGMA cluster analysis of three cohorts of *Spergularia salina* using Nei's (1978) distance measure. SB = persistent seed bank from 2000

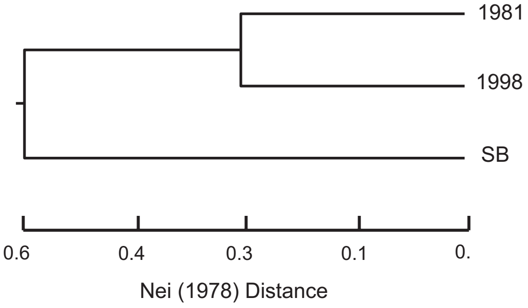

Fig. 7.6 UPGMA cluster analysis of three cohorts of *Salicornia depressa* using Nei's (1978) distance measure. SB = persistent seed bank from 2000

population when seeds were collected from plants at this time. Populations for *A. prostrata* and *S. depressa* were widespread throughout the marsh in 1981, explaining their higher diversity as compared to *S. salina.* Since salt mining began on the site in the late 1800s, it is most likely that these two species had well established populations. Genetic diversity also increased for *A. prostrata* over the 17 year period. This also may be attributed to multiple seed introductions over the time period by migratory birds or to changes in the genetic structure of the seed bank. Levin (1990) proposed that seed banks can be sources of new genetic variation due to seed aging accompanied by a reduction of seed viability, the relationship between the reduction of seed viability and chromosome breakage and mutations in viable seeds, and the relationship between chromosomal aberrations and the occurrence of heritable point mutations.

The seed bank of *A. prostrata* was more genetically diverse when compared to either the 1981 or 1998 cohorts. This finding is similar to other investigations of terrestrial species (McCue and Holtsford 1998; Cabin et al. 1998), but differs from Mandák et al. (2006) who found low genetic variation of the soil seed bank for *Atriplex tatarica* L. when compared to later developmental stages. Although *A. tatarica* is also an annual, this species is outcrossing and is wind and insect pollinated. In the Czech Republic it is found in terrestrial sites where it typically occurs in salt steppes, disturbed sites, and is typically an early successional species (Mandák et al. 2006). Mandak et al. (2006) explained that a relatively highly homozygous seed bank may be attributed to a temporal Wahlund effect created by season-to-season drift.

Seed banks of *S. salina* and *S. depressa* were less diverse than the aboveground vegetation. These findings bring into question Templeton and Levin's (1979) hypothesis, in which seed banks purportedly have more diversity than the aboveground vegetation since they are a collection of "genetic memory" from years past. When these species set seed in autumn, most seeds remain on or near the soil surface, ready to germinate the following spring. Ungar (unpublished data) found that most seeds found in the Rittman, Ohio, salt marsh and in coastal salt marshes in Wales and England, were located within the top two centimeters in the soil. Carter (2003) found that seeds of *A. prostrata*, *S. depressa*, and *S. salina*, when placed on the soil surface, germinated between 90 % and 100 % across all zonal communities in an inland salt marsh. Seeds that were buried (~15 cm) had less than 10 % germination, except for large seeds of *S. depressa* which do not have a light requirement for germination. However, *S. depressa* and *S. salina* do form large persistent seed banks. *S. salina* produces a seed bank with a mean density of 471,135 seeds m^{-2}, ranging from 170,525 seeds m^{-2} to 1,189,466 seeds m^{-2} (Ungar 1988a). Philipupillai and Ungar (1984) recorded approximately 38,000 seeds m^{-2} to 118,000 seeds m^{-2} for large and small seed morphs combined, depending on the season, for the seed bank of *S. depressa*. This indicates that some numbers of seeds are buried before the following spring, or they may be in an enforced dormancy due to high salinity levels. Although it would be interesting to know which years dominate the persistent seed banks for these species, designing and executing an experiment to assess composition based on multiple years would be a difficult task, especially in environmentally variable habitats like inland salt marshes. Nonetheless, a lack of diversity was found in the seed bank for *S. depressa* and *S. salina*. Our findings also differ substantially from Liu et al. (2014) who found high genetic diversity in both the seed bank and aboveground vegetation of *Heleocharis valleculosa* (Cyperaceae), a common perennial wetland species. They attributed the high genetic diversity of the seed bank of this species to the interconnectedness of the wetlands in their study sites. They asserted that flowing water between larger wetland areas would promote the accumulation of genotypes due to long distance seed dispersal from different parts of the lake. In our investigation, even though loci were found in the seed bank cohorts that were not present in the aboveground cohorts studied, they must have come from an aboveground population of a different year than the 1981 or 1998 populations. Lack of similarity of shared loci was indicated by the highly segregated non-overlapping cohorts produced by the PCoA, and by results of the AMOVA. It is possible that the seeds in the persistent seed bank, instead of functioning as a "bank" of diversity from which future populations may arise, actually function on a short time-scale as a "dump" of genetic material. Over the long-term, however, the seed bank does act as a genetic and physical reservoir that promotes the persistence of a population when responding to catastrophic or large-scale disturbance, or when a population is restored when a competitor is removed.

Diversity for *S. depressa* cohorts declined between 1981 and 1998. This may be attributed to having only nine samples from the 1981 cohort, yet 98.5 % of the variation was still captured. However, Kröger et al. (2002) used only 12 samples when comparing populations of *Salicornia remosissima* in Germany using RAPD analysis and found low genetic diversity. Jefferies and Gottlieb (1982) also found low genetic diversity in *Salicornia* populations from England.

Populations of *S. depressa* (s.l.) from northeastern North America also had low genetic diversity (Wolff and Jefferies 1987). They concluded that this could be due to three factors: an autogamous breeding system, founder effects, and isolation of populations. Because these findings represent genetic diversity for two distant years, it is unclear as to how genetic diversity in a single population varies from one year to the next. It would be interesting to assess genetic diversity over consecutive years for a single population to ascertain changes in diversity from one year to the next and to assess variability in the seed bank. Decline between the 2 years could also be explained by a loss of genotypes over the 17-year period. The 1981 cohort had 11 loci that were not present in the 1998 cohort; the 1998 cohort had 9 loci not found in the 1981 cohort.

In this investigation, we found that seed banks do not always function as a reservoir of genetic information, even though they may serve to restore a population after an environmental disturbance. We suggest that seed banks would be more appropriately labeled as seed dumps when the majority of genetic diversity or genotypes evident in the seed deposits is not contributing on a multi-year scale to the aboveground vegetation, as documented in three annual halophyte species by the present study. Additionally, these three species demonstrated different responses in a similar environment. These findings show that persistent seed banks can be less genetically diverse than an aboveground population from any year, thereby bringing into question Templeton and Levin's (1979) hypothesis. Our findings also differ substantially from Liu et al. (2014). Cohorts for *A. prostrata*, *S. depressa*, and *S. salina* were highly separated, indicating a high turnover in genetic composition from 1981 to 1998. This turnover may be due to environmental selection pressures in highly variable habitats such as inland salt marshes. Genetic diversity increased over the 17-y period for *S. salina* and *A. prostrata*, but declined for *S. depressa*. Low genetic diversity in these three species in this salt marsh habitat may be due to mainly autogamous breeding systems, founder effects, or isolation of these populations. It should be noted that a visit to this site by C. Carter on 16 October 2006 showed that *P. australis* had completely replaced these three annual halophytes in the aboveground vegetation. The presence of a seed bank for all three of these species would allow for regeneration of the aboveground populations if *P. australis* were removed as a competitor from these annual halophytes, but it would be expected that genetic diversity of these populations would be small. The recovery of these populations on this site is based on the longevity of these seeds in the soil for each species and the removal of *P. australis* in the aboveground vegetation. Further investigations are necessary to determine yearly fluctuations in genetic diversity in single populations and their seed banks and to assess the precise yearly source of seeds that are present in persistent seed banks. Clearly, more multi-year or cross-decade investigations on seed banks and aboveground vegetation in wetland species, especially annuals, are needed.

Acknowledgments We are grateful to Cheryl McCreary, Aurea Cortes-Palomec, Dr. Min Feng, Thomas Jackson, and Dr. Ross McCauley for assistance with ISSR procedures and data analysis. We recognize the Morton Salt Company for permitting access to their property. This investigation was supported by Sigma Xi—Grants in Aid of Research, Ohio University Student Enhancement Award, and the Ohio University John Houk Memorial Research Grant to C. T. C.

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8

The Impact of Lake Bonneville and Lake Lahontan on the Halophytes of the Great Basin

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Abstract

The rivers in the Great Basin in the Western United States do not drain into the Pacific Ocean. Some 30,000 years ago a lot of water was present in the Great Basin and two huge lakes (Bonneville and Lahontan) were formed. These lakes were very large and very deep. Over the next 17,000 years, the weather became very dry and the lakes began to evaporate leaving lots of salts on the land and in the few remaining smaller lakes. Great salt lake is the largest remaining lake in the Great Basin and is very salty. Because the dissolved salts were deposited mainly on the valley floors, only salt tolerate plants (halophytes) can grow in the high salt areas. Because of the mountains in the Great Basin area there is considerable diversity in the plant population. The area is ranked 4th out of 116 Eco regions in North America. The number of halophytic species is the highest in the Great Basin in North America. In addition a number of non-native salt tolerant plants have been introduced.

A number of halophytes are present in the Great Basin area in the Western United States. One of the reasons for the presence of the high number of halophytes is related to the geological history of the Great Basin. Because the Great Basin has no outlet to the ocean, large lakes developed about 32,000 years ago. Two major lakes (Lake Bonneville and Lake Lahontan) were formed. Lake Bonneville covered over 1/3 of the state of Utah and was very deep 304 m (1000 ft). Lake Lahontan covered a large part of Nevada and was also very deep 270 m (900 ft). Around 14,500 years ago, weather conditions changed and the lakes began drying up with only a couple of saline lakes remaining. Great Salt Lake is the largest remaining saline lake. As the water dried up, considerable salt from the water was deposited in the valleys. A range of halophytes have adapted to the salinity concentration in the soil. Because the area has a number of mountains and valleys the salinity varies according to elevation and location. Three plant shrub zones are characterized in the Great Basin area. A range of halophytes and other major plants are growing in the different zones. Non-native salt tolerant

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M.A. Khan et al. (eds.), *Sabkha Ecosystems Volume V: The Americas*,
Tasks for Vegetation Science 48, DOI 10.1007/978-3-319-27093-7_8

plants have been introduced into the Great Basin area.

1 The Significance of the Great Basin Region

The Great Basin is considered to be the center of halophytes in the Western United states. One could ask why is that the case? Utah and Nevada are dry high mountain areas, but being dry doesn't necessarily mean high saline. The geology area of Nevada and Utah is called the Great Basin because the rivers have no outlets to the ocean. The Great Basin covers 477,664 sq km (184,427 sq mi). It includes most of Nevada, the western half of Utah, a little part of Idaho, Oregon and California (Fig. 8.1). In addition there are a series of North-south mountain ranges that exist across the Great Basin area. Most of the area is cold desert which exists between 1219 m (4000 ft) and 1981 m (6500 ft) but includes mountains that range up to 3962 m (13,000 ft) with high valleys between the mountain ranges. The rainfall of the great basin region is between 18 and 30 cm (7–12 inches) per year. The Sierra Nevada and Cascade Mountains create a rain shadow in the Great Basin area causing the valleys to be a cold dry desert in the winter and a hot dry desert in the summer. There are rivers that drain the area but they flow to land locked lakes that exist between the mountain ranges.

The Great Basin is a land of striking contrasts containing considerable biological diversity. The area is ranked as the fourth highest in terms of the number of vascular plant species among 116 eco-regions throughout North America (Great 2011). This high biological diversity is produced by a blending of the surrounding eco-regions, flora and fauna populations with the unique species of the Great Basin including halophytes. The diversity is increased by the diverse habitats of the number of species of birds, butterflies and mammals found within the Great Basin's topography. The Great Basin is home to the Bristlecone Pine which grows to be 10,000–11,000 years old. Along the crest of the Ruby Mountains around Ruby Dome, annual precipitation ranges from 40 to 45 inches (102–114 cm) above 10,000 ft (3048 m) level, whereas at the lower elevations annual precipitation measures only around 7 inches (22.3 cm). In terms of plant coverage, sagebrush-grass constitutes the predominant plant cover over much of the Great Basin (Breshears et al. 2008).

In the Ruby Mountains area, the sagebrush overstory on the lower southern and western exposures yields to chokecherry (*Prunus virginiana*), snowberry (*Symphoricarpos spp.*), serviceberry (*Amelanchier alnifolia*), bitterbrush (*Purshia tridentata*) and small rabbitbrush (*Chrysothamnus viscidiflorus*) as the elevation increases (Weber et al. 1993). Between 7500 (2286 m) and 9000 ft, (2743.2 m) mountain mahogany is found on many of the southern and western exposures. Rockspirea (*Holodiscus discolor*) is also found in this same exposure and elevation zone on drier and rockier slopes. On the northern exposures and extended valleys of the mountains, dense groves of aspen (*Populus tremuloides*) may be found, giving way to scattered stands of limber pine (*Pinus flexilis*) and some white bark pine (*Pinus albicaulis*) above 8500 ft (2590 m). Small stands of subalpine fir (*Abies lasiocarpa*) and, rarely, white fir (*Abies concolor*), may also be found at these upper mountain elevations; however, none of these conifer stands presently offer any commercial logging value.

In the valleys, where there is less precipitation, the soils are more saline. In the case of the saline playas near the edges of the saline lakes, the salinity is very high (Greer 1977). Some playas of the western Great Basin are often nearly devoid of vegetation, but the margins of these playas support sparse communities of shrubs that can tolerate saline soils. *Allenrolfea occidentalis* (iodine bush) and *Sarcobatus vermiculatus* (black greasewood) can tolerate high saline soils (Donovan et al. 1997).

The level of salinity in the saline lakes can range from high to very high. In some cases, certain fish can tolerate the saline waters, but at higher salinity the fish can not survive. In the

Fig. 8.1 Map of the Great Basin (Courtesy of Wikipedia)

highly saline waters, brine shrimp (*Artemia franiciscana*) is common (Kojima et al. 2013). In terms of plant life, a blue-green algae (*Dunaliella viridis*) grows well. There is also a variety of salt-tolerant bacteria that thrive well in the saline waters. Brine flies (*Ephydra cinerea*) are also present in the area (Campos et al. 2003).

1.1 The Formation of Lake Bonneville

In relation to the geological history of the area, another event, the formation of Lake Bonneville, has played an important role. Around 32,000 years ago at the beginning of the Wisconsin Ice

Age, Lake Bonneville began to appear. With cooler temperatures and higher moisture in addition to the melting of the ice, Lake Bonneville increased in size until it became a huge lake (Fisher 1974). At its highest level, it was nearly 523 km long (325 miles) and 217 km wide (135 miles). It stretched from the southeast corner of Idaho to the bottom of Utah near Cedar City, Utah. It is estimated that it covered 11,000 km^2 (19,691 sq miles) (Fig. 8.2), and was almost as large as Lake Michigan but it was deeper. It was present from 32,000 to 14,500 years ago (Gilbert 1980). Lake Bonneville was not only large but it was also a very deep lake. The water level rose to an elevation of 1524 m (5150 ft) which was nearly 304 m (1000 ft) above the level of Great Salt Lake. Over the thousands of years that Lake Bonneville existed the depth of the lake varied some but it was still a very deep lake (Fig. 8.2).

2 Lake Lahontan and the Formation of Saline Areas

2.1 Formation of Lake Lahontan

In the western part of the Great Basin the weather changed at the same time that the weather changed in the eastern part of the Great Basin. Around 32,000 years ago at the beginning of the Wisconsin Ice Age, water began to accumulate in valleys and a large Pleistocene Lake appeared in the western Great Basin. It existed in northwestern Nevada, northeastern California and southern Oregon. It was called Lake Lahontan. At its peak about 12,700 years ago, it covered 8500 sq miles (22,000 km$^{2)}$ The lake ranged from the bottom of Oregon to almost the bottom of Nevada including Lake Tahoe in California. The depth at Pleistocene

Fig. 8.2 Map of the Great Basin area with showing the two prehistoric lakes (Courtesy of Wikipedia)

time was 900 ft (270 m^2) at the location of Pyramid Lake (Fig. 8.2).

3 Overflowing of Lake Bonneville

3.1 Lake Bonneville Overflows at Red Rock Pass

About 14,500 years ago, water from Lake Bonneville began to overflow at Red Rock Pass. The flowing water cut a channel through Red Rock Pass in Southern Idaho. The amount of water released was huge. The level of the lake fell 344 ft (114 m) to the Provo bench level. It is estimated that huge amounts of water flowed into the Snake River and on to the ocean in the first week of the lake's overflow.

After a period of time the flow of water from Bonneville Lake stabilized and no more water flowed through Red Rock Pass. The water level remained at the Provo bench level for 500 years. The stable water level and washing of materials from the mountains made a flatten area (bench) along the mountain slopes which is called the Provo Bench level.

The Provo bench is present at Logan, at Ogden, at Salt Lake, at Provo and other locations in Utah. Many towns are built on the Provo Bench. In the western Great Basin, the water loss at Red Rock Pass affected Lake Lahontan but was not as dramatic as in the East.

4 Reduction in the Size of the Large Lakes

4.1 Changes in the Size and Number of Lakes

Around 14,000 years ago, the climate began to change and it became warmer. The amount of moisture was reduced. The net effect was that the large lakes began to dry up over thousands of years. The remaining smaller lakes from Lake Bonneville were Great Salt Lake, Sevier Lake, and Rush Lake.

On the western side of the Great Basin, with the change in the weather and the reduction in rainfall. Lake Lahontan began to dry up. The smaller lakes were Lake Tahoe, and Pyramid Lake. These lakes are not as saline as the Great Salt Lake. Lake Lahontan broke up into a series of smaller lakes most of which eventually dried up into playas. The saline playas included Black Rock Desert, Carson sink, Honey lake, Mono lake, Winnemucca lake, Lake Manly and Humboldt sink (Fig. 8.3).

Lake Tahoe was formed from Lake Lahontan but Lake Tahoe had a flow of fresh water from the mountains and did not become highly saline (Banuelos et al. 2003). Lake Tahoe drains into Pyramid Lake. As the climate changed to a warmer period and the amount of rain and snow was greatly reduced. The water evaporated and the climate became desert-like. The water in the valleys contained a lot of salts which were deposited on the land. The effect was to make the valleys saline. The most saline areas were the salt playas (flat area of closed basins).

In the western Great Basin area the remaining major lakes were Pyramid Lake and Walker Lake. The major saline playas were Black Rock Desert, the Carson Sink, Honey Lake Basin, Mono lake, Winnemucca lake, Lake Manly and the Humboldt Sink (Fig. 8.4). The remaining saline lakes were Pyramid Lake and Walker Lake. Lake Tahoe is a lake that was formed from Lake Lahontan but it has a high flow of fresh water and is not highly saline. The water from Lake Tahoe drains into Pyramid Lake. The mountain ranges also changes the distribution of the water deposit (Fig. 8.4).

The vegetation of the Great Basin at the Pleistocene period was similar to today's species, but the plant communities included Las Vegas Valley's yucca, Joshua tree, creosote, and mesquite vegetation which was preceded by an ice age juniper woodland interspersed with sagebrush. Pinyon pine forests were absent in northern and central parts of the state of Nevada. Shadscale, a lower elevation desert shrub, grew within western juniper groves along the shore of Lake Lahontan within the Winnemucca Lake basin. Today, elevations of 2000 ft or more and

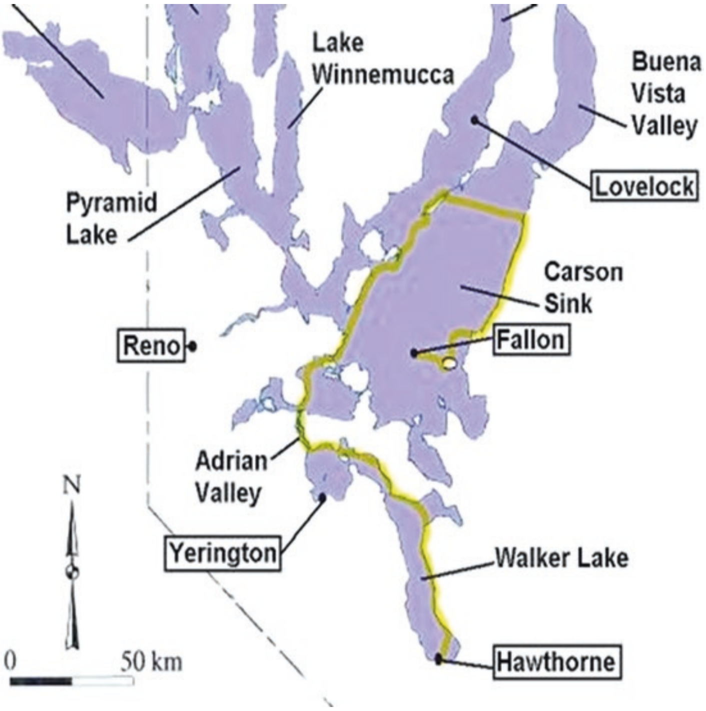

Fig. 8.3 Lakes and dry playa from Lake Lahontan (Courtesy from Wikipedia)

ten miles separate the two plant populations (Hunt 1974).

4.2 Characteristic of Pyramid Lake

Pyramid Lake is fed by the Truckee River. Pyramid Lake has no outlet to the sea. The lake loses water by evaporation or sub-surface seepage. The lake has about 10 % of the area of the Great Salt Lake but has 25 % more volume. The salinity is about 1/6 (5.5 ppt) of sea water. Three benthic invertebrates live in the lake (Galat et al. 1988). In the ninetieth century, Paiute Indians lived around the Pyramid Lake and collected Tui chub and cutthroat trout from the lake. Because more fresh water comes into the lake, fish can live in Pyramid Lake. The Lahontan cutthroat trout is a very large fish. The record weight was a trout of 41 lbs. The construction of Derby Dam in 1903 resulted in the extinction of the Lahontan cutthroat trout in most of the area, but in 1979 a scientist found in a small brook on the Nevada/Utah border, a remnant population of the Lahontan cutthroat trout. The Lahontan cutthroat population has been increased and is doing well in Pyramid lake. Now 20 lb Lahontan cutthroat trout are being caught (DeLong 2013).

4.3 Characteristics of Humboldt Sink

Humboldt Sink is a dry lake bed that is about 11 miles (17.7 km) long and 4 miles (6.4 km) wide. In ancient times (13,000 years ago) it was Humboldt Lake but now it is a dry playa which is about 50 miles (80.4 km) from Reno, Nevada. Some water makes it to the dry playa from the 330 mile (531 km) Humboldt river. The sink has no natural outlet. A connection was made with Carson Sink but the channel has been dry since 1986. The wetlands (Humboldt Salt Marsh) near the sink provides important nesting, foraging, and resting habitat to large numbers of migratory birds. Apparently the Humboldt sink has a long history of human habitation suggesting that Native Americans hunted and fished in the Humboldt Sink during wetter climatic periods.

Fig. 8.4 Lake Lahontan showing the mountain areas with remaining Lakes and Playas (Courtesy from Wikipedia)

4.4 Characteristics of Carson Sink

The Carson Sink is a saline playa that was previously fed by the Carson River. The area involved is 300 sq miles (482.8 km^2). Now it is mainly a dry saline playa but in the southeastern fringe of the sink some water enters the sink and a wetland has developed. A wildlife refuge exists and is an important stopover for migrating waterfowl.

4.5 Characteristics of Walker Lake

Walker Lake is a remnant of the prehistoric Lake Lahontan. The area is 50.3 sq miles (130 km^2). It is 18 miles (28.9 km) long and 7 miles (11.2 km) wide. The lake dried up several times at the end of the Pleistocene period. Fresh water is added to the lake by the Walker River. The area was inhabited by the Paiute Indian tribe during the centuries. In recent times, the level of Walker Lake has dropped due to diversion of water for irrigation purposes. At present time the lake level is 3923 ft above sea level. The TDS concentration was 19 g/L which is above the lethal limit for most native fish. The Lahontan cutthroat trout is no longer present. Some efforts have been made that indicate lengthy acclimations in simulated lake water may increase the survival rate of Lahontan cutthroat trout (Bigelow et al. 2010). The lake's Tui chub have declined dramatically and may soon disappear due to the salinity. Studies on the salt tolerance of some midges *Cricotopus ornatus, Tanypus grodhausi* and *Enallagma clausum* indicated that salinities needs to be below 25 g/l for them to survive (Herbst et al. 2013). Some conservation efforts have resulted in the protection of Walker Lake (Herbst et al. 2013).

4.6 Characteristics of the Black Rock Desert

The Black Rock Desert is a dry lakebed of the Pleistocene Lake Lahontan. It is a saline playa that is located 100 miles (160.9 km) north of Reno. The area includes 300,000 acres (120,000 ha) of land. The rainfall average for the years 1971–2000 was 7.90 inches. When the rains come, some shallow lakes can be formed and huge numbers of fairy shrimp develop. The area has been inhabited by the Paiute Indian for centuries. During the gold rush period, thousands of gold seekers crossed the Black Rock Desert on their way to California. Some 22 mountain ranges are within or bordering the Black Rock Desert region. In the flat regions of the desert, Lahontan salt shrub vegetation is present. The area has been mined for gypsum and gold. Because of the flatness of the area, two successful attempts at the World Land Speed Record were made in 1983 and 1997. The area was also used to test rocket launches from 1996 to 2013. During World War II, the area was used as a USAAF aerial gunnery training range. Travel by vehicles on these dry playas results in the development of branchiopod egg and ephippia density in the tracks of the vehicles (Sada et al. 2013).

4.7 Characteristics of Honey Lake Basin (California-Nevada)

Honey Lake Basin was part of the 22,000 km Lake Lahontan pluvial lake system that existed between 5000 and 40,000 years ago. The basin consists of two subbasins separated by a low elevation divide. The western subbasin had a total dissolved solids (TDS) content of 1300 mg/L, whereas the eastern subbasin had a TDS of 46,000 mg/L. Later there was a rebound and the western subbasin had the highest TDS content (Mayo et al. 2010).

4.8 Characteristics of Winnemucca Lake (Nevada)

Winnemucca Lake is a saline playa that has been studied with a remote sensing system to determine soil moisture levels (Glenn and Carr 2004).

4.9 Characteristics of Mono Lake, California

Mono Lake is on the east side of the Sierra Nevada mountains. It has no outlet but had fresh water streams draining into the lake. Over time many of the fresh water rivers were diverted to the populated Los Angles area. Mono Lake began to dry up and the salinity increased. It represents a transition zone between the Sierra Nevada mountains and the Great Basin desert. The saline waters contain brine shrimp, alkali flies and fungal populations. The isolation of fungi from Mono Lake yielded 67 fungal species from 23 samples. Around the area of Mono Lake there are 14 ecological zones and over 1000 plant species and 67 fungal species. The area has over 400 vertebrate species (Steiman et al. 2004). Four shrub species represented most of the 7–11 % cover of perennial vegetation. The sequence of shrubs started with *Sarcobatus vermiculatus* being the closest to the lake shore, then *Chrysothamnus nauseosus*, *Tetradymia tetrameres* and *Chrysothmanus viscidiflorus* being the furthest from the lake shore (Toft and Elliott-Fisk 2002).

4.10 Characteristics of Lake Manly

Lake Manly was a prehistoric lake in Death Valley, California. Death Valley is the lowest land point in the United States. During the Holocene period, Lake Manly filled the Death Valley basin of Inyo County, California. Manly Lake was represented as a group of lakes in Death Valley that later dried up. Most of the water in Lake Manly came from melting glaciers rather than rivers. The low elevation and the high temperatures have created a dry saline desert environment (Hunt 1975).

5 Characteristics of Great Salt Lake

5.1 The Properties of Great Salt Lake

The major saline lake that remained on the eastern side of the Great Basin is Great Salt Lake mainly because it was located at a lowest elevation in the Rocky Mountains. Other smaller salt lakes appeared in the great basin, but Great Salt Lake was the largest and the lake with the highest salinity. It is the largest saltwater lake in the Western Hemisphere and the fourth largest terminal lake in the world (Fig. 8.5). The dumping of the salts onto the land and into the lakes resulted in making the valleys and shorelines of the Great Basin area saline and most of the arid plants in the valleys could not survive because of the saline soils whereas halophytes could grow in the saline soil. Soils on the slopes of the mountain ranges above 1524 m (5000 ft) receive more than (12–14 inches) 305–356 mm of rain and are not highly saline. The soils in the valley where the rainfall is less than (7–12 inches) 305 mm per year are more saline. The most saline areas are the playas (flats of closed basins). Areas around the Great Salt Lake, Sevier Lake (a saline lake), Great Salt Lake Desert and some salt flats in the middle areas of Utah are highly saline playas. Often crystalline salt lay stratified on the surface of these high saline playas. Great Salt Lake is the terminal lake which fluctuates depending on the rainfall and evaporation that takes place. During the time period between 1851 and 1976, Great Salt Lake reached a high of 1284 m (4211 ft) above sea level in 1873, a low of 1278 m (4191 ft) in 1963. At the present time, the lake elevation is around 1280 m (4200 ft.). It is 128.7 km (80 miles) in length and 48.3 km (30 miles) in width. The salinity of the lake ranges from 5 to 27 % (50–270 ppt), the ocean being 3.5 % (35 ppt). Even though Great Salt Lake is very saline, it has an abundance of life living in it.

No fish exists in the highly saline waters of Great Salt Lake, but a brine shrimp (*Artemia franiciscana*) is common (Werner et al. 2014) and is harvested and sold as food for tropical fish (Kojima et al. 2013). There are two different types brine shrimp, a pathenogenetic *Artemia* (60 %) and a zygogenetic species (40 %). The two species appear almost identical (Campos et al. 2003). The value of selling the brine shrimp is a $57 million per year business. In terms of plant life, a blue-green algae (*Dunelilla viridis*) grows very well in high salinity ranging from 10 to 30 %. There are also a variety of salt-tolerant bacteria such as *Halorhabdus utahensis* that thrive well in the saline waters (Werner et al. 2014). Brine flies (*Ephydra cinerea*) are also present in the area. The southern part of the lake is normally blue-green in color whereas the northern part is higher in salinity and is reddish in color due to the presence of beta carotene in the algae (Brix et al. 2004). Two mudskippers are present in the saline lake. The alkaline pH has no effect on the ammonia excretion of the mudskipper *Periophthalmodon schlosseri*. In the case of the second mudskipper, *Boleophthalmus boddaerti*, it cannot breakdown ammonia. There are nine elements present in the waters of the Great Salt Lake. About 80 % of the lake solids is the salt, NaCl. The extraction of minerals from the salty brine is a multimillion dollar business.

Fig. 8.5 Map showing the area of Lake Bonneville (Courtesy from Wikipedia)

5.2 Another Remnant (Saline Lake) of Lake Bonneville Is Sevier Lake Located in Millard County

It is fed primarily by the Beaver and Sevier rivers. The first recorded observation was in 1872 which reported that the lake area was 487 sq km (188 sq miles) with a salinity of 86 ppm which is two and one half times the salinity of ocean water. The water from the rivers that drain into Sevier Lake has been diverted for irrigation and Sevier Lake is now mainly a dry saline playa. During the wet years of 1984 and 2011 the lake filled somewhat, but now it is mainly a dry playa. Potash mining occurs in some of the dry area of Sevier Lake (EPM mining Ventures 2014).

Many halophytes are present in the great basin area, perennial types are most common but a few exotic annuals are present. In Millard county rare edaphic endemic plants have been associated with mineral deposits. In 1983, Cronquist discovered a halophyte (*Frasera gypsicola*) growing on gypsum mounds. It only grows on the gypsum mounds and is called a gypsophyte (DeQueiroz et al. 2012).

6 The Three Shrub-Steppe Zones

6.1 Distribution of Plants into Three Shrub-Steppe Zones

In terms of describing the distribution of plants in the Great Basin, they can be grouped into three shrub-steppe zones. The populations of the plants will vary in distribution in different parts of the Great Basin. The three shrub-steppe zones are:

1. Salt-desert shrubs,
2. Sagebrush semi-desert,
3. Sagebrush steppe.

6.2 In the Salt-Desert Shrub Zone the Dominant Plants Are Halophyte Perennials

This zone has the highest saline conditions (121 mmho cm^{-1}). Often free NaCl is present on the surface of the soil. The following halophytic plants are normally present: *Atriplex gardneri, Allenrolfea utahensis, Distichlis spicata, Salicornia Utahensis, and Salicornia rubra* (Skougard 1979).

6.3 *Atriplex gardneri* (Moq.) D. Dietr (Syn *Atriplex nuttallii*) Gardner Saltbush

Atriplex gardneri is a widely distributed species of Atriplex. There are six varieties listed: var *bonnevillensis*, var *cuneata,* var *gardneri*, var *falcate*, var *welshii* and var *tridentate* (Welsh et al. 2003). The complex grows in fine-textured saline soils. Polyploidy occurs and diploids, triploids, tetraploids, hexaploids, and higher polyploids have been found (Welsh et al. 2003). The plant also forms hybrids between *A. gardneri* and *A. canescens, A. garrettii, A. carrugata* and *A. confertifolia*. Salo et al. (1999) tested the ability of several halophytes to grow in a saline waste marsh from a power generating plant and he found that *A. gardneri* was the most successful shrub grown. *Atriplex gardneri* can grow over an 80-fold range of salinity levels Goodman (1973). The amount of biomass produced depends on the salinity gradient. *Atriplex gardneri* is a good forage plant for livestock and wildlife and can withstand heavy grazing.

6.4 *Allenrolfea occidentalis* (Wats) Kuntze (Iodine Bush or Pickleweed)

This halophyte is highly salt tolerant. It can grow in saline soils where the salt concentration is 1027 mM (Hansen and Weber 1975; Weber et al. 2002). The plant produces an abundant of seeds even in very dry years (Young et al. 1995). The seeds are uniform in size and color and there is no evidence of polymorphism (Gul and Weber 1999, 2000a, b). The upper zone of the soil contain large numbers of seeds of *A. occidentalis* (Gul et al. 2000a). To maintain the populations of *A. occidentalis* a large seed bank is needed (Gul and Weber 2001). Temperatures of 25 °C night and 35 °C day provides the best conditions for seed germination to occur. Cooler temperature decreased the germination rate. The Inhibition of germination of the seed is greater in the dark than in the light (Gul et al. 2000b). The percent germination decreases with increased salinity, but seeds can germinate in 800 mM NaCl (Gul 2001). Seeds that have been placed in high saline solutions for 20 days and then transferred to distilled water germinated readily which indicates a high tolerance to exposure to high salt conditions (Gul et al. 2000b). The inhibitory effects of salinity on seed germination was reversed by Fusicoccin. The chemical, Ethephon, significantly promoted germination at all salinities tested (Gul and Weber 1998). The highest dry mass of roots of *A. occidentalis* occurred at 600 mM NaCl at low density (2000 plants m^3). Even at high salinities photosynthesis functioned reasonably well, but extremely high salinity did decrease dry mass of roots and shoots (Gul et al. 2000). With increasing salinity, the water potential of the plants became more negative (Gul et al. 2000b). The Na and Cl concentrations in shoots and roots increased when the NaCl level was increased while cations (K, Ca, Mg) decreased (Gul et al. 2001). High metabolism, respiration and growth were the highest during May and June and the lowest during the dry month of August (Harris et al. 2001a, b).

6.5 *Salicornia utahensis* Tidestr. Syn *Salicornia pacifica var utahensis* (Tidestr.) Munz. (Utah Samphire)

Saliconria utahensis is a succulent perennial that grows well in high saline playa (Keller et al. 2002). Although a seed bank exists in the salt playa, reproduction is mainly from the roots, (Gul and Weber 2001). The outer regions of shoots of *S. utahensis* contain chloroplasts which photosynthesize to obtain energy. The inner region (cortex) of the shoots lacks chloroplasts (Hansen et al. 1972). There is an osmotic range in the shoots from the base of the stem shoot (75–90 atms range) to the top (110–1707 atms range) (Hansen and Weber 1975). Over the growing season, the potassium ion concentration decreased slightly, on the other hand, the concentration of Na gradually increased to 16.1 % (Hansen and Weber 1975). A study tested the salt sensitive of the carbon fixing enzyme, RuBPCase from *S. utahensis* and *S. ruba* and found they were almost as salt sensitive as RuBPCase from Tomato (Chong-Kyun and Weber 1980). Using wavelength dispersive X-ray microanalysis to analyse the ion distribution in a cross section of *S. utahensis*, it was found that Na, K and Cl concentrations were very low in the palisade region but high in the cortex area. These results suggested that there was a compartmentalization of the ions in the non-photosynthetic cortex cells. Similar ion distribution of the ions were found using Energy Dispersive X-Ray Microanlysis (Khan et al. 1985, 1986). Using silver chloride precipitation to locate chloride ions in the cells of S. utahensis and S. rubra, Hess et al. 1975 found that the Cl ions were concentrated in the vacuoles in the palisade and cortex cells. Using the the silver chloride precipitation method, the Cl ions were low in organelles such as chloroplasts (Hess et al. 1975). Using lead phosphate as a marker for ATPase, it was found that the ATPase was located along the plasma membranes in the palisade and cortex cells of shoots (Weber et al. 1990). Chong-Kyun and Weber (1980) isolated ATPase from *S. utahensis* and they found ATPase was salt tolerant and could function in 3 M concentrations of NaCl. Over a period of time sections of the shoot accumulates so much salt that the palisade and cortex cells are killed, but the vascular tissue in the center of the shoot continues to function as water transport to the living sections above the dead section (Weber 1982). Analysis of the oil from seeds of *S. utahensis* indicates that it would be a good cooking oil.

6.6 *Salicornia europaea var rubra* L syn (*Salicornia rubra* A Nels). (Samphire Annual)

Salicornia rubra is a succulent annual and it is considered to be that an obligate halophyte. It reacts positively to certain levels of NaCl, in fact it does not grow well in the absence of NaCl. *Salicornia rubra* grows where the salinity is the highest (Harris et al. 2001a, b). The optimal growth of *S. rubra* is at 200 mM NaCl (Khan et al. 2001d). With increased salinity the fresh and dry weight of *Salicornia rubra* decreases, still some plants are able to grow in 1000 mM NaCl. Seeds of *S. rubra* can germinate at 1000 mM NaCl at 25/35 °C alternating temperatures regimes (Khan et al. 2000) Kinetin, GA, and ethephon substantially alleviated the effect of salinity in *Salicornia rubra* (Khan et al. 2000, 2002a, b).

6.7 *Distichlis spicata* (L.) Greene. (Native Saltgrass)

Distichlis spicata is very salt tolerant grass and is widely distributed in North America (Pataki 2008). It is not an exceptionally palatable forage but is often grazed in the winter for lack of other forages. Yensen (2002) developed a more palatable saltgrass (*Distichlis spicata var yensen*-4a) that grows on saline soils. *Distichlis spicata* provides excellent protection against wind and water erosion (Welsh et al. 2003). The highest metabolism, respiration, efficiency and growth occur during spring (May and June) and the lowest growth occurs during the hot dry month of August (Harris et al. 2001a, b). Six halophyte grasses were grown in arrange of salinities up to 600 mM NaCl and *Distichlis spicata var stricta* (Torr.) was the most salt tolerant (Marcum 1999). Six salt tolerant forage plants were irrigated with brackish water and *D. spicata* was the most salt tolerant (Pasternak et al. 1993). In certain areas, *D. spicata* is associated with mound formation (0.3 m in height). The mounds appear to help plant recruitment and survivorship (Blank et al. 1998). Ketchum et al. 1991 found that when NaCl-induced stress was present that proline accumulation occurred in *D. spicata.* The threshold salinity levels for *D. spicata* was around 0.5 M NaCl and the proline accumulation was 27.4 mu.mol/g fresh wt. (Cavalieri and Huang 1979).

Salsola liberica (Sennen & Pau) (Russian thistle) is a halophytic forb in the family Chenopodiacease and is widely distributed in the inland salt deserts of Utah. Seed germination increased when there was an decrease in soil salinity. Increased temperature increases seed germination, whereas lower temperatures decreased seed germination (Khan et al. 2002b).

7 Halophytes Present at Lower Salinity (96 Mmho Cm^{-1})

These species grow in areas some distance from the saline lake shore but the soils are saline The halophytes normally present are *Astragalus* species, *Atriplex falcate, Atriplex gardneri, Kochia Americana, Sarcobatus vermiculatus,* and *Suaeda torreyana*.

7.1 *Astragalus* Species

*Astragalu*s has at least 111 species and numerous varieties, it is probably the largest genus of flowering plants in the Great Basin. However some of the species are poisonous. The toxin is a combination of pyrrolizidine alkaloids and selenium. However, large amounts of the plant needs to be consumed before it has a poisonous effect. Some cattle become addicted to eating *Astragalus.* These cattle develop an odd behavior pattern called ‘loco disease’. Some of the species have high salt tolerance (Welsh et al. 2003).

Atriplex is a large complex genus with at least 23 species and at least 9 varieties. In addition, the genus forms hybrids with native and introduced species (Welsh et al. 2003). The result of this genetic plasticity is a range of plants that can occupy numerous habitats. *Atriplex corrugate* Watts (mat-saltbrush) is present in fine textured saline soils often with considerable slope. When compared with six *Atriplex* species, *Atripex corrugate* was the most salt tolerant plant in comparison to *A. obovata, A. cuneata, A. falcate, A. confertiolia* and *A. canescens* (Hodgkinson 1987). *Atriplex confertifolia* (Torr. & Frem.) Wats. (shadscale) is a wide spread salt tolerant shrub in the Great Basin region. Wildlife and livestock, especially sheep browse shadscale even though it has spikes. *Kochia Americana* and *A. confertifolia* forms hybrids with *A. canescens, A. garrettii, A. carrettii, A. carrugata* and *A. gardneri* (Welsh et al. 2003). Atriplex species are C_4 photosynthesis plants. Delta values suggest that salinity induces an increase in the bundle sheath leakiness (Sandquist and Ehleringer 1995). Salt bladders function for salt removal in these species (Sen and Rajpurohit 1982; Schirmer and Breckle 1982). Kenagy (1972) indicated that the peripheral tissues of the leaves are hypersaline not the inner tissues. Analysis of the seeds by EDAX analyzes reveals that the seed coat has the highest concentration of sodium, chlorine, potassium and calcium, but the endosperm is low in all elements except phosphorous which is the highest in the embryo (Khan et al. 1987). The best yield in reference to forage value of *A. confertifolia*, was obtained with pure stands (Goodman 1973). *Atriplex gardneri* grows well in the lower saline areas, but *A. gardneri* has to compete with other halophytes that can grow in the lower saline areas.

Kochia americana Wats is an excellent forage for sheep, cattle and deer. It is especially high in protein during the fall (Stubbendieck et al. 2003).

Sarcobatus vermiculatus (greasewood) is usually considered an indicator plant for saline soils. Donovan et al.(1997) found that *S. verminculatus* could accumulate large amounts of leaf Na and still maintain adequate uptake of N, P, K. Ca, and Mg over an extreme salinity gradient (non-saline to highly saline). Mound formation (0.3 m in height) is common with *S. vermiculatus*. Drenovsky and Richards (2003) found that *S. vermiculatus* was able to maintain high leaf nitrogen in spite of high sodium. The plant has very deep roots (nearly 13 m deep). There are two chromosome races (n = 18 and n = 36) with the dipoloid being the common form (Sanderson et al. 1999). Eddleman and Romo (1987) concluded that rapid uptake of Na by the germinating embryos and seedlings is an adaptive mechanism for developing and maintaining a favorable water balance in soils with low osmotic potentials. Dobb and Donovan (1999) suggested that the Na uptake of *Sarcobatus* seedling enhanced its ability to deal with declining psi(s) and to become established in more saline areas (Sen and Rajpurohit 1982). Some seeds of *S. vermiculatus* can germinate in salt solution of 800 mM NaCl. The optimal germination is at a temperature regime of 20/30 °C at all salinity concentrations. But even seeds placed in 1000 mM NaCl for 20 days germinate readily when transferred to distilled water. This indicates that high salinity is not detrimental to the seeds of this species (Khan et al. 2001c). The seed oil indicated that 79 % is unsaturated fatty acids and 21 % saturated (Weber et al. 2001). *S. vermiculatus* is considered a fair forage plant for livestock, big game, small mammals and birds. Soluble oxalates particularly in young twigs can cause mortality in sheep and in rare cases in cattle. The plant has some value as firewood (Gul et al. 2001).

Suaeda torreyana Wats. is present in the salt grass communities. The oil content of the seeds is 25 %. Lipid analysis of the seed oil indicates that 90 % is unsaturated fatty acids and 10 % saturated fatty acids. This mix of saturated and unsaturated fatty acid would make a good quality cooking oil (Weber et al. 2001).

8 Semi-Desert Sagebrush Zone

In the semi-desert sagebrush zone and sagebrush steppe, the dominant shrub would be *Artemisia tridentata*. The three subspecies of *Artemisia tridentata* include A. *tridentata* at low elevations, A. *wyomingensis* at a range of elevations and A. *vaseyana* at intermediate moisture levels and higher elevations (West 1983. Warner et al. 2012).

In the zone at the higher elevations on the mountains, the soils are well formed but in some areas may have high levels of sodium. The most conspicuous shrub species under these conditions is *Atriplex confertifolia* (Trimble 1989). Other perennial species include *Ceratoides lanata, Kochia americana, Artemisia spinescens* and several species of *Atriplex*. Perennial grasses that may be present in the salt gradient include *Sporobolus airoides, Elymus elymoides and Elymus cinereus* (Roundy 1985; Romney and Wallace 1980; Roundy et al. 1989). At the lowest levels of salinity, various species of *Atriplex* and *Ceratoides* may be present (Khan et al. 2004).

9 Exotic Annual Salt Tolerant Species

Perennials plants are dominant in the Great Basin and native annuals are extremely rare. On the other hand, exotic annual species are common and make up the majority of annuals in the Great Basin (Schirmer and Breckle 1982). Some of the exotic annuals are *Bromus tectorumn, Descurainia pinnata, Halogeton glomeratus, Lelpidium perfoliatuym, Malcomia africana* and *Salsola pestifer.* The exotic annual species normally develop when a disturbance such as a fire or overgrazing by cattle occurs. A healthy stand of native perennials can normally compete better than a stand of exotic annuals (Booth 2000).

Bromus tectorumn (June grass) has invaded and is present in large areas of the Great Basin. It grows most often in areas that have been burned by fire. It grows rapidly in the spring and can be grazed by cattle when the plants are tender. Then later in the summer the plants dry out and become a fire hazard. The seeds are not destroyed in a fire and germinate readily when the rains come (Haubensak et al. 2014).

Halogeton glomeratus (Bieb.) C. A. Mey. was introduced into the Great Basin from Eurasia in the early 1930s. *Halogeton* has spread through out the Great Basin area. *Halogeton* is rich in oxalates and if a large amount of the plant is ingested it can change the blood pH of the animal and cause death. Around 1250 sheep died from *Halogeton* poisoning in 1970 (Welsh et al. 2003). The populations of *H. glomeratus* have been reduced by planting more favorable salt tolerant plants (Young 2002). Increased salinity in the soil decreases the percent germination of *H. glomerstus* seeds but 10 % of the seeds can germinate in 800 mM NaCl. In terms of the temperature conditions, the rate of germination was the highest at 25/35 °C and the lowest at 5/15 °C. Germination of *H. glomeratus* seeds was higher in the light than in the dark. Seeds placed in a salt solution for 30 days and then transferred to low salt solution germinated readily (Khan et al. 2001b). The fatty acid content of the seeds was 84 % unsaturated fatty acid and 16 % saturated fatty acids (Weber et al. 2001).

Kochia prostrata (L.) Schrader. (Prostrate Kochia). Kochia is an annual that was introduced from Eurasia and is considered to be good forage. The seeds of *Kochia prostrata* do not mature until late October. The best germination (97 %) of the seeds was obtained after the seeds were air dried and stored for 3 month at 4 °C (Waller et al. 1983). The best germination occurred between 15 and 25 °C. *Kochia prostrata* can grow in highly saline soils (25–38 dSm^{-1}) (Rao et al. 1995). *Kochia prostrate* that were grown in saline soils (17 mmho/cm) accumulated $Na+$ and $Cl-$ contents of 50 and 85 meq/100 g dry matter respectively but the plants showed no salt injury symptoms (Francois 1976).

Kochia scoparia (L.) Schrader (Summer cypress). Annual introduced from Eurasia. *Kochia scoparia* is salt tolerant. The plant produced a high amount of seeds (single plant may produce 15,000 seeds). The best germination occurs at 25/35 °C. The seeds will germinated in a range of salinity up to 100 mM NaCl. Germination was high for seeds transferred from high saline solution to low saline water (Khan et al. 2001a). The oil content of seeds of *K. scoparia* was 10 %. The oil of the seeds was 81 % unsaturated and 19 % saturated fatty acids (Weber et al. 2001). The plant is considered to be good forage and cattle can be fed up to 40 % Kochia in their diet (Lieth and Al Masoom 1993).

Lepidium perfoliatum (L.) (Clasping pepperweed). The plant is native to Europe and Asia.

Salsola pestifer A. Nels. (tumble weed or Russian thistle). The plant was introduced from Russia. Seeds will germinate in a range of salinity (up to 1000 mM NaCl). Germination is inhibited at cooler temperatures whereas warmer nights (25 °C) and days (35 °C) show higher germination. Seeds transferred from salt solutions to low saline water after 20 days germinated readily (Khan et al. 2002b). *Salsola pestifer* is a C_4 photosynthesis halophyte (Glagoleva and Chulanovskaya 1996). In the early spring when the plant is tender, *Salsola pestifer* has fair forage value for cattle and sheep. Biomass yield of *Salsola pestifer* was increased by exposure to saline conditions (Fowler et al. 1988).

Tamarix ramosissimais (saltcedar) is an introduced plant from Eurasia. Tamarix establishes itself along saline and non saline streams. The plant form a thick wall of plant material. Tamarix tends to out compete the native tree, *Populus fremontii* (cottonwood) (Shafroth et al. 1995).

The Great Basin is a great area for halophytes that have adapted to the many saline conditions. Their ability to thrive under saline conditions is impressive.

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Halophytic Flora of Argentina: A Checklist and an Analysis of its Diversity

9

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Abstract

Saline terrestrial areas represent 3.32 % (92,600 km^2) of the Argentine continental territory. Halophytic vegetation is recognized in these regions like edaphic or azonal depending on its association with saline or alkaline soils, not on the ecoregion's climates. The aims of this contribution are: (1) to provide the first preliminary checklist of native vascular plants growing and completing their life cycle for saline continental areas of Argentina, and (2) to determine its endemism's, life forms and the ecoregions where these halophytes have been collected. A total of 673 halophytic taxa within 291 genera and 64 families of vascular plants were recorded in the various saline habitats of Argentina, 23.17 % of them are endemics. The halophytic flora represents 6.49 % of the total vascular flora of Argentina. Diversity shows a decreasing tendency from those geosystems that are less affected by hydro-halomorphic processes to those physically characterized by the maximum expression of the flooding-salinization processes. Historical factors along with occupational factors may have contributed in defining the current floristic pattern. Temporal fluctuations in depth, electrical conductivity and ionic composition of groundwater, are the main environmental factors determin-

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M.A. Khan et al. (eds.), *Sabkha Ecosystems Volume V: The Americas*,
Tasks for Vegetation Science 48, DOI 10.1007/978-3-319-27093-7_9

ing the compositional variation of the saline vegetation of the country. Nearly all halophytes are flowering plants, only 0.30 % correspond to Ferns. Dicots comprised 67.31 % of the total (453 taxa in 48 families), while the remainder consisted of 216 taxa of Monocots (14 families), and only two Gymnosperm species. The family with the highest number of genera was: Asteraceae (53) followed by Poaceae (50), Fabaceae (21), Amaranthaceae (13), Solanaceae and Cactaceae (11), and Verbenaceae (10). The most represented genera are *Atriplex* (19), *Lycium* (18 taxa), *Senecio* (16), *Chloris* (12), *Baccharis* (12), *Deyeuxia* and *Hordeum* (11), *Heliotropium* (10), *Gomphrena*, *Sporobolus, Solanum* and *Prosopis* (9), Grindelia (8), *Distichlis, Junellia*, *Glandularia* (7) and *Euphorbia*, *Aristida*, *Eragrostis* and *Festuca* with 6 species. Regarding the life-form forms spectra, Hemicryptophytes are the predominant life-form and constitute 52.9 % of all recorded species, followed by Chamaephytes (21.84 %), Therophytes (10.10 %), Phanerophytes (7.13 %), Geophytes (5.79 %), Succulents (2.08 %), and Parasites (0.15 %). In the study area, the largest number of taxa was found in the Dry Chaco (26.95 %) followed by Espinal (18.31 %), Pampa (11.97 %), Patagonian Steppe (8.01 %), Puna (6.97 %), Monte of Plains and Plateaus (9.69 %), Humid Chaco (4.57 %), High Andes (4.06 %), Monte of Hills and Valleys (3.12 %), Iberá Marshes (2.81 %), Paraná Flooded Savanna (2.71 %), and Mesopotamian Savanna (0.83 %). When comparing the distribution of total endemics between the different ecoregions, Dry Chaco (33.65 %), appeared with the highest values followed Monte of Plains and Plateaus (18.27 %), Espinal (16.35 %); Patagonian Steppe (12.02 %), Puna (8 %) and Pampa (7.2 %). Surprisingly the number of halophytic taxa that grows in Argentina is very high, representing nearly 22 % of the total number cited for the world.

1 Introduction

Argentina is the most extensive temperate country in South America. A large part of its biodiversity can be attributed to the fact that different biogeographical regions converge in this territory (Zuloaga et al. 1999). The wide expanse of its continental area (2,791,810 km^2) and its varied topographical, climatic and vegetation features are essential to the formation of one of the most diverse floras in the southern Neotropics.

Argentina is bordered by Uruguay, Brazil and the Atlantic Ocean to the east, Paraguay and Bolivia to the north and Chile to the west (Fig. 9.1). The country is characterized by a wide range of macrohabitats across elevation and climatic gradients, from 7000 m above sea level to the coastal plains and from subtropical to polar climates. Different ecoregions have been recognized among these macrohabitats: Dry Chaco, Espinal, High Andes, Humid Chaco, Iberá Marshes, Mesopotamian Savanna, Monte of Hills and Valleys, Monte of Plains and Plateaus, Pampa, Paraná Flooded Savanna, Paranaense Forest, Patagonian Forest, Patagonian Steppe, Puna and Yungas Forest (Burkart et al. 1999) (Fig. 9.1).

Argentina is also one of the 25 most diverse countries in the world due to its species richness and endemism (Caldecott et al. 1996). The northeast and northwest regions of Argentina have the highest number of families, genera and species, with Misiones and Salta being the most important provinces (Zuloaga et al. 1999). With a rich endemic flora, Argentina has 9938 species, distributed in 274 families and 2000 genera of which 1760 species are endemic (Zuloaga et al. 2008).

There are approximately 147 million ha of saline soils in the Americas (Szabolcs 1989).

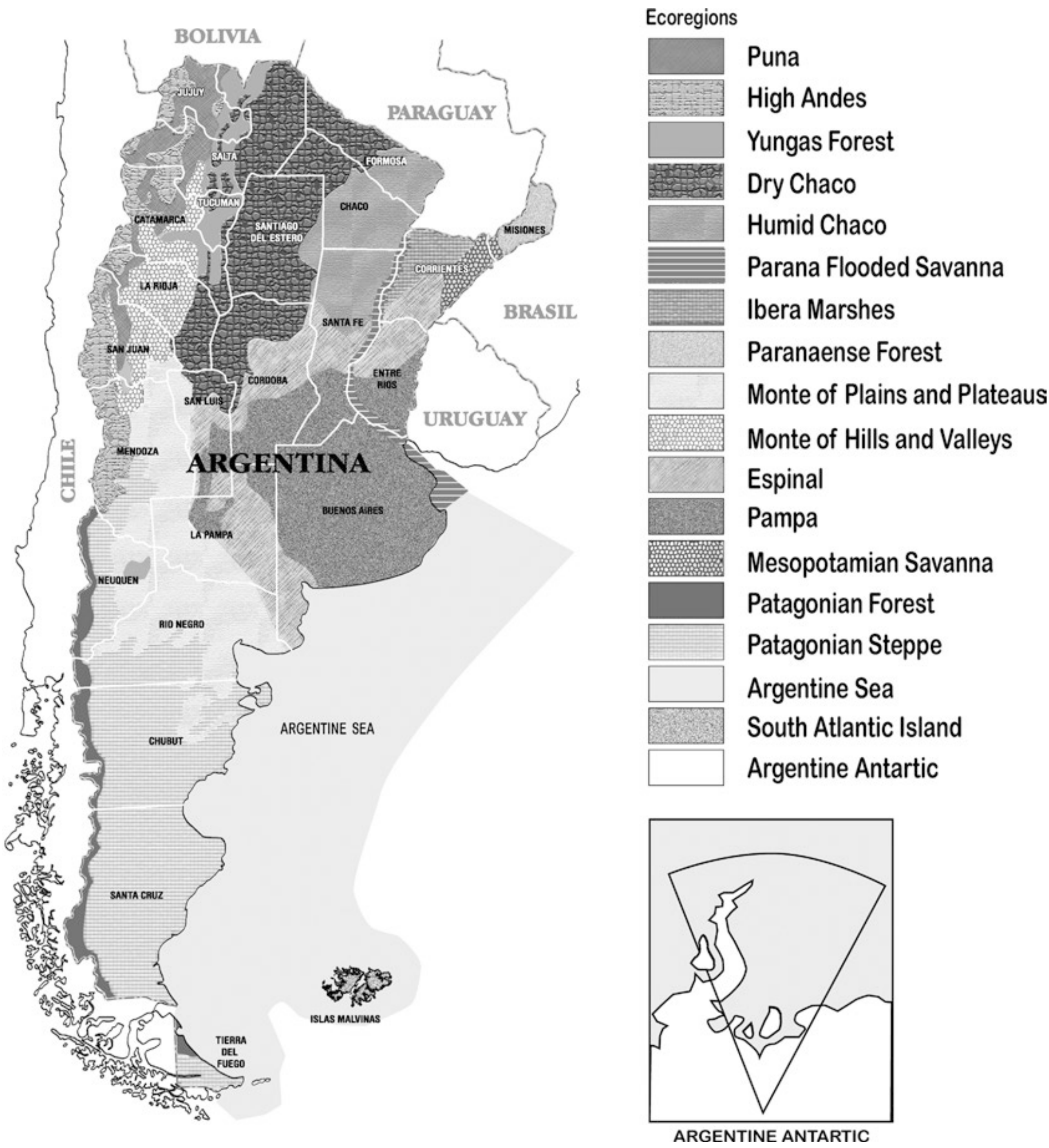

Fig. 9.1 Ecoregions of Argentina (Modified from Burkart et al. 1999)

Saline terrestrial areas represent 3.32 % (92,600 km^2) of the Argentine continental territory (INTA 2015) and are mainly present in: Puna (Fig. 9.2), Dry Chaco, Monte of Plains and Plateaus, Monte of Hills and Valleys, Patagonian Steppe, Espinal and Pampa ecoregions. Halophytic vegetation is recognized in these ecoregions, such as edaphic or azonal areas, depending on its association with saline or alcaline soils rather than the ecoregional climates (Figs. 9.3, 9.4 , and 9.5).

Continental evaporitic environments of Argentina are also important habitats for many endemic halophytes. They are represented by Miocene facies from the Bolivian border to the Mendoza province, as well as Quaternary deposits from the Puna to Patagonia. Two main saline environments are recognized: (a) Pampean (between Catamarca and Buenos Aires provinces), and (b) Patagonian (Fig. 9.1). In general, shallow saline deposits, with sodium chloride

Fig. 9.2 Carachi Pampa Salar, near Antofagasta de la Sierra, Catamarca Province, Argentina (Puna Ecoregion)

and sulfate, are present. The Puna is considered as an "Evaporite Province" with deep natural salt pans (Alonso 2005).

Large surfaces of the interior of the country are arid and have internal drainage. This situation is favorable to the formation of a wide diversity of lake water chemistry and playas. Saline and hypersaline lakes form the largest group in northwestern and central Argentina and in the Patagonian Plateau. In most of the saline and salt lakes situated in the central and northwestern arid regions of Argentina the major ions are Na^+ and Cl^-, originally old sea salt (Quiros and Drago 1999). Halophytic flora grows around these lakes and represents the main biological component of these saline ecosystems.

In some regions the area occupied by halophytic vegetation is very large, for instance in central Argentina, with 9 % of their landscapes being affected by hydrohalomorphic processes. In these environments the natural vegetation clearly reveals its dual ecological and stabilizing role, and it is also an indicator of soil productivity (Cantero et al. 1998a, b).

Even though considerable attention has been given to the vegetation of saline areas of Argentina for many years (Hauman-Merck 1913; Ringuelet 1939; Ragonese and Covas 1947; Vervoorst 1950, 1967; Ragonese 1951; Morello 1958; Sayago 1969; Anderson et al. 1970; Roig 1972; Bocher et al. 1972; León 1975; Lewis and Collantes 1975; Lewis et al. 1976, 1984, 1985; Cabrera 1976; Ragonese and Piccinini 1977; León et al. 1979; Cano 1980; Perelman et al. 2001; Bordon 1983; Burkart et al. 1990; Carnevali et al. 1987; Kruger and Peinemann 1996; Cantero et al. 1996, 1998a, b; Cantero and León 1996, 1999; Cantero and Petryna 1998; Karlin et al. 2011) a complete catalogue of the halophilous flora has not been yet produced.

Martínez Carretero (2001) proposed a syntaxonomical scheme of the Argentine saline vegetation. He recognized two classes and three orders in each one (Class *Salicornietea perennis*: O. *Sarcocornietalia perennis*, O. *Lepydophylletalia cupressiformae* and O. *Distichlietalia spicatae*; Class *Suaedetea divaricatae*: O. *Stenodrepano-Prosopietalia reptantis*, O. *Cortesio-*

Prosopietalia strombuliferae and O. *Lycio-Sporoboletum*) but a floristic description of the compositional variation of each of these categories was not undertaken.

By setting a dividing line between halophytes and glycophytes (salt sensitive plants) at a salt concentration of ~80 mM NaCl (a conductivity in the soil solution of 7.8 dS m^{-1}), Aronson (1989) listed ca. 1550 salt-tolerant plants. Using the same definition, Menzel and Lieth (2003) recorded ca. 2600 species.

Accordingly to the most recently interactive version of the initial Aronson's HALOPH, the eHALOPH database (compiled at http://www.sussex.ac.uk/affiliates/halophytes, Ventura et al. 2015) and using as filters all families, photosynthesis pathways, plant types, values of conductivity and salt glands as defaults of this database, a total of 469 species were recorded for Argentina, nevertheless many of them are non native or they are not integrated in the flora of the country and must be excluded.

The aims of this contribution are: (1) to provide the first preliminary checklist of native vascular plants growing and completing their life cycle in saline areas of continental Argentina, and (2) to determine its endemism, life forms and the ecoregions where these halophytes have been collected.

2 Materials and Methods

The area selected is the whole continental territory of Argentina, comprising the 24 provinces, covering an area of approximately 2,791,810 km^2. The Argentine territory in the Antarctic continent and its southern islands has not been considered in this contribution (Fig. 9.1).

For our purposes, the most accepted definition of halophytes is: plants that complete their life cycle in saline habitats (Flowers et al. 2010) which was accepted and used to evaluate the inclusion of different taxa in the checklist. Only the native taxa that grow in Argentina were included. The taxonomic information was compiled from different floristic and taxonomical works (Hauman-Merck 1913; Ringuelet 1939; Ragonese and Covas 1947; Vervoorst 1950, 1967; Ragonese 1951; Morello 1958; Sayago 1969; Anderson et al. 1970; Bocher et al. 1972; Roig 1972; León 1975; Lewis and Collantes 1975; Lewis et al. 1976, 1984, 1985; Cabrera 1976; Ragonese and Piccinini 1977; León et al. 1979; Cano 1980; Perelman et al. 2001; Bordon 1983; Burkart et al. 1990; Carnevali et al. 1987; Kruger and Peinemann 1996; Cantero et al. 1996, 1998a, b; Cantero and León 1996, 1999; Cantero and Petryna 1998). Selected target flowering plant taxa were those that grow for certain in saline areas. All the available information of the species in the country has been compiled and arranged systematically, mainly from the collections compiled in the database Documenta Florae Australis (http://www2.darwin.edu.ar/iris/), with additional collections from other herbaria in Argentina (CORD and RIOC).

Verification of the current names of species was carried out using the following data bases: Tropicos (http://www.mobot.org), International Plant Names Index (http://www.ipni.org/index.html), and Documenta Florae Australis (http://www2.darwin.edu.ar/iris/).

The circumscription of the flowering plant families is according to APG III (APG 2009). The list of taxa is arranged in an alphabetical sequence of families, genera and species.

The following data were included: status (endemic or native), life-forms, ecoregions according to Burkart et al. (1999), a selected reference site where the species was collected (first province, then locality), and figures of some obligate and representative halophytes. Categories of halophyte types were not considered in this preliminary checklist. The status of the species was taken from Documenta Florae Australis (http://www2.darwin.edu.ar/Proyectos/FloraArgentina/BuscarEspecies.asp) database; the endemic category refers to distribution in Argentina. The life-form was determined from information on the labels and *in situ* observations, when possible, and the terminology of Raunkiaer (1934) was used.

3 Results and Discussion

A total of 673 halophytic taxa within 291 genera and 64 families of vascular plants were recorded in the various saline habitats of Argentina (Appendix) and 23.17 % of them are endemics. The halophytic flora represents 6.49 % of the total vascular flora of Argentina.

Diversity shows a decreasing tendency, from those geosystems that are less affected by hydrohalomorphic processes to those physically characterized by the maximum expression of the flooding-salinization processes. Historical factors along with occupational factors may have contributed in defining the current floristic pattern. Temporal fluctuations in depth, electrical conductivity and ionic composition of groundwater are the main environmental factors determining the compositional variation of the saline vegetation of the country.

Nearly all halophytes are flowering plants, only 0.30 % correspond to Ferns (Table 9.1). Dicots comprised 67.31 % of the total (453 taxa in 48 families), while the remainder consists of 216 taxa of Monocots (14 families), and there are only two Gymnosperm species.

The family with the highest number of genera was: Asteraceae (53), followed by Poaceae (50), Fabaceae (21), Amaranthaceae (13), Solanaceae and Cactaceae (11), and Verbenaceae (10). However, regarding the number of taxa, the order of importance changes: Poaceae (170), Asteraceae (121), Amaranthaceae (48), Solanaceae (45), and Fabaceae (34) and Verbenaceae (26) (Table 9.2).

The most represented genera are *Lycium* and *Atriplex* (19 taxa), *Senecio* (16), *Chloris* (12),

Table 9.1 Major clades of halophytes vascular plants of Argentina and its composition

Groups	Family	Genus	Species and infraspecific taxa	% Species and infraspecific taxa
FERNS	1	1	2	0.30
GYMNOSPERMAE	1	1	2	0.30
MONOCOTYLEDONEAE	14	76	216	32.09
DICOTYLEDONEAE	48	213	453	67.31
Total	**64**	**291**	**673**	100.00

Table 9.2 Composition of the most numerous families, genera and species of the halophytic flora of Argentina

Family	Genera	Species and infraspecific taxa	(%) Species and infraspecific taxa
Poaceae	50	170	25.26
Asteraceae	53	121	17.97
Amaranthaceae	13	48	7.13
Solanaceae	11	45	6.68
Fabaceae	21	34	5.05
Verbenaceae	10	26	3.86
Cyperaceae	8	18	2.67
Cactaceae	11	17	2.52
Boraginaceae	5	14	2.08
Malvaceae	7	13	1.93
Brassicaceae	6	13	1.93
Apiaceae	6	12	1.78
Euphorbiaceae	5	11	1.63
Caryophyllaceae	4	10	1.48
Zygophyllaceae	4	8	1.18
Convolvulaceae	4	8	1.18
Amaryllidaceae	3	7	1.04
Portulacaceae	4	7	1.04

Baccharis (12), *Deyeuxia* and *Hordeum* (11), *Heliotropium* (10), *Prosopis* (9), *Gomphrena*, *Sporobolus, Grindelia* and *Solanum* (8), *Distichlis, Junellia*, *Glandularia* (7) and *Euphorbia*, *Aristida*, *Eragrostis* and *Festuca* with 6 species (Appendix).

Interestingly, and in comparison with northern hemisphere halophytic floras, the Solanaceae family is very important, not only due to the high representation within their genera, but also with the species (e.g. *Lycium* also occurs in the northern hemisphere but as a glycophyte / xerophyte, not as a halophyte).

Regarding the life-form spectra, Hemicryptophytes are the predominant life-form and constitute 52.9 % of all recorded species, followed by Chamaephytes (21.84 %), Therophytes (10.10 %), Phanerophytes (7.13 %), Geophytes (5.79 %) and Succulents (2.08 %) and Parasites (0.15 %).

In the study area, the largest number of taxa was found in the Dry Chaco (26.95 %) followed by the Espinal (18.31 %), Pampa (11.97 %), Patagonian Steppe (8.01 %), Puna (6.97 %), Monte of Plains and Plateaus (9.69 %), Humid Chaco (4.57 %), High Andes (4.06 %), Monte of Hills and Valleys (3.12 %), Iberá Marshes (2.81 %), Paraná Flooded Savanna (2.71 %), and Mesopotamian Savanna (0.83 %). When comparing the distribution of all the endemics between the different ecoregions, the Dry Chaco (33.65 %) showed the highest value, followed by Monte of Plains and Plateaus (18.27 %), Espinal (16.35 %), Patagonian steppe (12.02 %), Pampa (7.52 %), Puna (3.85 %) and Monte of Hills and Valleys (3.85 %) (Appendix).

Surprisingly the number of halophytic taxa that grows in Argentina is very high, representing nearly 22 % of the total number cited for the world (Khan and Duke 2001) and, for example, the same as for the whole Mediterranean climatic zone (Choukr-Allah 1991). The rich endemic halophyte flora of Argentina is also important and calls for urgent, cautious studies on the conservation of the very particular, invaluable and unprotected southernmost saline habitats of America where these species are found.

Appendix

List of halophytic taxa of Argentina with its status, life forms, and ecoregions and reference site where they grows

Family	Genus	Species	Status	Life form	Ecoregions	Reference site
Acanthaceae	Justicia	J. gilliesii (Nees) Benth.	Endemic	Chamaephyte	Dry Chaco	Córdoba, Salinas Grandes
	Ruellia	R. simplex Wright	Native	Chamaephyte	Espinal	Córdoba, Mar Chiquita
Aizoaceae	Sesuvium	S. portulacastrum (L.) L.	Native	Hemicryptophyte	Dry Chaco, Pampa	Buenos Aires, Arroyo Saladillo & NR 205
	Trianthema	T. argentina Hunz. & Cocucci	Endemic	Therophyte	Monte of Hills and Valleys	La Rioja, near Los Colorados
Alismataceae	Sagittaria	S. montevidensis Cham. & Schltdl. subsp. montevidensis	Native	Geophyte	Espinal	Córdoba, Laguna La Salada
Alliaceae	Tristagma	T. ameghinoi (Speg.) Speg.	Native	Hemicryptophyte	Patagonian Steppe	Chubut, Salina El Molle
		T. patagonicum (Baker) Traub	Native	Hemicryptophyte	Patagonian Steppe	Chubut, Valle del Lago Blanco
Amaranthaceae	Allenrolfea	A. patagonica (Moq.) Kuntze	Endemic	Chamaephyte	Dry Chaco, Espinal, Monte of Plains and Plateaus	Catamarca, Salinas Grandes
		A. vaginata (Griseb.) Kuntze	Endemic	Chamaephyte	Dry Chaco, Espinal, Monte of Hills and Valleys, Monte of Plains and Plateaus	Córdoba, Mar Chiquita
	Alternanthera	A. nodifera (Moq.) Griseb.	Native	Hemicryptophyte	Dry Chaco	Córdoba, Salinas Grandes
		A. paronychioides A. St.-Hil. subsp. chacoënsis (Morong ex Morong & Britton) Pedersen	Native	Hemicryptophyte	Dry Chaco	Formosa, La Rinconada
	Amaranthus	A. muricatus (Moq.) Hieron.	Native	Hemicryptophyte	Espinal, Monte of Hills and Valleys	Catamarca, Belén
		A. standleyanus Parodi ex Covas	Native	Therophyte	Dry Chaco	Santiago del Estero, Salinas Grandes

	Atriplex	A. argentina Speg.	Endemic	Chamaephyte	Dry Chaco, Espinal, Monte of Plains and Plateaus	Buenos Aires, Salitral de la Vidriera
		A. boecheri Aellen	Endemic	Chamaephyte	Monte of Plains and Plateaus	Mendoza, Salinas del Diamante
		A. cordobensis Gand. & Stuck. subsp. cordobensis	Endemic	Chamaephyte	Dry Chaco, Espinal	Córdoba, Mar Chiquita
		A. cordobensis Gand. & Stuck. subsp. grandibracteata Múlgura	Endemic	Chamaephyte	Dry Chaco, Puna	Jujuy, Salinas Grandes
		A. crenatifolia Chodat & Wilczek	Endemic	Chamaephyte	Monte of Plains and Plateaus	San Luis, Salinas del Bebedero
		A. deserticola Phil.	Native	Chamaephyte	Dry Chaco, Puna	Jujuy, Salinas Grandes
		A. imbricata (Moq.) D. Dietr. var. imbricata	Native	Chamaephyte	Puna	Salta, Salar de Pocitos
		A. lampa (Moq.) D. Dietr.	Endemic	Chamaephyte	Dry Chaco, Monte of Plains and Plateaus, Patagonian Steppe	San Juan, Salina de Mascasín
		A. lithophila A. Soriano	Endemic	Chamaephyte	Dry Chaco	La Rioja, Salina de Mascasín
		A. mendozensis Speg.	Endemic	Chamaephyte	Monte of Plains and Plateaus	Mendoza, NR 7, km 913
		A. montevidense Spreng.	Native	Chamaephyte	Dry Chaco, Mesopotamian Savanna, Pampa, Patagonian Steppe	Chubut, Salina Chica, Península Valdés
		A. nitrophiloides A. Soriano ex Múlgura	Native	Chamaephyte	Puna	Jujuy, Laguna de los Pozuelos
		A. oreophila Phil.	Native	Therophyte	Monte of Plains and Plateaus	Mendoza, Atuel
		A. pamparum Griseb.	Native	Chamaephyte	Dry Chaco, Pampa	Tucumán, El Puestito
		A. patagonica (Moq.) D. Dietr.	Endemic	Chamaephyte	Patagonian Steppe	Chubut, Salina Grande, Península Valdés
		A. quixadensis Del Vitto, Múlgura & Petenatti	Endemic	Chamaephyte	Dry Chaco	San Luis, NP Sierra de las Quijadas

(continued)

Family	Genus	Species	Status	Life form	Ecoregions	Reference site
		A. sagittifolia Speg.	Endemic	Chamaephyte	Patagonian Steppe	Patagonia Occidental
		A. spegazzinii A. Soriano ex Múlgura	Endemic	Chamaephyte	Monte of Plains and Plateaus	San Juan, 40 km S from Caucete
		A. undulata (Moq.) D. Dietr.	Endemic	Chamaephyte	Espinal	Buenos Aires, Bahía Blanca Estuary
	Chenopodium	C. parodii Aellen	Endemic	Therophyte	Patagonian Steppe	Chubut, Estancia Quichaura-Tecka
	Gomphrena	G. boliviana Moq. f. boliviana	Native	Therophyte	Dry Chaco	La Rioja, El Quicho
		G. elegans Mart. var. mesopotamica Pedersen	Endemic	Hemicryptophyte	Espinal	Corrientes, NR 14, before the Río Mocoretá
		G. martiana Gillies ex Moq. var. martiana	Native	Therophyte	Dry Chaco	Córdoba, Salinas Grandes
		G. mendocina (Phil.) R.E. Fr. subsp. mendocina	Endemic	Therophyte	Dry Chaco	San Juan, Salina de Mascasín
		G. perennis L. var. perennis	Native	Hemicryptophyte	Espinal	Entre Ríos, Ombúes to El Yunque
		G. pulchella Mart. subsp. pulchella	Native	Hemicryptophyte	Espinal	Santa Fe, Río Salado
		G. tomentosa (Griseb.) R.E. Fr. var. ruiz-lealii Subils & Hunz.	Native	Hemicryptophyte	Monte of Hills and Valleys	San Juan, Ischigualasto
		G. tomentosa (Griseb.) R.E. Fr. var. tomentosa	Native	Hemicryptophyte	Dry Chaco	Catamarca, Salinas Grandes
	Heterostachys	H. olivascens (Speg.) Speg.	Endemic	Chamaephyte	Dry Chaco, Monte of Plains and Plateaus	Río Negro, PR 58, 17 km N from intersection with PR 61
		H. ritteriana (Moq.) Ung.-Sternb.	Native	Chamaephyte	Dry Chaco, Espinal, Monte of Plains and Plateaus	Mendoza, Pampa Amarilla
	Holmbergia	H. tweedii (Moq.) Speg.	Native	Chamaephyte	Dry Chaco, Espinal	Córdoba, Mar Chiquita

	Nitrophila	N. australis Chodat & Wilczek var. australis	Endemic	Hemicryptophyte	Monte of Hills and Valleys	Catamarca, Santa María
		N. australis Chodat & Wilczek var. kuntzei (Ulbr.) A. Soriano	Endemic	Chamaephyte	Patagonian Steppe	Patagonia Occidental
	Oxybasis	O. macrosperma (Hook. f.) S. Fuentes, Uotila & Borsch	Native	Therophyte	Espinal, Pampa	San Luis, Laguna Sayape
	Pfaffia	P. glomerata (Spreng.) Pedersen	Native	Hemicryptophyte	Dry Chaco	Salta, 54 km NE from J.V.González, road to Puerta Blanca
	Sarcocornia	S. ambigua (Michx.) M.A. Alonso & M.B. Crespo	Native	Chamaephyte	Dry Chaco, Pampa, Monte of Plains and Plateaus, Patagonian Steppe	Tierra del Fuego, Bahía de San Sebastián
		S. neei (Lag.) M.A. Alonso & M.B. Crespo	Native	Chamaephyte	Pampa	Buenos Aires, Arroyo Las Garzas & NR 205
	Suaeda	S. argentinensis A. Soriano	Native	Chamaephyte	Espinal, Patagonian Steppe	Chubut, Salina Grande, Península Valdés
		S. densiflora A. Soriano ex Giusti	Endemic	Therophyte	Espinal	Buenos Aires, Laguna La Salada
		S. divaricata Moq (Fig. 9.6)	Native	Chamaephyte	Dry Chaco, Monte of Plains and Plateaus, Patagonian Steppe	Córdoba, Salinas Grandes
		S. neuquenensis M.A. Alonso, Conticello & Cerazo	Endemic	Therophyte	Monte of Plains and Plateaus	Neuquén, Los Barreales
		S. patagonica Speg.	Native	Therophyte	Espinal, Pampa, Patagonian Steppe	Buenos Aires, Laguna La Salada

(continued)

Family	Genus	Species	Status	Life form	Ecoregions	Reference site
Amaryllidaceae	Habranthus	H. andalgalensis Ravenna	Endemic	Geophyte	Dry Chaco	Córdoba, Salinas Grandes
		H. gracilifolius Herb.	Native	Geophyte	Dry Chaco, Pampa	Córdoba, Salinas Grandes
		H. jamesonii (Baker) Ravenna	Endemic	Geophyte	Espinal	Buenos Aires, Salitral de la Vidriera
	Hieronymiella	H. clidanthoides Pax	Endemic	Hemicryptophyte	Dry Chaco	La Rioja, Guayapas
		H. speciosa (R.E. Fr.) Hunz.	Endemic	Hemicryptophyte	Puna	Jujuy, Salinas Grandes
	Rodophiala	R. mendocina (Phil.) Ravenna	Endemic	Geophyte	Monte of Plains and Plateaus	La Pampa, La Reforma
	Zephyranthes	Z. mesochloa Herb. ex Lindl.	Native	Geophyte	Humid Chaco	Chaco, Resistencia
Anacampserotaceae	Grahamia	G. bracteata Hook. & Arn. (Fig. 9.7)	Endemic	Chamaephyte	Dry Chaco, Espinal, Monte of Plains and Plateaus	Buenos Aires, Bahía Blanca Estuary
Anacardiaceae	Schinus	S. johnstonii F.A. Barkley	Endemic	Phanerophyte	Espinal	Entre Ríos, Estancia La Vascongada
		S. longifolius (Lindl.) Speg. var. longifolius	Native	Phanerophyte	Iberá Marshes	Corrientes, Lomas de González
Apiaceae	Apium	A. commersonii DC.	Native	Hemicryptophyte	Dry Chaco, Pampa	Buenos Aires, Partido of La Plata
		A. sellowianum H. Wolff	Native	Therophyte	Espinal, Iberá Marshes, Pampa, Paraná Flooded Savanna	Corrientes, Santa Lucía, Salinas Grandes
	Azorella	A. trifurcata (Gaertn.) Pers.	Native	Hemicryptophyte	Monte of Plains and Plateaus	Mendoza, Atuel
	Cyclospermum	C. leptophyllum (Pers.) Sprague var. leptophyllum	Native	Hemicryptophyte	Espinal	Santa Fe, NR 19 & road to Iturraspe
	Eryngium	E. chubutense Neger ex Dusén	Endemic	Hemicryptophyte	Espinal	Santa Fe, NR 19 & road to Iturraspe
		E. coronatum Hook. & Arn.	Native	Hemicryptophyte	Dry Chaco, Espinal, Iberá Marshes, Paraná Flooded Savanna	Tucumán, Santa Rosa de Leales
		E. ebracteatum Lam.	Native	Hemicryptophyte	Espinal, Pampa	Córdoba, PR 17, near La Para

		E. eburneum Decne.	Native	Hemicryptophyte	Pampa	Buenos Aires, Depresión del Salado
		E. echinatum Urb.	Native	Hemicryptophyte	Pampa, Paraná Flooded Savanna	Entre Ríos, Victoria Department
		E. nudicaule Lam.	Native	Hemicryptophyte	Espinal	Santa Fe, road to Esperanza, Río Salado
	Hydrocotyle	H. bonariensis Lam.	Native	Geophyte	Espinal	Santa Fe, Las Colonias Department
	Mulinum	M. spinosum (Cav.) Pers.	Native	Hemicryptophyte	Patagonian Steppe	Chubut, Salina Chica, Península Valdés
Apocynaceae	Araujia	A. odorata (Hook. & Arn.) Fontella & Goyder	Native	Chamaephyte	Dry Chaco	Córdoba, Salinas Grandes
	Aspidosperma	A. quebracho-blanco Schltdl.	Native	Phanerophyte	Dry Chaco, Espinal	La Rioja, Salina de Mascasín
	Metastelma	M. tubatum Griseb.	Endemic	Chamaephyte	Dry Chaco	Córdoba, Salinas Grandes
	Philibertia	P. gilliesii Hook. & Arn.	Native	Chamaephyte	Dry Chaco	Córdoba, Salinas Grandes
	Tweedia	T. brunonis Hook. & Arn.	Native	Chamaephyte	Dry Chaco	Córdoba, Salinas Grandes
Asteraceae	Acmella	A. decumbens (Sm.) R.K. Jansen var. decumbens	Native	Hemicryptophyte	Pampa	Buenos Aires, Tolosa
		A. grisea (Chodat) R.K. Jansen	Native	Hemicryptophyte	Espinal	Corrientes, NR 126, 47 km NW from Sauce
		A. pusilla (Hook. & Arn.) R.K. Jansen	Native	Hemicryptophyte	Mesopotamian Savanna	Corrientes, Paso Naranjito
	Ambrosia	A. tenuifolia Spreng.	Native	Hemicryptophyte	Espinal, Pampa	Córdoba, Mar Chiquita
	Angelphytum	A. aspilioides (Griseb.) H. Rob.	Native	Hemicryptophyte	Dry Chaco	Formosa, Las Lomitas
	Austrobrickellia	A. patens (D. Don ex Hook. & Arn.) R.M. King & H. Rob. var. tomentosa (Hieron.) Ariza & S.E. Freire	Native	Chamaephyte	Dry Chaco	Córdoba, Salinas Grandes
	Austroespatorium	A. inulifolium (Kunth) R.M. King & H. Rob.	Native	Chamaephyte	Dry Chaco	Santiago del Estero, PR 5, Pto. El Saladillo

(continued)

Family	Genus	Species	Status	Life form	Ecoregions	Reference site
	Baccharis	B. acaulis (Wedd. ex R.E. Fr.) Cabrera	Native	Chamaephyte	Puna	Salta, Minas de Sijes
		B. articulata (Lam.) Pers.	Native	Chamaephyte	Dry Chaco	Santiago del Estero, Belgrano Department
		B. crispa Spreng.	Native	Chamaephyte	Espinal, Pampa	San Luis, Saladillo
		B. darwinii Hook. & Arn.	Native	Chamaephyte	Dry Chaco, Espinal, Humid Chaco, Monte of Plains and Plateaus, Pampa, Patagonian Steppe	Tucumán, Chañar Pozo
		B. divaricata Hauman	Endemic	Chamaephyte	Patagonian Steppe	Chubut, Salina Grande, Península Valdés
		B. dracunculifolia DC.	Native	Chamaephyte	Humid Chaco	Chaco, Pto. Tirol
		B. glutinosa Pers.	Native	Chamaephyte	Dry Chaco, Monte of Hills and Valleys	San Juan, around the airport
		B. juncea (Cass.) Desf.	Native	Chamaephyte	Espinal, Pampa, Patagonian Steppe, Puna	La Pampa, between El Carancho & Acha
		B. phyteuma Heering	Endemic	Chamaephyte	Pampa	Buenos Aires, between Tolosa & Ensenada
		B. salicifolia (Ruiz & Pav.) Pers.	Native	Chamaephyte	Dry Chaco, Espinal	Córdoba, Arroyo Plujunta, between Balnearia & Marull
		B. spartioides (Hook. & Arn. ex DC.) J. Remy	Native	Chamaephyte	Dry Chaco, Espinal, Monte of Hills and Valleys, Monte of Plains and Plateaus, Patagonian Steppe	Mendoza, Pampa Amarilla
		B. tenella Hook. & Arn. (Fig. 9.8)	Endemic	Chamaephyte	Dry Chaco, Espinal, Patagonian Steppe	Córdoba, Salinas Grandes
	Barrosoa	B. candolleana (Hook. & Arn.) R.M. King & H. Rob.	Native	Hemicryptophyte	Espinal	Córdoba, Jeanmaire
	Chaetanthera	C. lanata (Phil.) I.M. Johnst.	Native	Hemicryptophyte	Puna	Reserva de San Guillermo, Río de la Sal
		C. revoluta (Phil.) Cabrera	Native	Therophyte	Puna	La Rioja, General Sarmiento, 13 km E from Salina del Leoncito

	Chaptalia	C. integerrima (Vell.) Burkart	Native	Hemicryptophyte	Humid Chaco	Santiago del Estero, Lagunas Saladas, between PR 56 & Los Juríes
	Chromolaena	C. arnottiana (Griseb.) R.M. King & H. Rob.	Native	Chamaephyte	Espinal	Córdoba, Jeanmarie
		C. christieana (Baker) R.M. King & H. Rob.	Native	Chamaephyte	Dry Chaco	Formosa, ca. 30 km SW Va. Gral. Güemes
		C. hirsuta (Hook. & Arn.) R.M. King & H. Rob.	Native	Chamaephyte	Humid Chaco	Santiago del Estero, Lagunas Saladas, between PR 56 & Los Juríes
		C. squarroso-ramosa (Hieron.) R.M. King & H. Rob.	Native	Hemicryptophyte	Dry Chaco, Espinal	Salta, 17 km E from El Galpón
	Chuquiraga	C. atacamensis Kuntze	Native	Chamaephyte	Puna	Jujuy, along NR 40 to El Moreno
		C. aurea Skottsb.	Endemic	Chamaephyte	Patagonian Steppe	Río Negro, 52 km SW from Los Menucos in direction to Ing. Jacobacci
		C. avellanedae Lorentz	Endemic	Chamaephyte	Patagonian Steppe	Chubut, Salina Grande, Península Valdés
		C. erinacea D. Don subsp. erinacea	Endemic	Chamaephyte	Espinal, High Andes, Patagonian Steppe	Buenos Aires, Salitral de la Vidriera
		C. erinacea D. Don subsp. hystrix (Don) C. Ezcurra	Endemic	Chamaephyte	Monte of Plains and Plateaus	Mendoza, Salinas del Diamante
	Conyza	C. blakei (Cabrera) Cabrera	Native	Therophyte	Patagonian Steppe	Chubut, Salina Grande, Península Valdés
		C. bonariensis (L.) Cronquist var. angustifolia (Cabrera) Cabrera	Native	Therophyte	Espinal	Córdoba, Mar Chiquita
		C. laevigata (Rich.) Pruski	Native	Therophyte	Espinal	Buenos Aires, Salitral de la Vidriera
		C. lorentzii Griseb.	Native	Therophyte	Espinal	Córdoba, Mar Chiquita
	Cotula	C. mexicana (DC.) Cabrera	Native	Therophyte	Dry Chaco	Córdoba, Pampa de Achala
	Cyclolepis	C. genistoides D. Don	Native	Phanerophyte	Dry Chaco, Espinal, Monte of Plains and Plateaus, Patagonian Steppe	Catamarca, Salinas Grandes

(continued)

Family	Genus	Species	Status	Life form	Ecoregions	Reference site
	Doniophyton	D. anomalum (D. Don) Kurtz	Native	Phanerophyte	Monte of Plains and Plateaus	Mendoza, Salinas del Diamante
	Eiachaenium	E. magellanicum Sch. Bip.	Native	Hemicryptophyte	Patagonian Steppe	Santa Cruz, Estancia Las Vegas, Río Coyle
	Flaveria	F. bidentis (L.) Kuntze	Native	Therophyte	Dry Chaco, Espinal, Monte of Plains and Plateaus	Santiago del Estero, around Termas de Río Hondo
		F. haumanii Dimitri & Orfila	Native	Therophyte	Espinal, Humid Chaco	Córdoba, between Miramar & Río Plujunta mouth
	Gaillaria	G. megapotamica (Spreng.) Baker var. radiata (Griseb.) Baker	Native	Hemicryptophyte	Espinal	Córdoba, Mar Chiquita
	Gamochaeta	G. stachydifolia (Lam.) Cabrera	Native	Hemicryptophyte	Espinal	Buenos Aires, road to Puerto Cuatreros, General Cerri
		G. subfalcata (Cabrera) Cabrera	Native	Therophyte	Pampa	Santa Fe, La Samosita, Santa Lucía
	Grindelia	G. anethifolia (Phil.) A. Bartoli & Tortosa var. anethifolia	Native	Hemicryptophyte	Patagonian Steppe	Neuquén, La Negra
		G. brachystephana Griseb.	Endemic	Hemicryptophyte	Dry Chaco, Espinal, Iberá Marshes	Corrientes, Estero Pucú
		G. cabrerae Ariza var. alatocarpa Ariza	Endemic	Hemicryptophyte	Espinal	Córdoba, Mar Chiquita
		G. cabrerae Ariza var. cabrerae	Endemic	Hemicryptophyte	Pampa	Entre Ríos, Victoria
		G. puberula Hook. & Arn.	Native	Chamaephyte	Dry Chaco	Tucumán, Chañar Pozo
		G. pulchella Dunal var. discoidea (Hook. & Arn.) A. Bartoli & Tortosa	Native	Chamaephyte	Pampa	BuenosAires, Depresión del Salado
		G. pulchella Dunal var. pulchella	Native	Hemicryptophyte	Dry Chaco, Monte of Plains and Plateaus	Córdoba, Salinas Grandes
		G. scorzonerifolia Hook. & Arn.	Native	Hemicryptophyte	Espinal, Pampa, Paraná Flooded Savanna	Santa Fe, Coronda

	Gyptis	G. tanacetifolia (Gillies ex Hook. & Arn.) D.J.N. Hind & Flann	Native	Chamaephyte	Pampa	Córdoba, La Carlota
	Holocheilus	H. hieracioides (D. Don) Cabrera	Native	Hemicryptophyte	Espinal	Córdoba, between La Francia & Jeanmaire
	Hymenoxys	H. anthemoides (Juss.) Cass.	Native	Therophyte	Dry Chaco, Espinal, Mesopotamian Savanna, Pampa	Corrientes, Paso Naranjito
		H. cabrerae K.L. Parker	Endemic	Therophyte	Espinal	Buenos Aires, Salitral de la Vidriera
		H. robusta (Rusby) K.L. Parker	Native	Therophyte	Puna	Jujuy, Quebrada de Calete
		H. tweediei Hook. & Arn.	Native	Therophyte	Pampa	Entre Ríos, Ceibas a Médanos
	Hypochaeris	H. chondrilloides (A. Gray) Cabrera	Native	Hemicryptophyte	Espinal, Monte of Hills and Valleys, Monte of Plains and Plateaus, Puna	San Juan, PR 430, Río Jáchal
		H. meyeniana (Walp.) Griseb.	Native	Hemicryptophyte	Puna	Jujuy, Laguna de los Pozuelos
		H. patagonica Cabrera	Endemic	Hemicryptophyte	Patagonian Steppe	Santa Cruz, NR 40, Río Olnie to Bajo Caracoles
		H. petiolaris (Hook. & Arn.) Griseb.	Native	Hemicryptophyte	Pampa	Entre Ríos, Gualeguaychú, Arroyo Ñancay
	Isostigma	I. hoffmannii Kuntze	Native	Hemicryptophyte	Iberá Marshes	Corrientes, NR 12, 20 km S from NR 123
	Lepidophyllum	L. cupressiforme (Lam.) Cass.	Native	Chamaephyte	Patagonian Steppe	Tierra del Fuego, Bahía de San Sebastián
	Lessingianthus	L. rubricaulis (Bonpl.) H. Rob.	Native	Chamaephyte	Humid Chaco, Iberá Marshes, Paraná Flooded Savanna	Santiago del Estero, Lagunas Saladas, between PR 56 & Los Juríes
	Luciliocline	L. subspicata (Wedd.) Anderb. & S.E. Freire	Native	Hemicryptophyte	High Andes	Jujuy, Laguna de Vilama
	Micropsis	M. australis Cabrera	Endemic	Therophyte	Espinal	Buenos Aires, Salitral de la Vidriera

(continued)

Family	Genus	Species	Status	Life form	Ecoregions	Reference site
	Mikania	M. cordifolia (L. f.) Willd.	Native	Chamaephyte	Dry Chaco	Santiago del Estero, Río Salado
		M. periplocifolia Hook. & Arn.	Native	Chamaephyte	Espinal, Humid Chaco	Córdoba, Laguna La Salada
		M. urticifolia Hook. & Arn.	Native	Chamaephyte	Espinal	Córdoba, Mar Chiquita
	Noticastrum	N. diffusum (Pers.) Cabrera	Native	Hemicryptophyte	Pampa	Buenos Aires, Río Quequén Salado
		N. marginatum (Kunth) Cuatrec.	Native	Hemicryptophyte	Pampa	Buenos Aires, Río Quequén Salado
		N. sericeum (Less.) Less. ex Phil.	Native	Hemicryptophyte	Espinal	Buenos Aires, Laguna La Salada, Pedro Luro
	Ocyroe	O. armata (Wedd.) Bonifacino	Native	Chamaephyte	High Andes	Jujuy, Laguna de Vilama
	Panphalea	P. bupleurifolia Less.	Native	Hemicryptophyte	Paraná Flooded Savanna	Buenos Aires, Ribera del Río de La Plata: Juan Gerónimo
	Parastrephia	P. lucida (Meyen) Cabrera	Native	Chamaephyte	Puna	Jujuy, Salinas Grandes
	Parthenium	P. hysterophorus L.	Native	Therophyte	Dry Chaco, Espinal	Buenos Aires, Salinas Chicas
	Pascalia	P. glauca Ortega	Native	Hemicryptophyte	Dry Chaco	La Rioja, PR 28, between Portezuelo & San Ramón
	Perezia	P. pinnatifida (Humb. & Bonpl. ex Flüggé) Kunth	Native	Hemicryptophyte	High Andes	Jujuy, Laguna de Vilama
	Picrosia	P. longifolia D. Don	Native	Hemicryptophyte	Espinal, Pampa	Santa Fe, Bella Italia
	Pluchea	P. microcephala R.K. Godfrey	Native	Hemicryptophyte	Dry Chaco	Catamarca, Salinas Grandes
		P. sagittalis (Lam.) Cabrera	Native	Hemicryptophyte	Dry Chaco	Formosa, ca. 3 Km SW Va. Gral. Güemes
	Porophyllum	P. ruderale (Jacq.) Cass.	Native	Hemicryptophyte	Dry Chaco	Córdoba, Salinas Grandes
	Pseudognaphalium	P. cheiranthifolium (Lam.) Hilliard & B.L. Burtt	Native	Hemicryptophyte	Monte of Plains and Plateaus	Mendoza, Lagunas del Rosario
		P. lacteum (Meyen & Walp.) Anderb.	Native	Hemicryptophyte	High Andes	Jujuy, Laguna de Vilama
		P. leucopeplum (Cabrera) Anderb.	Native	Hemicryptophyte	Espinal	Buenos Aires, La Salada, Pedro Luro

	Pterocaulon	P. lorentzii Malme	Native	Therophyte	Dry Chaco	Tucumán, Chañar Pozo
		P. purpurascens Malme	Native	Hemicryptophyte	Dry Chaco	Córdoba, Salinas Grandes
		P. virgatum (L.) DC.	Native	Hemicryptophyte	Dry Chaco, Espinal, Humid Chaco, Mesopotamian Savanna	Entre Ríos, Ombúes to El Yunque
	Schkuhria	S. pinnata (Lam.) Kuntze ex Thell.	Native	Hemicryptophyte	Dry Chaco	Santiago del Estero, NR 34, SE from La Argentina
	Senecio	S. adenophyllus Meyen & Walp.	Native	Chamaephyte	High Andes	Jujuy, Laguna de Vilama
		S. barbarae Cabrera	Native	Hemicryptophyte	High Andes	Jujuy, Laguna de Vilama
		S. filaginoides DC.	Native	Chamaephyte	Espinal, Puna	Jujuy, Salar de Cauchari
		S. goldsackii Phil.	Endemic	Chamaephyte	Monte of Plains and Plateaus	La Pampa, Laguna Curru Lauquen
		S. helgae Cabrera	Native	Hemicryptophyte	High Andes	Jujuy, Laguna de Vilama
		S. humillimus Sch. Bip. ex Wedd.	Native	Hemicryptophyte	Puna	Jujuy, Laguna de Pozuelos
		S. melanopotamicus Cabrera	Endemic	Chamaephyte	Monte of Plains and Plateaus	La Pampa, Salitral Lavalle
		S. nutans Sch. Bip.	Native	Chamaephyte	High Andes, Puna	Catamarca, Salar del Hombre Muerto
		S. pampeanus Cabrera	Native	Hemicryptophyte	Dry Chaco, Espinal, Iberá Marshes, Pampa	Buenos Aires, road to Arroyo Chasicó
		S. pinnatus Poir. var. pinnatus	Native	Chamaephyte	Dry Chaco, Humid Chaco, Mesopotamian Savanna	Santa Fe, Lanteri
		S. pinnatus Poir. var. simplicifolius Cabrera	Endemic	Chamaephyte	Pampa	Entre Ríos, near Parque Unzué
		S. saltensis Hook. & Arn.	Native	Chamaephyte	Espinal, Humid Chaco	Córdoba, Mar Chiquita
		S. scorzonerifolius Meyen & Walp.	Native	Hemicryptophyte	High Andes	Jujuy, Laguna de Vilama
		S. subulatus D. Don ex Hook. & Arn. var. subulatus	Endemic	Chamaephyte	Paraná Flooded Savanna	Buenos Aires, Hudson (F. C. S.)
		S. vira-vira Hieron.	Native	Chamaephyte	Espinal	Buenos Aires, Salitral de la Vidriera
		S. xerophilus Phil. var. xerophilus	Native	Chamaephyte	Puna	Salta, Santa Rosa de Tastil

(continued)

Family	Genus	Species	Status	Life form	Ecoregions	Reference site
	Solidago	S. argentinensis López Laph. & Semple	Native	Chamaephyte	Monte of Plains and Plateaus	Mendoza, Río Salado Superior
		S. chilensis Meyen var. chilensis	Native	Hemicryptophyte	Espinal	Buenos Aires, Laguna La Salada
	Soliva	S. macrocephala Cabrera	Native	Therophyte	Espinal	Entre Ríos, Federación
	Symphyotrichum	S. patagonicum (Cabrera) G.L. Nesom	Endemic	Therophyte	Patagonian Steppe	Santa Cruz, Costa Oeste, San Martín
		S. squamatum (Spreng.) G.L. Nesom	Native	Hemicryptophyte	Pampa	Buenos Aires, Estancia San Miguel
	Taraxacum	T. gilliesii Hook. & Arn.	Native	Hemicryptophyte	Patagonian Steppe	Santa Cruz, near Esperanza
	Tessaria	T. absinthioides (Hook. & Arn.) DC.	Native	Chamaephyte	Monte of Hills and Valleys	Salta, NR 40, Animaná
		T. dodoneifolia (Hook. & Arn.) Cabrera subsp. dodoneifolia	Native	Chamaephyte	Dry Chaco, Monte of Hills and Valleys	La Rioja, between Olta & El Dique de Olta
	Trichocline	T. auriculata (Wedd.) Hieron. var. breviscapa Zardini	Endemic	Hemicryptophyte	High Andes	Jujuy, Vilama
		T. reptans (Wedd.) Hieron.	Native	Hemicryptophyte	Espinal	Buenos Aires, Salinas Chicas
	Trixis	T. cacalioides (Kunth) D. Don	Native	Hemicryptophyte	Dry Chaco	Córdoba, Salinas Grandes
		T. divaricata (Kunth) Spreng. subsp. divaricata	Native	Hemicryptophyte	Espinal	Córdoba, Mar Chiquita
	Verbesina	V. encelioides (Cav.) Benth. & Hook. f. ex A. Gray	Native	Therophyte	Monte of Plains and Plateaus	Mendoza, Campos de Salas
	Werneria	W. pygmaea Gillies ex Hook. & Arn.	Native	Hemicryptophyte	High Andes	Jujuy, Laguna de Vilama

Boraginaceae	Cryptantha	C. mendocina I.M. Johnst.	Endemic	Therophyte	Espinal	La Pampa, NR 148, Cano Quemado
	Ehretia	E. cortesia Gottschling	Native	Chamaephyte	Dry Chaco, Monte of Plains and Plateaus	Córdoba, Salinas Grandes
	Heliotropium	H. catamarcense I.M. Johnst.	Endemic	Hemicryptophyte	Dry Chaco	San Juan, Salina de Mascasín
		H. chrysanthum Phil.	Endemic	Hemicryptophyte	Dry Chaco	Mendoza, Salinas del Diamante
		H. curassavicum L. var. argentinum I.M. Johnst.	Native	Hemicryptophyte	Espinal, Pampa	La Pampa, NR 148, Estancia Poitaque
		H. curassavicum L. var. curassavicum	Native	Hemicryptophyte	Dry Chaco, Espinal, Monte of Hills and Valleys, Monte of Plains and Plateaus, Paraná Flooded Savanna	Salta, Luracatao, Laguna Brealito
		H. johnstonii Ragonese	Endemic	Hemicryptophyte	Dry Chaco, Monte of Plains and Plateaus	La Rioja, Salina La Antigua
		H. mendocinum Phil.	Endemic	Hemicryptophyte	Dry Chaco, Monte of Plains and Plateaus	San Luis, Salina del Bebedero
		H. nicotianaefolium Poir.	Native	Hemicryptophyte	Humid Chaco	Formosa, NR 11, Río Salado
		H. procumbens Mill.	Native	Hemicryptophyte	Dry Chaco	Tucumán, Chañar Pozo
		H. schreiteri I.M. Johnst.	Native	Hemicryptophyte	Dry Chaco	Córdoba, Lucio V. Mansilla
		H. veronicifolium Griseb.	Native	Hemicryptophyte	Dry Chaco	Salta, Coronel Moldes
	Phacelia	P. cumingii (Benth.) A. Gray	Native	Therophyte	Puna	San Juan, Reserva de San Guillermo, Río de La Sal
	Plagiobothrys	P. calandrinioides (Phil.) I.M. Johnst.	Native	Therophyte	Patagonian Steppe	Santa Cruz, 7 km S from Cañadón del Río Seco

(continued)

Family	Genus	Species	Status	Life form	Ecoregions	Reference site
Brassicaceae	Delpinophytum	D. patagonicum (Speg.) Speg.	Endemic	Chamaephyte	Patagonian Steppe	Santa Cruz, 5 km S from NR 3, San Julián
	Descurainia	D. antarctica (E. Fourn.) O.E. Schulz	Native	Hemicryptophyte	Monte of Plains and Plateaus	Río Negro, Cipolletti
		D. erodiifolia (Phil.) Prantl ex Reiche	Native	Hemicryptophyte	Dry Chaco, Espinal, Pampa	Catamarca, Salar de Pipanaco
	Exalimolobos	E. burkartii (Romanczuk & Boelcke) Al-Shehbaz & C.D. Bailey	Endemic	Therophyte	Dry Chaco	Tucumán, Las Salinas
	Lepidium	L. auriculatum Regel & Körn.	Native	Therophyte	Dry Chaco, Espinal, Pampa	Córdoba, NR 35, 35 km N from Huinca Renancó
		L. gracile (Chodat & Hassl.) Boelcke	Native	Therophyte	Iberá Marshes	Corrientes, Salinas Grandes
		L. myrianthum Phil.	Native	Therophyte	Monte of Plains and Plateaus	Mendoza, Salinas del Diamante
		L. parodii Thell.	Endemic	Hemicryptophyte	Pampa	Buenos Aires, La Plata
		L. pedersenii Al-Shehbaz	Native	Therophyte	Humid Chaco	Formosa, NR 11, 4 km S from Tatane, Río Salado
		L. spicatum Desv.	Native	Hemicryptophyte	Pampa	Santa Fe, Laguna del Chañar
		L. stuckertianum (Thell.) Boelcke	Endemic	Therophyte	Espinal	Corrientes, NR 126, 47 km W from Sauce
	Neuontobotrys	N. tarapacana (Phil.) Al-Shehbaz	Native	Hemicryptophyte	Puna	Salta, Salar de Gallego
	Schizopetalon	S. rupestre (Barnéoud) Reiche	Native	Therophyte	High Andes	San Juan, Reserva de San Guillermo, Río de la Sal
Bromeliaceae	Bromelia	B. urbaniana (Mez) L.B. Sm.	Native	Geophyte	Dry Chaco	Córdoba, Salinas Grandes
	Dyckia	D. floribunda Griseb. var. floribunda	Native	Geophyte	Dry Chaco	Córdoba, Salinas Grandes
		D. ragonesei A. Cast.	Endemic	Hemicryptophyte	Espinal	Córdoba, Mar Chiquita

Cactaceae	Cereus	C. aethiops Haw.	Native	Succulent	Monte of Plains and Plateaus	San Luis, Salinas del Bebedero
		C. argentinensis Britton & Rose	Endemic	Succulent	Iberá Marshes	Corrientes, PR 152, 2 Km N from Cerrito
		C. forbesii Otto ex C.F. Först.	Native	Succulent	Dry Chaco	Córdoba, Salinas Grandes
	Cleistocactus	C. baumannii (Lem.) Lem.	Native	Succulent	Dry Chaco, Espinal	Entre Ríos, Ombúes to El Yunque
	Echinopsis	E. leucantha (Gillies ex Salm-Dyck) Walp.	Endemic	Succulent	Dry Chaco, Monte of Plains and Plateaus	Córdoba, Salinas Grandes
	Gymnocalycium	G. ragonesei A. Cast.	Endemic	Succulent	Dry Chaco	Catamarca, Salinas Grandes
		G. schickendantzii (F.A.C. Weber) Britton & Rose var. schickendantzii	Endemic	Succulent	Dry Chaco	Córdoba, Salinas Grandes
	Maihueniopsis	M. glomerata (Haw.) R. Kiesling	Native	Chamaephyte	Dry Chaco	La Rioja, Salina de Mascasín
	Opuntia	O. sulphurea Gillies ex Salm-Dyck var. hildmannii (Fric) Backeb.	Native	Succulent	Dry Chaco	La Rioja, Salina de Mascasín
		O. sulphurea Gillies ex Salm-Dyck var. sulphurea	Native	Succulent	Dry Chaco, Monte of Plains and Plateaus	Santiago del Estero, 35 km S from road to Isla Verde, along NR 9
	Pterocactus	P. tuberosus (Pfeiff.) Britton & Rose f. tuberosus	Endemic	Succulent	Dry Chaco	La Rioja, Salina de Mascasín
	Setiechinopsis	S. mirabilis (Speg.) de Haas	Endemic	Chamaephyte	Dry Chaco, Monte of Plains and Plateaus	Mendoza, Fray Luis Beltrán
	Stetsonia	S. coryne (Salm-Dyck) Britton & Rose (Fig. 9.9)	Native	Succulent	Dry Chaco	Catamarca, Salinas Grandes
	Tephrocactus	T. aoracanthus (Lem.) Lem. (Fig. 9.10)	Endemic	Geophyte	Dry Chaco, Monte of Plains and Plateaus	Córdoba, Salinas Grandes
		T. articulatus (Pfeiff.) Backeb. var. articulatus	Endemic	Succulent	Dry Chaco	La Rioja, NR 38, between Castro Barros y Serrezuela
	Trichocereus	T. huascha (F.A.C. Weber) Britton & Rose var. huascha	Endemic	Succulent	Dry Chaco	La Rioja, between Pozo de la Vaca & Pozo Redondo
		T. strigosus (Salm-Dyck) Britton & Rose	Endemic	Succulent	Monte of Plains and Plateaus	Mendoza, Campos de Salas

(continued)

Family	Genus	Species	Status	Life form	Ecoregions	Reference site
Calyceraceae	Acicarpha	A.tribuloides Juss.	Native	Therophyte	Pampa	Santa Fe, Coronada
	Boopis	B. anthemoides Juss. var. anthemoides	Endemic	Hemicryptophyte	Pampa, Patagonian Steppe	Mendoza, Laguna Coipo Leuquén
		B.anthemoides Juss. var. subintegrifolia Hicken	Endemic	Hemicryptophyte	Dry Chaco	Tucumán, Chañar Pozo
		B. australis Decne.	Native	Hemicryptophyte	Monte of Plains and Plateaus	Neuquén, Zapala (F.C.S.)
	Nastanthus	N. ventosus (Meyen) Miers	Native	Hemicryptophyte	High Andes	La Rioja, Laguna Brava
Capparaceae	Capparis	C. atamisquea Kuntze	Native	Phanerophyte	Dry Chaco	Catamarca, Salar de Pipanaco
Caryophyllaceae	Arenaria	A. rivularis Phil.	Native	Hemicryptophyte	High Andes	La Rioja, Laguna Brava
		A. serpens Kunth	Native	Hemicryptophyte	Monte of Plains and Plateaus	Mendoza, Atuel
	Cardionema	C. ramosissima (Weinm.) A. Nelson & J.F. Macbr.	Native	Hemicryptophyte	Monte of Plains and Plateaus	La Pampa, La Reforma
		C. rosetta (Cambess.) A. Nelson & J.F. Macbr.	Native	Hemicryptophyte	Iberá Marshes	Corrientes, Santa Lucía, Salinas Grandes
	Colobanthus	C. quitensis (Kunth) Bartl.	Native	Hemicryptophyte	Puna	San Juan, Parque Nacional San Guillermo, Vega de Los Leones
	Spergula	S. grandis Pers.	Native	Hemicryptophyte	Pampa	Santa Fe, La Picaza
		S. laevis (Cambess.) D. Dietr.	Native	Hemicryptophyte	Pampa	Buenos Aires, Estancia San Carlos
		S. platensis (Cambess.) Shinners var. platensis	Native	Hemicryptophyte	Pampa, Paraná Flooded Savanna	Entre Ríos, Ceibas
		S. ramosa (Cambess.) D. Dietr. subsp. ramosa	Native	Hemicryptophyte	Espinal, Pampa	Córdoba, Laguna Las Salinas
		S. villosa Pers.	Native	Hemicryptophyte	Pampa	Córdoba, NR 7, 4 km E from General Levalle
Celastraceae	Maytenus	M. viscifolia Griseb.	Endemic	Phanerophyte	Dry Chaco	Catamarca, Salinas Grandes
		M. vitis-idaea Griseb. (Fig. 9.11)	Native	Phanerophyte	Dry Chaco	Catamarca, Salinas Grandes
	Moya	M. spinosa Griseb.	Endemic	Phanerophyte	Dry Chaco	Córdoba, Mar Chiquita
Celtidaceae	Celtis	C. chichape (Wedd.) Miq.	Native	Phanerophyte	Dry Chaco	Córdoba, Mar Chiquita

Commelinaceae	Commelina	C. erecta L. var. angustifolia (Michx.) Fernald	Native	Hemicryptophyte	Dry Chaco	Córdoba, Salinas Grandes
	Tripogandra	T. glandulosa (Seub.) Rohweder	Native	Hemicryptophyte	Espinal	Corrientes, Monte Caseros, La Potota
Convolvulaceae	Cressa	C. nudicaulis Griseb. (Fig. 9.12)	Endemic	Geophyte	Dry Chaco, Monte of Plains and Plateaus	Catamarca, Salina de Pipanaco
		C. truxillensis Kunth	Native	Geophyte	Espinal, Pampa, Patagonian Steppe	Chubut, Laguna Cona
	Evolvulus	E. arizonicus A. Gray	Native	Hemicryptophyte	Dry Chaco	Córdoba, Salinas Grandes
		E. glomeratus Nees & Mart. subsp. grandiflorus (D. Parodi) Ooststr.	Native	Hemicryptophyte	Iberá Marshes	Corrientes, NR 12, 10 km S from NR 123
		E. sericeus Sw. var. elongatus (Choisy) O'Donell	Native	Hemicryptophyte	Monte of Plains and Plateaus	Mendoza, Salinas del Diamante
	Ipomoea	I. amnicola Morong	Native	Hemicryptophyte	Dry Chaco	Santiago del Estero, NR 9, between Río Saladillo & Isla Verde
		I. stuckertii O'Donell	Endemic	Geophyte	Dry Chaco	Córdoba, Salinas Grandes
	Jacquemontia	J. decumbens O'Donell	Native	Chamaephyte	Iberá Marshes	Corrientes, NR 12, 10 km S from NR 123
Cucurbitaceae	Cucurbitellia	C. asperata (Gillies ex Hook. & Arn.) Walp.	Native	Hemicryptophyte	Dry Chaco	Córdoba, Salinas Grandes
	Halosicyos	H. ragonesei Mart. Crov. (Fig. 9.13)	Endemic	Chamaephyte	Dry Chaco	Córdoba, Salinas Grandes

(continued)

Family	Genus	Species	Status	Life form	Ecoregions	Reference site
Cyperaceae	Amphiscirpus	A. nevadensis (S. Watson) Oteng-Yeb.	Native	Hemicryptophyte	High Andes, Puna	Salta, Salar de Pocitos
	Bolboeschoenus	B. maritimus (L.) Palla ssp. paludosus (A. Nelson) T. Koyama	Native	Geophyte	Espinal	Córdoba, Mar Chiquita
	Bulbostylis	B. juncoides (Vahl) Kük. ex Herter var. juncoides	Native	Hemicryptophyte	Humid Chaco	Santa Fe, San Vicente
	Carex	C. sororia Kunth subsp. sororia	Native	Hemicryptophyte	Humid Chaco	Chaco, La Amalia
		C. vixdentata (Kük. ex Osten) G.A. Wheeler	Native	Hemicryptophyte	Pampa	Buenos Aires, Río Quequén Salado
	Cyperus	C. corymbosus Rottb. var. subnodosus (Nees & Meyen) Kük.	Native	Geophyte	Espinal, Pampa	Córdoba, Jeanmaire
		C. laevigatus L.	Native	Geophyte	Espinal, Pampa	Córdoba, Mar Chiquita
		C. oxylepis Nees ex Steud.	Native	Geophyte	Dry Chaco, Espinal	Santiago del Estero, Isla Verde
	Eleocharis	E. argentina Barros	Endemic	Geophyte	Monte of Plains and Plateaus	Mendoza, Los Morritos
		E. atacamensis Phil.	Native	Geophyte	Monte of Hills and Valleys, Puna	Catamarca, Laguna Blanca
		E. macrostachya Britton	Native	Geophyte	Pampa	Santa Fe, NR 16 & Arroyo Saladillo
		E. pseudoalbibracteata S. González & Guagl.	Native	Geophyte	High Andes	San Juan, Calingasta, near the Gendarmerie Shelter
	Phylloscirpus	P. acaulis (Phil.) Goetgh. & D.A. Simpson	Native	Geophyte	Monte of Plains and Plateaus	Mendoza, Río Salado
	Schoenoplectus	S. americanus (Pers.) Volkart ex Schinz & R. Keller	Native	Geophyte	Espinal, Monte of Hills and Valleys, Puna	Catamarca, Copacabana
		S. californicus (C.A. Mey.) Soják var. californicus	Native	Geophyte	Espinal, Pampa	Córdoba, near Jeanmaire
		S. pungens (Vahl) Palla var. badius (J. Presl & C. Presl) S.G. Sm.	Native	Geophyte	Espinal, Monte of Hills and Valleys, Pampa	Córdoba, Mar Chiquita

		S. pungens (Vahl) Palla var. longispicatus (Britton) S.G. Sm.	Native	Geophyte	Pampa	Santa Fe, between Saneti Spíritu & San Eduardo
		S. pungens (Vahl) Palla var. pungens	Native	Geophyte	Espinal	Córdoba, Río Cuarto or Saladillo, 8 km before W. Escalante
Ephedraceae	Ephedra	E. rupestris Benth.	Native	Chamaephyte	Puna	Jujuy, Laguna de Guayatayoc
		E. triandra Tul. emend. J.H. Hunz.	Native	Chamaephyte	Espinal	Buenos Aires, Salitral de La Vidriera
Equisetaceae	Equisetum	E. bogotense Kunth	Native	Hemicryptophyte	Patagonian Steppe	Mendoza, road to Paso Pehuenche boundary, 2000 m before Arroyo El Macho
		E. giganteum L.	Native	Hemicryptophyte	Monte of Hills and Valleys	San Juan, around the airport
Euphorbiaceae	Croton	C. bonplandianus Baill.	Native	Chamaephyte	Mesopotamian Savanna	Corrientes, Paso Naranjito
	Ditaxis	D. catamarcensis (Griseb.) Pax	Endemic	Chamaephyte	Dry Chaco	Salta, 54 km NE from J.V.González
		D. jablonszkyana Pax & K. Hoffm.	Endemic	Chamaephyte	Dry Chaco	La Rioja, Salina de Mascasín
	Euphorbia	E. berteroana Spreng.	Native	Therophyte	Dry Chaco	Córdoba, Salinas Grandes
		E. eichleri Müll. Arg.	Native	Hemicryptophyte	Dry Chaco	Córdoba, Salinas Grandes
		E. hieronymi Subils	Endemic	Hemicryptophyte	Espinal	Córdoba, Mar Chiquita
		E. klotzschii Oudejans var. argentina (Müll. Arg. ex Griseb.) Oudejans	Native	Therophyte	Dry Chaco	San Juan, Salina de Mascasín
		E. klotzschii Oudejans var. klotzschii	Native	Therophyte	Dry Chaco	Santiago del Estero, NR 34, between Pab. Negro y Argentina
		E. serpens Kunth var. microphylla Müll. Arg.	Native	Hemicryptophyte	Dry Chaco	Santiago del Estero, NR 34, between Pab. Negro y Argentina
	Jatropha	J. excisa Griseb.	Native	Chamaephyte	Dry Chaco	Córdoba, Salinas Grandes
	Tragia	T. hieronymii Pax & K. Hoffm.	Native	Chamaephyte	Dry Chaco	Córdoba, Salinas Grandes

(continued)

Family	Genus	Species	Status	Life form	Ecoregions	Reference site
Fabaceae	Acacia	A. aroma Gillies ex Hook. & Arn.	Native	Phanerophyte	Dry Chaco	La Rioja, Salina de Mascasín
		A. praecox Griseb.	Native	Phanerophyte	Dry Chaco, Paraná Flooded Savanna	Chaco, Colonia Benítez
	Adesmia	A. horrida Gillies ex Hook. & Arn.	Native	Chamaephyte	Puna	Salta, Salar del Gallego
	Albizia	A. inundata (Mart.) Barneby & J.W. Grimes	Native	Phanerophyte	Dry Chaco	Córdoba, Salinas Grandes
	Anarthrophyllum	A. rigidum (Gillies ex Hook. & Arn.) Hieron.	Native	Phanerophyte	Patagonian Steppe	Mendoza, Los Hoyos
	Caesalpinia	C. gilliesii (Wall. ex Hook.) D. Dietr.	Native	Phanerophyte	Espinal	Córdoba, Mar Chiquita
	Cercidium	C. praecox (Ruiz & Pav. ex Hook.) Harms subsp. glaucum (Cav.) Burkart & Carter	Endemic	Phanerophyte	Dry Chaco	Córdoba, Salinas Grandes
	Desmanthus	D. tatuhyensis Hoehne var. brevipes (B.L. Turner) Luckow	Native	Chamaephyte	Dry Chaco	Córdoba, between Jerónimo Cortéz & Altos de Chipión
	Geoffroea	G. decorticans (Gillies ex Hook. & Arn.) Burkart	Native	Phanerophyte	Dry Chaco	Catamarca, Salinas Grandes
	Glycyrrhiza	G. astragalina Hook. et Arn.	Native	Chamaephyte	Patagonian Steppe	Chubut, Salina Chica, Península Valdés
	Hoffmannseggia	H. erecta Phil.	Endemic	Hemicryptophyte	Monte of Plains and Plateaus, Puna	Salta, Salar de Arizaro
		H. eremophila (Phil.) Burkart ex Ulibarri	Native	Hemicryptophyte	Puna	Salta, Pastos Grandes, Salar Río Grande
		H. glauca (Ortega) Eifert	Native	Hemicryptophyte	Espinal	Buenos Aires, Laguna La Salada
		H. trifoliata Cav.	Native	Hemicryptophyte	Patagonian Steppe	Río Negro, Arroyo Valcheta
	Indigofera	I. parodiana Burkart	Native	Hemicryptophyte	Dry Chaco	Córdoba, Salinas Grandes
	Lathyrus	L. magellanicus Lam. var. glaucescens Speg.	Native	Hemicryptophyte	Patagonian Steppe	Tierra del Fuego, Bahía San Sebastián
	Mimosa	M. ephedroides (Gill.) Benth.	Endemic	Chamaephyte	Dry Chaco	La Rioja, Salina de Mascasín

	Mimozyganthus	M. carinatus (Griseb.) Burkart (Fig. 9.14)	Native	Chamaephyte	Dry Chaco	Córdoba, Salinas Grandes
	Neptunia	N. pubescens Benth.	Native	Chamaephyte	Humid Chaco	Santa Fe, 2 km S from Berna
	Poissonia	P. heterantha (Griseb.) Lavin	Native	Chamaephyte	Puna	Jujuy, Salinas Grandes
	Prosopidastrum	P. globosum (Hook. et Arn.) Burk.	Endemic	Phanerophyte	Patagonian Steppe	Chubut, Salina Grande, Península Valdés
	Prosopis	P. alpataco Phil. f. alpataco	Endemic	Phanerophyte	Dry Chaco, Patagonian Steppe	Chubut, Salina Grande, Península Valdés
		P. campestris Griseb.	Endemic	Phanerophyte	Dry Chaco	Córdoba, Mar Chiquita
		P. flexuosa DC. f. flexuosa	Native	Phanerophyte	Dry Chaco	La Rioja, Salina de Mascasín
		P. hassleri Harms var. hassleri	Native	Phanerophyte	Dry Chaco	Santiago del Estero, 35 km S from road to Isla Verde, along NR 9
		P. humilis Gillies ex Hook. & Arn.	Endemic	Chamaephyte	Espinal	Córdoba, Pacheco de Melo
		P. pugionata Burkart	Endemic	Phanerophyte	Dry Chaco	Córdoba, Salinas Grandes
		P. reptans Benth. var. reptans (Fig. 9.15)	Native	Phanerophyte	Dry Chaco, Humid Chaco	Córdoba, Salinas Grandes
		P. sericantha Hook. et Arn.	Native	Phanerophyte	Dry Chaco	La Rioja, Salina de Mascasín
		P. strombulifera (Lam.) Benth. var. strombulifera	Native	Phanerophyte	Dry Chaco, Monte of Plains and Plateaus	Mendoza, Tunuyán
	Senna	S. acanthoclada (Griseb.) H.S. Irwin & Barneby (Fig. 9.16)	Endemic	Phanerophyte	Dry Chaco	Córdoba, Salinas Grandes
		S. aphylla (Cav.) H.S. Irwin et Barneby	Native	Phanerophyte	Dry Chaco	Catamarca, Salar de Pipanaco
	Stenodrepanum	S. bergii (Harms)	Endemic	Chamaephyte	Dry Chaco, Humid Chaco	Santa Fe, Arroyo Golondrina & road to Fortín Olmos
	Zuccagnia	Z. punctata Cav.	Endemic	Phanerophyte	Monte of Hills and Valleys	Salta, NR 68, km 69, Arroyo Palo Seco

(continued)

Family	Genus	Species	Status	Life form	Ecoregions	Reference site
Frankeniaceae	Frankenia	F. juniperoides (Hieron.) M.N. Correa	Endemic	Chamaephyte	Espinal, Monte of Plains and Plateaus	Buenos Aires, Bahía Blanca Estuary
		F. patagonica Speg.	Endemic	Chamaephyte	Monte of Plains and Plateaus	Río Negro, 31 km S from Valcheta along road to Tembrao
		F. triandra J. Remy	Native	Chamaephyte	Monte of Hills and Valleys, Puna	Catamarca, between Nacimientos & Laguna Blanca
Halophytaceae	Halophytum	H. ameghinoi (Speg.) Speg.	Endemic	Therophyte	Monte of Hills and Valleys	San Luis, Sierra de Las Quijadas
Gesneriaceae	Sinningia	S. tubiflora (Hook.) Fritsch	Native	Hemicryptophyte	Espinal	Entre Ríos, Ombúes to El Yunque
		S. warmingii (Hiern) Chautems	Native	Hemicryptophyte	Dry Chaco	Salta, NR 34, km 1146, Río Saladillo
Iridaceae	Sisyrinchium	S. micranthum Cav. subsp. micranthum	Native	Hemicryptophyte	Espinal	Corrientes, NR 126, 47 km NW from Sauce
		S. pachyrhizum Baker subsp. pachyrhizum	Native	Hemicryptophyte	Paraná Flooded Savanna	Buenos Aires, Baradero
		S. platense I.M. Johnst.	Native	Hemicryptophyte	Pampa	Buenos Aires, Tolosa
Juncaceae	Juncus	J. acutus L. subsp. leopoldii (Parl.) Snogerup	Native	Geophyte	Monte of Hills and Valleys, Pampa	Córdoba, NR 36, km 555, near Huinca Renancó
		J. balticus Willd. subsp. mexicanus (Willd. ex Roem. & Schult.) Kirschner	Native	Geophyte	Puna	Catamarca, Laguna Blanca
		J. bufonius L. var. bufonius	Native	Therophyte	Humid Chaco	Santa Fe, Yugo Quebrado
	Oxychlöe	O. castellanosii Barros	Endemic	Hemicryptophyte	High Andes	San Juan, Quebrada Mula Muerta
Loasaceae	Caiophora	C. coronata (Gillies ex Arn.) Hook. & Arn.	Native	Hemicryptophyte	High Andes	Catamarca, Salina de la Laguna Verde
Malpighiaceae	Tricomaria	T. usillo Hook. & Arn.	Endemic	Chamaephyte	Dry Chaco	Córdoba, Salinas Grandes

Malvaceae	Cienfuegosia	C. argentina Gürke	Native	Hemicryptophyte	Dry Chaco, Iberá Marshes, Paraná Flooded Savanna	Chaco, Colonia Benítez
		C. drummondii (A. Gray) Lewton	Native	Hemicryptophyte	Dry Chaco	Formosa, Las Lomitas
		C. saraviae Krapov.	Endemic	Chamaephyte	Dry Chaco	Salta, 58 km NE from J.V.González, road to Puerta Blanca
		C. schulzii Krapov.	Endemic	Hemicryptophyte	Dry Chaco	Formosa, Las Lomitas
		C. ulmifolia Fryxell	Native	Hemicryptophyte	Humid Chaco, Iberá Marshes	Corrientes, PR 23, 3 km W from Río Santa Lucía
	Gaya	G. parviflora (Phil.) Krapov.	Native	Hemicryptophyte	Dry Chaco	Formosa, Las Lomitas
	Lecanophora	L. ameghinoi (Speg.) Speg.	Endemic	Hemicryptophyte	Monte of Plains and Plateaus	Mendoza, Salinas del Diamante
		L. ecristata (A. Gray) Krapov.	Endemic	Therophyte	Monte of Plains and Plateaus	Mendoza, Salinas del Diamante
	Malvastrum	M. amblyphyllum R.E. Fr.	Native	Hemicryptophyte	Dry Chaco	Santiago del Estero, NR 9, along Salinas Grandes, between Río Saladillo & Monte Redondo
		M. coromandelianum (L.) Garcke	Native	Hemicryptophyte	Dry Chaco	Salta, Ojo de Agua
	Malvella	M. leprosa (Ortega) Krapov.	Native	Hemicryptophyte	Pampa	Santa Fe, between Landeta & El Fortín
	Pavonia	P. revoluta Krapov. & Cristóbal	Native	Chamaephyte	Espinal	Córdoba, Mar Chiquita
	Sida	S. dictyocarpa Griseb.	Native	Chamaephyte	Dry Chaco	Córdoba, between Lucio V. Mansilla & El Tuscal
Martyniaceae	Ibicella	I. lutea (Lindl.) Van Eselt	Native	Therophyte	Dry Chaco	Santiago del Estero, NR 9, 35 km S from road to Isla Verde
		I. parodii Abbiatti	Endemic	Therophyte	Dry Chaco	Córdoba, Salinas Grandes
Najadaceae	Najas	N. guadalupensis (Spreng.) Magnus	Native	Geophyte	Dry Chaco	Córdoba, Salinas Grandes

(continued)

Family	Genus	Species	Status	Life form	Ecoregions	Reference site
Nyctaginaceae	Allionia	A. choisyi Standl.	Native	Hemicryptophyte	Monte of Plains and Plateaus	San Luis, Salina del Bebedero
		A. incarnata L.	Native	Hemicryptophyte	Dry Chaco, Monte of Plains and Plateaus	La Rioja, Salina de Mascasín
	Boerhavia	B. cordobensis Kuntze	Endemic	Hemicryptophyte	Dry Chaco	La Rioja, PR 21, between Solca & El Unquillal
	Bougainvillea	B. spinosa (Cav.) Heimerl	Native	Phanerophyte	Dry Chaco	Córdoba, Monte del Tigre
Olacaceae	Menodora	M. trifida (Cham. & Schltdl.) Steud.	Native	Chamaephyte	Pampa	Córdoba, PR 6, around Río Saladillo, between Pozo del Molle & Inriville
Oxalidaceae	Oxalis	O. conorrhiza Jacq.	Native	Hemicryptophyte	Espinal	Entre Ríos, Paso Yunque
Passifloraceae	Passiflora	P. elegans Mast.	Native	Hemicryptophyte	Iberá Marshes	Corrientes, Santa Lucía, Salinas Grandes
		P. morifolia Mast.	Native	Hemicryptophyte	Dry Chaco	Santiago del Estero, El Saladillo
		P. palmatisecta Mast.	Native	Hemicryptophyte	Dry Chaco	Córdoba, Salinas Grandes
Piperaceae	Peperomia	P. comarapana C. DC. f. comarapana	Native	Hemicryptophyte	Espinal	Entre Ríos, Paso Yunque
Plantaginaceae	Plantago	P. maritima L.	Native	Hemicryptophyte	Monte of Plains and Plateaus	Mendoza, Atuel
		P. myosuros Lam.	Native	Hemicryptophyte	Espinal, Pampa	Córdoba, Mar Chiquita
		P. pulvinata Speg.	Native	Hemicryptophyte	Patagonian Steppe	Santa Cruz, Pan de Azúcar
Plumbaginaceae	Limonium	L. brasiliense (Boiss.) Kuntze	Native	Hemicryptophyte	Monte of Plains and Plateaus, Pampa	Santa Fe, Laguna Santa Lucía
Poaceae	Amelichloa	A. ambigua (Speg.) Arriaga & Barkworth	Endemic	Hemicryptophyte	Espinal	Buenos Aires, Salitral de la Vidrera
		A. brachychaeta (Godr.) Arriaga & Barkworth	Native	Hemicryptophyte	Espinal	La Pampa, Salinas Grandes

	Aristida	A. adscensionis L.	Native	Hemicryptophyte	Dry Chaco, Monte of Plains and Plateaus	Santiago del Estero, Salinas de Ambargasta
		A. circinalis Lindm.	Native	Hemicryptophyte	Humid Chaco	Santiago del Estero, J.F.Ibarra, Lagunas Saladas
		A. mendocina Phil.	Native	Hemicryptophyte	Dry Chaco, Humid Chaco, Monte of Plains and Plateaus	La Pampa, Salitral Levalle
		A. pallens Cav. var. pallens	Native	Hemicryptophyte	Humid Chaco	Santiago del Estero, J.F.Ibarra, Lagunas Saladas
		A. spegazzinii Arechav.	Native	Hemicryptophyte	Espinal	Buenos Aires, Salitral de la Vidriera
		A. subulata Henrard	Endemic	Hemicryptophyte	Espinal, Patagonian Steppe	Buenos Aires, Salinas Chicas
	Blepharidachne	B. benthamiana (Hack. ex Kurtz) Hitchc.	Endemic	Hemicryptophyte	Dry Chaco	Catamarca, Salinas Grandes
		B. hitchcockii Lahitte	Endemic	Hemicryptophyte	Dry Chaco	La Rioja, PR 31, between Solca & El Unquillal
	Bothriochloa	B. laguroides (DC.) Herter var. laguroides	Native	Hemicryptophyte	Humid Chaco	Santiago del Estero, Ibarra, Lagunas Saladas
		B. saccharoides (Sw.) Rydb. var. saccharoides	Native	Hemicryptophyte	Pampa	Buenos Aires, Río Quequén Salado
	Bouteloua	B. aristidoides (Kunth) Griseb.	Native	Hemicryptophyte	Dry Chaco, Espinal	Córdoba, Mar Chiquita
		B. barbata Lag.	Native	Hemicryptophyte	Dry Chaco, Monte of Plains and Plateaus	San Juan, Salina de Mascasín
		B. megapotamica (Spreng.) Kuntze	Native	Hemicryptophyte	Espinal	San Luis, Saladillo
	Briza	B. subaristata Lam.	Native	Hemicryptophyte	Pampa	Buenos Aires, Carcalleros, Río Quequén Salado

(continued)

Family	Genus	Species	Status	Life form	Ecoregions	Reference site
	Bromus	B. catharticus Vahl var. catharticus	Native	Therophyte	Espinal, Monte of Plains and Plateaus, Puna	Río Negro, Cipolletti
		B. catharticus Vahl var. rupestris (Speg.) Planchuelo & P.M. Peterson	Endemic	Therophyte	Espinal	Buenos Aires, Ing. White, near the Club Naútico
		B. setifolius J. Presl var. brevifolius Nees	Native	Hemicryptophyte	Monte of Plains and Plateaus	Mendoza, Las Animas, Río Salado
		B. tunicatus Phil.	Native	Hemicryptophyte	Patagonian Steppe	Santa Cruz, San Julián
	Cenchrus	C. chilensis (E. Desv.) Morrone	Native	Hemicryptophyte	High Andes, Puna	Jujuy, Quebrada de Calete
		C. myosuroides Kunth	Native	Hemicryptophyte	Dry Chaco, Espinal	Córdoba, Jeanmaire
		C. pilcomayensis (Mez) Morrone	Native	Hemicryptophyte	Espinal	Santa Fe, near Esteban Rams
	Chaetotropis	C. chilensis Kunth	Native	Hemicryptophyte	Pampa	Santa Fe, between Rufino & Rosetti
		C. elongata (Kunth) Björkman	Native	Hemicryptophyte	Espinal, Pampa	Santa Fe, Capovur
		C. imberbis (Phil.) Björkman	Native	Hemicryptophyte	Espinal, Pampa	La Pampa, Laguna Grande del Guanaco
	Chloris	C. barbata Sw.	Native	Therophyte	Espinal	Santa Fe, 7 km NW from Esperanza
		C. berroi Arechav.	Native	Hemicryptophyte	Pampa	Buenos Aires, Ignacio Correas, Arroyo Pescado
		C. canterae Arechav.	Native	Hemicryptophyte	Espinal, Pampa	Entre Ríos, Concepción del Uruguay
		C. castilloniana Lillo & Parodi var. castilloniana	Native	Hemicryptophyte	Dry Chaco	San Juan, Salina de Mascasín
		C. ciliata Sw. f. breviseta Hack.	Native	Hemicryptophyte	Dry Chaco	Tucumán, Chañar Pozo
		C. ciliata Sw. f. ciliata	Native	Hemicryptophyte	Pampa	Entre Ríos, Concepción del Uruguay, Arroyo Isletas
		C. halophila Parodi var. halophila	Native	Hemicryptophyte	Dry Chaco, Espinal, Humid Chaco, Paraná Flooded Savanna	Santa Fe, Río Salado

		C. halophila Parodi var. humilis Christ	Native	Hemicryptophyte	Monte of Hills and Valleys	Tucumán, Alto de Las Salinas
		C. parvispicula Caro & E.A. Sánchez	Native	Hemicryptophyte	Dry Chaco	Córdoba, Salinas Grandes
		C. pycnothrix Trin.	Native	Hemicryptophyte	Paraná Flooded Savanna	Corrientes, Corrientes
		C. sesquiflora Burkart	Native	Hemicryptophyte	Pampa	Entre Ríos, Concepción del Uruguay
		C. virgata Sw.	Native	Hemicryptophyte	High Andes	Catamarca, Andes, E of Paso De San Francisco
	Cortaderia	C. rudiuscula Stapf	Native	Hemicryptophyte	Patagonian Steppe	Chubut, Salina Grande, Península Valdés
		C. selloana (Schult. & Schult. f.) Asch. & Graebn.	Native	Hemicryptophyte	Dry Chaco, Monte of Plains and Plateaus, Paraná Flooded Savanna	Buenos Aires, NP Campos del Tuyú
	Cottea	C. pappophoroides Kunth	Native	Hemicryptophyte	Dry Chaco	Córdona, Salinas Grandes
	Danthonia	D. cirrata Hack. & Arechav.	Native	Hemicryptophyte	Pampa	Buenos Aires, Río Salado
		D. montevidensis Hack. & Arechav.	Native	Hemicryptophyte	Pampa	Buenos Aires, Río Salado
	Deschampsia	D. antarctica E. Desv.	Native	Hemicryptophyte	Patagonian Steppe	Santa Cruz, Estancia Tapi Aike

(continued)

Family	Genus	Species	Status	Life form	Ecoregions	Reference site
	Deyeuxia	D. crispa Rúgolo & Villav.	Native	Hemicryptophyte	Puna	Jujuy, Laguna de Pozuelos
		D. curvula Wedd.	Native	Hemicryptophyte	Puna	Jujuy, Salar de Olaroz
		D. deserticola Phil. var. deserticola	Native	Hemicryptophyte	Dry Chaco	Salta, Laguna Blanca
		D. eminens J. Presl var. eminens	Native	Hemicryptophyte	High Andes, Puna	Jujuy, Laguna de Jama
		D. eminens J. Presl & C. Presl var. inclusa Rúgolo	Endemic	Hemicryptophyte	Puna	Jujuy, Laguna de Jama
		D. heterophylla Wedd.	Native	Hemicryptophyte	High Andes	Jujuy, Laguna de Vilama
		D. rigescens (J. Presl) Türpe	Native	Hemicryptophyte	Puna	Jujuy, Quebrada de Salitre
		D. spicigera J. Presl var. cephalotes (Wedd.) Rúgolo & Villav.	Native	Hemicryptophyte	Puna	Jujuy, Quebrada de Salitre
		D. velutina Nees & Meyen var. nardifolia (Griseb.) Rúgolo	Native	Hemicryptophyte	High Andes, Puna	Jujuy, Quebrada de Salitre
		D. velutina Nees & Meyen var. velutina	Native	Hemicryptophyte	Puna	La Rioja, Salina del Leoncito
		D. viridiflavescens (Poir.) Kunth var. montevidensis (Nees) Cabrera & Rúgolo	Native	Hemicryptophyte	Pampa	Buenos Aires, Arroyo Saladillo & NR 205
	Digitaria	D. californica (Benth.) Henrard var. californica	Native	Hemicryptophyte	Dry Chaco, Espinal	Córdoba, Mar Chiquita
		D. californica (Benth.) Henrard var. villosissima Henrard	Native	Hemicryptophyte	Dry Chaco	Santiago del Estero, PR 5, Pto. El Saladillo
		D. ciliaris (Retz.) Koeler	Native	Hemicryptophyte	Dry Chaco	Santiago del Estero, PR 5, Pto. El Saladillo
		D. eriostachya Mez	Native	Hemicryptophyte	Iberá Marshes	Corrientes, PR 152, 2 km N from Cerrito
		D. sacchariflora (Nees) Henrard	Native	Hemicryptophyte	Dry Chaco	Córdoba, Salinas Grandes
		D. similis Beetle ex Gould	Native	Hemicryptophyte	Espinal, Iberá Marshes	Santa Fe, Río Salado

	Distichlis	D. acerosa (Griseb.) H.L. Bell & Columbus (Fig. 9.17)	Endemic	Hemicryptophyte	Dry Chaco	La Rioja, Salina La Antigua
		D. australis (Speg.) Villamil	Endemic	Hemicryptophyte	Patagonian Steppe	Río Negro, 36 km S from Chasico
		D. humilis Phil.	Native	Hemicryptophyte	High Andes, Puna	Jujuy, Salinas Grandes
		D. laxiflora Hack.	Endemic	Hemicryptophyte	Pampa	Córdoba, PR 50, Laguna Las Salinas
		D. scoparia (Kunth) Arechav. var. erinacea (Beetle) Nicora	Endemic	Hemicryptophyte	Patagonian Steppe	Santa Cruz, Puerto Deseado
		D. scoparia (Kunth) Arechav. var. scoparia	Native	Hemicryptophyte	Espinal, Monte of Hills and Valleys, Pampa, Patagonian Steppe	Chubut, Salina Grande, Península Valdés
		D. spicata (L.) Greene	Native	Hemicryptophyte	Dry Chaco, Espinal, High Andes, Monte of Hills and Valleys, Pampa, Patagonian Steppe	Chubut, PR 20, 4 km E from Sarmiento
	Eleusine	E. tristachya (Lam.) Lam.	Native	Hemicryptophyte	Pampa	Buenos Aires, Río Quequén Salado
	Elionurus	E. muticus (Spreng.) Kuntze	Native	Hemicryptophyte	Espinal, Humid Chaco	San Luis, Saladillo
	Elymus	E. patagonicus Speg.	Native	Hemicryptophyte	Patagonian Steppe	Santa Cruz, 43 km from Perito Moreno to Los Antiguos
		E. scabrifolius (Döll) J.H. Hunz.	Native	Hemicryptophyte	Espinal, Paraná Flooded Savanna	Buenos Aires, NP Campos del Tuyú

(continued)

Family	Genus	Species	Status	Life form	Ecoregions	Reference site
	Eragrostis	E. bahiensis Schrad. ex Schult.	Native	Hemicryptophyte	Paraná Flooded Savanna	Santa Fe, Río Salado
		E. lugens Nees	Native	Hemicryptophyte	Espinal, Monte of Hills and Valleys	San Luis, Saladillo
		E. mexicana (Hornem.) Link subsp. virescens (J. Presl) S.D. Koch & Sanchéz Vega	Native	Therophyte	Dry Chaco	Catamarca, Salar de Pipanarco
		E. neesii Trin. var. expansiflora Nicora	Native	Hemicryptophyte	Humid Chaco	Santa Fe, Las Gamas
		E. nigricans (Kunth) Steud.	Native	Hemicryptophyte	Puna	Jujuy, Salinas Grandes
		E. orthoclada Hack.	Native	Hemicryptophyte	Paraná Flooded Savanna	Chaco, 13 km N from La Verde, Estancia Dos Tranqueras
	Eriochloa	E. acuminata (J. Presl) Kunth	Native	Hemicryptophyte	Dry Chaco	Córdoba, Salinas Grandes
		E. montevidensis Griseb.	Native	Hemicryptophyte	Espinal	Córdoba, NR 158, 23 km S from San Francisco
		E. punctata (L.) Desv. ex Ham.	Native	Hemicryptophyte	Dry Chaco, Espinal, Humid Chaco	Córdoba, Jeanmaire
		E. tridentata (Trin.) Kuhlm.	Native	Hemicryptophyte	Dry Chaco, Pampa	Santiago del Estero, Lagunas Saladas, road between PR 56 & Los Juríes
	Erioneuron	E. pilosum (Buckley) Nash var. longiaristatum (Kurtz) Anton	Endemic	Hemicryptophyte	Dry Chaco	Santiago del Estero, Salina de Ambargasta

	Festuca	F. argentina (Speg.) Parodi	Native	Hemicryptophyte	Patagonian Steppe	Santa Cruz, San Julián
		F. argentinensis (St.-Yves) Türpe	Native	Hemicryptophyte	High Andes	Salta, Salar de Arizaro
		F. dissitiflora Steud. ex Griseb.	Native	Hemicryptophyte	Puna	La Rioja, Salina del Leoncito
		F. humilior Nees & Meyen	Native	Hemicryptophyte	Puna	Jujuy, Laguna de los Pozuelos
		F. orthophylla Pilg.	Native	Hemicryptophyte	Puna	Jujuy, Laguna de Guayatayoc
		F. parodii St.-Yves	Endemic	Hemicryptophyte	Puna	La Rioja, Salinas del Leoncito
	Gouinia	G. latifolia (Griseb.) Vasey	Native	Hemicryptophyte	Espinal	Córdoba, Mar Chiquita
		G. paraguayensis (Kuntze) Parodi var. tortuosa (Swallen) Türpe	Native	Hemicryptophyte	Dry Chaco	La Rioja, E edge of Salina La Antigua
	Hordeum	H. comosum J. Presl	Native	Hemicryptophyte	Patagonian Steppe	Tierra del Fuego, Estancia Cullen, near N edge of Bahía San Sebastián
		H. cordobense Bothmer, Jacobsen & Nicora	Endemic	Hemicryptophyte	Dry Chaco, Pampa	Tucumán, Chañar Pozo
		H. erectifolium Bothmer, Jacobsen & M. Jørg.	Endemic	Hemicryptophyte	Espinal	Buenos Aires, Salinas Chicas
		H. euclaston Steud.	Native	Therophyte	Espinal, Monte of Plains and Plateaus	Corrientes, Estancia La Encarnación
		H. flexuosum Nees ex Steud.	Native	Hemicryptophyte	Pampa	Buenos Aires, Cascallares, Río Quequén Salado
		H. lechleri (Steud.) Schenck	Native	Hemicryptophyte	Patagonian Steppe	Tierra del Fuego, Bahía de San Sebastián
		H. muticum J. Presl	Native	Hemicryptophyte	Puna	Jujuy, Quebrada de Salitre
		H. procerum Nevski	Endemic	Hemicryptophyte	Pampa	Buenos Aires, Tres Arroyos, Río Quequén Salado
		H. pubiflorum Hook. f. subsp. halophilum (Griseb.) Baden & Bothmer	Native	Hemicryptophyte	Puna	Catamarca, Laguna blanca
		H. pubiflorum Hook. f. subsp. pubiflorum	Native	Hemicryptophyte	Patagonian Steppe, Puna	Santa Cruz, Estancia Tapi Aike
		H. stenostachys Godr.	Native	Hemicryptophyte	Espinal, Pampa	Buenos Aires, Bahía Blanca Estuary

(continued)

Family	Genus	Species	Status	Life form	Ecoregions	Reference site
	Hymenachne	H. amplexicaulis (Rudge) Nees	Native	Hemicryptophyte	Paraná Flooded Savanna	Buenos Aires, Río Salado
	Jarava	J. ichu Ruiz & Pav. var. ichu	Native	Hemicryptophyte	Espinal	La Pampa, Laguna Guatraché
		J. neaei (Nees ex Steud.) Peñailillo	Native	Hemicryptophyte	Puna	San Juan, Río de Sal
		J. plumosa (Spreng.) S.W.L. Jacobs & J. Everett	Native	Hemicryptophyte	Espinal	Buenos Aires, Salitral de la Vidriera
	Leptochloa	L. dubia (Kunth) Nees	Native	Hemicryptophyte	Dry Chaco	Santiago del Estero, Salinas Grandes
		L. fusca (L.) Kunth subsp. fascicularis (Lam.) N.W. Snow	Native	Hemicryptophyte	Dry Chaco, Pampa	Córdoba, Salinas Grandes
		L. fusca (L.) Kunth subsp. uninervia (J. Presl) N. Snow	Native	Hemicryptophyte	Dry Chaco, Espinal, Pampa, Puna	Córdoba, Salinas Grandes
	Melica	M. argyrea Hack.	Native	Hemicryptophyte	Pampa	Santa Fe, Arteaga
		M. glabrescens (Torres) Torres	Endemic	Hemicryptophyte	Pampa	Buenos Aires, Cascallares, Río Quequén Salado
		M. macra Nees	Native	Hemicryptophyte	Dry Chaco, Pampa	Tucumán, Salitral Pobre
		M. rigida Cav.	Native	Hemicryptophyte	Pampa	Buenos Aires, Río Salado
	Muhlenbergia	M. asperifolia (Nees & Meyen ex Trin.) Parodi	Native	Hemicryptophyte	Espinal, High Andes, Monte of Hills and Valleys, Patagonian Steppe	Catamarca, Carachi Pampa
	Munroa	M. andina Phil.	Native	Therophyte	Puna	Jujuy, Salinas Grandes
	Nassella	N. arcuata (R.E. Fr.) Torres	Native	Hemicryptophyte	Puna	Jujuy, Salinas Grandes
		N. formicarum (Delile) Barkworth	Native	Hemicryptophyte	Pampa	Buenos Aires, Cascallares, Río Quequén Salado
		N. nardoides (Phil.) Barkworth	Native	Hemicryptophyte	High Andes	Jujuy, Laguna de Vilama
		N. tenuis (Phil.) Barkworth	Native	Hemicryptophyte	Espinal, Monte of Plains and Plateaus, Patagonian Steppe	Mendoza, Salinas del Diamante

	Nicoraepoa	N. pugionifolia (Speg.) Soreng & L.J. Gillespie	Native	Hemicryptophyte	Patagonian Steppe	Patagonia Occidental
	Panicum	P. chloroleucum Griseb.	Endemic	Hemicryptophyte	Puna	Catamarca, Laguna Blanca
		P. urvilleanum Kunth	Native	Hemicryptophyte	Dry Chaco, Monte of Plains and Plateaus	La Rioja, Salina de Mascasín
	Pappophorum	P. caespitosum R.E. Fr.	Native	Hemicryptophyte	Dry Chaco, Espinal, Pampa	Buenos Aires, Salitral de la Vidriera
		P. pappiferum (Lam.) Kuntze	Native	Hemicryptophyte	Dry Chaco, Paraná Flooded Savanna	Tucumán, Chañar Pozo
		P. phillippianum Parodi	Native	Hemicryptophyte	Dry Chaco, Espinal, Monte of Plains and Plateaus, Pampa	Mendoza, Salinas del Diamante
		P. vaginatum Buckley	Native	Hemicryptophyte	Dry Chaco	Córdoba, Salinas Grandes
	Pappostipa	P. chrysophylla (E. Desv.) Romaschenko var. chrysophylla	Native	Hemicryptophyte	Patagonian Steppe	Mendoza, Laguna de Llancanelo
		P. humilis (Cav.) Romaschenko var. humilis	Native	Hemicryptophyte	Patagonian Steppe	Santa Cruz, Puerto Deseado
	Paspalum	P. almum Chase	Native	Hemicryptophyte	Humid Chaco	Chaco, NR 11, Río Salado
		P. buckleyanum Vasey	Native	Hemicryptophyte	Dry Chaco	Salta, NR 16, km 669, El Galpón
		P. denticulatum Trin.	Native	Hemicryptophyte	Dry Chaco	Salta, NR 16, between km 669 & 675, El Galpón.
		P. distichum L.	Native	Hemicryptophyte	Dry Chaco, Espinal	Tucumán, NR 9, Río India Muerta
		P. malacophyllum Trin.	Native	Hemicryptophyte	Dry Chaco	Tucumán, NR 9, 3 km from the boundary with Santiago del Estero
		P. vaginatum Sw.	Native	Hemicryptophyte	Espinal, Pampa	Buenos Aires, Pehuajó
	Phragmites	P. australis (Cav.) Trin. ex Steud.	Native	Hemicryptophyte	Espinal	Buenos Aires, Salina Chica

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Family	Genus	Species	Status	Life form	Ecoregions	Reference site
	Poa	P. atropidiformis Hack. var. atropidiformis	Native	Hemicryptophyte	Patagonian Steppe	Tierra del Fuego, Estancia Cullen, near N edge of Bahía San Sebastian
		P. lanigera Nees	Native	Hemicryptophyte	Pampa	Santa Fe, between Los Nogales & Río Carcarañá
		P. lanuginosa Poir. var. patagonica (Phil.) Giussani & Soreng	Native	Hemicryptophyte	Patagonian Steppe	Chubut, Salina Grande, Península Valdés
		P. ligularis Nees ex Steud. var. resinulosa (Nees ex Steud.) Fernández Pepi & Giussani	Endemic	Hemicryptophyte	Pampa	Córdoba, Pacheco de Melo
	Polypogon	P. interruptus Kunth	Native	Hemicryptophyte	High Andes	Catamarca, Andes, E of Paso De San Francisco
	Puccinellia	P. argentinensis (Hack.) Parodi	Native	Hemicryptophyte	High Andes, Puna	La Rioja, Laguna Brava
		P. frigida (Phil.) I.M. Johnst.	Native	Hemicryptophyte	High Andes, Puna	Jujuy, Cerro Sal
		P. glaucescens (Phil.) Parodi	Native	Hemicryptophyte	Pampa	La Pampa, Gral. Pico
		P. magellanica (Hook. f.) Parodi	Native	Hemicryptophyte	Patagonian Steppe	Tierra del Fuego, Río Grande Department
		P. mendozina (Hack.) Parodi	Endemic	Hemicryptophyte	Patagonian Steppe	Santa Cruz, Estancia Tapi Aike
		P. pusilla (Hack.) Parodi	Native	Hemicryptophyte	Patagonian Steppe	Santa Cruz, PR 12, between Cañadón Seco & Caleta Olivia
	Schizachyrium	S. microstachyum (Desv. ex Ham.) Roseng., B.R. Arrill. & Izag.	Native	Hemicryptophyte	Dry Chaco, Humid Chaco	Santiago del Estero, J.F.Ibarra, Lagunas Saladas, road between PR 56 & Los Juríes

	Setaria	S. geminata (Forssk.) Veldkamp	Native	Hemicryptophyte	Pampa	Buenos Aires, Depresión del Salado
		S. hunzikeri Anton	Native	Hemicryptophyte	Dry Chaco	La Rioja, NR 79, between Chamical & Casa de Piedra
		S. lachnea (Nees) Kunth	Native	Hemicryptophyte	Dry Chaco, Espinal	Córdoba, Jeanmaire
		S. leucopila (Scribn. & Merr.) K. Schum.	Native	Hemicryptophyte	Dry Chaco	La Rioja, Salina la Antigua
		S. macrostachya Kunth	Native	Hemicryptophyte	Dry Chaco	Tucumán, Chañar Pozo
		S. pampeana Parodi ex Nicora	Native	Hemicryptophyte	Dry Chaco, Espinal, Monte of Plains and Plateaus	La Pampa, Salitral Negro
		S. parviflora (Poir.) Kerguélen var. parviflora	Native	Hemicryptophyte	Dry Chaco, Humid Chaco, Iberá Marshes, Pampa	Santa Fe, Tostado, Río Salado
	Spartina	S. densiflora Brongn.	Native	Hemicryptophyte	Espinal, Humid Chaco, Pampa, Paraná Flooded Savanna	Córdoba, Mar Chiquita
		S. fasciculata (Lam.) P. Beauv.	Native	Hemicryptophyte	Espinal, Paraná Flooded Savanna	Buenos Aires, Bahía de Samborombón
		S. spartinae (Trin.) Merr. ex Hitchc.	Native	Hemicryptophyte	Humid Chaco, Pampa, Paraná Flooded Savanna	Chaco, Río Salado

(continued)

Family	Genus	Species	Status	Life form	Ecoregions	Reference site
	Sporobolus	S. indicus (L.) R. Br. var. indicus	Native	Hemicryptophyte	Dry Chaco, Iberá Marshes, Pampa	Corrientes, Rincón de Luna, Estancia Los Tres Rincones, Alto Cué
		S. maximus Hauman	Endemic	Hemicryptophyte	Monte of Hills and Valleys	Tucumán, Rio Santa Maria
		S. mendocinus E. Méndez	Endemic	Hemicryptophyte	Monte of Plains and Plateaus	Mendoza, Arroyo Blanco
		S. monandrus Roseng., B.R. Arrill. & Izag.	Native	Hemicryptophyte	Espinal	Entre Ríos, Paso Yunque, on tha Guayquiraró
		S. phleoides Hack.	Endemic	Hemicryptophyte	Dry Chaco, Espinal, Humid Chaco, Pampa, Monte of Plains and Plateaus	La Pampa, Salitral de La Perra
		S. pyramidatus (Lam.) Hitchc.	Native	Hemicryptophyte	Dry Chaco, Espinal, Humid Chaco, Pampa	San Juan, Salina de Mascasín
		S. rigens (Trin.) E. Desv. var. atacamensis (Parodi) Asteg.	Endemic	Hemicryptophyte	Puna	Jujuy, Salinas Grandes
		S. rigens (Trin.) E. Desv. var. rigens	Native	Hemicryptophyte	Espinal, Monte of Plains and Plateaus, Patagonian Steppe	Chubut, Salina Chica, Península Valdés
	Steinchisma	S. hians (Elliott) Nash	Native	Hemicryptophyte	Espinal	Santa Fe, between San Cristóbal & Crespo, Estancia La Fortuna
	Stenotaphrum	S. secundatum (Walter) Kuntze	Native	Hemicryptophyte	Pampa	Buenos Aires, Arroyo San Clemente
	Trichloris	T. crinita (Lag.) Parodi	Native	Hemicryptophyte	Dry Chaco, High Andes	Catamarca, Salinas Grandes
	Urochloa	U. adspersa (Trin.) R.D. Webster	Native	Hemicryptophyte	Dry Chaco	Tucumán, Monteagudo
		U. paucispicata (Morong) Morrone & Zuloaga	Native	Hemicryptophyte	Dry Chaco	Córdoba, Salinas Grandes

Portulacaceae	Calandrinia	C. compacta Barnéoud	Native	Hemicryptophyte	High Andes	La Rioja, Reserva Laguna Brava, Río Salado
	Portulaca	P. confertifolia Hauman var. cordobensis D. Legrand	Endemic	Hemicryptophyte	Dry Chaco	Córdoba, Salinas Grandes
		P. echinosperma Hauman	Endemic	Therophyte	Dry Chaco	San Juan, Salina de Mascasín
		P. grandiflora Hook.	Native	Therophyte	Dry Chaco	San Juan, Salina de Mascasín
		P. obtusifolia D. Legrand var. obtusifolia	Endemic	Hemicryptophyte	Dry Chaco	Córdoba, Saladillo, Villa Candelaria
		P. ragonesei D. Legrand	Endemic	Hemicryptophyte	Dry Chaco	Córdoba, Salinas Grandes
	Talinum	T. polygaloides Gillies ex Arn.	Native	Geophyte	Dry Chaco	Córdoba, Salinas Grandes
Potamogetonaceae	Stuckenia	S. filiformis (Pers.) Boehm. ssp. alpina (Blytt) R.R. Haynes, Les & M. Král	Native	Geophyte	High Andes	San Juan, Quebrada Mula Tuerta
		S. striata (Ruiz & Pav.) Holub	Native	Geophyte	Pampa	Buenos Aires, Río Quequén Salado
Ranunculaceae	Halerpestes	H. cymbalaria (Pursh) Greene	Native	Geophyte	Monte of Hills and Valleys, Pampa	Catamarca, from NR 40 to Famabalasto
		H. exilis (Phil.) Tamura	Native	Geophyte	High Andes, Puna	La Rioja, Laguna Brava
Rhamnaceae	Discaria	D. chacaye (G. Don.) Tortosa	Native	Phanerophyte	Patagonian Steppe	Tierra del Fuego, Bahía San Sebastián
	Ziziphus	Z. mistol Griseb.	Native	Phanerophyte	Dry Chaco	Catamarca, Salinas Grandes
Ruppiaceae	Ruppia	R. cirrhosa (Petagna) Grande	Native	Geophyte	Dry Chaco, Espinal	Córdoba, Salinas Grandes
Sapindaceae	Urvillea	U. chacoënsis Hunz.	Native	Chamaephyte	Dry Chaco	Córdoba, Salinas Grandes

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Family	Genus	Species	Status	Life form	Ecoregions	Reference site
Scrophulariaceae	Bacopa	B. monnieri (L.) Pennell	Native	Therophyte	Humid Chaco, Monte of Plains and Plateaus	Mendoza, Ciénagas de Resolana
	Limosella	L. australis R. Br.	Native	Therophyte	Patagonian Steppe	Santa Cruz, Estancia Tapi Aike
	Monttea	M. aphylla (Miers) Benth. & Hook. var. aphylla	Endemic	Chamaephyte	Monte of Plains and Plateaus	La Pampa, Laguna Curru Lauquen
	Scoparia	S. dulcis L.	Native	Hemicryptophyte	Dry Chaco	Tucumán, Chañar Pozo
		S. montevidensis (Spreng.) R.E. Fr.	Native	Hemicryptophyte	Pampa	Córdoba, La Nacional
Simaroubaceae	Castela	C. coccinea Griseb.	Native	Phanerophyte	Dry Chaco	Códoba, Mar Chiquita
Solanaceae	Bouchetia	B. anomala (Miers) Britton & Rusby	Native	Hemicryptophyte	Dry Chaco, Espinal	Córdoba, Mar Chiquita
	Calibrachoa	C. humilis (R.E. Fr.) Stehmann & Semir	Native	Chamaephyte	Espinal	Corrientes, road from Mercedes to Paso de los Libres & Río Miriñay
		C. parviflora (Juss.) D'Arcy	Native	Hemicryptophyte	Espinal, Humid Chaco, Pampa	Corrientes, Monte Caseros
	Fabiana	F. denudata Miers	Native	Phanerophyte	Monte of Plains and Plateaus	Mendoza, Salinas del Diamante
		F. densa J. Remy	Native	Chamaephyte	Puna	Jujuy, Quebrada de Salitra
		F. patagonica Speg.	Native	Phanerophyte	Patagonian Steppe	Santa Cruz, Lago Salitroso
	Jaborosa	J. bergii Hieron.	Endemic	Hemicryptophyte	Espinal	Buenos Aires, Salina Chica
	Leptoglossis	L. linifolia (Miers) Griseb.	Endemic	Hemicryptophyte	Dry Chaco, Espinal, Humid Chaco, Pampa	Córdoba, Mar Chiquita

	Lycium	L. americanum Jacq.	Native	Chamaephyte	Dry Chaco, Espinal, Iberá Marshes	Formosa, Laguna La Salada
		L. boerhaviifolium L. f.	Native	Chamaephyte	Dry Chaco, Espinal, Iberá Marshes, Pampa	Córdoba, Mar Chiquita
		L. chanar Phil.	Native	Chamaephyte	High Andes	Catamarca, around Antofagasta de la Sierra
		L. chilense Miers ex Bertero var. chilense	Native	Chamaephyte	Dry Chaco, Espinal	Buenos Aires, Salitral de la Vidriera
		L. chilense Miers ex Bertero var. confertifolium (Miers) F.A. Barkley	Native	Chamaephyte	Monte of Plains and Plateaus	La Pampa, Salar Levalle
		L. chilense Miers ex Bertero var. filifolium (Miers) Bernardello	Native	Chamaephyte	Dry Chaco, Espinal, Monte of Plains and Plateaus	Córdoba, Mar Chiquita
		L. chilense Miers ex Bertero var. minutifolium (Miers) F.A. Barkley	Native	Chamaephyte	Dry Chaco, Monte of Plains and Plateaus, Patagonian Steppe	La Pampa, Salar Levalle
		L. ciliatum Schltdl.	Native	Chamaephyte	Dry Chaco, Espinal	Córdoba, Salinas Grandes
		L. elongatum Miers	Endemic	Chamaephyte	Dry Chaco	Tucumán, Cajón del Río Luro
		L. humile Phil.	Native	Chamaephyte	High Andes, Puna	Catamarca, Salina de Antofalla
		L. infaustum Miers	Endemic	Chamaephyte	Dry Chaco, Espinal, Humid Chaco, Pampa	Córdoba, between R. D. de Guzmán & Pacheco de Melo
		L. morongii Britton	Native	Chamaephyte	Iberá Marshes, Paraná Flooded Savanna	Chaco, Colonia Benitez
		L. nodosum Miers	Native	Chamaephyte	Dry Chaco	Tucumán, Chañar Pozo
		L. repens Speg.	Endemic	Chamaephyte	Patagonian Steppe	Santa Cruz, Río Gallegos
		L. tenuispinosum Miers var. calycinum (Griseb.) Bernardello	Native	Chamaephyte	Dry Chaco	Tucumán, Tapia, Quebrada de Lules
		L. tenuispinosum Miers var. friesii (Dammer) C.L. Hitchc.	Endemic	Chamaephyte	Dry Chaco	Santiago del Estero, Quimili Paso
		L. tenuispinosum Miers var. tenuispinosum	Native	Chamaephyte	Dry Chaco, Espinal, Monte of Plains and Plateaus	La Pampa, Laguna Colorada Grande
		L. vimineum Miers	Native	Chamaephyte	Espinal	Santa Fe, between Esperanza & Santa Fe, Río Salado

(continued)

Family	Genus	Species	Status	Life form	Ecoregions	Reference site
	Nicotiana	N. corymbosa J. Remy var. corymbosa	Native	Therophyte	Puna	San Juan, Reserva de San Guillermo, Río de la Sal
		N. longiflora Cav.	Native	Hemicryptophyte	Espinal, Puna	Córdoba, Mar Chiquita
		N. paa Mart. Crov.	Native	Hemicryptophyte	Dry Chaco	Catamarca, Pipanaco
	Petunia	P. axillaris (Lam.) Britton, Stern & Poggenb. subsp. axillaris	Native	Therophyte	Espinal	Córdoba, Mar Chiquita
		P. inflata R.E. Fr.	Native	Therophyte	Humid Chaco	Formosa, Río Salado
	Physalis	P. viscosa L.	Native	Hemicryptophyte	Espinal, Pampa	Córdoba, Mar Chiquita
	Sclerophylax	S. arnottii Miers	Endemic	Hemicryptophyte	Dry Chaco	San Juan, Salina de Mascasín
		S. difulvioi Del Vitto & Petenatti	Endemic	Hemicryptophyte	Monte of Hills and Valleys	San Luis, Sierra de Las Quijadas
		S. lorentzianus O. Hoffm.	Native	Hemicryptophyte	Mesopotamian Savanna	Corrientes, NR 127 & Arroyo Ayui
		S. spinescens Miers	Native	Therophyte	Espinal, Paraná Flooded Savanna	Córdoba, Mar Chiquita
		S. trispermum Di Fulvio	Endemic	Therophyte	Dry Chaco	Formosa, Las Lomitas
	Solanum	S. atropurpureum Schrank	Native	Hemicryptophyte	Humid Chaco	Formosa, NR 11, km 1144, Arroyo Salado
		S. brevicaule Bitter	Native	Hemicryptophyte	Monte of Hills and Valleys	Salta, Río Salado
		S. elaeagnifolium Cav.	Native	Hemicryptophyte	Dry Chaco, Monte of Plains and Plateaus	San Luis, Salina del Bebedero
		S. euacanthum Phil.	Native	Hemicryptophyte	Dry Chaco,Monte of Plains and Plateaus, Patagonian Steppe	Córdoba, Salinas Grandes
		S. hieronymi Kuntze	Native	Hemicryptophyte	Monte of Plains and Plateaus	San Luis, Salina del Bebedero
		S. juvenale Thell.	Native	Hemicryptophyte	Dry Chaco	Tucumán, Chañar Pozo
		S. pilcomayense Morong	Native	Hemicryptophyte	Dry Chaco	Tucumán, Chañar Pozo
		S. triflorum Nutt.	Native	Therophyte	Pampa	Buenos Aires, Estancia Salalé

Sterculiaceae	Ayenia	A. odonellii Cristóbal	Native	Chamaephyte	Iberá Marshes	Corrientes, NR 12, 10 km S from NR 123
	Melochia	M. anomala Griseb.	Native	Chamaephyte	Dry Chaco	Córdoba, Salinas Grandes
		M. hermannioides St.Hil	Native	Chamaephyte	Iberá Marshes	Corrientes, NR 12, 10 km S from NR 123
Typhaceae	Typha	T. domingensis Pers.	Native	Geophyte	Dry Chaco	San Juan, Baño El Salado
Valerianaceae	Valeriana	V. castellanosii Borsini	Native	Hemicryptophyte	High Andes	Jujuy, Laguna de Vilama
Verbenaceae	Aloysia	A. gratissima (Gillies & Hook. ex Hook.) Tronc. var. gratissima	Native	Phanerophyte	Dry Chaco, Espinal, Iberá Marshes	Entre Ríos, Paso Yunque, Río Guayquiraró
	Glandularia	G. flava (Gillies & Hook. ex Hook.) Schnack & Covas	Endemic	Hemicryptophyte	Espinal, Monte of Plains and Plateaus	Río Negro, Cipolletti
		G. lilloana (Moldenke) Botta	Endemic	Hemicryptophyte	Monte of Hills and Valleys	Catamarca, El Saladillo
		G. microphylla (Kunth) Cabrera	Native	Hemicryptophyte	Puna	Jujuy, Quebrada del Salitre
		G. nana (Moldenke) Tronc.	Native	Therophyte	Humid Chaco	Chaco, Margarita Belín
		G. tenera (Spreng.) Cabrera	Native	Hemicryptophyte	Espinal, Pampa	Buenos Aires, Lago Epecuén
		G. tweedieana (Niven ex Hook.) P. Peralta	Native	Hemicryptophyte	Iberá Marshes	Corrientes, 19.5 km SE from San Luis del Palmar
		G. venturii (Moldenke) Botta	Endemic	Hemicryptophyte	Espinal, Puna	San Luis, Saladillo

(continued)

Family	Genus	Species	Status	Life form	Ecoregions	Reference site
	Junellia	J. bisulcata (Hayek) Moldenke var. bisulcata	Native	Chamaephyte	Puna	Jujuy, El Moreno to Abra de Lipan
		J. connatibracteata (Kuntze) Moldenke	Endemic	Chamaephyte	Monte of Plains and Plateaus, Patagonian Steppe	Chubut, Salina del Pito
		J. hookeriana (Covas & Schnack) N. O'Leary & P. Peralta var. hookeriana	Endemic	Chamaephyte	Espinal, Monte of Plains and Plateaus	Buenos Aires, Laguna La Salada
		J. micrantha (Phil.) Múlgura	Native	Chamaephyte	Patagonian Steppe	Santa Cruz, 5–7 km from San Julián
		J. patagonica (Speg.) Moldenke	Endemic	Chamaephyte	Patagonian Steppe	Chubut, Estancia La Begonia
		J. seriphioides (Gillies & Hook. ex Hook.) Moldenke	Native	Chamaephyte	Monte of Plains and Plateaus, Puna	Jujuy, Salinas Grandes
		J. thymifolia (Lag.) Moldenke	Native	Chamaephyte	Patagonian Steppe	Chubut, NR 25, 42 km S from Paso de Indios
	Lippia	L. grata Schauer	Native	Phanerophyte	Dry Chaco	Catamarca, Salinas Grandes
		L. salsa Griseb.	Endemic	Phanerophyte	Dry Chaco, Espinal, Monte of Plains and Plateaus, Pampa	La Pampa, Salitral de La Perra
	Neosparton	N. aphyllum (Gillies & Hook. ex Hook.) Kuntze	Endemic	Chamaephyte	Monte of Plains and Plateaus	Mendoza, Salinas del Diamante
		N. patagonicum Tronc.	Endemic	Chamaephyte	Patagonian Steppe	Chubut, Colonia Sarmiento
	Parodianthus	P. ilicifolius (Moldenke) Tronc.	Endemic	Chamaephyte	Dry Chaco	Córdoba, Salinas Grandes
	Phyla	P. nodiflora (L.) Greene var. minor (Hook.) N. O'Leary & Múlgura	Native	Hemicryptophyte	Espinal, Iberá Marshes, Pampa	Corrientes, PR 152, 2 km N from Cerrito
	Pitraea	P. cuneato-ovata (Cav.) Caro	Native	Geophyte	Dry Chaco	Tucumán, Chañar Pozo, Río Saladillo
	Stachytarpheta	S. cayennensis (Rich.) Vahl	Native	Chamaephyte	Humid Chaco	Formosa, Río Salado

	Verbena	V. bonariensis L. var. bonariensis	Native	Therophyte	Espinal	Santa Fe, Campo Buriasco, near María Juana
		V. gracilescens (Cham.) Herter var. gracilescens	Native	Hemicryptophyte	Espinal, Mesopotamian Savanna	Córdoba, Río Cuarto or Saladillo
		V. litoralis Kunth var. subglabrata (Moldenke) N. O'Leary & Múlgura	Native	Hemicryptophyte	Humid Chaco	Santa Fe, Arroyo Golondrina & road to Fortín Olmos
Viscaceae	Phoradendron	P. argentinum Urb.	Native	Parasitic	Monte of Hills and Valleys	Salta, Los Castillos
Vitaceae	Cissus	C. verticillata (L.) Nicolson & C.E. Jarvis	Native	Phanerophyte	Dry Chaco	Córdoba, Salinas Grandes
Ximeniaceae	Ximenia	X. americana L. var. americana	Native	Phanerophyte	Dry Chaco	Córdoba, Salinas Grandes
Zannichelliaceae	Zanichelia	Z. palustris L.	Native	Geophyte	Pampa, Paraná Flooded Savanna	Buenos Aires, Oriente, Río Quequén Salado
Zygophyllaceae	Bulnesia	B. bonariensis Griseb.	Native	Phanerophyte	Dry Chaco	Formosa, El Descanso
		B. foliosa Griseb.	Native	Phanerophyte	Dry Chaco	La Rioja, E edge of Salina La Antigua
		B. retama (Gillies ex Hook. & Arn.) Griseb.	Native	Phanerophyte	Dry Chaco, Monte of Plains and Plateaus	La Rioja, Salina de Mascasín
	Larrea	L. ameghinoi Speg.	Endemic	Phanerophyte	Patagonian Steppe	Río Negro, NR 23, 52 km SW from Los Menucos in direction to Ing. Jacobacci
		L. cuneifolia Cav.	Endemic	Phanerophyte	Dry Chaco, Monte of Plains and Plateaus	Catamarca, Salar de Pipanaco
		L. divaricata Cav.	Native	Phanerophyte	Dry Chaco	Catamarca, Salinas Grandes
	Plectrocarpa	P. tetracantha Gillies ex Hook. & Arn	Endemic	Phanerophyte	Dry Chaco, Monte of Plains and Plateaus	Catamarca, Salinas Grandes
	Porlieria	P. microphylla (Baill.) Descole, O'Donell & Lourteig	Native	Phanerophyte	Dry Chaco, Monte of Plains and Plateaus	Mendoza, Salinas de Guasayán

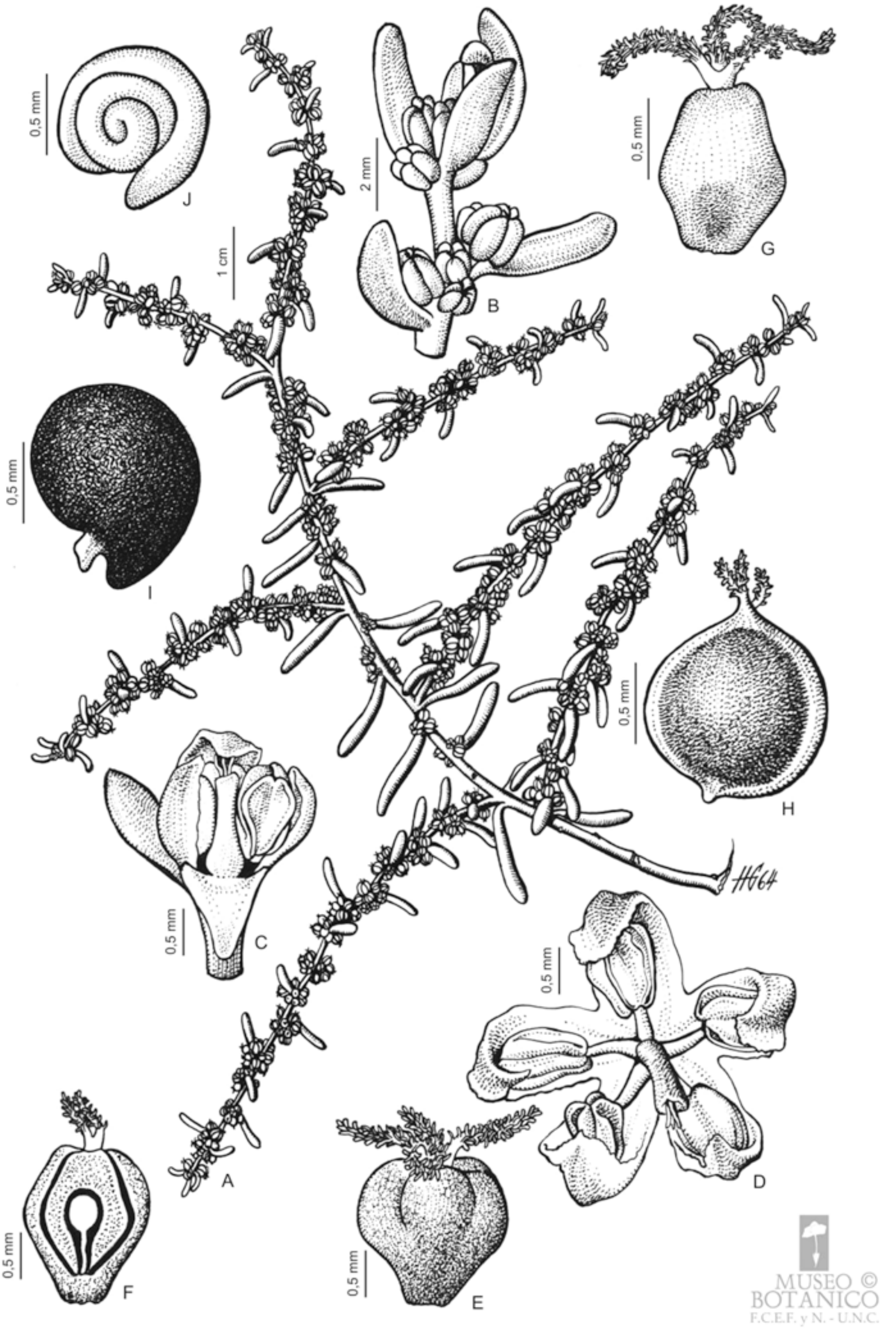

Fig. 9.3 *Suaeda divaricata*. (**a**) Branch of female plant. (**b**) Apex of female branch. (**c, d**) Male flower, in longitudinal section and upper view, respectively. (**e**) Female flower. (**f**) Female flower in longitudinal section. (**g**) Gynoecium. (**h**) Fruit. (**i**) Seed. (**j**) Embryo

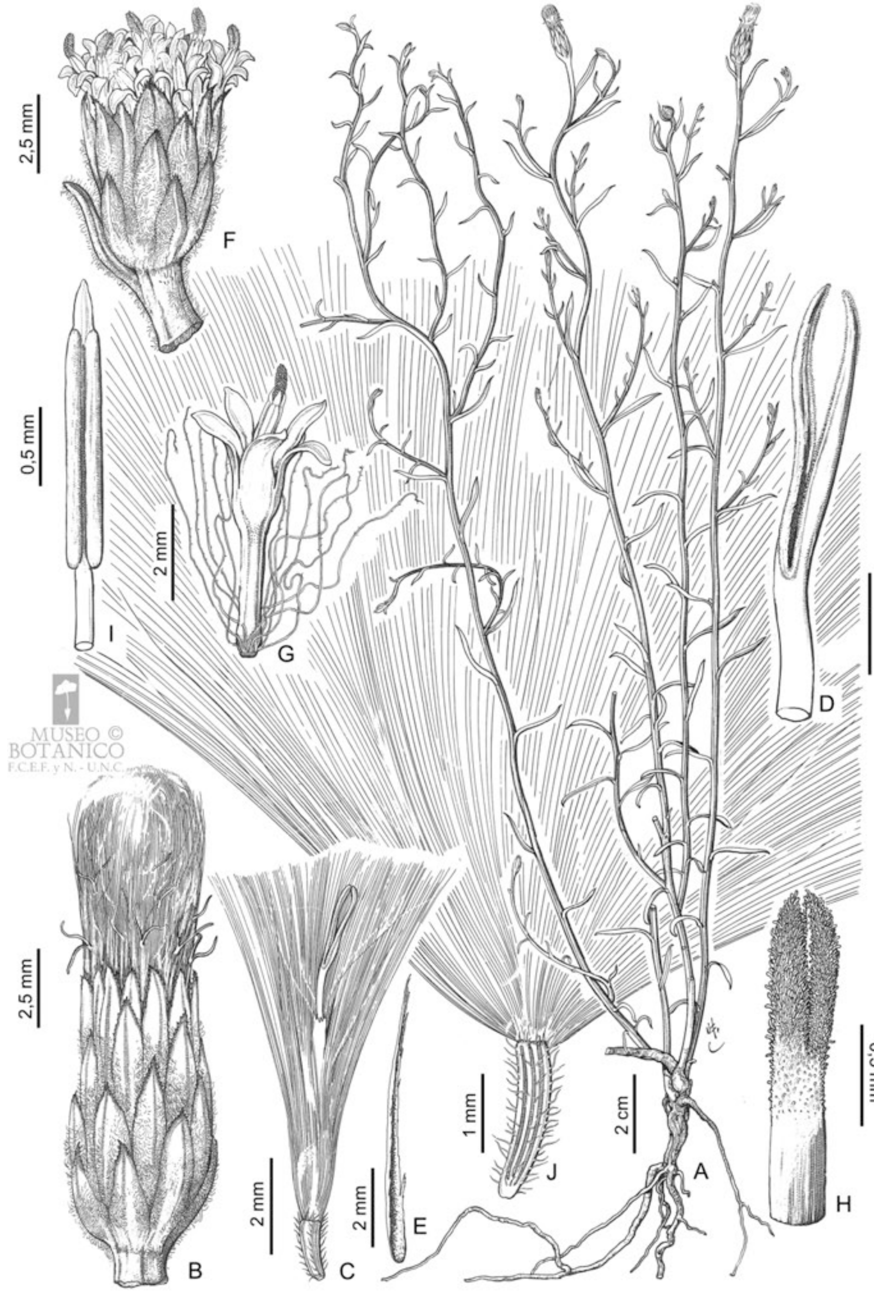

Fig. 9.4 *Baccharis tenella*. (**a**) Habit. (**b**) Female head. (**c**) Female flower. (**d**) Stigma of female flower. (**e**) Palea. (**f**) Male head. (**g**) Male flower. (**h**) Stigma of male flower. (**i**) Stamen. (**j**) Fruit

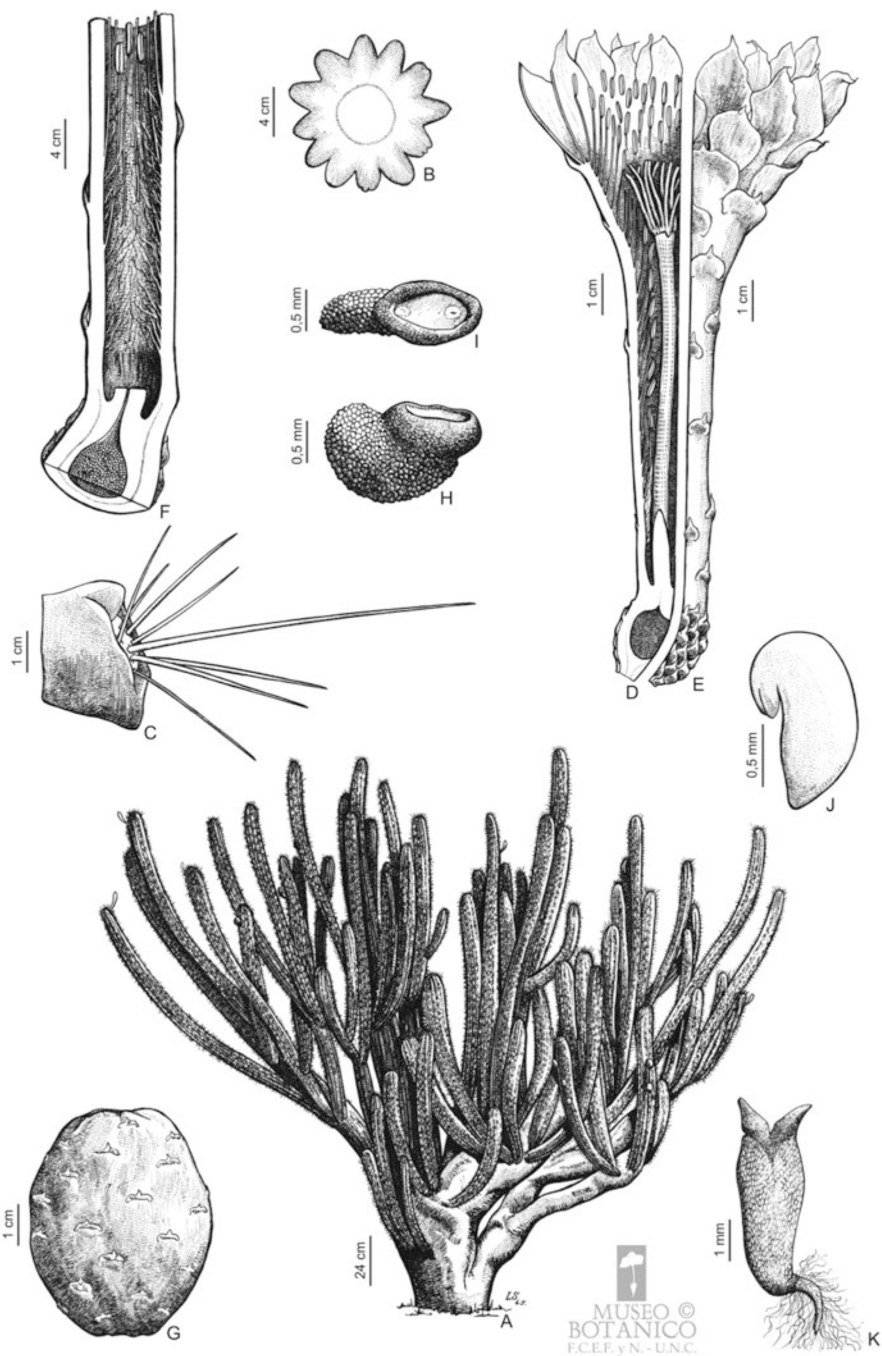

Fig. 9.5 *Stetsonia coryne*. (**a**) Habit. (**b**) Stem, cross section. (**c**) Areole. (**d, e**) Flower, longitudinal section and general view, respectively. (**f**) Opened floral tube. (**g**) Fruit. (**h–i**) Seed, lateral and hilar view

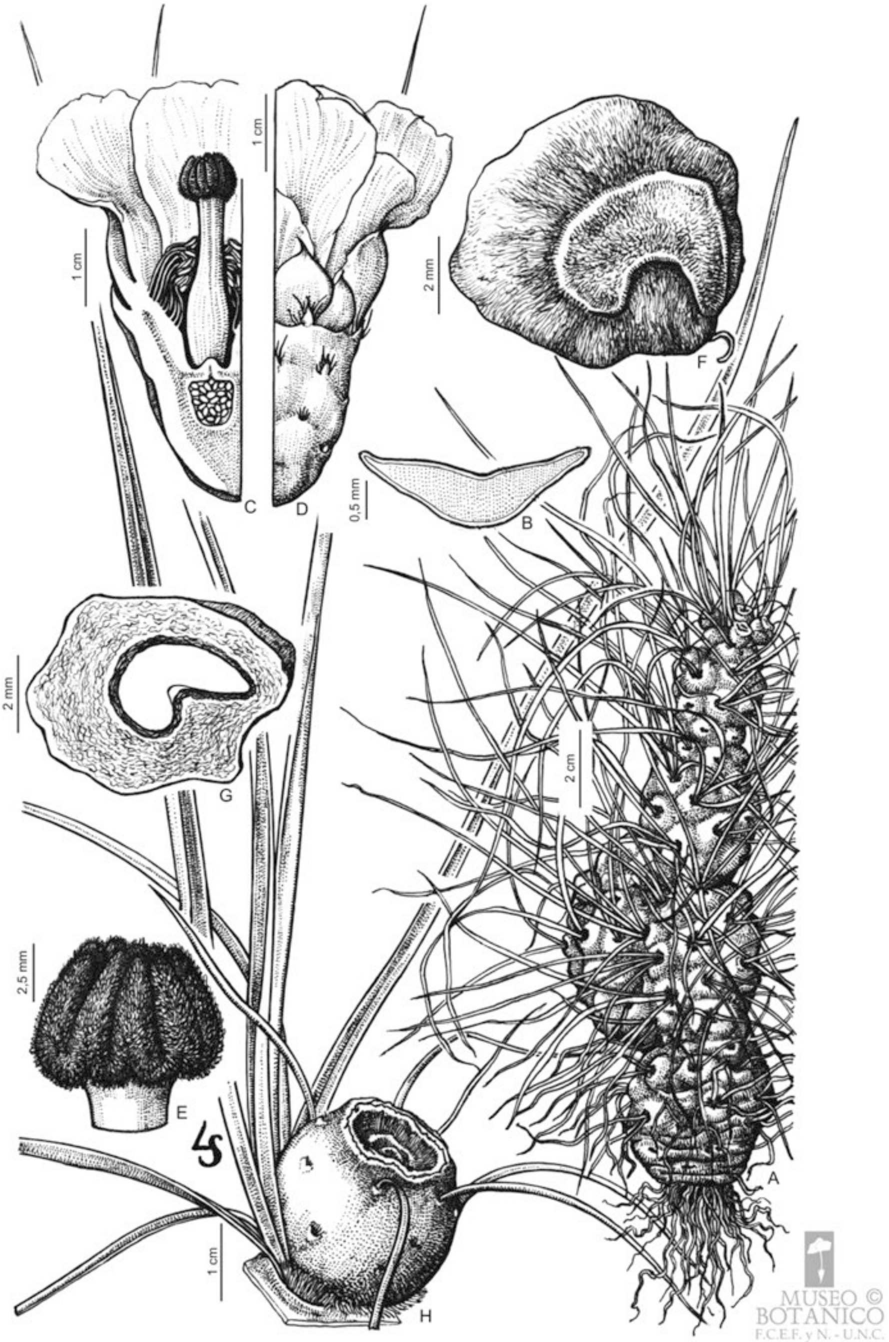

Fig. 9.6 *Tephrocactus aoracanthus*. (**a**) Plant. (**b**) Spine, cross section. (**c**) Flower, longitudinal section. (**d**) Flower, general view. (**e**) Stigma. (**f, g**) Seed, lateral view and cross section, respectively

Fig. 9.7 *Grahamia bracteata*. (**a**) Flowering branch. (**b**) Sepal. (**c**) Flower, longitudinal section. (**d**) Stamen, dorsal view. (**e**) Ovary, cross section. (**f**) Fruit. (**g**) Seed. (**h**) Seed, cross section. (**i**) Embryo

Fig. 9.8 *Maytenus vitis-idaea*. (**a**) Fruiting branch. (**b**) Male flower. (**c**) Female flower. (**d**) Basal view of female flower in longitudinal section

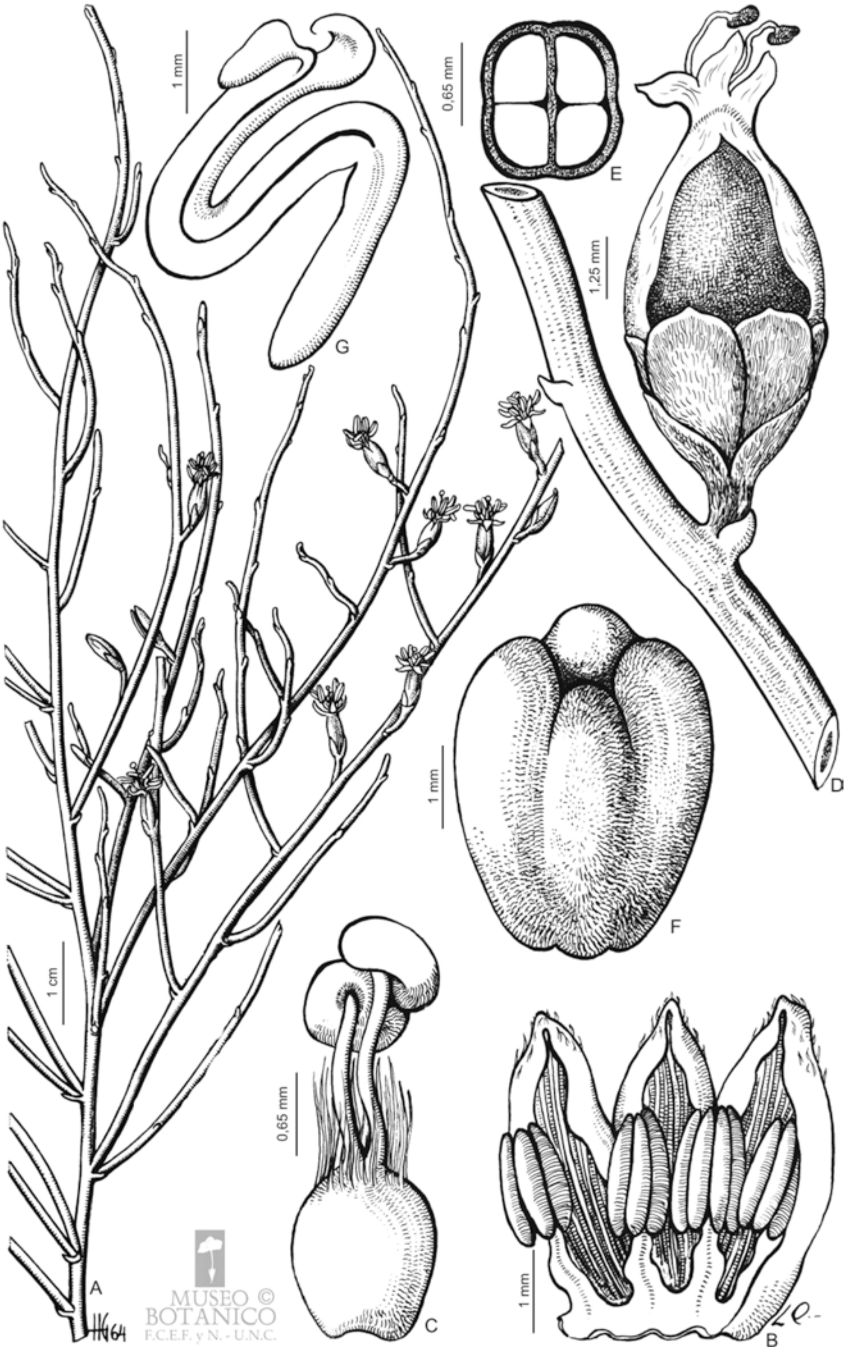

Fig. 9.9 *Cressa nudicaulis*. (**a**) Branch. (**b**) Opened corolla. (**c**) Gynoecium. (**d**) Branch with fruit. (**e**) Fruit, cross section. (**f**) Seed. (**g**) Embryo

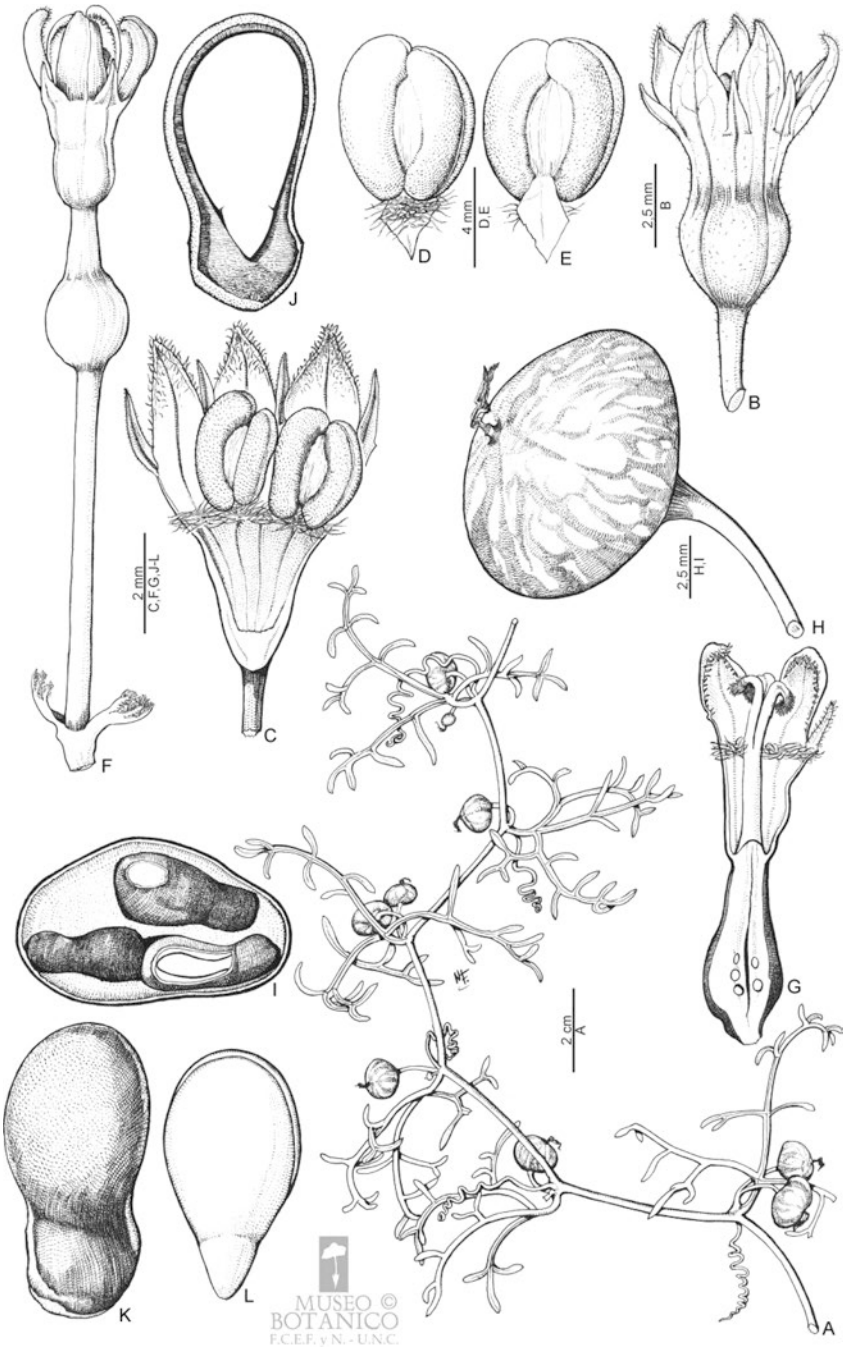

Fig. 9.10 *Halosicyos ragonesei*. (**a**) Fruiting branch. (**b, c**) Male flowers. (**d, e**) Anthers, ventral and dorsal view, respectively. (**f**) Female flower. (**g**) Female flower, cross section. (**g**) Fruit. (**i**) Fruit, cross section. (**j, k**) Seed, longitudinal and lateral view, respectively. (**l**) Embryo

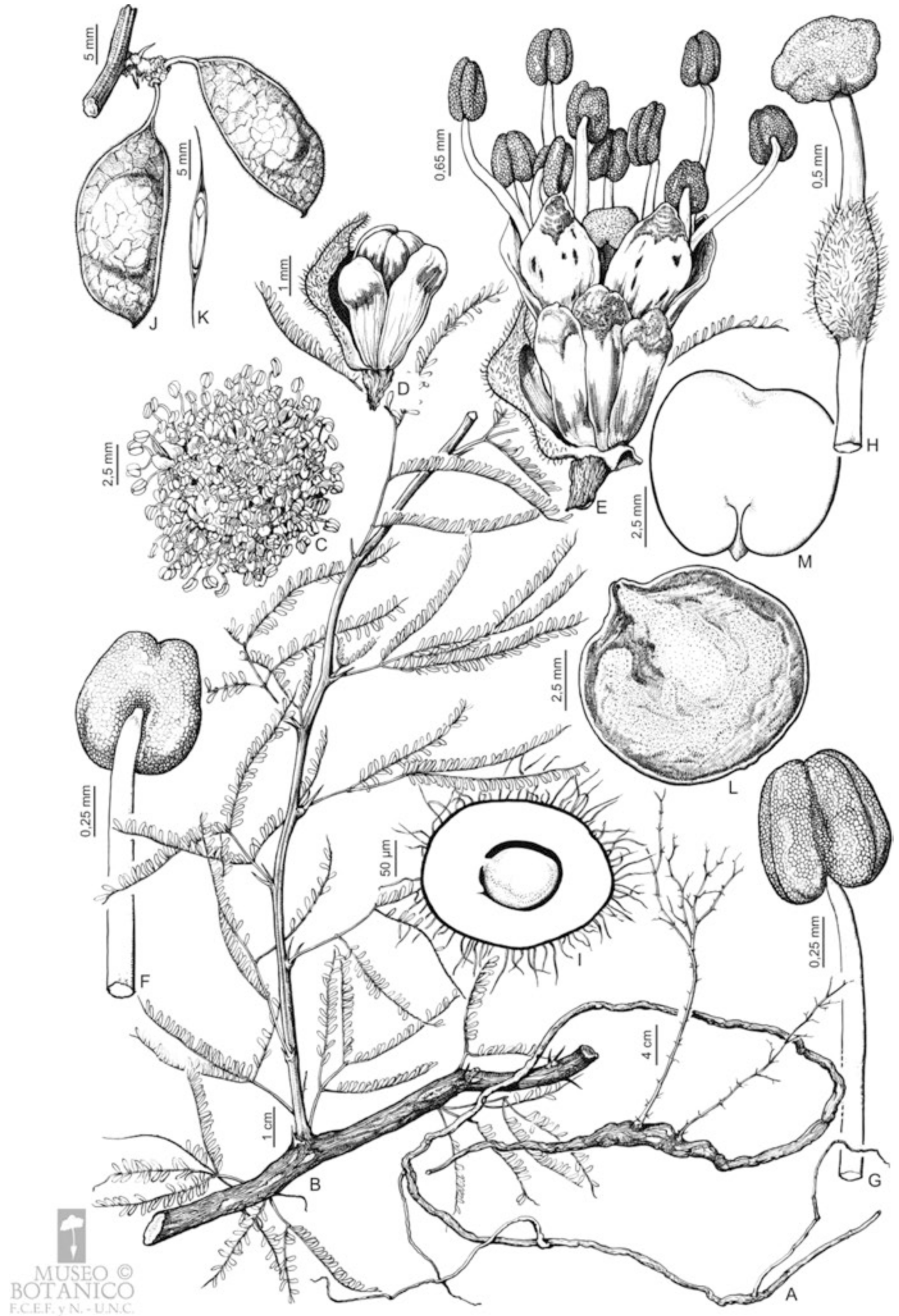

Fig. 9.11 *Mimozyganthus carinatus*. (**a, b**) Branches. (**c**) Inflorescence. (**d**) Flower bud and bract. (**e**) Flower. (**f, g**) Stamens, dorsal and ventral view, respectively. (**h**) Gynoecium. (**i**) Ovary, cross section. (**j**) Fruit. (**k**) Fruit, longitudinal section. (**l**) Seed. (**m**) Embryo

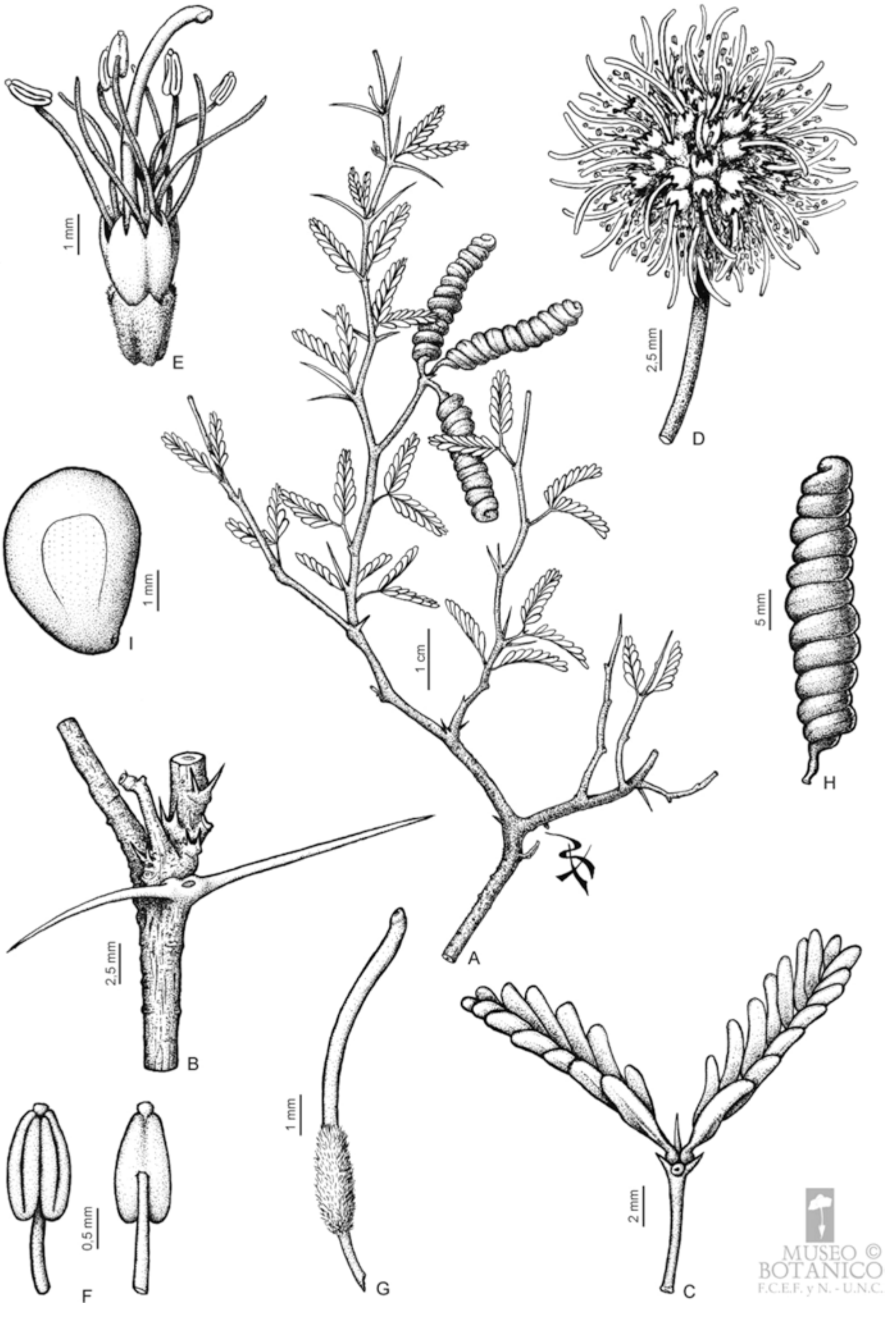

Fig. 9.12 *Prosopis reptans* var. *reptans*. (**a**) Fruiting branch. (**b**) Node with spines. (**c**) Leaf. (**d**) Inflorescence. (**e**) Flower. (**f**) Stamens, dorsal and ventral view. (**g**) Gynoecium. (**h**) Fruit. (**i**) Seed

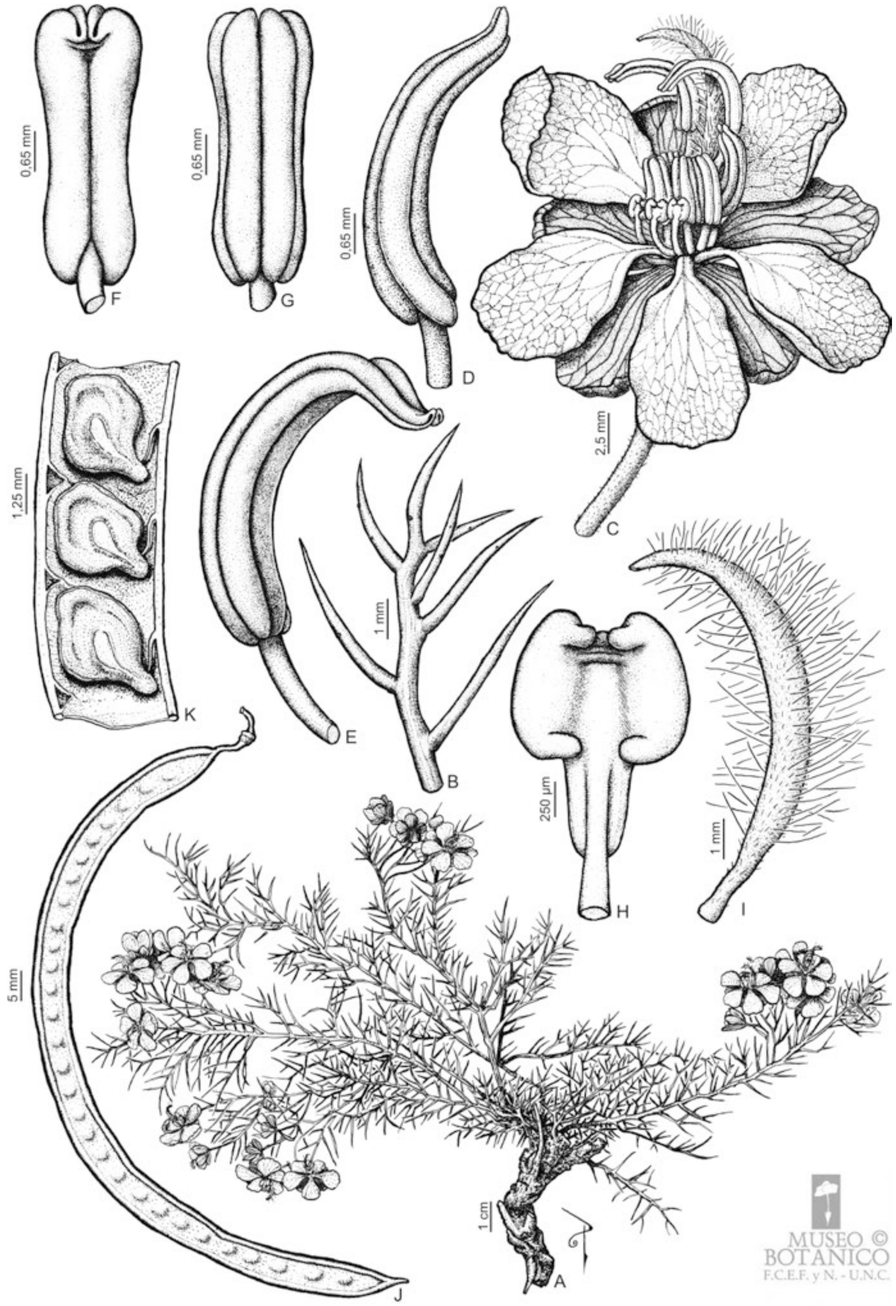

Fig. 9.13 *Senna acanthoclada*. (**a**) Plant. (**b**) Branch. (**c**) Flower. (**d, e**) Fertile basal stamens. (**f, g**) Fertile medium stamens. (**h**) Staminode. (**i**) Gynoecium. (**j**) Fruit

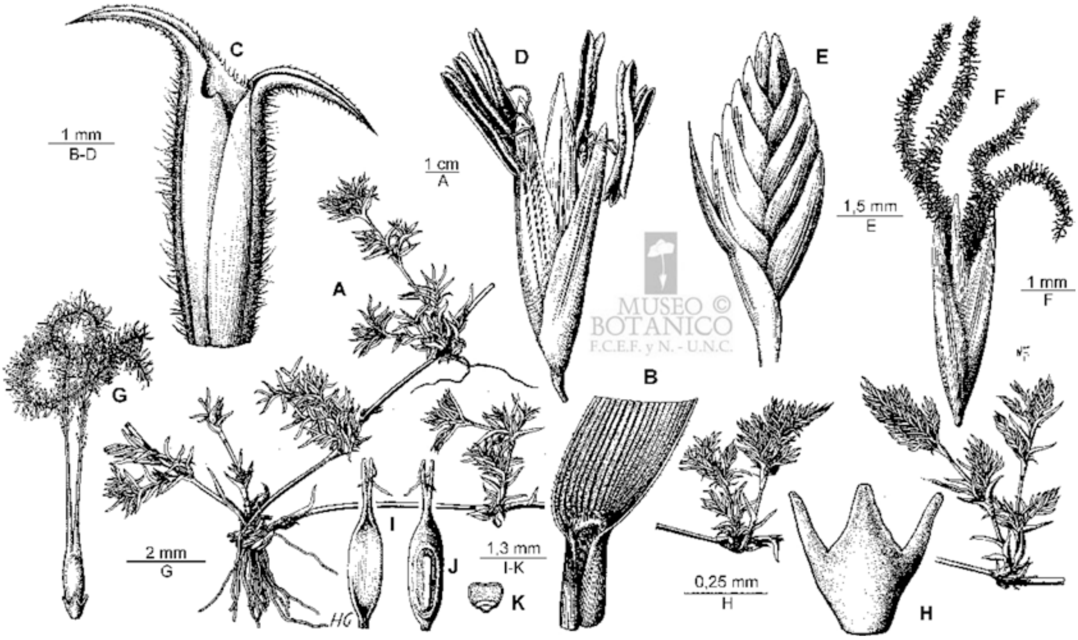

Fig. 9.14 *Distichlis acerosa*. (**a**) Habit. (**b**) Ligule. (**c**) Profiles. (**d, e**) Staminate spikelets. (**f**) Female spikelet. (**g**) Pistillate flower. (**h**) Staminode. (**i–k**) Fruit, scutelar, hilar and cross sections respectively

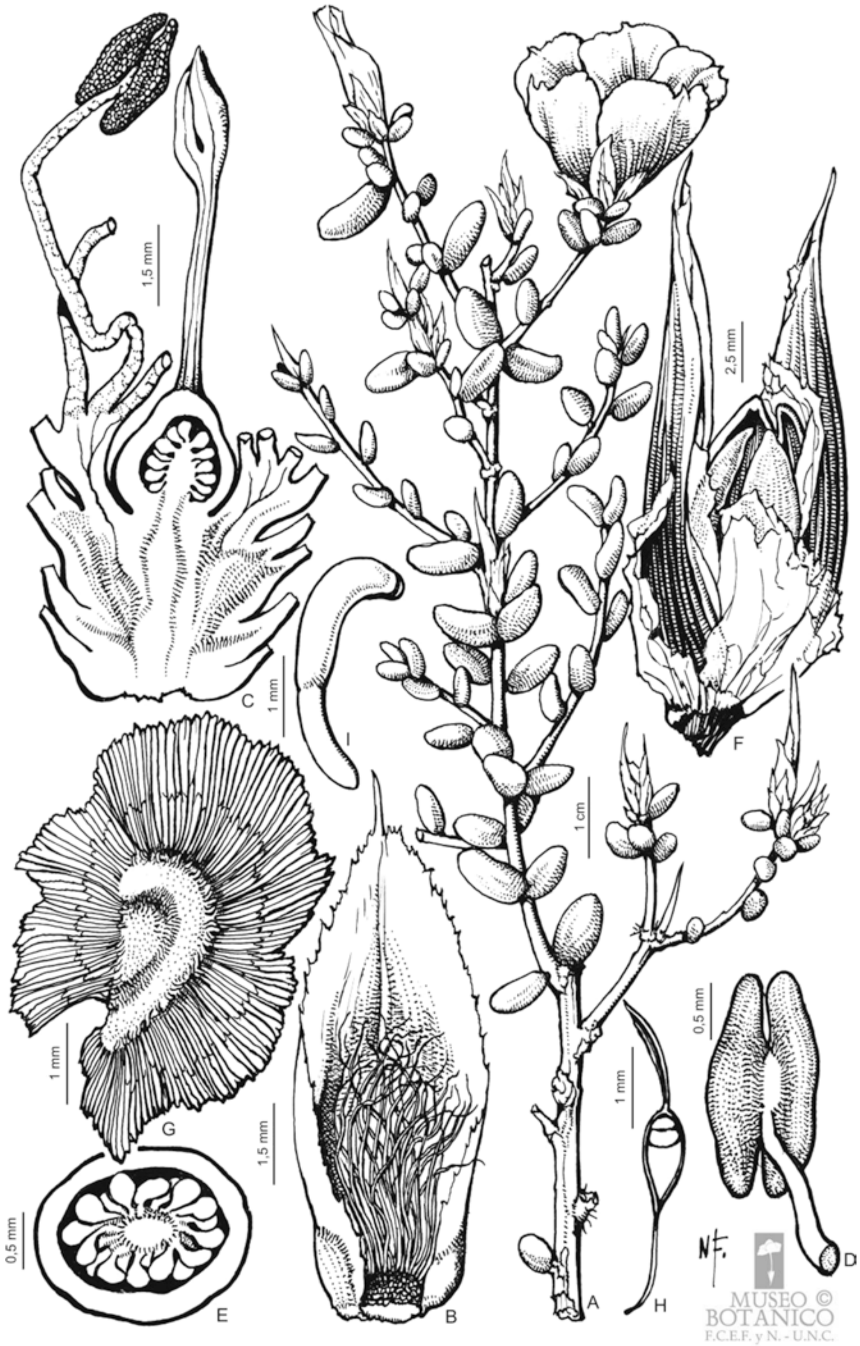

Fig. 9.15 *Grahamia bracteata*. (**a**) Flowering branch. (**b**) Sepal. (**c**) Flower, longitudinal section. (**d**) Stamen, dorsal view. (**e**) Ovary, cross section. (**f**) Fruit. (**g**) Seed. (**h**) Seed, cross section. (**i**) Embryo

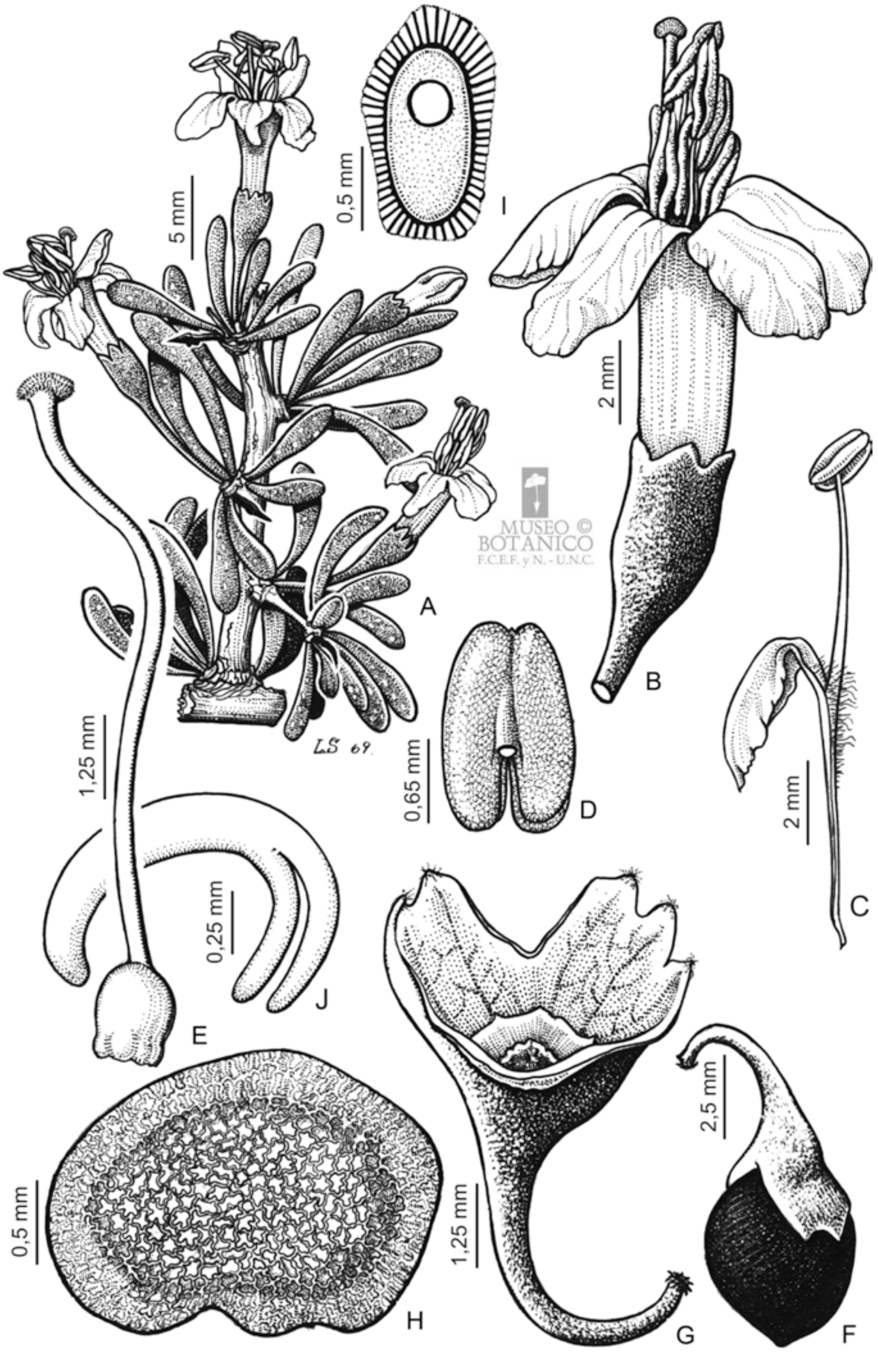

Fig. 9.16 *Lycium infaustum*. (**a**) Flowering branch. (**b**) flower. (**c**) Corolla sector. (**d**) Anther. (**e**) Gynoecium. (**f**) Fruit. (**g**) Calyx. (**h**) Seed. (**i**) Seed, cross section. (**j**) Embryo

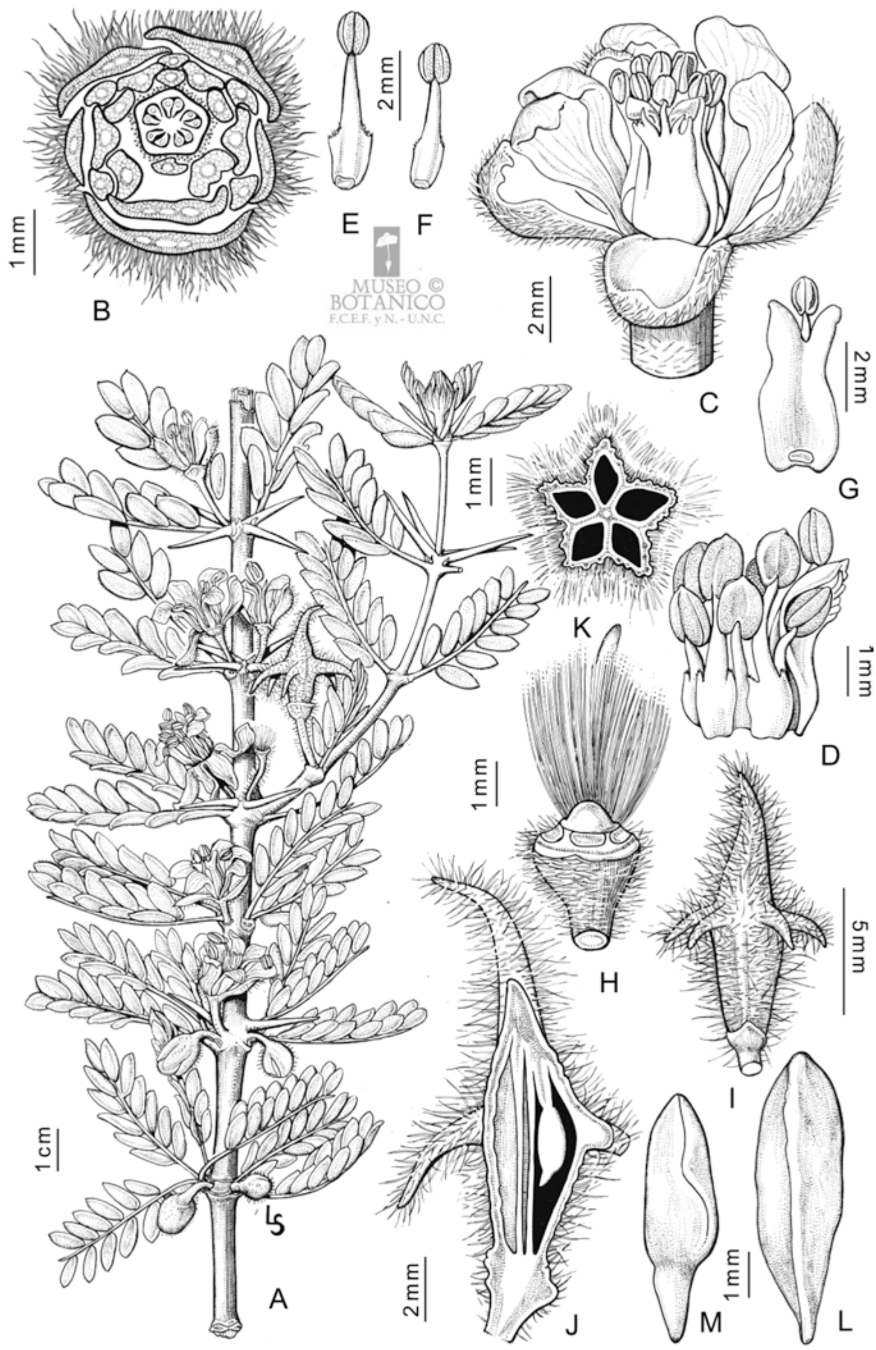

Fig. 9.17 *Plectrocarpa tetracantha*. (**a**) Flowering plant. (**b**) Flower bud, cross section. (**c**) Flower. (**d**) Androecium. (**e, g**) Stamens. (**h**) Gynoecium, showing nectaries and hairs on the ovary. (**i**) Fruit. (**j**) Fruit, longitudinal section. (**k**) Fruit, cross section. (**l**) Seed. (**m**) Embryo

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Coastal Environments in the Bahía Blanca Estuary, Argentina

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Abstract

The Bahía Blanca Estuary is a coastal system placed in a sharp transition between humid subtropical and semiarid climates, shaped by a unique combination of large interanual climatic variations and a transgressive sea level during the Holocene. In the region, the late Holocene marine transgresion resulted in low coastal landforms inherited from the former estuarine dynamics. These environments are commonly occupied by coastal ecosystems that can be roughly classified into intertidal and inland (perimarine) wetlands. Within the intertidal zone, most of the area is covered by extensive barren mudflats, and marshes are dominated by *Spartina alterniflora* or *Sarcocornia perennis*. A supralittoral zone can be defined in an intermediate position, irregularly inundated by sea water. Vegetation in this zone is sparse, with a mosaic of salt flats, halophytic steppes and shrubs forming mound-intermound complexes. The Old Marine Plain, in the inland limits of the marine transgression is not affected by tidal flooding, but an irregularly humid zone develops due to saline seepage from the uplands. These wetlands are subjected to episodic disappearance, and may get dry for several years, relying on the occurrence of rainy years during humid periods to resurge. Because of their highly dynamic nature, and the particular climatic settings of the area, these wetlands are sensitive indicators of climate change and variations in large scale circulation patterns. This chapter describes climatic patterns, geomorphological settings, and

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M.A. Khan et al. (eds.), *Sabkha Ecosystems Volume V: The Americas*,
Tasks for Vegetation Science 48, DOI 10.1007/978-3-319-27093-7_10

plant communities, as well as the major physical and biological interactions defining landscape structure.

1 Introduction

The Bahía Blanca Estuary is a major wetlands system in the southern coast of the Pampa region, Argentina. The name Bahía Blanca (White Bay) makes allusion to the ground surface incrusted with salts, giving a bright white color to soils in the coastal zone. Charles Darwin, in his famous chronicles of the voyage on board HMS Beagle, mentioned the observation of this phenomenon, when he visited Bahía Blanca on September 6, 1832. Salt incrustations occur in many coastal environments of Atlantic South America, even under moderately dry climate. However, bright white crusts, mainly of Sodium sulfate crystals are particularly abundant near Bahía Blanca (Darwin 1845). Locally known as *salitrales*, these extensive plains composed of fine grained sediments, commonly devoid of vegetation, or supporting scattered tussocks of salt tolerant species, may appear as a dark muddy surface when they are wet. During humid periods, after several months of excess precipitation, shallow ponds form in topographic depressions, but under dry weather conditions, hot summer temperatures, or strong winds, a rapid evaporation takes place, and the surface appears as, in the words of Darwin "*…square miles of the plain white, as if from a slight fall of snow…*" (Darwin 1845, p. 78).

The coastal landscape in the area has been deeply modeled by the Holocene marine transgression. While the eustatic (globally averaged) sea level has been rising from the Last Glacial Maximum (LGM) to the present, the relative height of the sea with respect to land can vary from place to place due to local tectonic and hydrographic effects. A falling or fluctuating relative sea level during the late Holocene characterized most coastlines of the southern hemisphere and eastern Asia (Pirazzoli 1991). In the northern coasts of Argentina, several authors have identified a high stand about 6000 years ago when the relative sea level reached around 6 m above present (Isla 1989; Violante and Parker 2000; Cavallotto et al. 2004). Southwards, along the Patagonian coasts, several Holocene marine shorelines can be found at different elevations, with a southward increase in terrace elevation for terraces of the same age, suggesting a tectonic uplift effect (Rostami et al. 2000). The late Holocene falling trend in relative sea level has resulted in wide low-lying areas of former estuarine environments, and typical regressive forms, like extensive plains composed of beach-ridge and lagoonal deposits.

In Bahía Blanca, the present configuration of the estuary responds to a complex morphological transformation, that involves not only the Holocene transgression but also a record of complex climatic changes. Since the Pleistocene, the area was affected by an alternation of dry and humid periods (Aguirre 1995). After the last glaciation, under warmer and more humid conditions, and a relative sea level close to the present position, rivers brought large sediment loads developing a delta, in the area presently occupied by the estuary. Sea level continued rising until a high stand of 8–10 m above present, that was reached at a radiocarbon age of 5990 year BP (González 1989). During this transgressive period the former deltaic sediments were redistributed by the estuarine dynamics developing tidal flats, shoals, spits, and islands (Melo et al. 2003). The present temperate-dry climate has established about 3000 year BP. As the relative sea level sank to the current position, rivers progressively disappeared and depressions were replaced by aeolic environments and salt flats. The Colorado River, which once discharged into the Bahia Blanca area, progressively migrated southward until its present position (Melo et al. 2003).

In the region, the late Holocene marine regression resulted in low coastal landforms inherited from the former estuarine dynamics. These coastal environments are commonly occupied by wetlands, typically salt marshes, halophyte steppes, and salt flats, which undergo increasing inundation under the current rising trends in relative sea level (Pratolongo et al. 2013). This chapter describes landscape structure and halophytic vegetation cover in the Bahía Blanca coastal zone. This temperate Atlantic estuary, placed in a sharp transition between humid subtropical and semiarid climates has a unique combination of large interanual climatic variations and a transgressive sea level during the Holocene. We describe climatic patterns, geomorphological settings, and plant communities, as well as the major physical and biological interactions defining landscape patterns.

1.1 Physical Drivers Shaping the Estuarine Dynamics

The Bahia Blanca estuary is a system of north-west to south-east channels separated by islands and wide tidal flats (Fig. 10.1). The northern portion of the estuary is dominated by Canal Principal, a funnel shaped channel that has a total length of 61 km, and varies in width from 200 m at the head to about 3–4 km at the mouth (Piccolo and Perillo 1997). From north to south, major inlets in the system are Bahía Falsa and Bahía Verde, which are also funnel shaped channels with total lengths of about 30 km, and average widths of 4 and 6 km respectively (Fig. 10.1).

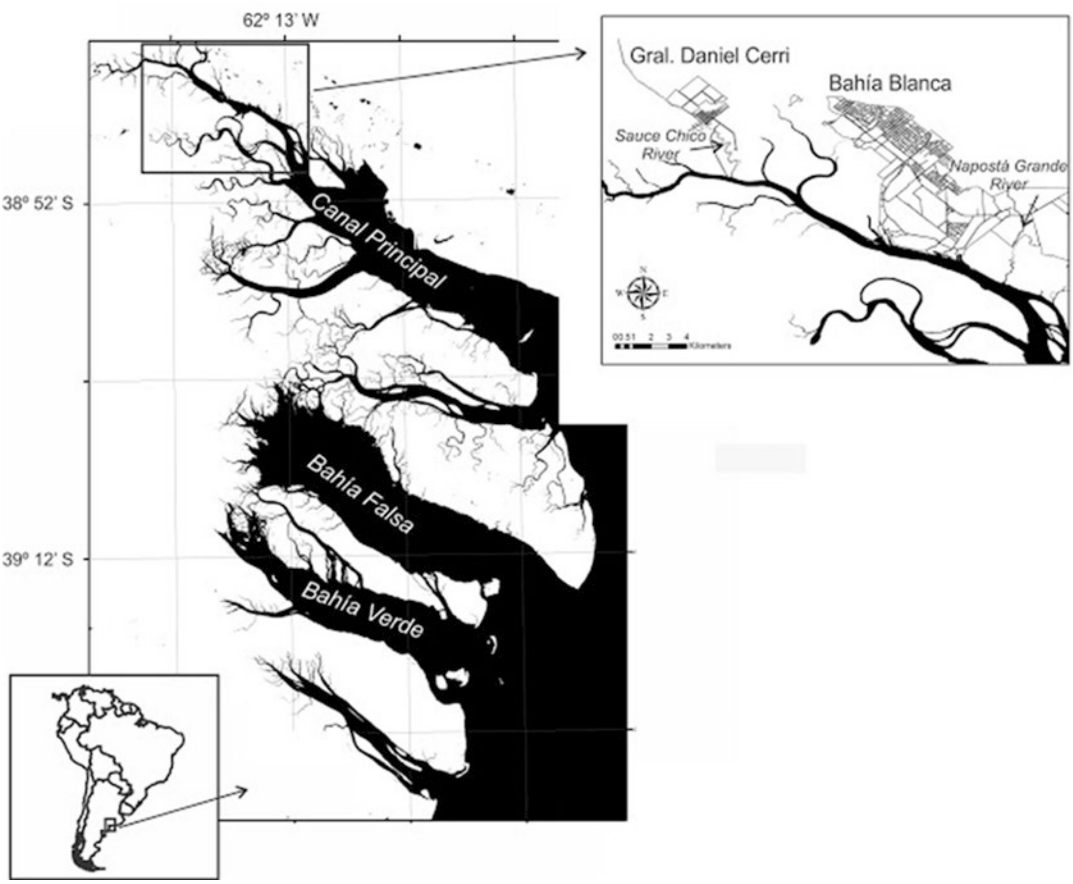

Fig. 10.1 Geographical location of the Bahía Blanca Estuary in South America. *Inset*: detail of the inner zone of Canal Principal, showing mayor urban developments. The Sauce Chico and Napostá Grande Rivers are the only permanent sources of freshwater to the system

Although these secondary channels represent the largest area, they are still understudied, and there is little information on their circulation patterns and ecological processes.

The Sauce Chico and Napostá Grande Rivers, discharging 1.9 and 0.8 $m^3 s^{-1}$, respectively, enter the estuary from the northern shore of Canal Principal, and represent the only permanent source of freshwater to the system. Although mean annual runoff from these rivers is extremely low, large variations can be observed, with peak values up to 200 $m^3 s^{-1}$ (Piccolo et al. 2008). Freshwater inflow from other sources is restricted to periods of high local rainfall (Melo et al. 2003). Tidal energy is provided by a quasi-stationary semidiurnal tidal wave. Tidal amplitude increases steadily from 2.2 m at the mouth of Canal Principal to 3.5 m through the head. Persistent winds blowing all year round are commonly responsible for tidal perturbations and storm surges. Mean wind velocity is 22.5 km h^{-1}, and there is a mean number of 196 days $year^{-1}$ with winds over 43 km h^{-1}. Predominant NW and N winds produce a set down of the predicted water levels, advancing low tide, and delaying high tide (Piccolo et al. 2008).

1.2 Climatic Patterns

Although winds have the strongest influence on the estuarine circulation, rainfall patterns largely control vegetation structure in the area. Bahía Blanca is located in the Semiarid Pampas, a sharp transition between humid and arid climates. Annual rainfall distribution has a winter minimum and usually two maxima: autumn and spring, with intermediate values in summer months (January to February) and very restricted water availability due to high evaporation rates (Krepper et al. 1989). Large temporal rainfall variability has been regarded as the most significant climatic feature for the region (Scian 1999). Dry and wet periods that may last decades alternate in a cyclical oscillation, with annual precipitation values that may range from less than 300 mm $year^{-1}$ during the arid phase, to values exceeding 900 mm $year^{-1}$ in extremely wet years. Continuous temperature and pluviometric measurements in the region started during the second half of the nineteenth century. Based on the available information, Galve (2006) defined four time periods that also relate to changes in the mean global temperature (Agosta and Compagnucci 2008).

1870–1925: During this period rainfall was above the long term average. The whole region was covered by dense vegetation and tall grasses with higher water retention capacity.

1925–1975: Precipitation significantly dropped, winter temperatures turned cooler, and stronger winds affected the region. Typically warm and dry summers promoted the loss of vegetation cover, which resulted in accelerated aeolic erosion of soils.

1975–2005: Summer rainfall above the average characterized this humid phase. Precipitation excess was responsible for changes in water table depth, and flooding affected large areas of natural and cultivated lands.

2005–2013: Summer rainfall sharply decreased producing the most severe dry period for the region. Year 2009 was particularly dry, after annual precipitation dropped to less than 300 mm. Major consequences of drought in the area were soil erosion and salinization (Ferrelli et al. 2012). In 2014, after several years of severe drought, rainfall records for the area show a strong positive anomaly, with monthly means largely exceeding historical values (Fig. 10.2).

Most of these variations can be associated to large scale circulation patterns (Scian 1999; Vargas et al. 2002). According to Grimm et al. (2000), Southern South America is one of the extratropical regions most affected by El Niño Southern Oscillation (ENSO) and precipitation anomalies at different time scales have been associated to El Niño and La Niña events (Vargas et al. 1999). Recent studies have shown that interannual variability in Southern South American is not only modulated by ENSO, but also by the Pacific Decadal Oscillation (PDO). Kayano and Andreoli (2007) suggested that rainfall variability might be explained by the ENSO signal in those cases when ENSO and PDO are in the same phase. More precisely, Silva et al. (2011) pointed out that El Niño events during positive PDO

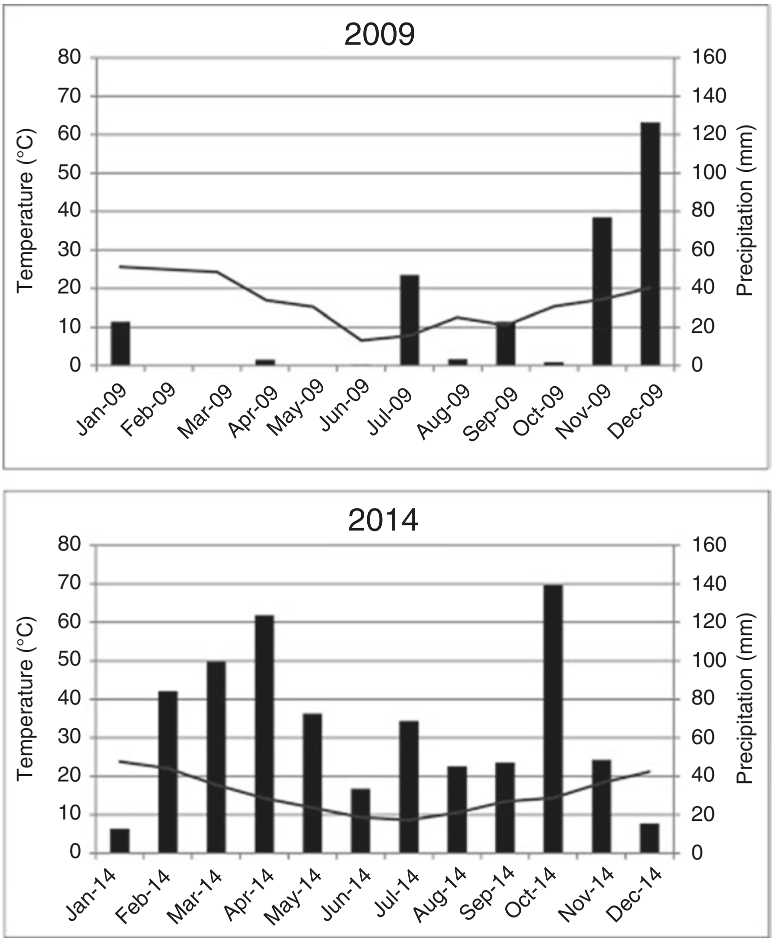

Fig. 10.2 Monthly rainfall and mean monthly temperatures registered in Bahía Blanca, during years 2009 and 2014

phases affect moisture transport and tropical-extratropical circulation patterns in austral summer over the region. These variations after 1975 seem to be associated with an increase in the frequency and intensity of El Niño events and positive precipitation anomalies (Ambrizzi et al. 2004), consistently with the last warm PDO that occurred during the period 1977 to mid-1990s (Robertson and Mechoso 2000).

1.3 A Coastal Landscape Modeled by the Holocene Marine Transgression

Based on the geomorphic map by González-Uriarte (1984), we identified five major landscape units in the area, and we used topographic charts, satellite images (Landsat TM and ETM+), and aerial photographs to develop the map presented in Fig. 10.3a. The evidences of past changes in sea level in the coastal area of Bahía Blanca (Fig. 10.3b) early captured the attention of naturalists and geologists. Raised Holocene deposits in the Bahía Blanca Estuary formed after the maximum Holocene Transgression (ca.6000 BP) during high energy periods identified as Transgressive Stages (González and Weiler 1983). In the northern shore of Canal Principal, González (1989) studied a sequence of intermixed Holocene beach ridges and tidal flats deposits, corresponding to high and low depositional energy periods. The oldest and highest deposits, located in the inner section, form a spit composed of several sand-shell ridges up to 10 m above present sea level (González et al. 1983;

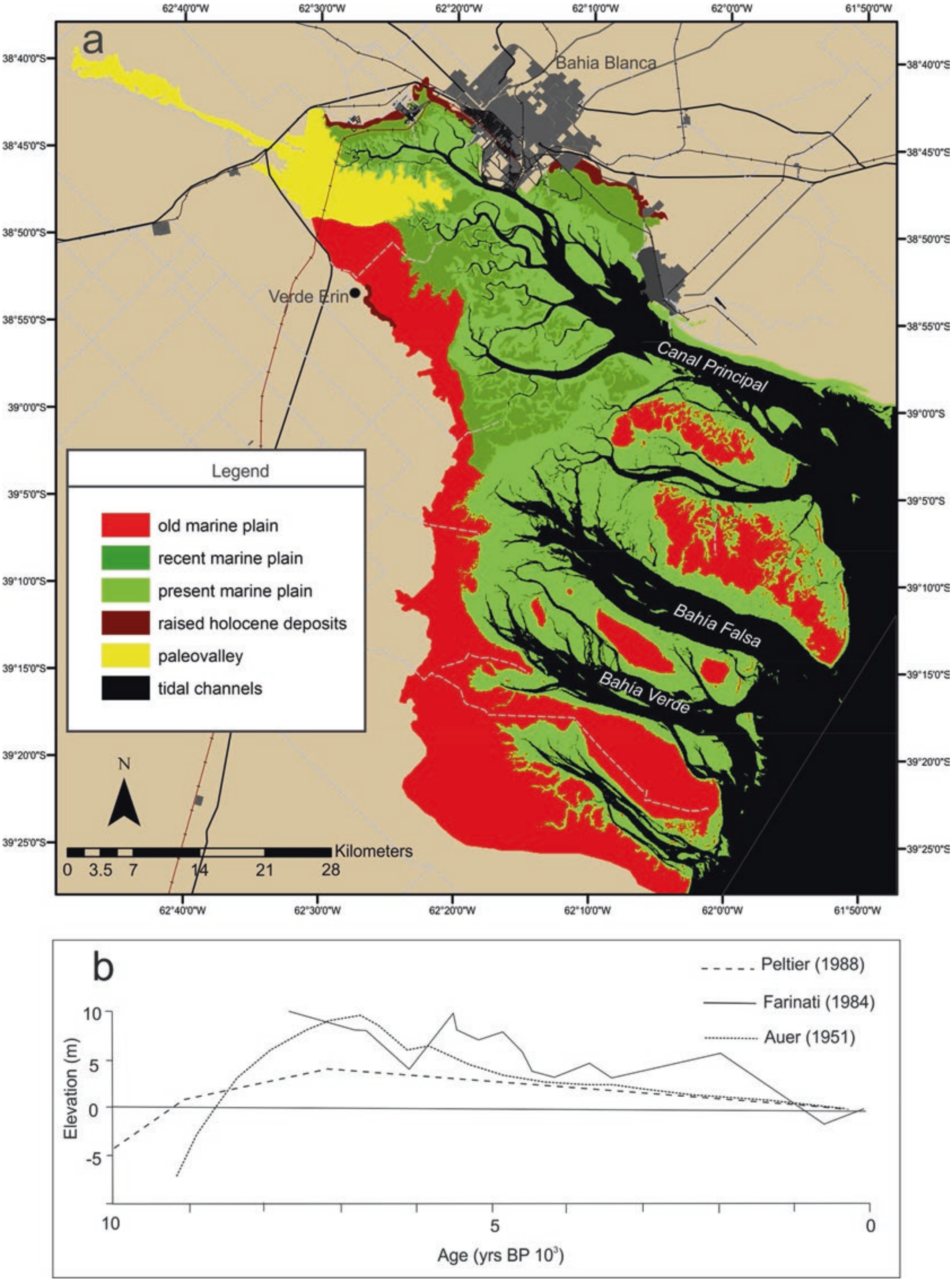

Fig. 10.3 (**a**) Major landscape units in the coastal zone of the Bahía Blanca Estuary. (**b**) Different estimations of the relative sea level curve during the Holocene in the study area

Aliotta and Farinai 1990). Through the middle zone, Holocene deposits appear about 6–7 m above mean sea level, and form a relatively continuous sand ridge parallel to the coast (Giagante et al. 2011). Based on ^{14}C dates, González (1989) described at least five Holocene transgressive peaks that occurred between 5990 ± 115 BP and 3560 ± 100 BP, with the maximum transgressive episode represented by the inland beach ridge.

Canal Principal extends inland through a narrow depressed landform locally known as *Salitral de la Vidriera*. The axis Canal Principal-Salitral de la Vidriera separates two major structural domains in the area: the elevated Positive of Ventania to the North, and the Colorado River Basin to the South (González-Uriarte 1984). The raised Holocene deposits, described in the northern margin of the study area outline the base of the frontal scarp dividing both domains. The depression containing Salitral de la Vidriera would be part of a paleo drainage formed by a plentiful river and tributaries ending in the estuary about 7000 year BP, which built a delta under a relative sea level close to the present. During the subsequent transgressive phase, this deltaic area was completely covered by the sea, and fluvial sediments were reworked by the estuarine dynamics forming wide tidal flats, spits, and shoals (Melo 2004). The marine influence in the area ended about 3000 year BP, approximately at the same time that present temperate-dry climate established, as suggested by palynological records of a psammophytic herbaceous steppe after 2610 year BP (Quattrocchio et al. 1990). As the relative sea level felt to the current position, rivers progressively disappeared, and the Colorado River, which once discharged in the Bahia Blanca area, progressively migrated southward until its present position (Spalletti and Isla 2003). Fluvial deposits were subsequently mobilized by eolic processes, and depressions were replaced by dune fields and salt flats (Grill and Quattrocchio 1996; Melo et al. 2003). Because of the presence of a structural control in the alignment Canal Principal-Salitral de la Vidriera, González-Uriarte (1984) described the arrangement as a Polygenic Valley, with its steep northern shore indicating the northern limits of influence of the Colorado River, before the drainage migrated southwards.

South of Canal Principal, in the western margin of the estuary, the gentler slope allows the clear distinction of at least two marine terraces of different elevations. In Verde Erin, Farinati (1983) described a shelly ridge at the base of a paleo-cliff, which would correspond to storm deposits indicating the inland limits of the marine transgression, at a ^{14}C age of 5406 ± 227 years BP. In the coastal plain extending towards Canal Principal, two successive levels can be identified, which formed at different ages during the regressive phase (González-Uriarte 1984). The Old Marine Plain, at an average elevation of 5 m above present sea level is a nearly continuous plain surface covered by different types of halophytic shrub communities. The Recent Marine Plain, 2–3 m above mean sea level is a mosaic of topographic highs, covered by halophytic shrubs, and elongated depressions corresponding to former tidal cannels, surrounded by salt flats. In this last unit, the gentle slope creates a gradual transition to the Present Marine Plain, composed of active tidal channels, mudflats and salt marshes, currently affected by the estuarine dynamics.

1.4 Coastal Wetlands and Landscape Patterns

In a broadest sense, coastal wetlands include a wide spectrum of environments, from low marshes and tidal flats, to non-tidal wetlands at the landward edge, whose hydrology is still influenced by sea level. Hageman (1969) first used the term *perimarine* zone to refer to the area where non-tidal wetlands persist under the control of relative sea level. In humid climates, freshwater seepage and high groundwater levels provide the waterlogged conditions necessary for the development and persistence of perimarine fresh water swamps, marshes, and fens (Waller et al. 1999; Gardner et al. 2000). In the perimarine zone of arid climates, under a combination of high evaporation and low freshwater inputs, soils develop extremely high salinities that eliminate all but the most tolerant plants. In tropical and subtropical areas, where precipitation is commonly less than 250 mm/year, flat and barren *sabkhat*, covered by evaporite accumulations commonly occur close to the high tide level (Barth and Böer 2002). From a hydrogeomorphic point of view, coastal sabkhat frequently inundated by seawater, occupy the landscape position of a high marsh, and the equivalent to perimarine fresh water fens and swamps, in these arid environments are inland sabkhat in the coastal zone, that are never flooded by tides, but where sea level keeps a near surface groundwater table.

Wetlands in arid and semiarid environments commonly occur in areas where flooding is intermittent and substrate is saturated to the surface only irregularly. In coastal landscapes, beyond the limits of the tidal inundation, wetlands may have a pulsed ephemeral nature what makes them difficult to identify (Cintron-Molero and Schaeffer Novelli 2002). Soils have been widely used for wetlands identification and delineation (Tiner 1999). Extended flooding or waterlogging has a significant effect on soil-forming processes, resulting in a set of unique and recognizable soil properties. When water fills the soil pore spaces replacing air, the supply of oxygen is depleted and chemical processes change (Henderson and Patrick 1982). Wetlands soils, that are saturated with water and chemically reduced to the point that dissolved oxygen is virtually absent, have an *aquic* moisture regime (Soil-Survey-Staff 1975). The term *aquic* (Vepraskas 1996) applies to soils that undergo saturation and reduction, and display morphological evidence of these conditions (i.e., redoximorphic features). Common indicators of a wetland soil include gray colors, iron and manganese concretions near the surface, and the wetness state of the soil (Tiner 1999).

Wetlands are more common in humid climates, but they also occur in dry and seasonally dry conditions, and their soils are considerably different from those in wetlands from humid climates. Wetland soils in arid climates concentrate salts in their surface and usually contain carbonates, gypsum, and even more soluble salts, and biomass accumulation is often limited. The combination of high salinities and low concentration of organic matter hinders typical processes expected in humid climates, such as microbial activity and chemical reduction of iron. If the soil color changes upon drying and soluble salts are present, redoximorphic features and hydric soil indicators may not form, and seasonally dry or intermittent wetlands would be difficult to identify. To overcome this problem, Boettinger (1997) suggest that salts more soluble than gypsum in the upper 30 cm indicate a hydric soil, and the presence of a salt crust should be sufficient as a field indicator of a wetland soil, subject to periodic saturation from a saline water table.

Coastal wetlands in Bahía Blanca can be roughly classified into intertidal and inland (perimarine) wetlands (Fig. 10.4). We considered here the upper limits of the intertidal zone as the area frequently inundated by tides, close to the elevations of mean high tides. Within this intertidal zone, most of the area is covered by extensive barren mudflats. Pure stands of *Spartina alterniflora* are commonly restricted to lower marshes in the middle reach of the estuary, but do not appear in the inner zone. *Spartina densiflora* marshes occasionally appear as pure stands that form a transition zone between *S. alterniflora* and *Sarcocornia perennis* in places influenced by freshwater discharges. Through the shallow inner section of Canal Principal, seasonally hypersaline conditions commonly develop, because of the higher evaporation rates, and vegetated marshes in this zone are restricted to elevations close to the mean high tide level, with *S. perennis* as the dominant species (Pratolongo et al. 2010). A supralittoral zone can be defined in an intermediate position, irregularly inundated by sea water, above the elevation of the mean high tide and below the limits of the highest tides (spring high tides and storm surges). Vegetation in this zone is sparse, with a mosaic of salt flats, halophytic steppes and shrubs forming mound-intermound complexes (Piovan et al. 2014).

Soils in intertidal and supralittoral wetlands are classified as Aquisalids (formerly Salorthids), and usually have an A horizon that is enriched in organic matter with respect to the underlying strata. In highly productive intertidal marshes, the organic rich layer may extend up to 25–50 cm

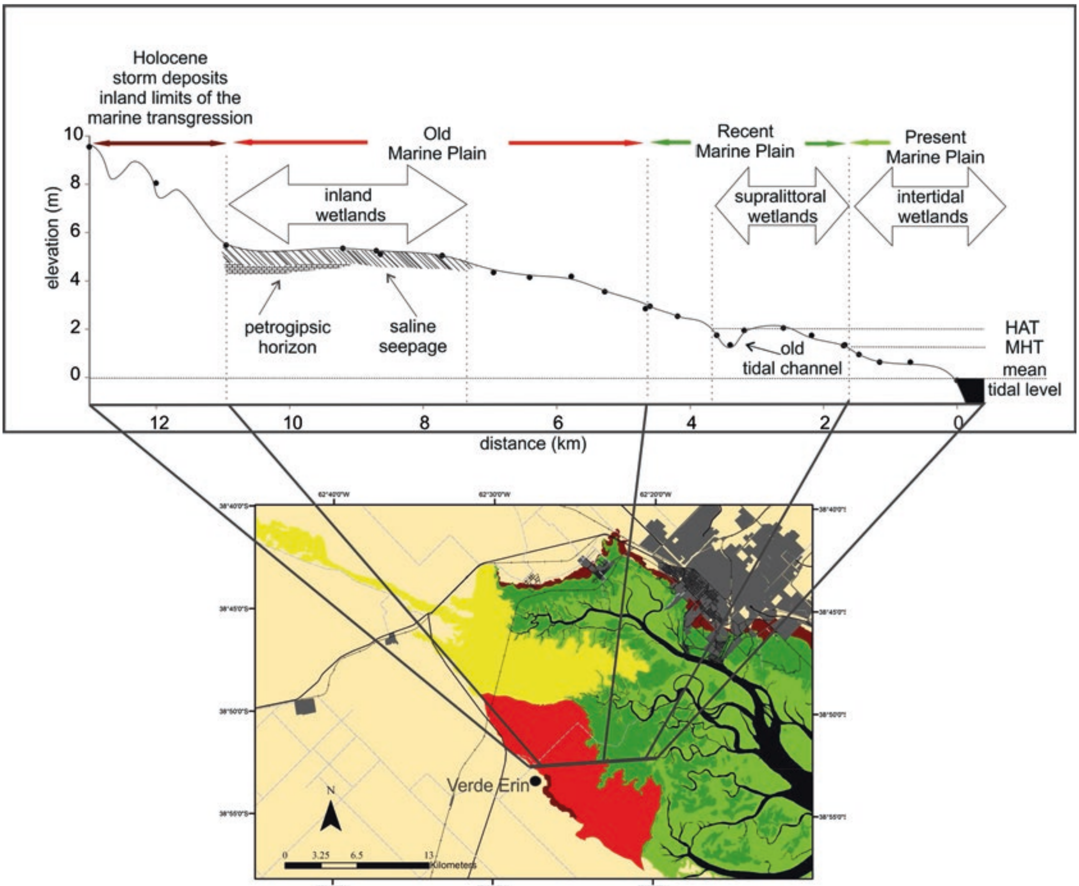

Fig. 10.4 Wetland types across an elevation profile covering different landscape units. *Black dots* are actual elevation values (RTK GPS) related to the local mean tidal level. *MHT* mean high tide, *HAT* highest astronomical tide

depth, but in halophytic steppes, A horizons rarely exceed 8–10 cm depth. In barren intermound areas, the A horizon may be difficult to identify or may not be present at all, and the parental material is often exposed at the soil surface (Kruger 1989). In more elevated landscape positions, less affected by tidal inundation, a highly saline groundwater table (measured values ranged from 41 to 45 PSU; PSU = practical salinity unit; 35 = seawater) fluctuates from −3 to −0.3 m during dry years, but rises to the soil surface during wet years, leaving soils ponded for several months. Soluble salt crystals form brittle salt crusts that disappear after tidal flooding and rain events, but reappear after a few days of high evaporation.

Intertidal and supralittoral wetlands form a gentle sloped continuum that extends from the Present through the Recent Marine Plain. Landscape pattern in this later unit is dissected by narrow depressions corresponding to former tidal channels, presently draining rain water. Within channels, soils are permanently flooded or saturated, even in dry years. The water table fluctuates around the surface (−0.4 to 0.5 m), and closely reflect rainfall events in the area. Continuous records of groundwater levels in wells show increases of more than 50 cm within hours after a single precipitation event (Piovan et al. 2014). Groundwater salinities in these channels are significantly lower (23–26 PSU) than those registered in more elevated environments within the unit, allowing for the development of highly productive *S. densiflora* marshes, and soils with a deeper layer enriched with organic matter.

The Old Marine Plain is not affected by tidal flooding, but an irregularly humid zone develops due to saline seepage from the uplands. The permanent field indicator of a dryland saline seepage in the area is salt accumulation in a fringe at the base of the scarp, in the inland limits of the marine transgression. During humid periods that may last several years, rain water is in excess of the retention capacity of soils in the uplands. As rain water infiltrates, it reaches the groundwater table and moves laterally downslope. At the discharge area, the groundwater rises to the soil surface; water seeps laterally out and evaporates, accumulating salts. Soils in the seepage spot, at the base of the slope, are classified as Petrogypsids (formerly Petrogypsic Gypsiorthids) because of the presence of a subsurface soil horizon cemented by gypsum (Kruger 1989). Gypsum formations commonly occur by evaporation of a fluctuating water table enriched in calcium and sulphate (Gomez-Miguel et al. 1984). In a fringe zone downslope of the discharge area soils are classified as Aquic Ustifluvents, and show typical redoximorphic features denoting saturation. Soils in this saline seepage area develop fluffy, almost snow-like crusts that form intermittently, when the capillary fringe reaches the soil surface.

Wetlands in the Old Marine Plain could be characterized as dry-end wetlands (Whigham 1999). They occur in landscape positions where flooding is irregular and soil saturation to the surface occurs occasionally. These wetlands are subjected to episodic disappearance, and may get dry for several years, relying on the occurrence of rainy years during humid periods to resurge. Plant communities in these environments are very reactive to small changes in climate, and quickly respond to exceptionally humid or dry periods. Because of their highly dynamic nature, and the particular climatic settings of the area, these wetlands are sensitive indicators of climate change and variations in large scale circulation patterns. Out of the seepage area, soils in the Old Marine Plain are well drained and have lower contents of soluble salts. These non-wetland areas typically develop brushwood associations with a halophytic grassy understory, which represent a valuable and commonly overused source of fodder in marginal grazing lands (Verettoni 1961).

1.5 Plant Communities

Several authors described plant associations in the Bahía Blanca coastal zone (Verettoni 1974; Kruger and Peinemann 1996; Nebbia and Zalba 2007). Based on this previous information and extensive field work carried out in the area, Piovan et al. (2014) defined nine major land cover classes, which were used to derive a spatial representation al the landscape level. The methodological approach involved the processing of a 30 years long time series of Landsat TM and ETM+ satellite images to obtain surface reflectance data, and the implementation of numerical classification algorithms, masking and reclassification, to produce the final land cover map presented in Fig. 10.5.

The upper and lower limits of the intertidal fringe were defined as the land-water interface detected in the image acquired during the highest and lowest tide registered in the time series. Within this intertidal fringe, non-vegetated tidal flats are the dominant land cover type (836 km^2). Salt marshes of *Spartina alterniflora* (196 km^2) appear as monospecific associations with variable plant heights and densities, from sparse plants, up to 20 cm tall (González et al. 2013), to dense stands taller than 1 m in places subject to high sedimentation rates (Pratolongo et al. 2010). Intertidal marshes of *Sarcocornia perennis* are less represented (72 km^2). In these marshes, the dominant species commonly forms circular mounds, sometimes in association, at higher elevations, with *Heterostachys ritteriana* or *Spartina densiflora* (Pratolongo et al. 2013). Vegetation cover of this type of marshes is highly uneven, from a few isolated patches in a matrix of bare soil, to an almost continuous carpet at some locations (Fig. 10.6). Intertidal marshes dominated by *Spartina densiflora* are rarely observed, and

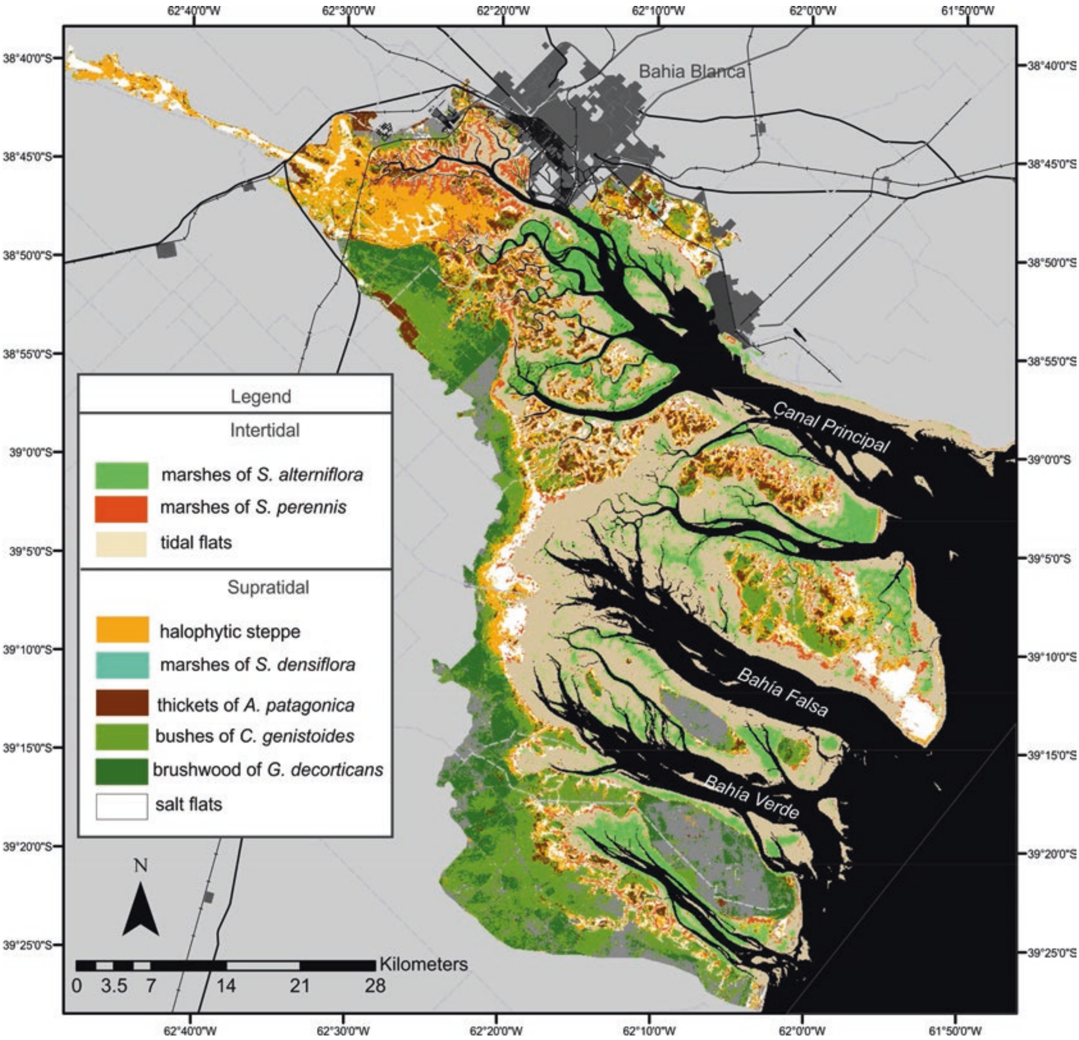

Fig. 10.5 Land cover map showing major plant associations in the coastal zone of the Bahía Blanca Estuary. Land cover classes were previously defined, based on field surveys, and the map was further obtained through digital classification of satellite images from the Landsat series

typically associate to freshwater discharge of the few permanent small rivers in the estuary. Because of their scattered distribution and small size, intertidal marshes of *Spartina densiflora* cannot be represented at the landscape scale. In the supralittoral zone, however, this type of marshes occupies the old tidal channels of the Recent Marine Plain (Fig. 10.7), covering 1.8 km^2. *Spartina densiflora* is the clear dominant species in these marshes, forming dense stands about 50 cm tall, and *Sarcocornia perennis* may be also present with relatively high percent cover (Piovan 2016).

Tidal inundation becomes less frequent upslope from the mean high tide level, and there is a gradual transition from *Sarcocornia perennis* marshes to halophytic steppes. Vegetation in this later class keeps a similar mound-intermound structure, but barren areas lengthen close to the limits of the highest tides, and soils between mounds develop more permanent salt crusts (Fig. 10.8a). At some locations, vegetation patches are sparse enough to allow for the distinction of salt flats as a pure land cover type (Fig. 10.8b). *Sarcocornia perennis* is also a dominant species in halophytic steppes but, as tidal inundation decreases, the number of spe-

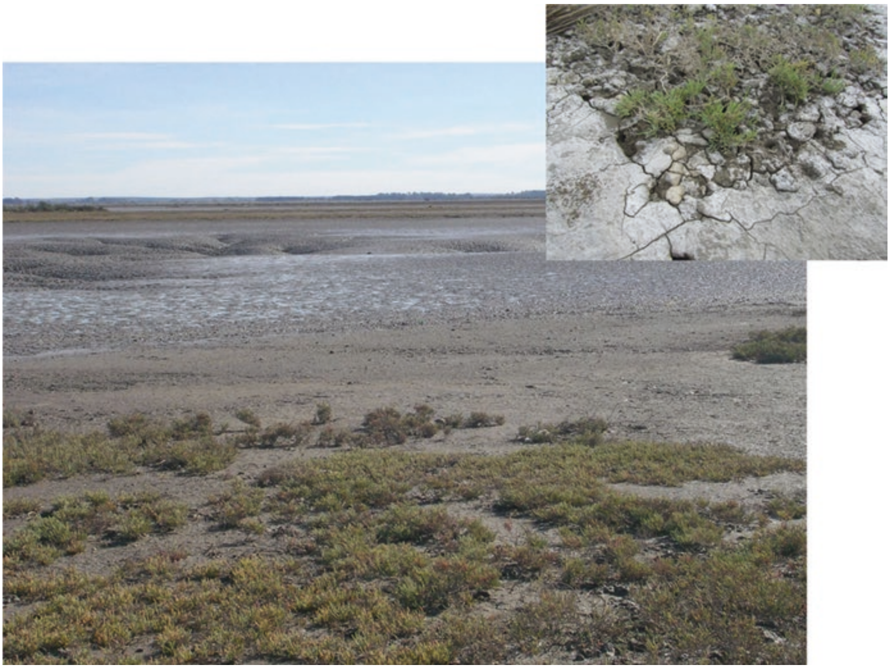

Fig. 10.6 Marshes of *Sarcocornia perennis*. *Inset*: plant detail. Close to the limits of mean high tides, salt crusts develop in bare soil between patches

Fig. 10.7 Marshes of *Spartina densiflora* occupying old tidal channels in the Recent Marine Plain. *Inset*: plant detail showing salt crystals from salt glands

cies within vegetation patches increases. Typical accompanying species are *Heterostachys ritteriana* and *Spartina densiflora*, with higher abundances than those observed in marshes. At higher elevations, vegetation is more complex, and different species like *Atriplex undulata*, *Limonium brasiliensis*, and *Frankenia juniperoides* may also appear in mounds.

Three different types of woody associations can be discriminated in the area. Dense thickets

Fig. 10.8 (**a**) Halophytic steppe with sparse vegetation patches, and barren areas between plants showing salt crusts. *Inset*: details of an association of *Sarcocornia perennis* and *Spartina densiflora* within a patch. (**b**) Pure salt flat, devoid of vascular vegetation, with polygonal soil cracks caused by desiccation

dominated by *Allenrolfea patagonica* form a continuous fringe in the inland limits of the Old Marine Plain (45 km^2). Vegetation height is about 1 m, and *Allenrolfea patagonica* has an average 60 % cover, sometimes in association with *Cyclolepis genistoides* (Fig. 10.9). Most species in the undergrowth appear in response to episodic rainfall, but *Sarcocornia perennis* and *Lycium chilense* are always present, even in dry periods. *Grahamia bracteata* and cactus from the genus *Trichocereus* are also commonly observed. Downslope from thickets of *Allenrolfea patagon-*

Fig. 10.9 Thickets of *Allenrolfea patagonica* and puffy salt crusts developing between plants. *Inset*: plant detail

ica, vegetation is slightly taller and the amount of bare soil increases. In bushes dominated by *Cyclolepis genistoides* (261 km^2), *Atriplex undulata* appears as a common species in the underbrush, replacing *Allenrolfea. patagonica* (Fig. 10.10). *Sarcocornia perennis, Frankenia juniperoides, Cressa truxiliensis*, and *Limonium. brasiliensis* also appear in this lower stratum. In the Recent Marine Plain, these two plant associations appear as a discontinuous mosaic, jointly mapped as halophytic shrubs in Fig. 10.11. In this landscape unit, *Allenrolfea. patagonica*, *Cyclolepis. genistoides, Atriplex undulata*, and *Sarcocornia perennis* are all common species, whose relative abundance is determined by specific site conditions. The last association described is the brushwood dominated by *Geoffroea decorticans* (150 km^2), which is indicative of well drained soils and lower salinities. The dominant species, *Geoffroea decorticans* is a tall shrub, exceeding 2 m height, which forms dense thorny bushes. The diverse underbrush is composed of *Lycium chilense, Atriplex undulata, Atriplex heterosperma, Grindelia brachystephana, Ephedra triandra*, and several grasses (*Poa lanuginosa*, *Trichloris crinita*, and *Stipa spp*, among others).

1.6 Non Vegetated Environments

Tidal mudflats cover more 836 km^2, almost 76 % of the intertidal area, and the ecological processes that take place in the benthic-pelagic interface of tidal flats are critical for the entire estuarine dynamics (Zapperi et al. in press). In these extensive flats devoid of vascular vegetation, associations of autotrophic microorganisms collectively known as microphytobenthos, are the most important primary producers (MacIntyre et al. 1996). The microphytobenthos is composed of unicellular eukaryotic algae and cyanobacteria that grow within the upper several millimeters of illuminated sediments, and play a major role in sediment stabilization (Stal 2010). Mobile diatoms secrete large amounts of extracellular polymeric substances (EPS), which are highly

Fig. 10.10 Bushes dominated by *Cyclolepis genistoides* (Asteraceae). *Inset*: detail of *Atriplex undulata*, a typical accompanying species in bushes

adhesive mucilages, consisting mostly of carbohydrates that bind sediment particles together (Decho 1990). In addition, cyanobacterial filaments weave among soil grains entangling them and forming a microbial mat that stabilizes and protect the surface from erosive forces, like tidal currents (Noffke 2010) and waves (Cuadrado et al. 2014).

According to Pan et al. (2013), surface sediments in the area present a biofilm composed of microbial communities embedded in EPS. The microphytobenthos community integrating the surface biofilm and microbial mats is composed of unicellular (epipelic diatoms) and filamentous algae (cyanobacteria). Assemblages contain smaller pennate diatoms (<40 μm) of the genera *Diploneis*, *Nitzschia* and *Navicula*, and larger species of the latter two genera, *Gyrosigma*, *Cylindrotheca*, and *Pleurosigma* (all genus names in *italics*). Centric diatoms include *Cyclotella meneghiniana* and *Paralia sulcate*, and also species of the genera *Thalassiosira* and *Coscinodiscus*. In the upper intertidal zone, close to the lower limits of *Sarcocornia perennis* marshes, the cyanobacterium *Microcoleus chthonoplastes* is the most abundant species, which typically has many trichomes forming a mesh of interweaving filaments, and is reported to significantly increase sediment cohesiveness (de Winder et al. 1999). The dominance in biomass of *Microcoleus chthonoplastes* is indicative of well-developed microbial mats presenting an elevated resistance to erosion, and a protective cover to the underlying sediments. In this zone, a distinct seasonal cycle was described in microphytobenthos biomass, chlorophyll a and colloidal EPS contents, with clear peak values in winter, and the lowest in summer (Pan et al. 2013; Zapperi 2015).

A winter-early spring phytoplankton bloom is a major component of the estuarine dynamics in the inner zone of the Bahía Blanca Estuary (Popovich and Gayoso 1999). The study area is a temperate, turbid, and nutrient-enriched estuary (Popovich et al. 2008) hence sufficient light penetration in the water column is a potential trigger for phytoplankton cell proliferation (Cloern 2001; Chassot et al. 2010). It is commonly believed that rivers are the major source of suspended sediments to estuarine systems, and con-

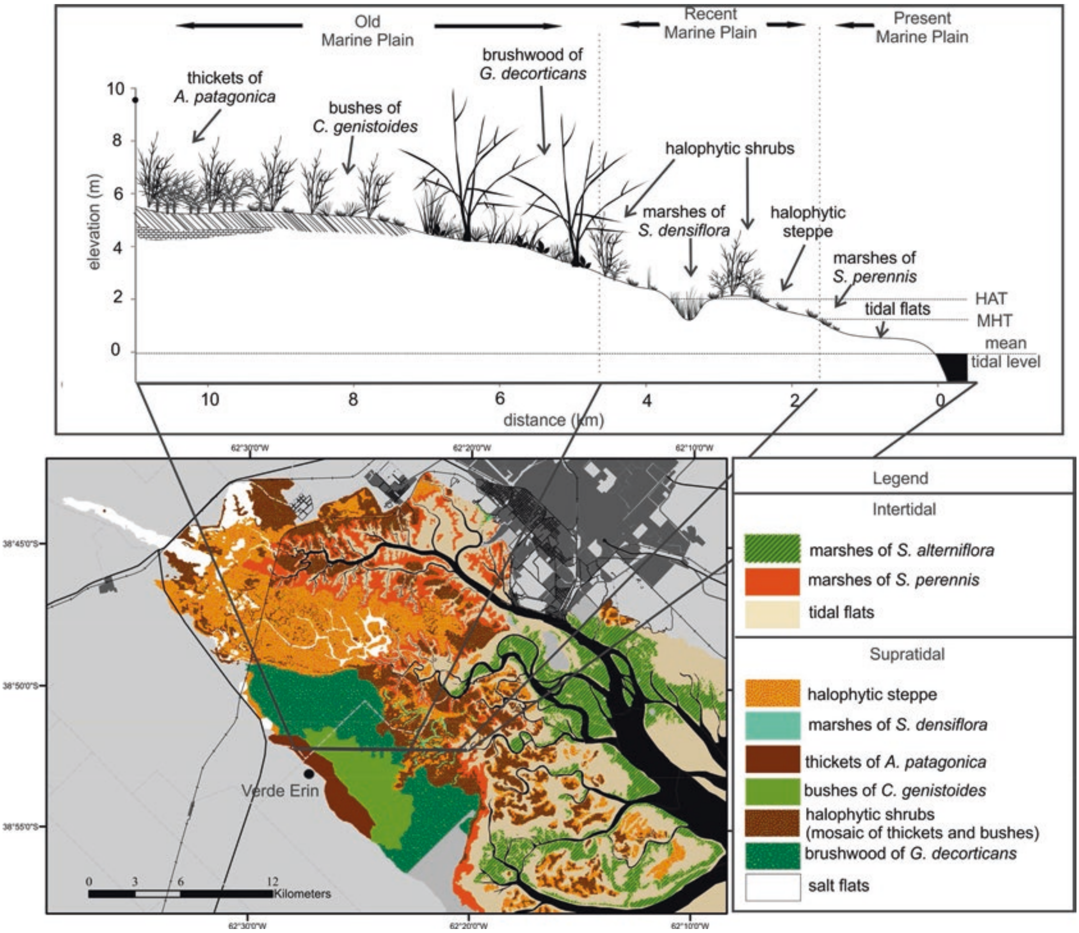

Fig. 10.11 Typical location of the different plant associations across an elevation transect. The land cover map showing plant associations in the inner zone of Canal Principal was obtained through on-screen digitizing over aerial photographs. Elevation values are referred to the mean tidal level

trol the associated turbidity (Syvitski and Kettner 2011). In the Bahía Blanca Estuary, however, river runoff is not a significant source of suspended solids to the water column. Recent studies revealed that general marsh erosion is a dominant landscape process in the inner zone of the estuary (Pratolongo et al. 2013). Land loss by erosion of *Sarcocornia perennis* marshes would be about 267 ha year^{-1}, and the eroded marshes may supply, on the average, more than 2360 Tons of particulate matter per day to the tidal sediment budget. Generalized erosion at the edge of *Sarocornia perennis* marshes is the major mechanism of shoreline retreat and salt marsh loss, and is also a major source of sediments to the water column. In this upper section of tidal flats, microphytobenthos biomass, and hence sediment stability peak in winter, what would contribute to generate the window of lower turbidity that triggers the phytoplankton bloom (Zapperi 2015).

Beyond tidal influence, an area of almost 195 km^2 is classified as salt flats. In addition, more than 273 km^2 are covered by halophyte steppes, mainly composed of barren soil between vegetated patches. However, despite the wide area that they cover, inland salt flats in the region are virtually absent from the literature. Pioneer work carried out by Cuadrado et al. (unpublished) described an inland sabkha in Bahia San Blas (about 100 km south from the Bahia Blanca Estuary). In this area, an elongated salt flat about 3 km length extends at the end of a tidal channel, separated from the sea by a barrier and flanked by gravel ridges to the north and sand spits to the south. Except for a few isolated patches of *Spartina densiflora* and *Sarcocornia perennis* bordering the area, most of the surface is covered by thick, coherent, and laminated microbial mats. A shallow ground water table rises above the surface after rainfall, forming small shallow (<15 cm) ponds at both sides of the microbial flat, and central pools with extremely high salinities (between 71 and 89). Noteworthy features in the area are small turbid ponds (~0.5 m^2, 5 cm deep) of hypersaturated (up to 110 PSU) "milky water" (as was called by Shin and Kendall) that appear in depressions covered by impervious microbial mats. Water clouding occurs as a result of degasing of carbon dioxide in the presence of cyanobacteria, increasing carbonate concentrations and fine suspended precipitates (Hanson et al. 1990). As ponded water evaporates, large amounts of halite and needles of aragonite (8 m in size) accumulate on the surface.

Dominant mat-constructing microbial species are mostly non-heterocystous, trichome-forming cyanobacteria (order *Oscillatoriales*), but benthic diatoms are also present with significant abundances. A microscopic analysis of surface sediment showed large spatial variations in algal composition, but pennate diatoms were always more abundant than centrics, represented by species from the genus *Navicula, Diploneis, Gyrosigma*, and *Nitzschia*. Centric diatoms of the genus *Melosira* and *Podosira* were also present. Filamentous cyanobacteria (like *Microcoleus chthonoplastes* and *Symploca sp*) were found at high densities (up to $376 \pm 15 \times 10^3$ trichomes per cm^3). Trichomes provide a dense and coherent fabric for the binding of sedimentary particles, what results in a highly elastic behavior and a remarkable leathery appearance, especially in physically-deformed structures.

2 Conclusions

The present work offers an insight on the factors shaping landscape structure and wetlands dynamics at the Bahía Blanca estuary, a coastal environment in the southern coasts of South America that has been deeply modeled by the Holocene marine transgression. The area is affected by strong interannual variations in rainfall, due to the influence of large climatic oscillations like El Niño and the Pacific Decadal Oscillation. Vegetation is dominated by halophytic species, associated in salt marshes, steppes, and shrubs, but barren surfaces are also extensive. While tidal mudflats cover most of the intertidal fringe, salt flats and bare soil in sparsely vegetated steppes thoroughly spread beyond the limits of tidal influence. Sabkha ecosystems are predictable landscape features in tropical and subtropical areas, where precipitation is commonly less than 250 mm/year. In the study area, however, barren surfaces incrusted with salts are widespread, in spite of its temperate semiarid regime, probably due to the combination of high amounts of inherited salts in soils, and strong winds augmenting evaporation. Because of their particular location in a sharp climatic transition, coastal wetlands in the Bahía Blanca Estuary are potential indicators of climate change and variations in large scale circulation patterns, as well as long term changes in sea level.

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11

Sarcocornia magellanica (Phil.) M. A. Alonso & M. B. Crespo: A Halophyte Native of Tierra Del Fuego (Argentina) Irrigated With Sea Water for Human Consumption and Sheep Meat Production

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and Alicia Y. Blessio

Abstract

Sarcocornia magellanica (Phil.) Alonso & Crespo, comb. Nova (salicornia) is a native perennial halophyte species of marshes in southern Patagonia, with a great potential to be developed as a crop, irrigated with seawater or salt-affected waters and as a natural pasture for domestic livestock feed. In order to evaluate the productive potential of the terrestrial species, such as fresh products for human consumption, cultivation possibilities and suitability of the same for sheep production, studies were conducted initially in marshes north of Tierra del Fuego-Argentina, after which culture was developed commercially. To this end, tests were conducted in natural environments, on communities called as "Carpet of Salicornia" (*Sarcocornia*), and crops planted on the Costa del Beagle Channel; in both cases with tunnel protection with plastic cover and witnesses unprotected; in which environmental, biological production and biomass parameters were measured. In natural environments irrigated daily tides, the production of green shoots in the second period of plant

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M.A. Khan et al. (eds.), *Sabkha Ecosystems Volume V: The Americas*,
Tasks for Vegetation Science 48, DOI 10.1007/978-3-319-27093-7_11

growth, yields showed 4–4.5 kg/m^2 and 0.70 kg fresh weight/dry weight m^2, with protective plastic tunnel LTD; and unprotected from 1.6 to 3.4 kg/m^2 in fresh weight (from 0.50 to 0.60 kg/m^2 dry weight). In the established culture, watered by pumping seawater and from the second year of production, the yield of green product selection and cutting of shoots was 4.7 kg/m^2 in protected plots and planting density of 12 pl/m^2, while in unprotected plots the yield was 1.8 kg/m^2 with the same planting density. From the third year the production of green shoots, stabilized at lower levels of performance: 2.6 Kg/m^2 with tunnel protection and 1.8 Kg/m^2 unprotected, with little variation between densities. Proximate analysis of green biomass *Sarcocornia* gave high values in essential fatty acids (47 %) – omega 3 and omega 6 – and high in salts K, Ca, Na and Mg. Feeding natural saline pastures of *Sarcocornia* and *Puccinellia* (lower middle marsh), lambs had a weight gain of 12–15 kg in 24 days of grazing, similar to the control lambs fed *Festuca* pastures. Chemical analysis of the meat determined that *Sarcocornia* fed animals had 50 % less cholesterol and 120–400 % increase in calcium, potassium, magnesium and sodium, in respect to traditional pasture fed. We conclude on the feasibility of growing this halophyte species by artificial irrigation with seawater, impersonate the natural irrigation of the tides, becoming the first direct Patagonian vegetable consumption as fresh products and unique nutritional properties; this along with the production of meat with reduced cholesterol content in saline *Sarcocornia* natural grasslands constitute a potential answer to reducing the consumption of fresh water in farming and salinized environments incorporating sustainable production.

1 Introduction

Conventional agriculture based on irrigation competes with industrial and domestic consumption, fighting 1 % of the water available on the planet in the form of fresh water. Another similar percentage saline waters constitute the remaining 98 % is seawater. The FAO estimates that 70 % of the usable water worldwide is used in agricultural production and a 14 % increase in water use for irrigation in 2050 is expected is undoubtedly – fresh water – a well sparse, especially considering sober estimated at 9000 million people world population by 2030. Moreover the total land under irrigation for agriculture (230 million ha.), 20 % are salinized. Salinized and inland marshes could be grown and produced food from 1 % of terrestrial plant species tolerant or highly adapted to salinity (Rozema and Flowers 2008). In particular, as the genus quenopodiaceas *Sarcocornia* have shown tolerance to high salinities around 18–40 g/L NaCl (Bianciotto et al. 2003, 2004; Costa et al. 2006b).

Worldwide halophyte species are being tested as crops for human consumption, animal fodder (Swinge et al. 1996; Bianciotto et al. 2004; Abdal 2009) or producing oils for production of biodiesel, drugs and edible oils (Hodges et al. 1993). As indicators of increased UV-B due to the depression of the stratospheric ozone layer radiation (Bianciotto et al. 2003; Costa et al. 2006a) or scrubber wastewater from shrimp culture (Costa et al. 2006b.). *Salicorniabigelovii* in particular, it has been the most studied quenopodiacea from the agricultural point of view, now cultivated successfully in the Sonoran desert in large areas (about 50,000 ha.) irrigated with seawater. It is a major producer of seed oil content (30 %), high contents of omega 6 and omega 3 – essential fatty acids with bióticas- properties and possibilities of producing biodiesel quality (Glenn et al.1998). Moreover, Rueda et al. (2003, 2011, 2013) worked on the possibilities of bio fertilization cultivars *S. bigelovii* – SOS and SOS-10 – 7 with growth-promoting bacteria (*Azospirillum* and *Klebsiella*) in order to avoid the effects of increased salinity in soils, the use of chemical nitrogen fertilizer commonly used in crops grown in desert environments of shoreline. The cultivation of the coastal deserts and enhancement of wetlands, major hostel halophytes, study around the world, represent new paradigms in agricultural production with significant advances in our day.

The marshes are coastal wetlands marine salinized by daily tides and home to most of the halophyte plant species (adapted to salinity). Ungar (1987) estimated 7 million km^2 in the coastal areas of the world and 1.3 million km^2 potentially usable agricultural area irrigated with salinized water. In Argentina and especially in Tierra del Fuego, the marshes of the Atlantic coast are little valued environments, despite fulfilling a key ecological role in both protective, operational, and supply of environmental goods and services. Most of these intertidal areas are used as waste dumps, as areas of oil exploitation and the best, feed for grazing sheep and cattle (Bianciotto et al. 2006, 2014). In Tierra del Fuego, marshes cover an area of about 60,000 ha.

In the area of these marshes the first related to the cultivation of halophytic species of greater vegetation cover work began initially known as *Salicornia ambigua* and then reformulated as *Sarcocornia magellanica* by Alonso and Crespo (2008). Early studies were aimed at determining the ability of the species in question as bio-indicator of increased UV-B radiation resulting from the depression of stratospheric ozone-the ozone hole-which occurs every year during the austral spring (Bianciotto et al. 2003, 2007; Costa et al. 2006a). Then and from the knowledge gained about the biology of *Sarcocornia*, trials were initiated to determine its potential as a producer of fresh food for human consumption and as forage for animal production.

2 Materials and Methods

During 2004–2012 the possibilities of growing *Sarcocornia magellanica* species perennial halophyte native of Tierra del Fuego were evaluated. Three trials were established: one in *Sarcocornia* natural grasslands (*Salicornia* Carpets with 80–90 % coverage) in the lower middle Chico River marsh (53 ° 30 ′S and 68 ° 00′ O, north of Tierra del Fuego – Figs. 11.6 and 11.8) **(R. Chico)**. This location has a macro tidal tide with an amplitude of 9 m regime. Which moistens the soil infiltration during each flood tide and 2 times a month. Another on the coast of the Beagle Channel (Ushuaia:54° 48′S – Figs. 11.8) (**B. Chanel 1**), in low marsh zone, by transplanting clumps of *Salicornia* (final soil cover 60–75 %), with daily tidal flooding; with three treatments: two with vegetation protection against environmental conditions (high winds and low temperatures) one with protection of plastic tunnel (“Tunel Claro”), another tunnel with mesh cover (“Tunel Malla”) and control without coverage. And third, as culture assay also in the Beagle Channel (Fig. 11.7) **(B. Chanel 2)**, transplant seedlings in the greenhouse developed from cuttings (stolons) of 10 cm in length, with two planting densities: 12 plants (17 cm between plants) and 18 plants (11 cm between plants) per square meter; seedlings planted on ridges were drawn every 30 cm., irrigated by pumping seawater and harvest methodology for selection of major outbreaks 5 cm. in length. Plots were delimited in each location of 250 m^2 with two treatments: one through tunnels (10 m long × 1.20 m wide × 0.90 m high) cover with plastic LTD and control without coverage.

The production test was conducted on lambs in the marsh R. Chico, using a design with three paddocks of 210 m^2 (6 m × 35 m.): A control with grazing on coironal (*Festucagracillima*) and two in *Salicornia* meadow with two animals each paddocks (total: 6 lambs). Those who were confined for 24 days with initiallivebodyweight between 8 and 12 kg.

For all assays environmental parameters were measured: wind, air temperature and soil moisture, salinity and out of tunnels; growth of the species and production (biomass and marketable yield); different forms of crop plant production were tested by multiplication by runners. Growth in body weight of lambs and proximal composition and nutritional analysis of meat and the green shoots of *Salicornia* were evaluated.

The statistical treatment to verify differences between treatments was performed by analysis of variance (ANOVA), calculated with the program Statistic 6.0; correlation analysis between environmental variables and production through SPSS STATISTICS 18 W PAS program.

3 Results

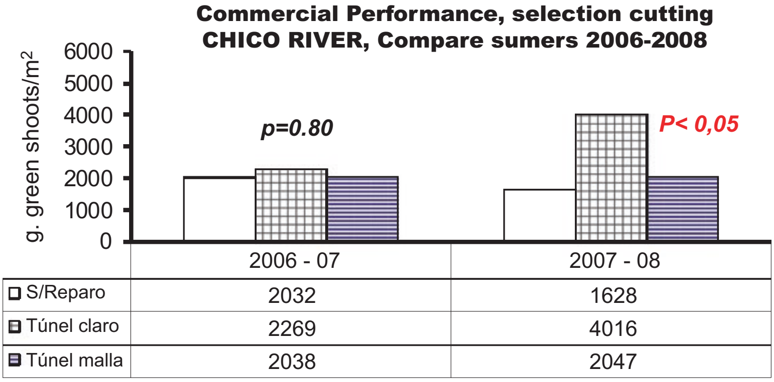
3.1 In the Marsh R. Chico

The trial was installed on natural field of *Sarcocornia* (Fig. 11.6) in a stratified sandy clay alluvial soil, with annual rainfall of 330 mm. and strong winds (35–40 km/h annual average). Rainfall in the period of plant growth, from October to March, amounted to 140 mm (2006/2007) and 230 mm. (2007–2008), representing 45–60 % of the annual precipitation. The average temperature in the months of vegetation growth was 8°. In the field, temperatures recorded in the treatments ranged from 17 to 28 °C for air and, soil ranged 11–18 °C, verifying the higher temperatures in the treatment of Tunnel Plastic protection. Soil moisture during the test was 30–35 % and soil salinity 17–19 g/l. Low salinities were explained by the mixing of fresh water of Chico River with seawater. The shoot length Plastic Tunnel (**Tunel Claro**) treatment (80 mm +/– 12.2) was significantly greater than control (**Sin Reparo**) (50 mm +/– 8.8) as in the density of green shoots where the difference in Plastic Tunnel (28,000 br/m^2 +/– 1,433.43) is 30 % higher than in the control unprotected. Production in green shoots during the second period (2007–2008) reported significant ($p < 0.005$) differences between treatment Plastic Tunnel (4,000 +/– 568.1 g/m^2) with a production 40 % higher fresh weight than the control without protection (1,600 +/– 763.6 g/m^2) (Fig. 11.1). Dry matter weights were registered 500 to 600 +/– 216.5 g/m^2 (17 % dry weight) (Fig. 11.3). This represents a production of 16–40 t/ha of fresh weight with an average 28 tons/ha of green fresh biomass and 5–7 tons/ha dry weight (Tables 11.1, 11.2 and 11.3).

3.2 Beagle Channel Coast, Trial 1

The trial was conducted on an alluvial soil of gravel and sand. During the growing season, rainfall in the summers of 2006/2007–2007/2008 (October to March) were 215 mm and 217 mm respectively, which represents 40 % of annual precipitation (550 mm); average temperatures from October to March, 9.5 °C; soil temperature 10–12 °C and salinity differentiated between years of 15–30 g/l. Soil moisture was 30 %. As for the biological parameters, and after 90–100 days growth cycle (January), the density of green shoots per square meter, showed significant differences between treatments, with values 30–35 % higher for Plastic Tunnel (9,000 br/m^2+/– 324.53)

Fig. 11.1 Performance of green shoots in the trial *S. magellanica* R. Chico, harvest end of December. Sin Reparo: Control; Tunnel Claro: Plastic tunnel; TunelMalla: mesh covered



	2006 - 07	2007 - 08
☐ S/Reparo	2032	1628
▦ Túnel claro	2269	4016
▤ Túnel malla	2038	2047

Table 11.1 Distribution of fatty acids, lipid, cholesterol and minerals in lambs fed in *S. maguellanica community* vs. Lambs grazing *Festuca* community

	Grazingon natural pasture of *S. maguellanica* (Salin pasture – PS)		Grazingon natural pasture of *Festuca spp.* (Coironal – PF)	
	%	ds	%	ds
Saturatedfattyacids	47.42	0.73	45.77	0.01
Monoenoicos	32.00	0.00	42	0.11
Polienoicos	18.42	0.40	9.49	0.51
Unsaturated	50.42	0.40	51.48	0.4
Trans	3.73	0.26	3.68	0.56
Omega 3 (n – 3)	4.29	0.16	2.17	0.08
Omega 6 (n – 6)	14.13	0.24	7.32	0.43
n – 3/n – 6	0.31	0.01	0.3	0.01
g lipids/100 g weight	1.96	0.01	7.80	0.01
mg colesterol/100 g	52.44	0.9	122.2	6.80
Ca %	0.12	0.02	0.04	0.01
Mg %	0.12	0.02	0.09	0.01
K %	1.40	0.02	1.15	0.02
Na %	0.70	0.01	0.37	0.01

Table 11.2 Distribution of fatty acids, lipid, Digestibility, salts and energy in *S. maguellanica*

Fattyacid[1]–lipids[2]– Digest. – Energy	Beagle 1		Río chico		Beagle 2		Festuca pasture
	%	ds	%	ds	%	ds	%
Protein (% dryweight)[3]	13.5		9.3		14.9		2.7
Saturados	29.20	0.53	25.41	0.10	24.54	0.51	
Monoenoicos	6.94	0.06	6.08	0.17	6.05	0.55	
Polienoicos	61.91	0.12	63.32	1.49	64.57	1.23	
Insaturados	68.85	0.06	69.40	1.32	70.62	0.72	
18:2n – 6 trans	0.56	0.01	0.34	0.04	0.42	0.03	
18:2n – 6 cis	19.87	0.00	20.78	0.46	25.63	0.52	
18:3n – 3 cis	41.49	0.11	42.19	1.07	38.53	0.74	
Lipids %	0.40	0.03	0.547	0.007	0.536	0.02	
Digestibility of Organicmatter (%)[4]	62.4		77.8		62.0		42
Energy (Mcal/kg OM)	2.2		2.9		2.2		
Ca[5]	0.6		0.4		1.3		0.4
Mg	1.3		1.2		1.3		0.2
K	1.9		2.4		1.7		<3
Na	14.1		13.5		10.5		>0.1

Methodology: 1. Gas Chromatografi; 2. Folch; 3. Kjeldhal; 4. NIRS technical (reflactance spectrography); 5. Atomic Absorption Spectrophotometry

Table 11.3 Lambs weight and daily gain in Trial Río Chico (n = 6)

Lambsweigth (kg/animal)	*Sarcocornia sligt lambs (PS)*	*Sarcocornia* heavy lambs (PS)	*Festuca spp.* lambs (PF)
Initial weigth	8.15	11.95	11.8
Final weight	22.25	26	22.5
Daily gain	0.58	0.58	0.44

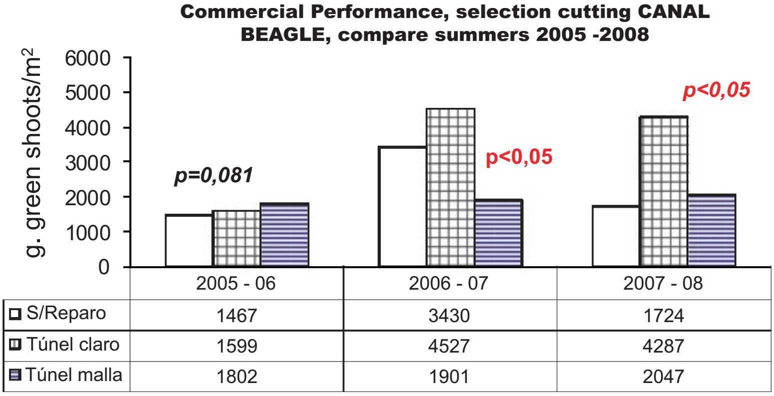
compared to control (7,000 br/m^2+/− 322.08). Regarding the shoot length varied between 70 and 95 mm +/− 16.21, no significant differences, with increased height in the treatment tunnel plastic. In terms of performance in green shoots, treatment Plastic Tunnel (4,100 g/m^2) shows values greater than 25 % control unprotected (3,400 g/m^2), with an overall average of 3,700 g/m^2 +/− 1.48 (Fig. 11.2). In terms of dry weight yields were observed between 500 and 700 g/m^2 (15 %) in control and Tunnel Plastic respectively (Fig. 11.4), with a mean value of 600 g/m^2 +/− 175.98 Production at farm level can be estimated at 37 t/ha of fresh weight and 6 t/ha of dry weight.

Highly significant correlations between air temperature ($r=0.750$, $p<0.001$) and floor ($r=0.807$, $p<0.001$) with the production of green shoots and dry matter, as a result of treatment were observed protective tunnels.

3.3 Beagle Channel, Trial 2

Located near the mouth of the Rio Olivia, with similar climatic site Costa Canal Beagle low marsh conditions, but on sandy loam soil, with gravel and irrigation by pumping seawater. Different planting densities showed significant differences in yields and production of green sprouts harvest selection. The plots with density of 18 plants/m^2 and protective plastic tunnel, showed the highest yields in the first year.

Fig. 11.2 Commercial performance of *S. magellanica* green shoots in the trial C. Beagle 1. Sin Reparo: Control; Tunnel Claro: Plastic tunnel; TunelMalla: mesh covered



	2005 - 06	2006 - 07	2007 - 08
☐ S/Reparo	1467	3430	1724
▦ Túnel claro	1599	4527	4287
▤ Túnel malla	1802	1901	2047

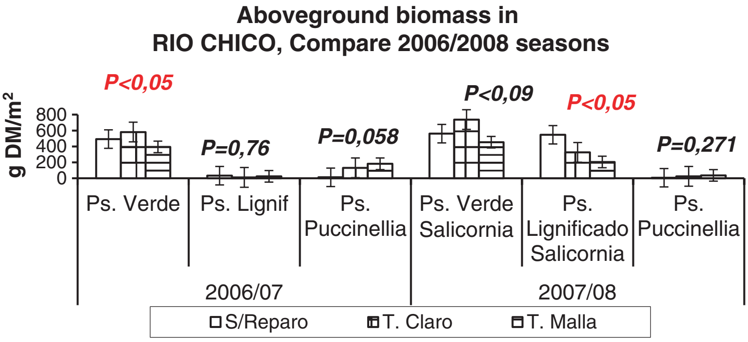


Fig. 11.3 Production of dry matter (DM) trial Rio Chico. Data detailed Green biomass and woody sprouts of *S. maguellanica* – dry matter of Puccinellia, by its status as a Natural Environment (*Sarcocornia* and *Puccinellia Grassland*). Ps verdesalicornia (dry weight of green shoot), Ps lignif. Salicornia (dry weight of lignified shoot), Ps *Puccinellia* (dry weight of *Puccinellia*)

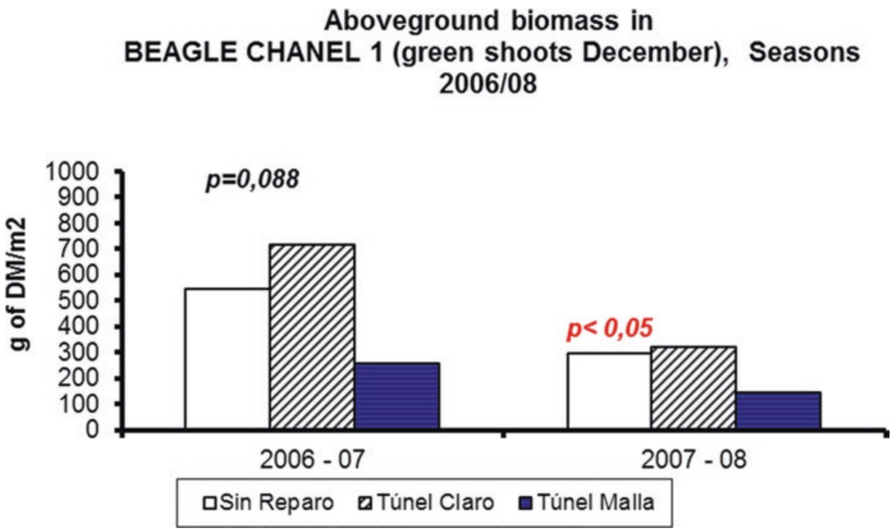


Fig. 11.4 Aboveground biomass of *Sarcocorniamagellanica*, BeagleChannel 1 trial. Sin Reparo: Control; Tunnel Claro: Plastic tunnel; TunelMalla: mesh covered

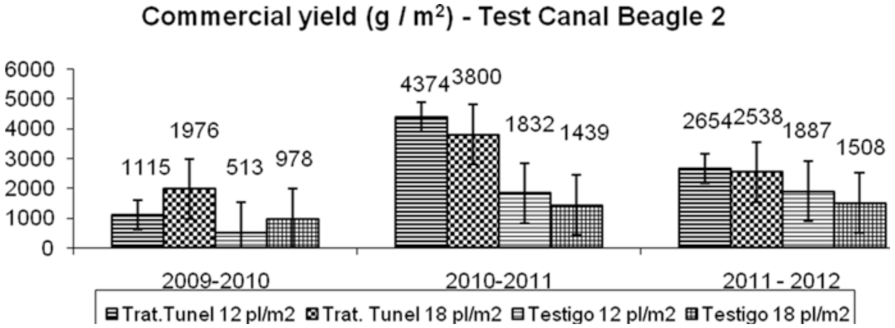


Fig. 11.5 Business Performance – cutting selection, Canal Beagle 2 trial. With two planting densities: 12 plants/m^2 and 18 plants/m^2 and two treatments with protective plastic tunnel and unprotected. Trat. Tunel 12 pl/m^2: plastic covered treatment – density of 12 pl/m^2; Trat. Tunel 18 pl/m^2: plastic covered tunnel – density of 18 plants/m^2; Testigo 12 pl/m^2: control 12 plants/m^2; Testigo18 pl/m^2:control 18 plants/m^2

In the 2nd year of cultivation, planting density of 12 plants/m^2 and protection tunnel, produced 4500 g/m^2, yields half past two times higher than controls and 20 % higher than the plots with density of 18 plants/m^2. The ground cover was approximately 75 % in this period. In the following years the production has stabilized at 1.7 Kg/m^2 unprotected and 2.6 Kg/m^2 with protection; with ground cover of 90 % (Fig. 11.5).

3.4 Nutritional Quality of *Sarcocornia* and Meat Lamb

The proximate composition of salts and essential fatty acids of *Sarcocornia magellanica*, as well as the characteristics of sarcocornia-fed ovine meat compared to Festuca-fed ovine meat in Tierra del Fuego, were described by Bianciotto and Col. (2004, 2013) from chemical analyzes of the INTI and are discussed below.

Fig. 11.6 Río Chico marsh – Tierra del Fuego, Argentina. *Sarcocornia maguellanica* plant

Regarding the proximate composition of oils and nutritional analysis in S. *magellanica* (Fig. 11.9), the results showed values of 9.3–14.9 % protein; 0.40 +/− 0.03 % lipid. As the salt content: 0.40–1.3 % in Ca; 1.3 % Mg; 1.7–2.4 % in K and 10–14 % of Na. By means of gas chromatography in *Sarcocornia* green shoots, a content of unsaturated fatty acids (65–68 %) was found, which doubles that saturated fatty acid (25–29 %). Moreover, *trans* fatty acid content was low (0.34–0.56 % of total fatty acids). The content of essential fatty acids: linoleic

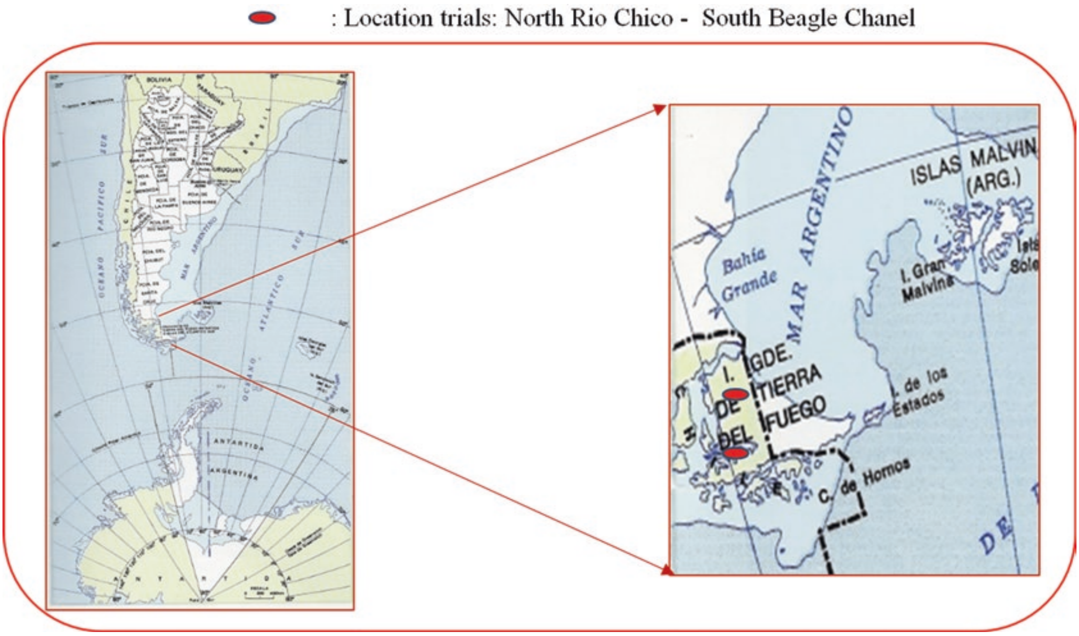


Fig. 11.7 Culture of *S. maguellanica* in Beagle Chanel 2

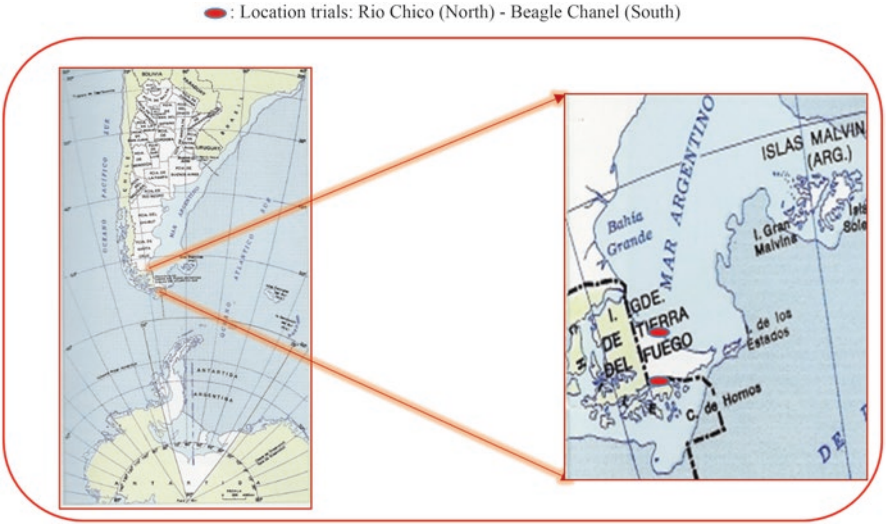


Fig. 11.8 Location of Tierra del Fuego

(19.8–25.6 %) and linolenic (38.5–42.1 %) conferred similar qualities to some vegetable oils, high in linoleic acid (40–75 % in sunflower, corn, soybean) or linolenic (linseed 58 %); with potential applications in prolonged therapy to control cholesterol.

The nutritional analysis of meat from lambs fed on natural pastures *Sarcocornia* (saline pasture – PS), compared with those fed on common natural pastures *Festuca sp.* (coirónal – PF) (Fig. 11.8), they showed increased content of 300 % in Ca, 30 % in Mg, 22 % in K, 90 % in Na and a

Fig. 11.9 Culture of low marsh zone – Beagle Chanel 1

cholesterol level 50 % lower, in the PS lamb. In the content of essential fatty values doubled in the *Salicornia* pasture fed (n – 3 = 4.3 mg/100 mg and n – 6 = 14.3 %), compared to the PF lambs (n – 3 = 17 % and n – 6 = 7.2 %). The content of fatty acid *trans*/100 gr. w/w in lambs PS (0.07 g/100 g) was 4 times lower than the PF (0.29 g/100 g) lambs. It is possible to see in a preliminary way that may be feasible completion of lambs to slaughter weight in *Salicornia* pastures, with special and distinct in meat quality. Final weights achieved at 24 days were similar in the six lambs fed on both grassland: saline grassland and pasture of *Festuca*. Daily gain of lambs was 0.40 kg (PF lambs) to 0.58 kg (PS lambs).

4 Discussion and Conclusions

The climate in Tierra del Fuego is a strong determinant of environmental parameters and biological production plants in general, and in *Sarcocornia*, despite being a native species. The plant growth occurs between the months of November to March and harvesting of green shoots from early January. Small changes in the temperature and wind speed, is reflected in the production of biomass. This was observed in the natural environment where the species grows, when it was observed higher shoot length on slopes of the banks of the rivers that flow into the sea, which protect the plants from drying and cooling effect by high winds. This led to the idea of testing economic forms of protection that would allow further development of the plants.

As the results, the protection tunnel showed a strong positive correlation between the parameters of green sprout production and an increase in temperature and reduction of the wind speed, the effect of the plastic cover. This led to production increases between 25 and 150 %. This antecedent corresponding to the Río Chico tests and Costa Canal Beagle 1 defined the form of cultivation on a commercial scale experience Canal Beagle 2 (mouth of R. Olivia), opting for the protection tunnels covered with plastic LTD. Yields in natural environments (R. and C. Beagle Boy 1, natural irrigation tide) and protection tunnels produced results in production of green shoots, similar to those achieved in the cultivation implanted artificial irrigation pumping. In the latter trial (Growing Beagle Channel 2), planting density played an important role, where the highest yields at the farm level (4.3 kg/m^2), occurred at the lowest planting density (12 pl./m^2) in the second period of growth; then stabilized production at a lower average yield (2.6 kg/m^2) in protected plots. The decline in yields could be related to plant cover reached 90 % in the third year, generating a decrease in farm productivity, by intraspecific competition. However, these production levels are consistent with those obtained by other authors in *Sarcocornia* and *Salicornia* (Costa et al. 2006b; Glenn et al. 1998).

During the 2nd culture period, coverage was 75 %, with a spacing between plants still evident about 5–8 cm, then disappeared in the third year for the most coverage. Other authors found that the degree of spacing between plants, related to the final planting density, growth form of the species or cultivar, spacing between rows, are generators of intraspecific competition in monospecific cultures (Mead 1970; Zanine and Santos 2004). With high densities of plants per unit area decrease was observed in aboveground biomass in populations of halophytes such as *Salicornia* and European *Saprtina alterniflora* (Ellison 1987; Brome et al. 1986).

Sarcocornia is a creeping plant in general, which is specially shaped multiplied agamic (stolons) in Tierra del Fuego and exceptionally by seeds; which generates almost pure populations that are true carpet, with high densities of shoots per unit area (8000 br./m^2) and 90 % vegetation cover. This coverage problems possibly caused competition between plants and reduced production. Besides the diversity of life forms with different growth habits from creeping and prostrate to erect, long growth cycle (nearly 6 months) before development cycles not exceeding 4 months, makes harvesting and performance of this species farm level in cultured decline over 3 years. Future work will be necessary to analyze the effects of chemical fertilization and biofertilization, besides the selection of cultivars with the best skills to achieve increases in the production of green shoots and oil content.

The composition of salts and essential fatty acids – linoleic and linolenic – give this species as a food special abilities that can be eaten as fresh outbreak. The omega 3 and 6 fatty acids are well known as drivers of high levels of cholesterol in blood. Sun et al. (2006) discussed the use of herbaceous *Salicornia* preventing atherosclerosis, hypertension and tumors, along with the synthesis of polysaccharides immunomodulatory cancer control. Control of diabetes and possibly hyperlipidemia, and found Park et al. (2006) from hyperglycemic and hyperlipidemic diets IRC induced in mice, which were then fed *Salicornia herbacea*.

Regarding the quality of lambs fed on natural pasture *Sarcocornia*-Saline Grassland-in short periods (24 days); the analyzes showed a decrease in cholesterol of 50 %, coupled with substantial increases (100 %) salts, essential fatty acids omega 3 and 6-and polineicos. Well as the amount of *trans* fatty acids were 4 times lower in lambs fed *Sarcocornia*. This would give, these meat advantageous features deferential respects to nutritional content.

In conclusion it is envisioned that the domestication of southern environment native halophyte irrigated with seawater, has a great potential as a crop. With chances of becoming a green product for human consumption and, an interesting fodder for sheep meat production of differentiated quality. It is also a way to put in value the marshes as potentially productive areas; because, most of these intertidal areas are used as waste dumps.

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12

Design Concept of a Reverse Osmosis Reject Irrigated Landscape: Connecting Source to Sabkha

Cylphine Bresdin, Margaret Livingston,
and Edward P. Glenn

Abstract

Feasibility studies in Arizona (U.S.A.) have determined that ocean delivery is a viable disposal option for saline waste water when sourced from near coastline regions. Use of open canals to transport waste water and use of evaporation ponds to reduce waste water volume are standard engineering practices. Engineered designs tend to focus on practicality and efficiency without regard to principles of landscape ecology. The concept of a saline ecosystem with landscape pattern incorporated as the vehicle for an evapotranspiration induced sequence of ecotopes along a directional saline gradient is proposed. This model will serve as a constructive, ecologically-based method to reduce reverse osmosis concentrate waste volume while increasing salinity during transport from source (RO facility) to sink (sabkha). In the process, biota is allowed to self-organize into marsh habitat and the system of pattern creates potential for plant and microbial crops. Potential for research use of the ecosystem is illustrated in light of a conceptual plan for the Santa Clara Slough, located at the northern end of the Sea of Cortez in the Gulf of California.

1 Introduction

As humans use fresh water it becomes more saline and as the broad salinity level of fresh water increases, there is demand to desalinate and return potable water for human consumption. As the number of desalination operations increase, the volume of concentrated waste also increases, but desalination is not the only source of brine waste streams. According to Lefebvre and Moletta (2006) the leather, textile, petroleum, agro-food, and chemical industries

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M.A. Khan et al. (eds.), *Sabkha Ecosystems Volume V: The Americas*,
Tasks for Vegetation Science 48, DOI 10.1007/978-3-319-27093-7_12

generate large volumes of saline waste. Industrial waste brine has been successfully used to irrigate ornamental landscapes and agricultural crops in arid regions of the Southwest (Gerhart et al. 2006; Glenn et al. 2009; Riley et al. 1997). Van der Gaag et al. (2010) proposes that we can responsibly deal with industrial waste brine by creation of remedial saline wetlands, but system salinity increases due to evaporation and consumptive water use by plants leading to increased soil salinity problems especially at inland locations. The movement of water from source to sink via an open canal system also subjects water to evaporation and a consequent increase in salinity. Alternative ideas for management and disposal of saline water in central Arizona were investigated during 2003–2006 by the Central Arizona Salinity Study (CASS 2003, 2006) and the Central Arizona Salinity Interceptor (CASI 2004). Both Arizona studies concluded that salts should be delivered to the ocean. Three routes of disposal for brine waste generated from the Yuma Desalting Plant in Yuma, Arizona were suggested in the reports: (1) gravity flow to the Salton Sea, (2) supplement flow to Cienega de Santa Clara, a natural saline wetland filtering agricultural runoff, or (3) transport via open canal to Puerto Penasco, Mexico for ocean delivery into the Sea of Cortez, which was determined to be the best option. Since concentration of brine waste from desalting source is 3–10 g L^{-1} total dissolved solids (TDS) and concentration at ocean sink is 35 g L^{-1} (TDS), the issue is how to move waste volume from source in an ecologically sensitive manner so that it is delivered to sink in site context while providing ecosystem services. An ecological solution to this problem might be creation of coastal depressions akin to evaporation ponds in the intertidal zone, essentially creating synthetic tide pools or tidal marshes to dispose of brine waste in a manner confluent with natural tidal regimes (Yechieli and Wood 2002). Results of the CASI study and success of Cienega de Santa Clara (Baeza et al. 2013; Mexicano et al. 2013) combined with the salinity gradient that underlies sequential cell structure of traditional salterns and the idea of saline wetlands functioning as concentrators was the thrust for design concept.

2 Methods/Approach

The goal of this work was to generate a conceptual design for a saline system; an ecological-based landscape along a directional gradient of increasing salinity which uses halophytic vegetation and sequential pools in accordance with a salinity continuum (Silvestri et al. 2005; Ungar 1998) to reduce volume and increase salinity of waste brine through evapotranspiration (Fig. 12.1).

It is assumed that correctly structured ecosystems will resort to self-organization or allogenic succession (Mitsch and Gosselink 2007) where energy flows are causal in saline zonation patterns. Self-organization is defined here as, a lateral diffusion of biota through the landscape matrix creating heterogeneity in the ecosystem. Structural landscape ecology, the foundation of complex patterns in landscapes, will allow and encourage evolution of ecological process. If landscape is the spatial pattern of the environment, ecology is the temporal processes. In his abstract, Franklin (1993) communicates that matrix and an appropriate biotic system is the concern of ecological landscape design. He presents an argument that the role of the matrix is to maintain diversity; highly functional ecosystems are generally associated with high species diversity with ample connectivity among edged patches.

This work designs an idea of ecosystem structure where the principle of landscape design and environmental sensitivity suggests that site analysis be an investigation of contextual pattern designed into existing structure (Makhzoumi 2000). In this sense, site location becomes important for this work. The project site is in the delta of the Colorado River in the Mexican state of Sonora, located in the arid southwest region of the North American continent south of Yuma, Arizona. Sonora has a coastal desert environment and is separated from Baja California by the Salton Slough and Colorado River Delta at the northern boundary of the Gulf of California (Fig. 12.2).

The CASI proposed canal and route from Yuma to the Gulf of California is used as guidance to propose an alternative route for regional

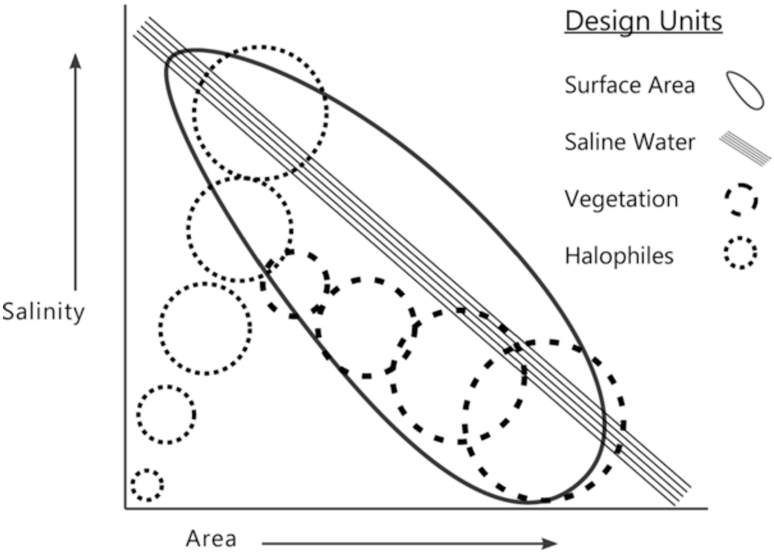

Fig. 12.1 Graphical representation depicting area versus salinity relationships of major design units constituting the concept. As salinity increases, surface area and area of water and vegetation decrease in a linear fashion. There is a minimal increase in surface area of halophilic microbes with a steep increase in system salinity

Fig. 12.2 Regional location of project site located at the southern end of the Santa Clara Slough on the eastern side of the Colorado River Delta, just north of El Golfo, Mexico. A surface conveyance canal from Yuma, AZ, shown as a *solid grey line* parallel to the pre-existing Mode Canal, that carries farm runoff to Cienega de Santa Clara, turns and follows Highway 3 south to the abandoned shrimp farm indicated by the *backward letter F*

considerations and design location. Figure 12.2 shows a regional route which parallels the existing MODE canal that feeds Cienega de Santa Clara until Highway 3, where it becomes the Bypass Canal that parallels the Highway until the southern end of the delta and enters Santa Clara Slough tidal basin. This basin was chosen to serve as sink due to its geologic relation to tidal flux, proximity to proposed canal, and existing infrastructure of an abandoned shrimp farm (Fig. 12.3). This site serves as vehicle for design of an idea which employs ecotope pattern as basis for a serial evapotranspiration induced saline gradated ecosystem for sustainable disposal of brine waste.

Site Analysis (Fig. 12.4): Abiotic components analyzed are substrate, topography and tidal flux. Basin soil is quaternary sediment, sand and clay which have been delivered onto the estuarine bed from river flow and tidal action. Encrusted salt layers residual in the basin are approximately 250–300 g L^{-1}. Soil structure within the shrimp farm boundary is expected to be rich in nitrogenous nutrients and harbor dormant microbes. Topographic quality of Santa Clara Slough basin ranges from approximately minus 1–6 m. Its

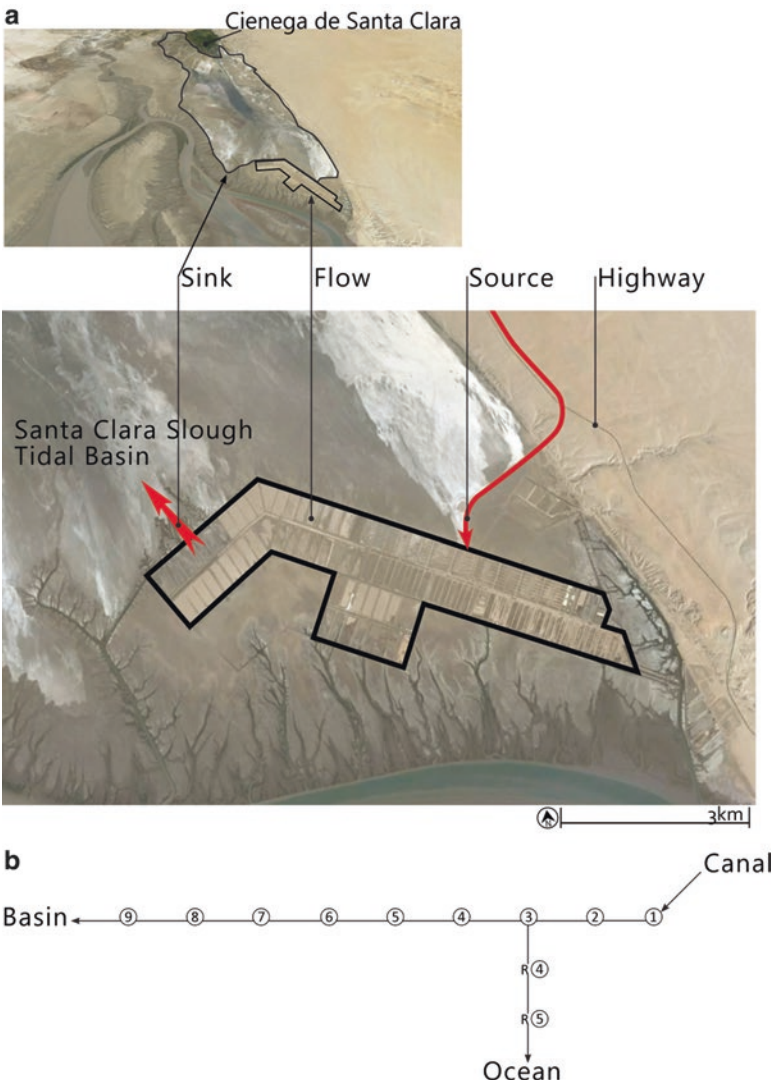

Fig. 12.3 (**a**) Imagery of the local environment showing physical relationship of the shrimp farm boundary to Santa Clara Slough, Cienega de Santa Clara and conveyance canal. (**b**) Simple schematic that shows ecotope alignment from input canal to outputs; ocean and basin

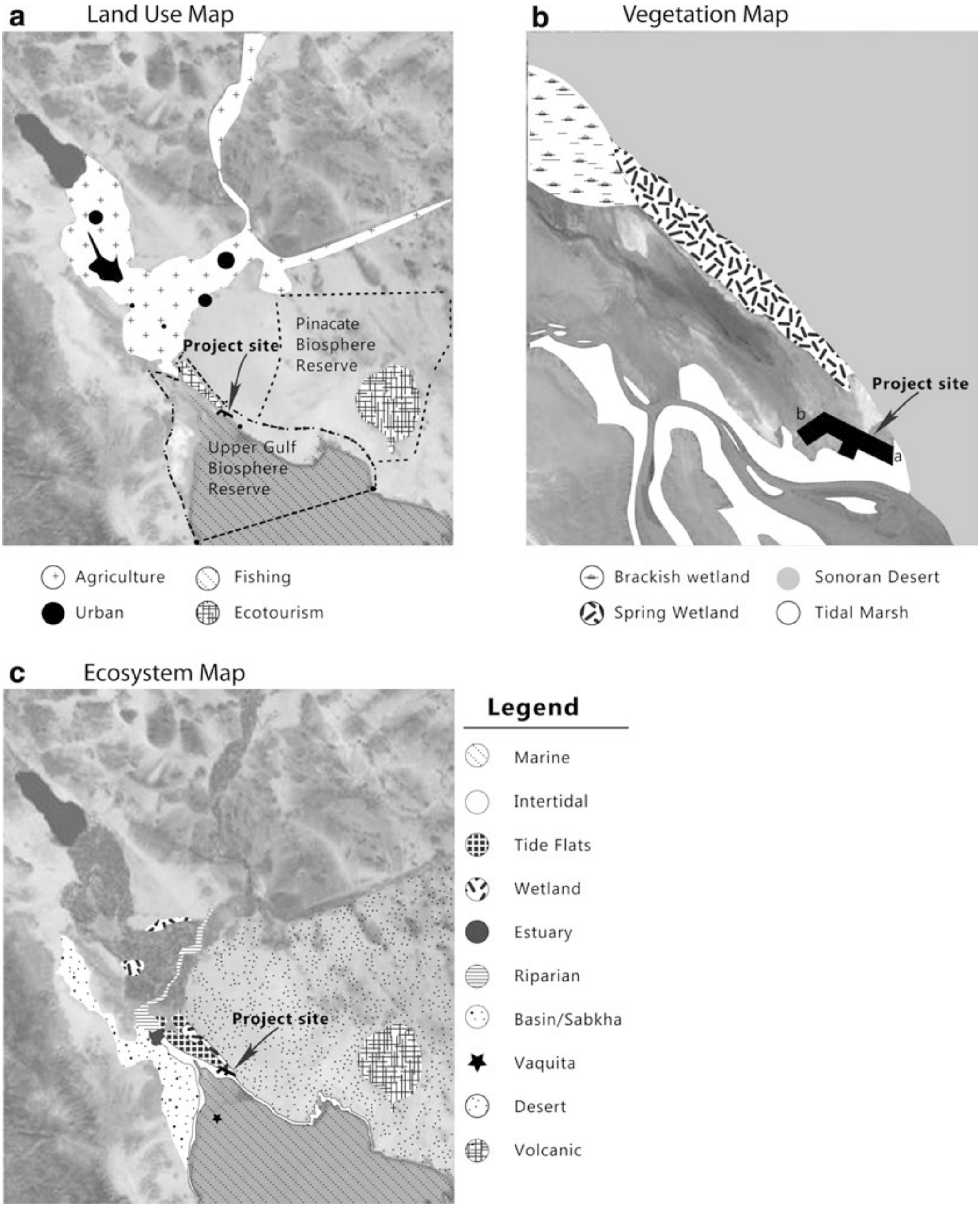

Fig. 12.4 (**a**) Land use map of existing conditions shows that the project site is located within the Upper Gulf Biosphere Reserve and that the Pinacate Biosphere Reserve is adjacent. Fishing and Agriculture dominate the economy of the region. (**b**) Vegetation map shows that the project site is west of desert and abutted to tidal marsh and down-grade from spring wetland habitat (El Doctor). Elevation drops from 4 m at inflow (*a*) to −1 m at outflow (*b*) relative to sea level. (**c**) Ecosystem map shows that desert dominates the region and the project site is ocean-side between desert and sabkha where ecotourism has a viable potential

eastern border is an escarpment which increases in grade from an elevation of 4–50 m along a north-south transect in line with the Cerro Prieto fault (Nelson et al. 2013). Elevation of the design site is approximately 4 m. It drops below 1 meter eight kilometers northward to the northwestern border where it abuts a low point in the slough. The southwestern border abuts a low point marine-side where there is potential for tidal interchange. Low point abutments are potential outflow locations. Tidal flux resulting in basin flushing occurs when tides exceed 5 m, approximately nine times a year at monthly intervals.

The site has full solar exposure, an annual precipitation of 54 mm and evaporation of 2 m. The average humidity is 44 %, average high temperature is 32 °C and average low is 17 °C.

Biotic components analyzed mainly consist of vegetation systems: Sonoran Desert, intertidal saltgrass meadows dominated by Distichlis palmeri, brackish wetlands (Cienega de Santa Clara), and fresh water spring wetlands (El Doctor); a corridor vegetated with over 29 wetland species which buffers slough and escarpment. Santa Clara Slough is a crusted mudflat with a mosaic of bacteria and a variety of shore birds; the Colorado River Delta is a major Pacific Flyway stop-over for migrating birds (Hinojosa-Huerta et al. 2013). For species detail the reader is referred to, Conservation Priorities in the Colorado River Delta Mexico and the United States (Zamora-Arroyo et al. 2005) available at www.sonoran.org. Protected vaquita (an endemic species) habitat is located off shore in the northern Sea of Cortez.

3 Results/Design

Design implications and applications are focused on development of flow between source and sink. When viewed at a fine grain, this situation becomes a saline system with a source of channeled waste brine, flow within the shrimp farm boundary, and sink to sabkha. Presence of preexisting structure is advantageous because earthwork for gravity flow and containment from east to west has been done. Use of this engineered structure as a framework for a productive sequential eco-evaporator of brine waste and biosphere research would be a beneficial repurpose for human education and wildlife.

Concept: Premise of concept is to inflow channeled water from Yuma Desalting Plant and flow it through a series of saline ecotopes that are spatially arranged to create a sequence of saline based communities with each community being more saline than the previous (Fig. 12.3c).

Ecotopes are in a heterogeneous linear pattern along a saline gradient. Within the confines of shrimp farm boundary, the pathway folds back onto itself and displays some sinuosity prior to sink. Brackish ecotopes (~35 g L^{-1}) are situated adjacent to marine-side low points to allow discharge of excess flow and potential ocean interchange of equivalent salinities during high tides. This requires design to consider tidal marsh stratification with the most saline ecotope situated adjacent to Santa Clara Slough where high saline outflow into the basin can be flushed out by monthly high tides that flood the basin, mixing sediment then recedes carrying salts out to open ocean leaving lagoons that evaporate. Geological positioning and climactic conditions of Santa Clara tidal basin defines it as a sabkha, a supratidal lagoon/playa where salt deposits (250–300 g L^{-1}) remain in contact with alluvial mud. Ecological design of the idea of a linear flow of saline ecotope pattern from source to sink is dependent on an appropriate natural saline sink; a sabkha. The system as a whole is dependent on supply of source water. Central Arizona Salinity Interceptor study reported an expected volume of 26.5 million gallons per day (MGD) at a salinity of 4.5 g L^{-1} TDS. This is design inflow salinity. If a microbial pre-filter or combination of pre-filter and RO are expected, they should be implemented prior to landscape system design. Salinity input into the landscape system would be at a greater concentration following wetland and mechanical treatment. Calculation to quantify water loss required within each successive ecotope is based upon difference of salinity

Table 12.1 Design of excel based model provides definitions, units and equations used behind the interface of the model shown in Fig. 12.6

	Equation	Variable	Units	Constants
		ET^o = pan evaporation	af $year^{-1}$	$ET^o = 8.268$ af $year^{-1}$
		af $year^{-1}$ = acre feet per year		af $year^{-1} = MGD \times 1121$
		A_{site} = area of site	acre	
		A_{Te} = total ecotope area	acre	
		A_r = area remaining	acre	
		S_i = salinity inflow	ppt	
		S_o = salinity outflow	ppt	
		W_i = volume water in	MGD	
Equation 1	$W_i \times (S_i \div S_o)$	W_o = volume water out	MGD	
Equation 2	$W_i - W_o$	W_c = volume water consumed	MGD	
Equation 3	$W_c \wp ET^o$	A_e = area needed per ecotope	acre	
Equation 4	$A_{site} - A_{Te}$	Maintenance		
Equation 5	$A_e = (W_i - (W_i \times (S_i \div S_o))) \times 1121 \div ET^o$			
Equation 6	$A_{Te} = \sum A_e < A_{Te}$			

inflow and desired outflow per ecotope. Area necessary to evapotranspire determined quantity of water can be calculated from known variables. Creative aspect of design is embedded in ecotope pattern; placement and proportion of units: size and shape of areas, depth of open water versus vegetation, and chromomorphic behavior of microbes.

Calculations: Premise of calculations was a simple sequential mass balance model built with Microsoft Excel and was based upon chosen salinity range spanned per ecotope. Hence, area of each ecotope required to increase salt concentration from inflow to outflow for each salinity range was mathematically deduced using equation 5 (Table 12.1 and Fig. 12.6). Outflow salinity of preceding ecotope equals inflow salinity of next ecotope and volume of water out of preceding ecotope equals volume of water into next ecotope (Fig. 12.5). This is the basis of sequence in the saline ecosystem pattern. Exploration of possible salinity ranges was the variable used to control area required per ecotope so that total area dedicated to ecotope pattern space is less than total area of project site which allows for human and mechanical space.

Assumptions were: (1) there is no water loss during canal transport, (2) there is no biotic uptake of salt, (3) there is no water loss due to biotic retention, (4) all water consumed by vegetation is transpired, (5) total water consumption equals pan evaporation: 8.268[1] af $year^{-1}$ (acre feet per year), and (6) calculations are per annum and based on CASI reported values of flow and salinity.

Site situation of the abandoned shrimp farm allows for perimeter expansion or reduction when accommodation of volume variability is needed. Calculated values for monthly fluctuations are reported in the Appendix. They will need to be considered in future design development. Future construction calculations which address assumption 2 and 3 may need to consider zonal mecha-

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[1] Annual number reported for Yuma Citrus Station is 99.21 in., standard value for Yuma area is 72 in.. Use of the higher value is justified by offset for potential volume reduction during transport and generality of application of theory.

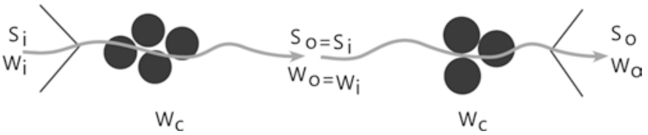
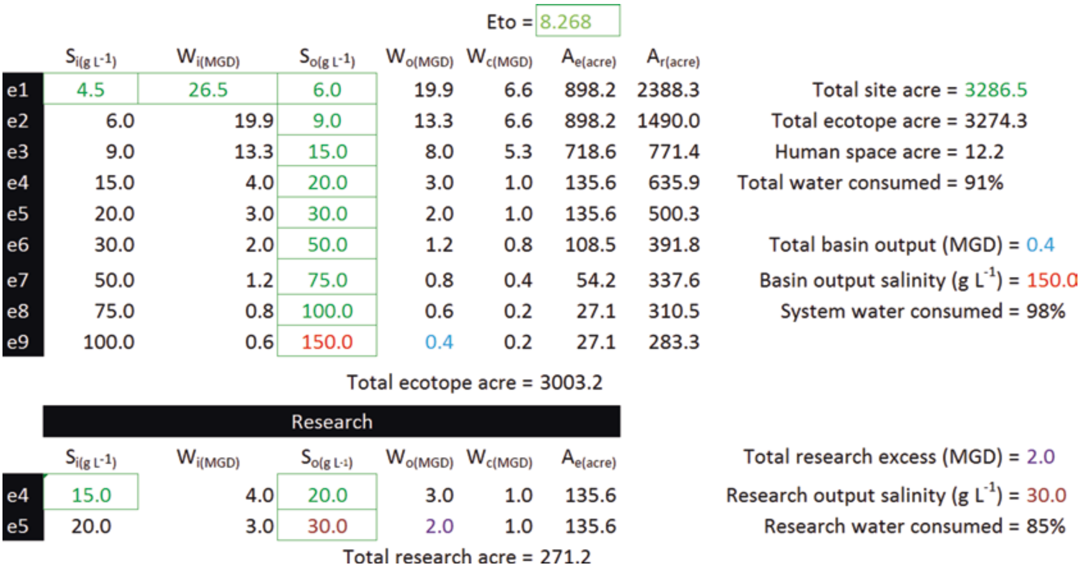


Fig. 12.5 Schematic of flow through the system showing how output of a previous ecotope becomes the input of the next ecotope, hence, the process of serial flow where water is continually consumed in sequential fashion



Eto = 8.268

	$S_{i(g\,L^{-1})}$	$W_{i(MGD)}$	$S_{o(g\,L^{-1})}$	$W_{o(MGD)}$	$W_{c(MGD)}$	$A_{e(acre)}$	$A_{r(acre)}$
e1	4.5	26.5	6.0	19.9	6.6	898.2	2388.3
e2	6.0	19.9	9.0	13.3	6.6	898.2	1490.0
e3	9.0	13.3	15.0	8.0	5.3	718.6	771.4
e4	15.0	4.0	20.0	3.0	1.0	135.6	635.9
e5	20.0	3.0	30.0	2.0	1.0	135.6	500.3
e6	30.0	2.0	50.0	1.2	0.8	108.5	391.8
e7	50.0	1.2	75.0	0.8	0.4	54.2	337.6
e8	75.0	0.8	100.0	0.6	0.2	27.1	310.5
e9	100.0	0.6	150.0	0.4	0.2	27.1	283.3

Total ecotope acre = 3003.2

Total site acre = 3286.5
Total ecotope acre = 3274.3
Human space acre = 12.2
Total water consumed = 91%

Total basin output (MGD) = 0.4
Basin output salinity (g L^{-1}) = 150.0
System water consumed = 98%

Research

	$S_{i(g\,L^{-1})}$	$W_{i(MGD)}$	$S_{o(g\,L^{-1})}$	$W_{o(MGD)}$	$W_{c(MGD)}$	$A_{e(acre)}$
e4	15.0	4.0	20.0	3.0	1.0	135.6
e5	20.0	3.0	30.0	2.0	1.0	135.6

Total research acre = 271.2

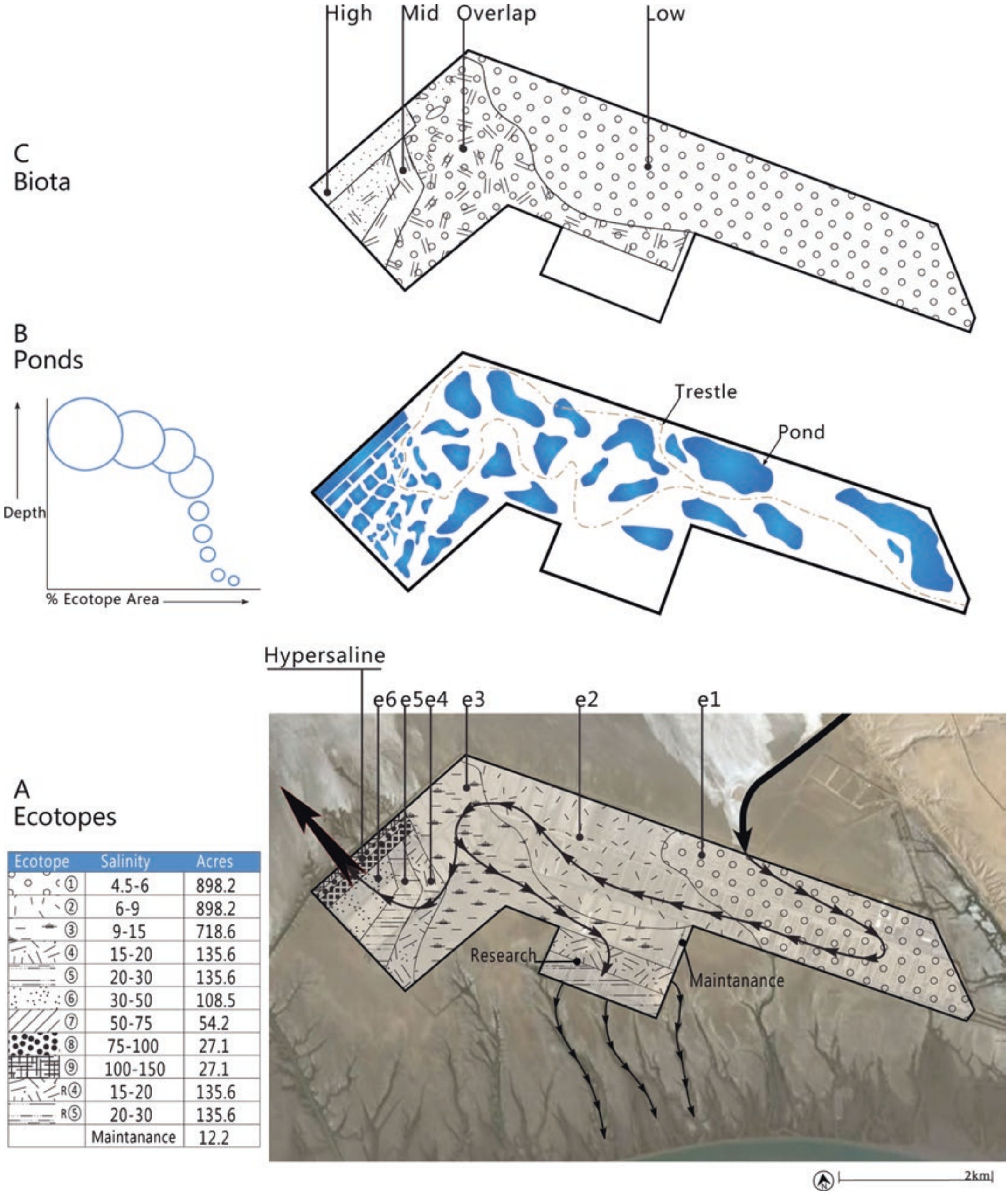
Total research excess (MGD) = 2.0
Research output salinity (g L^{-1}) = 30.0
Research water consumed = 85%

Fig. 12.6 Screen snip of the excel model interface. Outlined cells are user input cells used to calculate surface area required per ecotope based upon assigned salinity range. Area values are dependent on: total system area, input water volume and salinity, and evapotranspiration rate

nism of plant tolerance: exclusion, sequestration and secretion. Secretion in the intertidal zone will cycle salts through a vegetation/environment interface. Sequestration in the supratidal zone will remove a small amount of salt but release it upon decay. Detailed calculations should help enumerate balance between open pools and vegetation areas to seed. Microbial water consumption is considered negligible for theoretical design related calculations.

Design (Fig. 12.7): Abiotic focus is on pattern of open pool network created by subtle elevation changes within the microtopography of each ecotope. Since design related abiotic pattern has a foundation in elevation, raised human circulation is included in abiotic pattern, not land use. Land use is dedicated to ecologically constructive consumption of saline water. It is understood that larger sinuous pools have islands to accommodate wildlife needs.

Elevation affects soil moisture; low equates to hydric soils, high equates to dry sandy soils that wick water upwards causing salts to accumulate in substrate pores. Soil moisture level and amount of soil wicking will vary with seasonal variation and evapotranspiration. Consequently, soil salinities may be higher than open pool salinities which means that resident halo-xerophytes or psammophiles require a higher tolerance to salt induced stress than halo-hydrophytic plants. Annual per month mass balance spreadsheet results for the system are reported in the Appendix. Average MGD outflow derived from monthly calculations correlate closely with those derived by an annual approach. Figure 12.1 is the graphical representation of design elements under design restrictions of area, volume and salinity input. Seasonal variation in water consumption, outflow and resultant salinity



Ecotope	Salinity	Acres
①	4.5-6	898.2
②	6-9	898.2
③	9-15	718.6
④	15-20	135.6
⑤	20-30	135.6
⑥	30-50	108.5
⑦	50-75	54.2
⑧	75-100	27.1
⑨	100-150	27.1
R④	15-20	135.6
R⑤	20-30	135.6
	Maintanance	12.2

Fig. 12.7 (**a**) Diagram of basic landscape and process concept where input water flows sinuously down-grade through the system to outflow points. The table shows salinity range and area per ecotope of the system and indicates that oceanside outflow is at brackish seawater salinity while outflow into Sabkha is hypersaline at greater than 150 g L^{-1}. (**b**) Diagram of potential layout of ponds indicating spatial relationship of size to ecotope area. As ecotope salinity increases, ecotope area, and single pond area and depth decrease while ponds become the dominant landscape unit. (**c**) Biotic concept plan uses a general approach to salinity tolerance mirroring that used in horticulture because the system, as a whole, is intended to be self-organizing

Table 12.2 Short list of suggested species and vegetation forms for seeding or inoculation of ecotope ranges; a: shrub, b: grass, c: semi-succulent prostrate, d: reed

Unit	Ecotope	Latin	Common
 a  b  c  d * submerged species	① ② ③ ④	Anemopsis california	Yerba mansa
		Atriplex spp.	Saltbush
		Baccharis salicifolia	mule-fat
		Cressa truxillensis	Spreading alkali weed
		Heliotrope curassavicum	Alkali heliotrope
		Lycium brevipes	wolfberry
		Nitrophila occidentalis	Boraxweed
		Sesuvium verrucosum	Seaside purslane
		Sporobolus airoides	Alkali sacaton
	③ ④ ⑤ ⑥	Allenrolfea occidentalis	Iodine bush
		Batis maritima	Saltwort
		Distichlis spp.	Salt grass
		Juncus spp.	Rush
		Najas marina*	Najad
		Ruppia maritima*	Widgeon grass
		Scirpus maritimus	Salt bulrush
		Salicornia spp.	Glasswort
		Sueda linearis	Sea blite
	① ----- ⑦	Cyprinodon macularis	Desert pupfish
	① ----- ⑦	Gambusia affinis	Mosquitofish
	⑥ ⑧ ⑦ ⑨	Artemia spp.	Brine shrimp
		Dunaliella spp.	Dunaliella
		Chromomorphic Diatoms, Bacteria	

define the designed ecosystem as a poikilohaline[2] environment which will demand seasonally adaptive management.

Biotic focus of this work is pattern structure of a heterogeneous saline ecosystem for purpose of controlled volume reduction. Spatial relationship of area designation accomplished in a logical and environmentally sensitive manner does not require design specifics of each pattern block or ecotope. Generalities can be implemented. Design is not based upon intent to create wildlife habitat. However, design is sensitive to needs of migratory birds. Ecotopes are treated as self-realization units, broad spectrum planting of vegetation and microbial inoculation can be warranted, but should be relinquished to self-organization under adaptive management techniques. Suggested biota in Table 12.2 is arranged by unit type, salinity range, then alphabetically by genus. Suggested microbial organisms, and their related salinity and light intensity are shown in Fig. 12.8.

Ecotope 1 – 898.2 acre; 4.5–6 g L^{-1}. Saline water enters an open pool just below surface level causing turbulence which will hasten evaporation. Deeper pools (1.37 m minimum) can serve as reservoirs, buffering against drought, increasing zonation and heterogeneity. Wicking will cause soil salinity to rise beyond

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[2] Poikilohaline, saline environment where salinity range is a seasonally dynamic variable that affects biota.

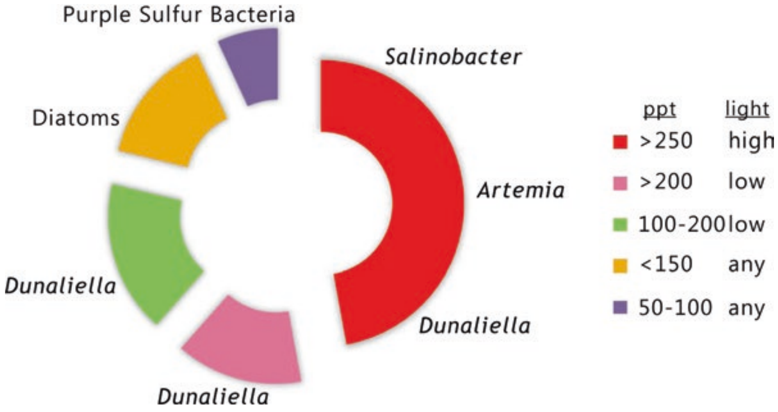


Fig. 12.8 Potential halophiles that can be seeded at specified salinities, light and nutrient levels are suggestions to get the system started in self-organization.

the salinity of pools. Grading will be required to direct water eastward so that it can gravity flow down-slope through the system.

Ecotope 2 – 898.2 acre; 6–9 g L^{-1}. Similar to e1 but requires a fan shaped slope to spread water going into e3. Consequently, meandering streams are more plentiful and pools are flat bottomed.

Ecotope 3 – 718.6 acre; 9–15 g L^{-1}. Vegetation pattern begins to shift from low to mid salinity. Pools are shallower (1 m minimum) and represent a higher percentage of ecotope surface area. Water flow is diverted in two directions to accommodate system continuance and potential research volumes.

Ecotope 4 – 135.6 acre; 15–20 g L^{-1}. Similar to e3, but area shape has begun to transform into geometric confines and pool to surface area has increased. Attempt to control Salt Cedar's invasive nature is accomplished through area of water greater than 1 m deep. Vegetation pattern is overlapped.

Ecotope 5 – 135.6 acre; 20–30 g L^{-1}. Vegetation pattern has fully shifted from low to mid salinity. Reeds are no longer present. The upper salinity level of e5, 30 g L^{-1} equates to the upper level of brackish environments. Pools continue to increase in percentage of surface area as shape becomes more geometric.

Ecotope 6 – 108.5 acre; 30–50 g L^{-1}. Contains sea water salinity and pools have become shallower (1 m maximum) and more geometric with a structure that resembles holding ponds of Aviero Salinas complex (Rodrigues et al. 2011).

Ecotope 7 – 54.2 acre; 50–75 g L^{-1}. Constitutes a broader salinity range where vegetation can no longer survive. Microbial populations increase and begin to display chromomorphic behavior; diatoms appear yellowish brown, anaerobic bacteria can lend a purplish hue, and Dunaliella, if present, is green. Pools have been conformed into straight sided cells.

Ecotope 8 – 27.1 acre; 75–100 g L^{-1}. Fish are no longer present and brine shrimp is first seen. Pools are large rectilinear evaporation cells consuming total ecotope surface area. Water retention time becomes an engineering issue to address. Chromatic dynamism of microbes becomes a dominant visual feature.

Ecotope 9 – 27.1 acre; 100–150 g L^{-1}. Highest salinity range as endpoint ecotope within the designed saline ecosystem. It supplies output flow into Santa Clara tidal basin at a projected rate of 0.4 MGD. Chromatic dynamism of microbes remains a dominant visual feature.

Salinity increases as volume and area decrease, open pool depth decreases, diversity of vegetative form and distribution decreases, vegetative zonation becomes more distinct and microbial presence becomes prominent. It is the view of the author that salinity range-appropriate seeding of biota can and should be initiated, but then left to an adaptive style of management that will allow self-organization to mature. It is anticipated that ecotope 1 will develop emerging marshes while ecotope 6 will develop into a submerging marsh. The site affords an offset dedicated area for experimental research where there is potential for tidal interaction. Since the idea design site lies within Gulf Biosphere Reserve boundary, research could potentially be managed by that entity. Appropriate research is vast, some possibilities are: halophyte agriculture, nursery stock production for coastal rehabilitation, microbial farming for polymer production, solar pond and energy research, and ornithological research. Human circulation should be limited to confined pathways atop sturdy rock trestles built to withstand and drain tidal surges.

4 Discussion

Based upon current knowledge of zonation pattern, its abiotic causes and plant stress coping mechanisms, an image of self-directed maturation could be suggested. However, this requires knowledge of contour details and hydrologic regime within the site context. Design development to this detail is beyond the scope of this work. To accommodate flow dynamics, grading will be necessary. Human investment is required for seasonal consideration and maintenance of ecological services. These include: wildlife habitat, halophytic agriculture for food, fiber or nursery stock, fish and brine shrimp production, or polymer extraction from microbes. Space for human related circulation and activities has been considered, and 12 acres have been allotted for the design. Four MGD in the salinity range of 10–30 g L^{-1} on an approximate 271 acre allotment satisfies research needs. Research ecotope 5 is located adjacent to research ecotope 4 and sea level to allow for 2.0 MGD leak-out of 30 g L^{-1} into tidal streams. CASI proposed solution was to flow 26.5 MGD of 4.5 g L^{-1} directly into the Sea of Cortez. Certainly there would be consequential biotic effects from a fresh water (4.5 g L^{-1}) plume alteration on the abiotic conditions of the sea (35 g L^{-1}). 3274 acres was required to reduce 4.5 g L^{-1} saline waste from 26.5 MGD to the sum of 0.4 MGD at 150 g L^{-1} and 2.0 MGD at 30 g L^{-1}. 0.4 MGD of 150 g L^{-1} gravity flows into Santa Clara tidal basin. This translates into:

0.4 MGD × 694.4 = 277.8 gpm | 0.4 MGD × 1121 = 448.4 a fyear^{-1} delivered to the sabkha.

Primary goal of this work was to derive an environmentally compatible and feasible landscape approach to mitigate anthropogenic saline waste. Volume is reduced from 26.5 MGD inflow to 2.4 MGD total outflow. Pathway of the flow through sequential ecotopes is divided into two directions which provide an option for research applications and wildlife habitat. Along the main path, salinity (TDS) is increased from an input salinity of 4.5 g L^{-1} to a discharge of 150 g L^{-1} into a tidal basin for periodic tidal flushing. If research dedicated flow is not consumed in experimentation, it discharges 2 MGD of 30 g L^{-1} into bidirectional tidal streams. Design is sensitive to existing contextual pattern. Vegetation and biota are seeded in a manner that should be conducive to maturation of self-organization. Variety in pool structure results in variety of vegetation diversity (Soga et al. 2013) and zonation patterns. Varieties in zonation patterns provide diversity in unit associations; the greater the diversity, the greater the heterogeneity, the greater the heterogeneity, the greater the stability. The system is designed to be dynamic and to establish its own equilibrium over time. The approach of using landscape pattern based upon salinity range allows for alterations in inflow and outflow salinity and volume, making this approach directly transferable to other shoreline disposal sites.

The proposed ecosystem was based upon annual data. Calculations used a pan evaporation of 8.268 af year^{-1}, this exceeds customary Yuma area ET^{o} of 6 af year^{-1}. Future design development will require extensive analysis of seasonal conditions and engineering aspects of hydrologic flow. Exact details of pool design and structure must be clarified and developed in accordance with substrate type, seasonal fluctuations, and available management practices. How will this saline waste water driven eco-evaporation system available for research and habitat be managed? What potential ecosystem services and goods could be harvested? Future considerations should focus on design of a small nearby pilot system that can mature into a public road-side park accessible to visitors.

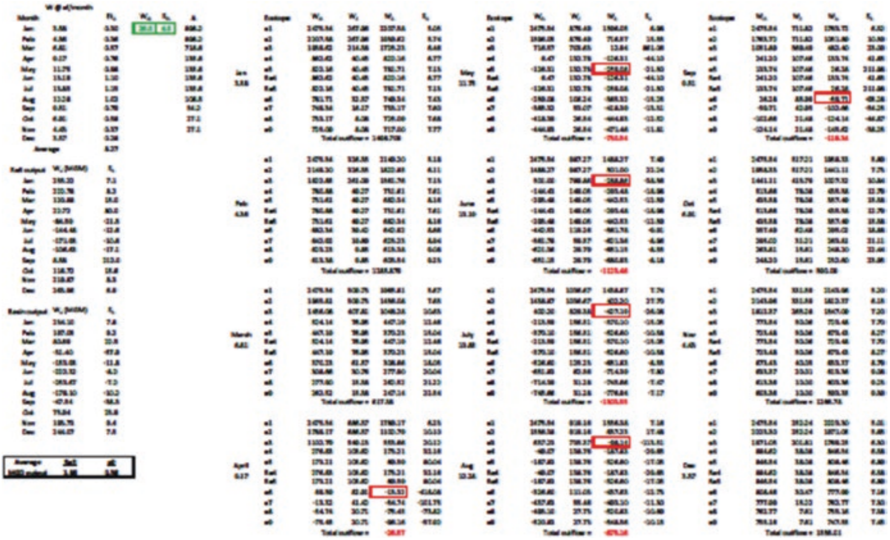
5 Conclusion

We have presented a concept to dispose of inland sourced anthropogenic saline waste water by use of landscape pattern and structure to enhance evapotranspiration and reduce volume in a contextual and environmentally sensitive manner with a favor toward self-design. An abandoned shrimp farm in the Colorado River Delta was repurposed into a tidal ecology with potential economic and research value as it was used to communicate general ecological design implications of pattern structure in relation to a sequential saline gradient. Each salinity stop-point along a salinity continuum in a heterogeneous horizontal flow ecosystem serves as a node or ecotype of the saline continuum which conveys concentrated brine to ocean via the sabkha sink.

Acknowledgements This manuscript partially fulfills requirements for the Degree of Doctor of Philosophy, University of Arizona and was originally published as a Masters of Landscape Architecture thesis by Cylphine Bresdin; Committee Chair, Elizabeth Scott. *Theory and Design Considerations of a Saline Ecological Landscape: A constructive method to reduce brine waste volume*, 2013. College of Architecture, Planning and Landscape Architecture of the University of Arizona, Tucson, AZ 85719, U.S.A. http://arizona.openrepository.com/arizona/. Cylphine would like to acknowledge and thank Dr. Charles Moody from the Yuma Desalting Plant for testing accuracy of the model.

Appendix

Monthly Values



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13

The Seed Bank of a Hypersaline Shrub Community in the Bahamas

Kendall A. Hanley, Brianne M. Walsh,
and Todd P. Egan

Abstract

Along the Fresh Lake causeway on San Salvador Island, the Bahamas, the seed bank was compared to the above ground vegetation in May 2006. Vegetation was dominated by a shrub canopy of *Conocarpus erectus*. A 49 m transect was run along the south side of the Fresh Lake causeway, and 10 secondary transects were randomly run from it towards Fresh Lake. Percent above ground cover was determined, and soil cores were taken along secondary transects at 0, 1, and 2 m. Percent above ground cover was calculated in 15 × 15 cm quadrats, and 6.0 cm diameter × 7.5 cm deep soil samples ($n = 30$) were collected. Species diversity was low, with only *Borrichia arborescens* (1.7 %), *Sporobolus virginicus* (16.8 %) and a member of the Poaceae (<1 %) representing aboveground vegetation. Only *Conocarpus erectus* represented the canopy. The majority of each quadrat along the secondary transects was bare ground. Percent above ground vegetation along the transects was determined and compared to number of seeds present. Only 43 (15,208 seeds/m^2) *Conocarpus erectus* seeds were present in the entire seed bank, and were found at plots 2, 8, and 10. Shrubs of this species were found at plots 1, 2, 7, and 10. No seeds of any other species were found in any transect. Tidal action may be the main force in distributing seeds along the causeway and out of the sampled area. A second factor accounting for low seed numbers may have been that seeds germinated but seedlings died before being recruited into the canopy.

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M.A. Khan et al. (eds.), *Sabkha Ecosystems Volume V: The Americas*,
Tasks for Vegetation Science 48, DOI 10.1007/978-3-319-27093-7_13

1 Introduction

This study was performed on San Salvador Island, Bahamas in May 2006. San Salvador is located about midway down the Bahamian archipelago at 24° 3′N latitude and 74° 30′W longitude, approximately 640 km southeast of Miami, Florida (Murphy et al. 1998). San Salvador is 11.2 km east to west and 19.25 km north to south (Fig. 13.1). The Antilles Current, part of the North Atlantic Gyre, flows past San Salvador and cools the island in the summer when temperatures range from 22 to 32 °C, and warms the island in the winter when temperatures range from 17 to 27 °C. San Salvador averages 100 cm of annual rainfall. The rainy season runs from September to November and is caused by tropical depressions, tropical storms, and hurricanes (Gerace et al. 2005). Average day/night temperatures were 28 °C/14 °C in January, 31 °C/16 °C in April, and 33 °C/20 °C in July (Gamble 2002).

Soils on the island are often shallow, poorly developed, and retain little water. Therefore, the island is home to species that can survive poor soil conditions, full sun, and periods of drought. Vegetation is generally scrub, with 524 species of vascular plants, representing 265 genera in 26 families. The island is divided into three vegetative zones – coastal, near shore, and inland. The interior of the island is made up of many saline or hypersaline lakes, surrounded by white or red mangroves. Vegetation in mangrove areas is sparse, and tends to grow in cracks between rocks. Shrub communities are dominated by haulback (*Mimosa bahamensis* L.), red calliandra (*Calliandra haematomma* L.) and poison wood (*Metopium toxiferum* L.). Near-shore vegetation is further from the ocean, and therefore less affected by salt spray. This community consists of silverthatch (*Coccothrinax argentata*(Jacq.) L.H. Bailey), shrubs and thickets (Gerace et al. 2005).

1.1 Seed Bank: Overview

Seed banks are ecologically important for many reasons. One reason is that they store seeds for future generations. Another important aspect is that they allow seed germination to occur during a more favorable time of year (Ungar 1995). Seed banks are especially important in highly stressful environments because they allow for recruitment after a devastating disturbance (Ungar 1991; Egan and Ungar 2000). Persistent seed banks allow populations to recover quickly from environmental hazards that cause mortality, and diminish the numbers of a certain species in an area (Ungar 1991). Seed germination and plant establishment occurs during favorable environmental conditions when soil salinity levels are reduced (Ungar 1991).

Seed banks can vary in size, mainly being affected by the number of seeds produced by the above ground vegetation, and seeds of various species can be found in all vegetation zones (Ungar 1995). However, above ground vegetation zones within seed banks may shift from year to year (Ungar 1995), and seeds often remain in the soil after the germination period to form a persistent seed bank (Ungar 1991).

Zonation of plant species may occur in the above ground vegetation even though seeds of all species are found along a salt marsh's salinity gradient (Egan and Ungar 2000). Zonation of vegetation in salt marshes suggests that location of different species is related to a species' ability to compete along a salinity gradient. Halophytic species are limited to zones based on a plant's ability to compete with other species and tolerate a saline environment (Egan and Ungar 1999). A plant's ability to compete is often negatively correlated with its ability to withstand a saline environment (Egan and Ungar 2000).

When seeds from limited salt tolerant species are dispersed into soil with a high salt concentration they may not germinate due to physiological restrictions. However, when seeds from highly salt tolerant species are dispersed into soils with low salt concentration they may not survive because they are poor competitors. As salt tolerance increases, the ability to compete decreases (Egan and Ungar 2000). Many halophyte seeds can withstand long periods of exposure to highly stressful conditions, then are able to germinate after the osmotic stress is removed (Ungar 1991).

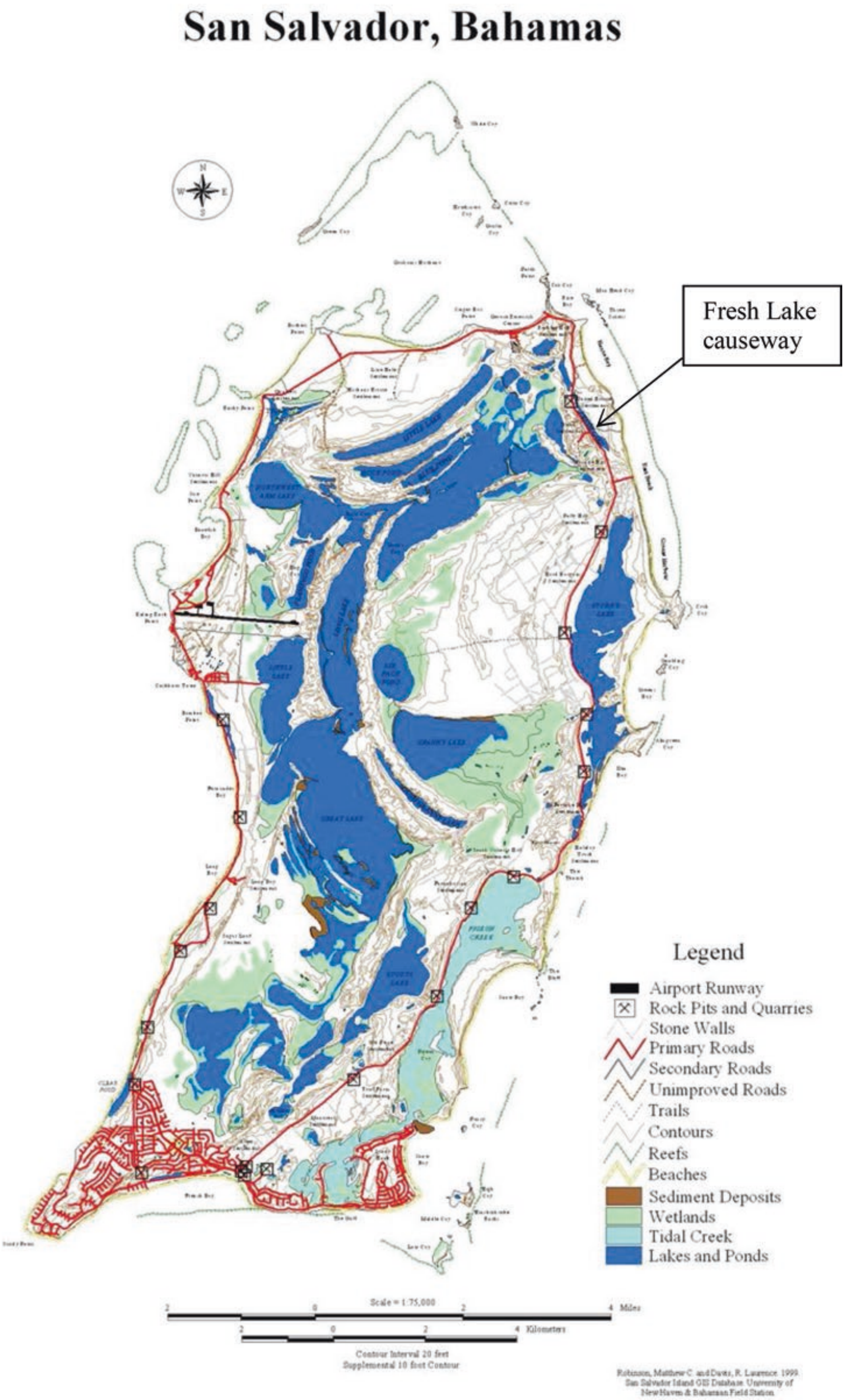

Fig. 13.1 Map of San Salvador Island, the Bahamas with arrow indicating location of the Fresh Lake causeway. Map used with permission of Robinson and Davis 1999

Dominant species in aboveground vegetation do not normally appear as the dominant species present in the seed bank (Ungar 1991). Hypersaline conditions appear to inhibit halophyte seed germination, thus maintaining a persistent seed bank (Egan and Ungar 2000). An increase in salinity appears to decrease seed germination (Egan and Ungar 1999), and salinity may inhibit the germination process at salinities greater than an adult plant of that species can tolerate (Ungar 1991).

Soil salinity helps determine whether or not germination will occur, and if a plant will grow to maturity (Egan and Ungar 2000). Seed germination usually occurs during periods of high precipitation when soil salinities are reduced in saline environments (Ungar 1982). Halophytes have adapted various germination strategies in order to establish a plant community within saline communities (Ungar 1995). Avoidance mechanisms appear to allow halophytes to resist stress, and halophytic species have evolved different mechanisms of dormancy in order to prevent seeds from germinating under extremely saline conditions (Ungar 1995).

Precipitation is heaviest in the spring or fall months in temperate climates (Ungar 1995), and from September to November on San Salvador Island, the Bahamas (Murphy et al. 1998). It has been found that a decrease in soil salinity due to rainy seasons stimulates the germination of halophytic species (Ungar 1995). Soil salinity increases during the summer months due to a decrease in soil moisture caused by increasing evaporation in warmer temperatures (Ungar 1995).

1.2 *Conocarpus erectus*: Overview

Conocarpus erectus is a halophytic member of the Combretaceae and is native to Bermuda, southern Florida, the Bahamas, the West Indies, the coasts of Mexico, Central and South America, and the Galapagos Islands (Francis 2007). *Conocarpus erectus* is commonly referred to as button mangrove or buttonwood (Francis 2007), however it is not considered a true mangrove because it is not restricted to a typical mangrove habitat (Rathcke et al. 1996). *Conocarpus erectus* provides a reproductive habitat and food for many animals (Rathcke et al. 1996) and helps prevent soil erosion (Francis 2007).

Conocarpus erectus flowers throughout the year in the Bahamas (Rathcke et al. 1996), producing purple and white flowers (Gilman and Watson 1993). The plants may have male, perfect, or female flowers (Rathcke et al. 1996). Kass et al. (2007) describe *Conocarpus erectus* as cryptically hermaphroditic because 11 % of plants with apparently male flowers had low fruit sets. Therefore these “male” flowers had a functional ovule (Kass et al. 2007). Pollination does not appear to rely on insects (Rathcke et al. 1996). *Conocarpus erectus* males produce no fruiting heads; female flowers produced high fruit set, while perfect flowers have low fruit set (Rathcke et al. 1996). *Conocarpus erectus* produces achene fruits (Guppy 1917) in compact heads or “buttons” (Rathcke et al. 1996) densely packed into 5–15 mm spherical clusters (Francis 2007). The fruits are dry, and can be brown or red in color (Gilman and Watson 1993); often with 35–56 fruits per head (Francis 2007). In many cases however, the plant will produce many achene fruits, but very few fruits will have mature seeds (Guppy 1917).

Conocarpus erectus usually occurs open-grown (Francis 2007) and can tolerate clay, loamy, sandy, acidic, and alkaline soils (Gilman and Watson 1993). *Conocarpus erectus* needs full sunlight to grow, and is shade intolerant (Francis 2007); however it is drought tolerant (Gilman and Watson 1993).

Water is the main source of seed dispersal, and *C. erectus* can grow up to 20 m tall; however, this species is usually found in shrub form with a height of 1.5–4 m (Francis 2007). Plants can live for several years with a medium growth rate (Francis 2007). *Conocarpus erectus* usually grows above the high tide line, just landward of other mangroves, and along beaches (Francis 2007). Tolerant to salt water spray and over-wash from storm surges; *C. erectus* is able to live near bodies of water with high salinities (Francis 2007). The plant’s bark is gray or brown in color and approximately 8 mm thick (Francis 2007). *Conocarpus erectus* may have one or multiple trunks (Francis 2007); leaves are somewhat fleshy and range from 2 to 10 cm long (Francis 2007). The leaves are oblong in shape, simple, exhibit pinnate venation, and are alternately arranged (Gilman and Watson 1993).

Ungar (1991) states that above ground vegetation does not always reflect the seed bank. Therefore, we hypothesized that seeds in the soil will be different from the above ground vegetation along the Fresh Lake causeway. Thus, not many *C. erectus* seeds may be present in the soil.

2 Materials and Methods

2.1 Study Site

The study occurred on San Salvador Island, the Bahamas, along the Fresh Lake causeway (long. 74°2.837′ W, lat. 24°06.008′ N, Fig. 13.2). Fresh Lake is hypersaline, and therefore vegetation is limited. Plants growing along the causeway included *Conocarpus erectus* L. (Combretaceae), *Borrichia arborescens*L. (Asteraceae), *Sporobolus virginicus*(L.) Kunth (Poaceae), and another species of grass.

2.2 Seed Bank

A primary 49 m transect was run parallel to the road along the Fresh Lake causeway. Ten secondary transects were selected along the primary transect at determined meter intervals using a random numbers table. Along the south side of the primary transect at 0, 1, and 2 m intervals into Fresh Lake, percent ground cover was determined and soil cores were collected to examine the seed bank. At each interval, percent ground cover was recorded using a 15 × 15 cm quadrat. Soil cores (6.0 cm diameter × 7.5 cm) were taken on the alternate side of the transect. A coin toss was used to determine if the right or left side of the secondary transect would be an aboveground quadrat measurement, or a soil sample. There were a total of 30 quadrats and 30 soil cores.

Fig. 13.2 Photograph of Buttonwood community along Fresh Lake causeway. Note the overwhelming growth form of shrubs

After the soil cores were extracted, they were dried and placed in plastic bags. Upon return to the U.S., samples were sorted into trays and sifted using a no. 10 (2 mm) soil sieve. Seeds were identified using reference samples collected directly from *Conocarpus erectus* shrubs.

3 Results

3.1 Seed Dispersal

Conocarpus erectus shrubs were found in 4 out of 10 plots (plots 1, 2, 7, and 10), whereas seeds of this species were only present in 3 plots (plots 2, 8, and 10). Along transect number 2, seeds were found at 1 and 2 m from the primary transect line, with 4 and 3 seeds, respectively. A total of 7 (2476 seeds/m^2) seeds were collected from soil core 2. In plot 8, seeds were found at 0 and 2 m from the primary transect line, with 1 (354 seeds/m^2) seed at each secondary plot. A total of 2 seeds were collected from plot 8. In plot 10, seeds were found at 0, 1, and 2 m from the primary transect line, with 3 (1061 seeds/m^2), 15 (5305 seeds/m^2), and 16 (5659 seeds/m^2) seeds, respectively. A total of 34 (12,025 seeds/m^2) *Conocarpus erectus* seeds were collected from secondary transect 10 (Fig. 13.3). Seeds of no other species were found. Overall, the seed bank was small and not diverse in regard to seed species.

3.2 Above Ground Vegetation

Bare ground dominated most of the 49 m transect, however three plants were present in various secondary transects aside from *C. erectus*. Plant species included *Borrichia arborescens*, *Sporobolus virginicus*, and another grass species. In secondary transects 1 through 6, *Sporobolus virginicus* was usually the only plant, and covered most of the area. An exception to this trend was secondary transect 2, where *Borrichia arborescens* (16.7 % cover) was present along with *Sporobolus virginicus* (13.3 % cover). In secondary transects 7 through 9, no above ground vege-

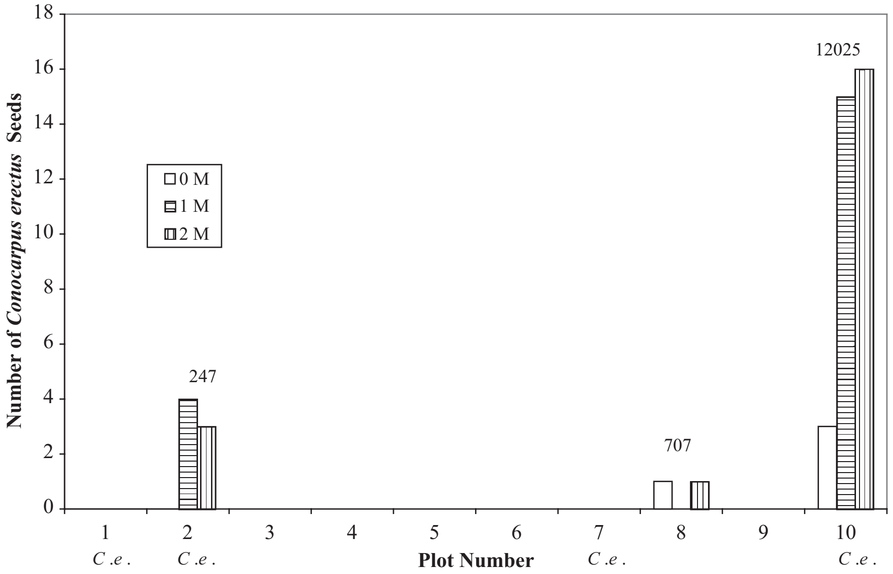

Fig. 13.3 Distribution of *Conocarpus erectus* seeds on 7 May 2006 at the San Salvador Island Fresh Lake causeway along a 49 m transect on the road's south side. A total of 10 plots were sampled at 0, 1, and 2 m in from the edge of the road. *Conocarpus erectus* plants were located in plots 1, 2, 7, and 10 (*C. e.*). Numbers above bars indicate the number of seeds/m^2 in core samples at each of three, 1 m^2 quadrats. No seeds where found at plots 1, 3, 4, 5, 6, 7, or 9. Not all secondary transects containing seeds had seeds present at each sub-plot (0, 1, and 2 m)

tation was present. Secondary transect 10 consisted predominately of bare ground, with one species of Poaceae present (3.3 % cover) (Fig. 13.4). Overall, there was low diversity in above ground coverage along the causeway.

There was low species diversity under the *Conocarpus erectus* canopy; *Borrichia arborescens* (1.7 %), *Sporobolus virginicus* (16.8 %), and another member of the Poaceae (<1 %) representing the aboveground vegetation. The remainder was bare ground.

3.3 Similarity Between Vegetation and Seed Bank

Similarities between the seed bank and above ground vegetation for each of the zones varied. *Conocarpus erectus* seeds were found in soil cores at secondary transects 2, 8, and 10. Of these, secondary transect 2 had *Borrichia arborescens* (16.7 % cover) and *Sporobolus virginicus* (13.3 % cover) both present; however bare ground was the dominant feature. Also, at secondary transect numbers 2 and 7, seeds of *C. erectus* were found along with *C. erectus* shrubs. Secondary transect 8 was comprised of bare ground because no aboveground vegetation was present, 2 (707 seeds/m^2) *Conocarpus* seeds were found, but no shrubs were present. Secondary transect 10 was dominated by bare ground; however, a small percentage of Poaceae was present (3.3 % cover). Also, in secondary transect 10, 34 (12,025 seeds/m^2) *C. erectus* seeds were found, along with a shrub (Figs. 13.3 and 13.4). *Conocarpus erectus* shrubs were found at secondary transects 1 and 7; however, no seeds were collected in these zones. Secondary transect 1 contained 38.3 % *S. virginicus* while secondary transect 7 had 100 % bare ground (Fig. 13.4). From the samples gathered at the Fresh Lake causeway it appeared that above ground vegetation and the seed bank were fairly similar; however, only *C. erectus* seeds were found within the seed bank and no other species of seeds were present.

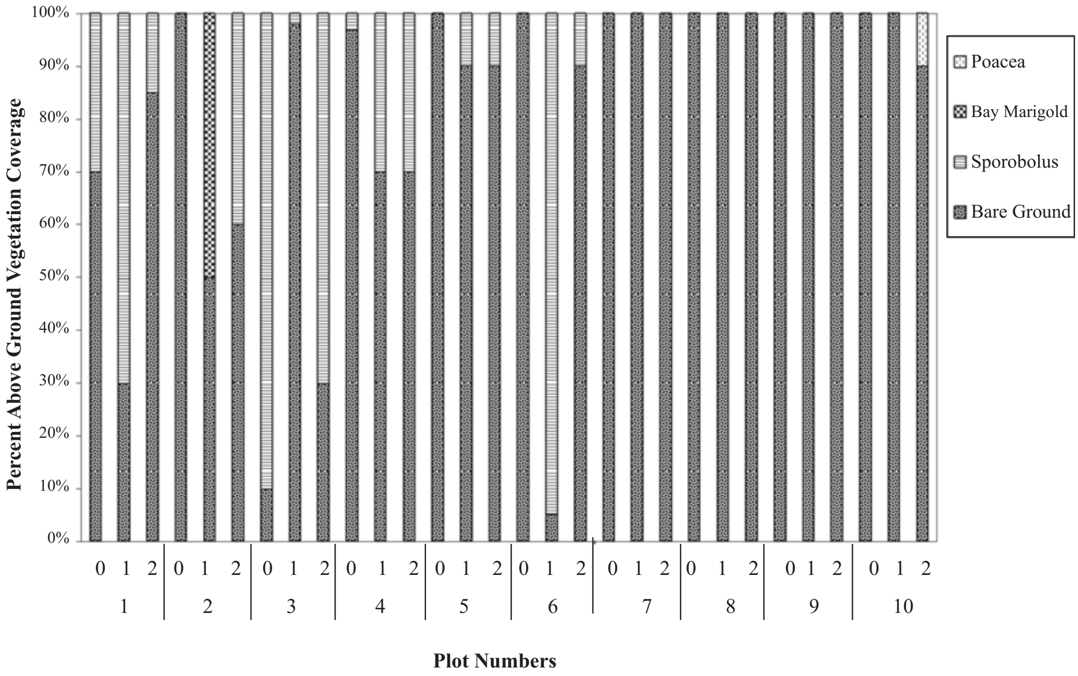

Fig. 13.4 Percentage of above ground vegetation present under a *Conocarpus erectus* canopy along a 49 m transect on 7 May 2006 on the San Salvador Island Fresh Lake causeway. Ten plots were sampled using 15 cm × 15 cm quadrat samples taken at 0, 1, and 2 m in from the edge of the road

4 Discussion

The data did not support the hypothesis that the seed bank and above ground vegetation along the Fresh Lake causeway would be dominated by different species. While, the number of seeds recovered in the samples was low, the entire seed bank consisted only of *Conocarpus erectus* seeds. The above ground vegetation along the causeway was dominated by *Conocarpus erectus* shrubs.

Ungar and Woodell (1993) observed that similarity between aboveground vegetation and seed banks in a perennial dominated community like this *C. erectus* community is low. Seed banks may also over-represent some halophyte species, while under representing other halophyte species, and annuals normally produce a large and persistent seed bank, while perennials generally do not (Ungar 1995; Ungar and Woodell 1996). The results of our seed bank study were contrary to this trend, even though numbers were low. Only seeds of the perennial *C. erectus* were present in the May 2006 samples of the Fresh Lake causeway seed bank. Seeds of other perennials represented in the above ground vegetation including *Borrichia arborescens* and *Sporobolus virginicus* were not present in the seed bank. However, the lack of annuals in the seed bank should not be too surprising since there was only one potentially annual species, a grass, and that was poorly represented. In addition, many grasses spread via rhizomes so reproduction by seeds may be less important. However, the question of why there were so few annual species present is worthy of investigation.

Although our seed bank contrasted with many other studies in that it was dominated by perennials and not annuals, our data were consistent with other halophyte seed bank studies reporting that the above ground vegetation was dominated by a perennial species (Ungar 1995; Ungar and Woodell 1996).

The number of *C. erectus* seeds found within the May 2006 samples at the Fresh Lake causeway was lower than expected based on the dominance of this species. Environmental and biological factors may reduce the number of seeds in a seed bank, but we believe that since our study site was in a tidal zone it was tidal action that was the main force in dispersing seeds from the sampled area (Ungar 1991; Ungar 1995; Ungar and Woodell 1996). *Conocarpus erectus* seeds have been noted to be buoyant due a to spongy aerenchyma layer which develops on the outer wall of the seed (Guppy 1917), and buoyancy could allow the seeds to be carried away from the seed bank by tidal action. Another factor that may have contributed to the low number of seeds in the seed bank is that most of the seeds may germinate soon after being shed, but then die before being recruited into the canopy (Ungar and Woodell 1993; Ungar 1995).

Soil samples at Fresh Lake causeway were collected in May, but the rainy season occurs from September to November on San Salvador Island, and the seed bank soil may have had elevated salt content which may have killed *C. erectus* seedlings. Halophytes usually remain dormant during exposure to high saline levels (Ungar 1982), however salinity tests were not performed, and salinity tolerance levels for *C. erectus* is only now being studied.

Lack of dormancy mechanisms, death of seeds, and poor salt tolerance may also have contributed to the lack of a persistent seed bank (Ungar 1995). Seed dormancy appears to be an important survival mechanism in halophytes because seeds can avoid extreme environmental conditions by delaying germination, and remain within the seed bank until a period of reduced salt stress occurs (Ungar 1982; Ungar 1995). Seed dormancy appears to occur due to physiological, physical, or morphological factors, and appears to allow seeds to germinate in conditions with moderate soil salinities. This may increase the likelihood of survival and recruitment (Ungar 1995). Dormancy mechanisms of *C. erectus* are not yet known.

Additional factors that may have decreased the number of seeds in the seed bank include herbivory by birds, mammals, insects, and arthropods; water logging; hypersaline conditions; and fungal and bacterial degradation (Ungar and Woodell 1993; Ungar 1995). Halophytes have also been known to cause allelopathic effects in germinating seeds (Abbas and Ali 2012).

Further research on the *C. erectus* seed bank appears to be necessary to understand the relationship between above ground coverage and seed bank composition. Further research on the salt tolerance and dormancy mechanism of *C. erectus* also appears to be necessary. To help answer these questions, seed bank studies of *C. erectus* that vary sampling at different times of the year are suggested. Buttonwood reproductive biology is only now being understood (Kass et al. 2007), therefore, a logical next step is to conduct artificial seed burial experiments which may elucidate information regarding the effects of moisture, CO_2, microorganisms, and seed predators (Baskin and Baskin 1998). In addition, Carter and Ungar (2004) used similar techniques to study the effects of seasonal light and temperature, potential changes in dormancy, and plant zonation with the halophyte *Spergularia marina*, and therefore could be employed with the upshore mangrove species buttonwood.

Acknowledgements The authors thank Vincent Voegeli and personnel of the Gerace Research Centre, San Salvador, The Bahamas for their help and use of field station equipment and facilities. We also thank J. Forrest Meekins for her helpful comments preparing the manuscript, and Elmira College, Elmira, NY, USA for helping fund this research.

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Salt Contaminated Water Phytotreatment by Constructed Wetland

14

B. Morteau

Abstract

Soil and water salinization can be reclaimed using halophytes. Salt contaminated water are usually treated with membrane processes and thermal methods. However, constructed wetland an efficient and affordable technology has been proposed to remove salt from water using halophytes. Efficiency of constructed wetlands are reported in this paper. Studies generally observed salt absorption by plants and salt accumulation issues in soil. An analysis of the literature demonstrates that phytoextraction partially removes salt from salt contaminated water and must be coupled with other technologies for increased effectiveness. The use of brine volume reduction, to reduce the volume of contaminated water, used in conjunction with phytoextraction is proposed as an alternative. Brine volume reduction also provides the possibility of generating income by cash crop cultivation. Recommendations are proposed to improve the treatment of salt contaminated water. A constructed wetland with basins planted with incrementally higher salt tolerant species is presented. Its design is based on evapotranspiration modelling and species selection.

1 Introduction

Salinization is the degradation of soil or water due to an increase in their salinity. It is occurring in many regions of the world (Vengosh 2007; Kaushal 2009) and is having an impact on a number of physical and chemical parameters that impair growth and metabolic activity in fauna and flora. The preponderance of research on salinization is concerned with soil salinization (Rozema and Schat 2013; Ventura and Sagi 2013) which reduces crop yields significantly, and this in a context of increasing world population and scarcity of new suitable land for agriculture (Panta et al. 2014).

Halophytes, or salt-tolerant species, grow in saline soil or water and absorb salt in their tissues

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M.A. Khan et al. (eds.), *Sabkha Ecosystems Volume V: The Americas*,
Tasks for Vegetation Science 48, DOI 10.1007/978-3-319-27093-7_14

(Ungar 1991; Manousaki and Kalogerakis 2011). Due to this characteristic, their use in salt phytoremediation is now widely accepted (Ungar 1991; Manousaki and Kalogerakis 2011). Phytoremediation is a viable alternative in reclaiming salinized soils and researchers around the world have been proposing halophyte agriculture both as a way to make effective use of salinized soils, and as a way of reclaiming them (Khan et al. 2014; Panta et al. 2014). Some researchers have also been experimenting with salt contaminated water treatment by phytoremediation (Morteau et al. 2009, 2014; Freedman et al. 2014; Rozema et al. 2014).

Commonly used methods in the treatment of saltcontaminated water (membrane processes and thermal methods) consume a considerable amount of energy. They generally cost less than \$1 per m^3, but can cost as much as \$19 per m^3, depending on the level of salt concentration and the energy source employed (Karagiannis and Soldatos 2008). Phytoremediation has been proposed as a cost effective treatment (Manousaki and Kalogerakis 2011). It requires low maintenance and represents a possible source of income from cash crop species (Khan et al. 2014).

Historically, treatment of salt contaminated water was limited to the treatment of drinking water. Cost has been the main obstacle in treating other type of effluents. Since the 1990s, soil salinization issues in California (Schoups et al. 2005) have led to the development of technologies based on drainage management (San Joaquin Valley Drainage Program 1990), the Integrated on-Farm Drainage Management system (IFDM) and haloagriculture irrigated with brine (Jordan et al. 2009). IFDM is based on the reuse of drainage water from salt-sensitive crops for irrigating halophyte crops, and on reducing the volume of water until complete evaporation (Díaz et al. 2013). More recently, the halophyte biofilter has been developed to treat saline aquaculture effluents (Brown et al. 1999; Lymbery et al. 2006, 2013; Sindilariu et al. 2007; Webb et al. 2012; Buhmann and Papenbrock 2013).

A number of industrial sectors have been conducting research on their effluents to develop both efficient and cost effective salt removal treatments: the greenhouse, nursery, and floriculture sector (Rozema 2014), the storm water management sector (Morteau et al. 2009, 2014), the soda ash production industry (Mirck and Volk 2012), the oil sands industry (Alberta Environment 2008; Trites and Bayley 2009), and others (Freedman et al. 2014). This paper looks at salt phytotreatment by constructed wetland (CW) in these industries.

The author focuses on the plant species used in the Americas. In the first part of this paper, phytotreatment of salt contaminated water is briefly described. Then two approaches (phytoextraction and brine volume reduction) for treating salt contaminated water are presented. Issues concerning the ability of plants to efficiently absorb salt and the importance of the evapotranspiration process in phytoremediation of salt contaminated water are discussed. In the second part of this paper, recommendations to improve the treatment of salt contaminated water by CW are presented.

2 Salt-Contaminated Water Phytoremediation

High-salt effluent is produced by a number of industries. Due to their impact on the environment, effluents have to be treated to minimize the level of salt released into the environment, or in such a manner so that the effluent can be reused (Morteau et al. 2009, 2014; Shelef et al. 2012; Freedman et al. 2014; Rozema et al. 2014). The proposed treatments, currently being studied, have been performed under different meteorological conditions and with different species. Climates have been arid (Freedman et al. 2014) and continental. Treatments have been performed outdoors and in greenhouses. The treatment systems therefore differ from one case to the next. However, regardless of the variation in these factors, the treatments are designed to deal with the same issues and are performed by subsurface CW (Morteau et al. 2009, 2014; Shelef et al. 2012; Freedman et al. 2014; Rozema et al. 2014).

IFDM and the halophyte biofilter were the first treatment systems developed for salt contaminated water. Although the purpose of the latter is to treat nutrients, as opposed to salt, the halophyte biofilter also manages the salt content, and like the IFDM are interesting in this capacity. Both treatment systems can be considered as efficient in dealing with salt. The IFDM is based on evapotranspiration: it increases the salt concentration of drainage water irrigating a series of species with increasing salt tolerances. However, studies conducted on salted effluents in constructed wetlands are solely focused on phytoextraction by plants. These studies examine treatment efficiency of one plant at a time and they usually report salt accumulation issues in soil (Lymbery et al. 2006; Shelef et al. 2012).

CW treat a broad range of contaminants, including organic material, suspended solids, nitrogen, phosphorus, metals, halogens, sulfurs and pathogens (Kadlec and Wallace 2009). They recreate and accelerate natural processes occurring in wetlands, such as salt absorption and evapotranspiration. Treatment is achieved by chemical, physical and biological processes. Plants are usually considered to have a positive effect on treatment, certain plants more than others, and this varies depending on conditions (Kadlec and Wallace 2009; Chazarenc et al. 2010; Vymazal 2011). As a consequence, species selection is a part of the design of a constructed wetland.

Although a high number of plant species are found in nature, only a few have been studied for their potential use in salt removal (Manousaki and Kalogerakis 2011). Species selected for phytoremediation must be salt tolerant (Manousaki and Kalogerakis 2011; Padmavathiamma et al. 2014). As highlighted in Buhmann and Papenbrock (2013), salt tolerance differs among species, which makes it possible to vary the level of salt concentrations treated. Salt contaminated water is treated by phytoextraction and brine volume reduction. Their specificities orientate plant selection. Phytoextraction is the absorption of contaminants by the plants in the aboveground biomass, and the subsequent harvesting of these plants (McCutcheon and Jørgensen 2008). Brine volume reduction is the reduction of the volume of water to be treated, by plant transpiration (McCutcheon and Jørgensen 2008). Phytoextraction requires a high level of biomass and salt accumulator species (Manousaki and Kalogerakis 2011). High levels of biomass linked to high salt accumulation leads to a higher salt yield (Reeves 2006).

In brine volume reduction, high transpiration rates must guide species selection. Transpiration is the water lost by plants through their leaves (Taiz and Zeiger 2006). It is driven by the difference in the water vapor concentration between the leaves and the air, and by the diffusional resistance. These factors cannot be controlled. However transpiration varies depending on the species, on the amount of transpiring leaves (and hence plant biomass (Chazarenc et al. 2010; Freedman et al. 2014), and on the general condition of the plants (e.g. impact of pollutants as salt) (Vico et al. 2014).

Finally, the ideal species would be those for which well-known agricultural practices have been developed, and to those which are cash crops. Species with well-known agricultural practices should be prioritized, as their maximum growth will be easier to achieve (Landmeyer 2012), as well as species with the economic benefit of being cash crops, to lower the net cost of treatment (Grattan et al. 2008).

Species selection influences treatment efficiency, but the choice between phytoextraction, which extracts salt from the water, and brine volume reduction, which reduces the volume of water, significantly affects the results as well.

3 Phytoextraction

Above a certain concentration, salt is toxic for most plants. Halophytes can live and grow at concentrations that would be detrimental for most plant (Flowers and Colmer 2008). For certain halophytes, this capacity is due to salt sequestration in their tissues and more specifically in their vacuoles (Touchette et al. 2009; Shabala and Mackay 2011) and their use of salt for osmotic adjustment (Shabala and Mackay 2011). Phytoextraction processes take advantage of this property. These plants extract salt from water and are then harvested.

Table 14.1 presents species used for salt-contaminated water phytoextraction, and their chloride and sodium accumulation. All studies observed salt absorption by plants, for example, (Shelef et al. 2012), found an accumulation of sodium in plants (average of 48 mg/g dry weight (DW)) permitting a removal of 51 % of sodium in lower concentrations (51 mg Na^+/L) and 13 % in higher concentrations (3067 mg Na^+/L). Selected species absorbed and removed a quantity of the salt contained in water. However, some authors consider plant absorption too low to efficiently remove most of the salt (Mirck and Volk 2012; Morteau 2014; Rozema et al. 2014).

One of the highest treatment capacities presented in Table 14.1 was for *Salicornia bigelovii*. Plants were exposed to 2827 mg Na^+/L and 2293 mg Cl^-/L and evapotranspiration was 1599 mm during the growing season. This species removed 2304 kg/ha out of 81,800 kg/ha (2.8 %) of the salt spread during the experiment. Other species (*Salicornia europaea, Typha angustifolia* and *Atriplex patula*) grown in horizontal CW pilots, watered with a solution of 1500 mg NaCl/L for 6 weeks, removed at most, 2.2 % of the salt (Morteau 2014). Most of the chloride and sodium was accumulated by the substrate. Furthermore, (Mirck and Volk 2012) achieved a total salt removal rate between 62 and 92 %, but only 0.5 % of the salt was retained by the plants. Finally, (Shelef et al. 2012) found *Bassia indica* removed 9 % of the sodium from the 730.8 g introduced, in an experiment in a recirculating vertical flow constructed wetland (RVFCW), and 300 l of water treated per day. The amount of salt removed by phytoextraction was low (maximum of 9 %) in all the studies. This result is comparable to nutrient (nitrate, phosphorus and COD) uptake by plants (Langergraber 2005). Nutrient uptake increased the efficiency of the treatment by 6.7 %. As well, (Vymazal 2011) considered nutrient uptake by the plants to be at less than 5 % of the inflow.

Salt-contaminated water treatment by phytoremediation results in a constant influx of salt, sometimes resulting in dozens of tons of salt to be treated. As noted by (Mirck and Volk 2012; Morteau 2014; Rozema et al. 2014), phytoextraction has limitations in the amount of salt it can remove. Furthermore, its efficiency is inversely proportional to the salt concentration (Shelef et al. 2012, 11). Research to optimize salt uptake, plant growth, and species selection would improve phytoextraction. However to reach higher efficiency, phytoextraction should be combined with other technologies or processes such as conventional method including membrane process, a thermal method, or by brine volume reduction.

4 Brine Volume Reduction

Brine volume reduction is a phytoremediation process that has not yet been thoroughly tested in the treatment of salted effluents from the industries looked at on in this paper. Brine volume reduction consists of reducing the volume of water to be treated by plant evapotranspiration. Indeed, plants can increase evaporation by a factor of 6.4–8.6 (Freedman et al. 2014; Borin et al. 2011). This process tends to increase the water salinity (Freedman et al. 2014) and soil salinity (Zalesny et al. 2008), possibly leading to unsuitable growth conditions for most species. For example, (Mirck and Volk 2012) presents an evapotranspiration cover (ET cover) with willow varieties to decrease percolation and the volume of water to be treated by conventional methods. Transpiration rates of willow can be twice as high as the grass reference crops. Willow varieties (*Salix miyabeana* (SX64), *S. purpurea* (9882-34), and *S. sachalinensis* × *S. miyabeana* (9870-40)) were exposed to salt concentrations up to 8125 mg $Cl^-.L^{-1}$ and salt accumulations in soil and plants were measured. The plants absorbed Cl^- and Na^+ but most of the salt remained in the soil, increasing the salinity and possibly deteriorating growth conditions for the plants. As a result, evapotranspiration is sometimes considered as having a detrimental impact on salt phytoremediation. (Freedman et al. 2014) proposed shortening the hydraulic resistance time to minimize evapotranspiration, which increases soil salinity. This is the opposite of what the IFDM system does, as it uses salt contaminated water

Table 14.1 Sodium and chloride accumulation by species proposed in the salted water phytoremediation in the Americas

Species	Treatment system	Dry weight (tons/ha)	Salt exposition (mg/L)	Na^+ accumulation (g/kg DW)	Cl^- accumulation (g/kg DW)	Salt removed (kg/ha)	Sources
Typha latifolia	CW microcosms	11.2	180 mg Na^+/L and 276 mg Cl^-/L	8.2	24.4	364	Rozema 2014
Schoenoplectus tabernaemontani		6.7		5.9	27.2	221	
Juncus torreyi Coville.		12.8		4.4	20.1	315	
Typha angustifolia		11.3		7.3	27.9	399	
Atriplex prostrata	CW microcosms	8.8	0–1500 mg NaCl/L	Up to 21	Up to 7	156	Morteau 2014
Typha angustifolia		3.1		Up to 10	Up to 10	64	
Salicornia europaea		0.7		Up to 38	Up to 10	313	
Allenrolfea occidentalis	Outdoor lysimeter	10–24	2827 mg Na^+/L and 2293 mg Cl^-/L	125	71	4704	Díaz et al. 2013
Atriplex lentiformis		3–15		49	42	1365	
Salicornia bigelovi		8		169	119	2304	
Distichlis spicata		10–12		15.8	13.1	346.8	
Spartina gracilis		8		9	23	416	
Salicornia bigelovii	Greenhouse lysimeter	Up to 13.9	Up to 12,000 mg/LofNa$^+$andCl$^-$	158	179	4684	Grattan et al. 2008

until complete evapotranspiration. As indicated above, phytoextraction has to be coupled with another treatment process. A system based on the IFDM in a CW is an alternative for improving salt treatment. To design such a treatment, two aspects must be taken into consideration: the control of salt accumulation in the substrate, and the salt-tolerance of the plant species.

To maintain salt concentration in the substrate, a leaching fraction (LF) higher than consumptive plant needs is appropriate to flush excess salts (Brown et al. 1999). Glenn et al. (2009) presents a formula to compute the leaching fraction:

$$LF = \frac{S_i}{(S_t - S_i)}$$

where S_i is the irrigation water salinity and S_t is the salinity of the soil water. S_i should remain close to S_t to attain the maximum yield. This approach is general and more complex model are in development (Skaggs et al. 2014).

Plant physiological phenomena such as transpiration and salt accumulation vary as a function of salt concentration. Some halophytes decrease their transpiration when salinity increases (Shabala and Mackay 2011). This phenomenon was observed in *Suaeda esteroa, Salicorniabigelovii* and *Atriplexbarclayana* (Brown et al. 1999). However *Suaeda* consumed more water than the others, and *Atriplex* didn't treat a large volume at high salinity (35,000 mg NaCl). Brown et al. (1999) explains these differences by the higher salt tolerance of *Suaeda*. In the same vein, *Sarcocornia fructicosa* (Redondo-Gómez et al. 2006) was capable of maintaining its stomatal conductance up to 30,000 mg NaCl/L while *Atriplex portulacoides* had a stomatal conductance lowered to 1100 mg NaCl (Redondo-Gómez et al. 2007) Likewise a better salt uptake for salinities lower than species tolerance was observed (Shelef et al. 2012). Other authors (Ungar 1991; Rozema et al. 2014; Morteau et al. 2014) found similar results suggesting that the removal potential is higher when plants are exposed to salt concentrations lower than their salt tolerances. Therefore, the anticipated salt water and soil concentrations of the treatment system have to be taken into consideration during its design, to assure higher efficiency.

The reuse of effluent by means of phytoextraction coupled with brine volume reduction is impossible. Greenhouses, nurseries and floricultures have been attempting to reuse their effluent treated by phytotreatment. Their results have been mixed (Rozema et al. 2014). However some researchers have been developing salt-resistant flowers which could be a source of income and a way to extract salt at the same time (Carter et al. 2005; Grieve 2011).

To summarize the present situation:

1. phytoextraction can partially remove salt content and has to be coupled with other treatments;
2. brine volume reduction is one possible way to reduce the volume of water that has to be treated and;
3. design should be based on evapotranspiration modeling to determine a leaching fraction and planned species selection in relation to their salt tolerances.

5 Recommendations

5.1 CW Design

A proposed CW is presented in Fig. 14.1. The substrate would be rich in nutrient and the water level would be high to increase ET (Chazarenc et al. 2010; Beebe et al. 2014). Different basins are to be connected in series with selected species having incrementally higher salinity tolerances located nearer the end of the system.

Salt concentration estimation in each basin permits to determine a leaching fraction and to plan species selection in relation to their salt tolerances. Salt concentration varies as a function of ET and precipitation. Hence, estimating ET in a water budget is crucial in the design of CW treating salt-contaminated water (Beebe et al. 2014; Skaggs et al. 2014).

ET impacts temperature, hydraulic retention time, water budget (Papaevangelou et al. 2012; Beebe et al. 2014) and treatment efficiency

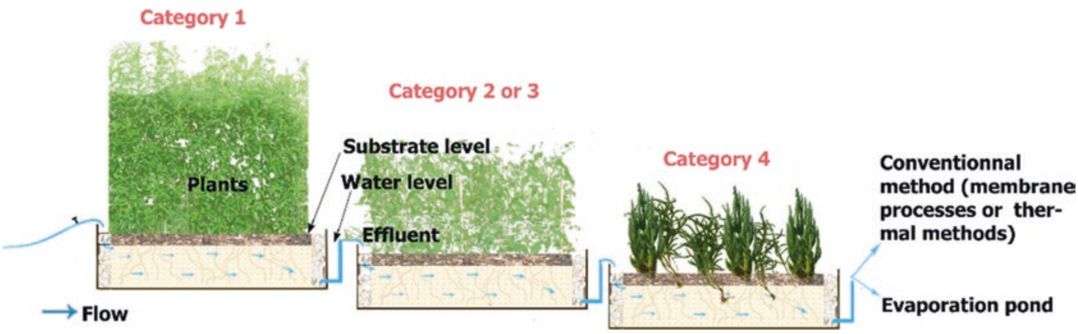

Fig. 14.1 Phytoextraction and brine volume reduction in constructed wetland in series

(Chazarenc et al. 2010; Beebe et al. 2014; Białowiec et al. 2014). It is influenced by a number of factors such as: meteorological factors (temperature, humidity, radiation, and wind speed) and CW variables (size, species soil type) (Allen et al. 1998; Chazarenc et al. 2010; Białowiec et al. 2014). For example, plant development and soil with rich nutrient content increase ET (Chazarenc et al. 2010; Białowiec et al. 2014).

A multitude of methods exist, such as the Bowen ratio energy balance and the eddy covariance (Drexler et al. 2004), but the pan evaporation equation and the Penman-Monteih equation (presented below) are used more frequently to estimate the reference evapotranspiration (ET_o) (Mohamed et al. 2012; Beebe et al. 2014; Sutherland et al. 2014).

$$ET_0 \frac{0.408\Delta\left(R_n - G\right) + \gamma \frac{900}{T+273} u_2\left(e_s - e_a\right)}{\Delta + \gamma\left(1 + 0.34u_2\right)}$$

Where

ET_o: reference ET [mm/day],
R_n: net radiation at the crop surface [MJ/m^2 day],
G: soil heat flux density [MJ/m^2 day],
T: air temperature at 2 m height [°C],
u_2: wind speed at 2 m height [m/s],
e_s: saturation vapour pressure [kPa],
e_a: actual vapour pressure [kPa],
$e_s - e_a$: saturation vapour pressure deficit [kPa],
Δ: slope vapour pressure curve [kPa/°C],
γ: psychrometric constant [kPa/°C].

The actual ET (ET_c) is then calculated using a crop coefficient (determined experimentally and adjusted to the climatic conditions) (K_c) with the following equation:

$$ET_c = K_c ET_o$$

ET is influenced by a variety of components (Papaevangelou et al. 2012) complicating its determination, and its estimation has to be calibrated to site characteristics. For example, the Penman-Monteih method has to be calibrated as a function of climate, wetland characteristic, and plant species. To reduce this uncertainty more accurate models are under development to simulate forage production under irrigation and dealing with salinity. The UNSATCHEM model is based on crop yield, average root zone salinity, water leaching fraction, and salt leaching fraction models (Skaggs et al. 2014).

5.2 Species Selection

Salt absorption and ET are higher when selected species are exposed to salt concentrations equal to or lower than their salt tolerances. A selection of some halophytes or salt-tolerant species used in agriculture irrigated with salt contaminated waters are presented in Table 14.2 (the author is focusing here on species found in the Americas). The agriculture practice, the accumulation, and in some cases the ET of the species have been estimated. However, the ET is difficult to capsulize from studies as it is climate dependent, and few studies highlights the

Table 14.2 Phytoremediation potential of salt contaminated water by halophyte and salt tolerant species

Species (varieties)	Salinity exposition	Biomass (tons DW/ha)	Na^+ concentration (g/kg DW)	Cl^- concentration (g/kg DW)	Commercial benefit	Sources	ET (mm/day)
Salinity tolerance (Category 1): 0–25 % seawater, 0–9000 mg NaCl/L							
Salix miyabeana (SX64)	Up to 8125 mg Cl^-/L	N. D.	2.6	67	Energy crop	Mirck 2012	N.D.
Salix purpurea (9882-34)		N.D.	7	62	Energy crop	Mirck 2012	N.D.
Salix (sachalinensis) × *Salix (miyabeana) (9870-40)*		N.D.	7	79	Energy crop	Mirck 2012	N.D
Polar (NC13460)	Up to 1250 mg Cl^-/L and 1200 mg Na^+/L[1]	1.3	2.5	5.5	Energy crop, paper, wood	Zalesny 2008	N.D.
Poplar (NC14018)		1.13	5.0	12.4	Energy crop, paper, wood	Zalesny 2008	N.D.
Poplar (NC14104)		3.0	1.8	12.1	Energy crop, paper, wood	Zalesny 2008	N.D.
Poplar (NC14106)		1.1	2.4	13.0	Energy crop, paper, wood	Zalesny 2008	N.D.
Poplar (DM115)		1.1	2.0	12.9	Energy crop, paper, wood	Zalesny 2008	N.D.
Poplar (DN5)		1.736	1.8	6.9	Energy crop, paper, wood	Zalesny 2008	N.D.
Poplar (NM2)		2.6	3.3	14.0	Energy crop, paper, wood	Zalesny 2008	N.D.
Poplar (NM6)		3.14	3.1	16.0	Energy crop, paper, wood	Zalesny 2008	N.D.
Atriplex lentiformis	Up to 2300 mg Cl^-/L and 2800 Na^+ mg/L	Up to 17	49.2	41.8	Forage	Jordan 2009, Diaz 2013, Glenn 2009	1.00
Schoenoplectus tabernaemontani	180 mg Na^+/L and 276 mg Cl^-/L	6.7	5.9	27.2		Rozema 2014	N.D.
Atriplex prostrata	0–1500 mg NaCl/L	8.8	Up to 21	Up to 7	Forage	Morteau 2014	N.D.
Festuca arundinacea	1000 mg Cl^-/L and 1500 mg Na^+/L		11.5		Forage	Suyama 2007, Zhang et al. 2014	N.D.

Salinity tolerance (Category 2): 25–50 % seawater, 9000–18,000 mg NaCl/L							
Medicago sativa L. (salado)	5600 mg Na^+/L and 3 800 mg Cl^-/L	14*	Between 4.2 and 11.5	Between 9 and 13.5	Forage	Grattan et al. 2004	N.D.
Lotus glaber Greene		8*	Between 11.5 and 40	Between 16 and 42.5	Forage	Grattan et al. 2004	N.D.
Medicago sativa L. (SW 9720)		16*	Between 4 and 11	Between 9.5 and 14	Forage	Grattan et al. 2004	N.D.
Pennisetum clandestinum		15*	Between 1 and 22	Between 28.5 and 42.5	Forage	Grattan et al. 2004	N.D.
Sporobolus airoides		9*	Between 4.5 and 16	Between 13 and 18.5	Forage	Grattan et al. 2004	N.D.
Paspalum vaginatum (Swartz)		7*	Between 14 and 17	Between 8 and 21	Forage	Grattan et al. 2004	N.D.
Paspalum vaginatum (PI 299042)		10*	Between 7 and 13	Between 8.5 and 13.5	Forage	Grattan et al. 2004	N.D.
Agropyron elongatum		17*	Between 10 and 20.5	Between 15 and 28.5	Forage	Grattan et al. 2004	N.D.
Distichlis spicata	Up to 2300 mg Cl^-/L and 2800 Na^+ mg/L	Up to 12	15.8	13.1	Forage	Diaz 2013, Buhman 2013	N.D.
Sporobolus virginicus	1000 mg Cl^-/L and 1500 Na^+/L	6.7	1.3	N.D.	Forage	Suyama 2007	N.D.
Leymus triticoides	1000 mg Cl^-/L and 1500 Na^+/L	N.D.	1.8	N.D.	Forage	Suyama 2007, Benes 2012	4.01
Typha latifolia	180 mg Na^+/L and 276 mg Cl^-/L	11.2	8.2	24.4		Rozema 2014	N.D.
Juncus torreyi Coville.	180 mg Na^+/L and 276 mg Cl^-/L	12.8	4.4	20.1		Rozema 2014	N.D.
Typha angustifolia	180 mg Na^+/L and 276 mg Cl^-/L	11.3	7.3	27.9		Rozema 2014	N.D.
Typha angustifolia	0–1500 mg NaCl/L	3.1	Up to 10	Up to 10		Morteau 2014	N.D.

(continued)

Table 14.2 (continued)

Species (varieties)	Salinity exposition	Biomass (tons DW/ha)	Na^+ concentration (g/kg DW)	Cl^- concentration (g/kg DW)	Commercial benefit	Sources	ET (mm/day)
Salinity tolerance (Category 3): 50–75 % seawater, 18,000–26,000 mg NaCl/L							
Spartina gracilis	Up to 2300 mg Cl^-/L and 2800 Na^+ mg/L	Up to 8	21.6	17.8	Forage	Diaz 2013, Johnson greene 1995	N.D.
Salinity tolerance (Category 4): 75–100 % seawater, 26,000–35,000 mg NaCl/L							
Allenrolfea occidentalis	Up to 2300 mg Cl^-/L and 2800 Na^+ mg/L	Up to 24	125	79	Forage	Diaz 2013	N.D.
Salicornia europaea	0–1500 mg NaCl/L	0.74	Up to 38	Up to 10	Food, forage	Morteau 2014	N.D.
Salicornia europaea	39,700 mg NaCl/L	Up to 15.4	139	180	Food, forage	Panta 2014, O'leary 1985	N.D.
Salicornia bigelovii	24,000 NaCl/L	Up to 17	158	179	Forage	Buhman 2013, Grattan, 2008	9
Salicornia bigelovii	Up to 2300 mg Cl^-/L and 2800 Na^+ mg/L	Up to 9	169	120	Forage	Diaz 2013, Buhman 2013	7.5
Spartina patens	35,000 mg NaCl/L	Up to 14				Buhman 2013, Gallagher, 1985	N.D.
Suaeda salsa	15,600 mg NaCl/L	Up to 7.7	15.5	14.3		Zhao et al. 2005	N.D.

N.B.:*multiple harvest

crop coefficient of halophytes (Suyama et al. 2007). All species presented are economically viable as cash crops.

At lower ranges of salt concentration (between 0 and 9000 mg NaCl/L) a broad selection of species is available (Table 14.2). *Typha latifolia* or *T. angustifolia*are not fully considered halophytes but could absorb high amounts of salt besides producing a high level of biomass. Buhmann and Papenbrock (2013) analyzed Cl^- and Na^+ content in leaves of *Salix* varieties exposed to salt concentrations up to 8125 mg/Land found chloride values of up to 72 g/kg, while the results for sodium were lower, a maximum of 2.6 g/kg. More than the salt accumulation by plants, transpiration capacities of willow were used to manage salt-contaminated water. Evaporation capacities of willow, *Salix* and reeds are used in the volume reduction of landfill leachate (Białowiec et al. 2014) and zero discharge wetlands. They would be of great efficacy in the first stage of treatment of brackish water.

More concentrated waters would require species with higher salt tolerance (particularly salt includers). Some of them have high yield and high salt accumulation *Salicornia bigelovii* and *europaea* had high biomass and chloride and sodium accumulation at high 35,000 mg NaCl/L or low salinity 2300 mg Cl^-/L and 2800 Na^+ mg/L (O'Leary et al. 1985; Karagiannis and Soldatos 2008; Benes et al. 2012). They appear to be the best suited species for high salt concentrations. The selection of species presented in Table 14.2 is non exhaustive. Local species that can thrive in the meteorological conditions present onsite should be chosen.

To improve salt contaminated water treatment, two propositions were presented: factoring improved evapotranspiration models into CW design, selecting species as a function of their salinity tolerance in relation to the salt concentration of the water to be treated. However models are complex and sometimes inaccurate due to site specific characteristic and change of ET due to salinity (Khan et al. 2014). In the same vein almost no information were found about crop coefficient of halophytes.

6 Conclusions

Due to scarcity of water and suitable land for agriculture, salinization is an issue for the economic and social future of the planet. Treatment have been proposed using halophytes for soil and water contaminated by salt. CW coupled with halophytes has been proposed. However, phytoextraction partially removes salt. Less than 10 % was usually removed in the studies consulted. ET has to be maximized by the selection of appropriate species as a function of the salt concentration in the effluents. This approach requires a multibasin CW in which the salted-contaminated water is concentrated by ET to the point that the volume of treated water remaining can be removed by another technology or evaporation basins.

CW designs require an estimation of ET. Appropriate species selection as a function of the salt concentration expected in the CW improves salt absorption and ET. Such models are complex and need to be adapted for that particular case.

An analysis of the cost-effectiveness and benefits of this treatment is needed to deepen our knowledge of the necessity and the possible effectiveness of salt-contaminated water phytoremediation by CW.

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Agriculture and Sheep Production on Patagonian Sabkhas with *Sarcocornia neei* Irrigated with Seawater (Chubut – Argentina)

15

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Abstract

Extensive sheep farming is one of the main economic activities in the Patagonian steppe of Argentina. In environments with saline grasslands of marshlands on the Atlantic coast, sheep rearing and agriculture, is a recent technological innovation, which might become an important alternative for production in the marginal ecosystems of America. In these arid ecosystems, the agricultural activity is limited to the area of valleys with scarce fresh water resources. In these cold temperate steppes, plains with salinized lakes and wetlands – salt flats – are the main features. Growing native halophyte *Sarcocornia neei* for human consumption and as natural halophyte grassland for sheep rearing, appeared as a possibility after preliminary studies carried out in marshlands in the southernmost tip of Patagonia, Tierra del Fuego. In Comodoro Rivadavia (Province of Chubut – Argentina), a potting test was carried out to define biological parameters of growth, phenology, and biomass production in two conditions, seawater irrigated (33, 59 g/l) and freshwater irrigated (4,3 mS/cm). The plants irrigated with seawater produced longer shoots (approx. 30 % longer) and branches (approx. 10 % longer) than the ones irrigated with fresh water without significant differences and had a significant higher number of sprouts and ramifications. There were no significant differences in the average dry biomass. Phenological differences in the treatments were not observed. At the same time, in Malaspina Cove (Province of

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M.A. Khan et al. (eds.), *Sabkha Ecosystems Volume V: The Americas*,
Tasks for Vegetation Science 48, DOI 10.1007/978-3-319-27093-7_15

Chubut – Argentina) tests were run to assess the productivity of 1 ha grassland of *S. neei* for feeding weaning lambs and slaughtering after 21 days. These were compared with control lambs fed in steppe grasslands of Argentine *Festuca* with a load of 0.3 animals/ha. Both the control sheep and the sheep fed on halophyte grasslands gained similar weight. Differences were shown on the quality of the *Sarcocornia* grassland, which bore 9–10 times more load (10 animals/ha) and in the meat analysed by the National Institute of Industrial Technology, which showed 14 % less cholesterol and 400 % less trans and saturated fats. Forage production in these salt flats was 3400 Kg/ha.

1 Introduction

Fresh water is a limited resource worldwide and therefore the increasing salinity in soils requires the development of new crops able to tolerate high concentrations of salts (Glenn et al. 1999). Several authors (Bianciotto et al. 2004, 2006; Rueda-Puente et al. 2011; Ventura et al. 2011a, b; Feng et al. 2013; Boscaiu and Vicente 2013; Salazar et al. 2014) point out that *Salicornia* and *Sarcocornia* species are promising pioneering crops for using seawater or water with high salinity since they grow naturally along the coastline (Davy et al. 2001).

The cultivation of the coastal deserts and enhancement of wetlands represents a new paradigm in agricultural production with significant advances in our day.

Coastal wetlands salinized by daily tides are home to most of the halophyte plant species adapted to salinity. Ungar (1987) estimated that there are seven million km^2 in the coastal areas of the world and 1.3 million potentially usable agricultural areas irrigated with salinized water. In Patagonia, one million km^2 of Atlantic coast shows a desertification process and 35–40 % represents Arid Ecosystems (PROSA 1996). In northeastern Brazil, salt affected soils are common with estimated areas of one million has (Costa et al. 2006).

Until recently, these areas were considered a problem for traditional production. Recent studies worldwide have defined these ecosystems as highly productive given their ecological importance for both their economic and social value. In some parts of the world they show diverse vegetation such as the Boreal type, while other regions are usually dominated by a few plants such as the West Atlantic grassland type (Adams 1990). Isacch et al. (2006) state that the south western Atlantic marshlands constitute the temperate type, with transitional characteristics between the Austral-South African marshlands and those from the western Atlantic, and they belong to the *Spartina* and *Sarcocornia* halophytes. Bortolus et al.(2009) remark that the distribution of the types of marshlands on the South American Atlantic coast clearly depends on the latitude, with an abrupt change in the Valdes Peninsula (Central Patagonia) since South of 40° latitude the landscape is dominated by *Sarcocornia*. Along the 225 km coastline of Patagonia, the presences of 27 marshes have been observed, with the provinces of Río Negro and Chubut having the greatest variety of muddy and rocky substrate. Alonso and Crespo (2008) taxonomic review of the South American taxa, identified two species: *Sarcocornia neei* (Lag.) M.A. Alonso & M.B. Crespo and *S. magellanica* (Phil.) M.A. Alonso & M.B. Crespoin Patagonia. Both species are perennial and usually with agamic reproduction, occasionally by seeds. *S. neei* saline soils is distributed in South America, in the Pacific from Peru to Chile and Argentina in the west, center and south, and the Atlantic coast to the Strait of Magallanes (Alonso and Crespo 2008).

Previous studies on the biology and productivity on *Sarcocornia* spp. in Patagonia (Bianciotto et al. 2014; Boraso et al. 2013), helped to design new trials in order to learn about the biology and productivity of *S. neei* irrigated with seawater and to determine the properties of the grasslands dominated by *Sarcocornia* sp. as fodder for cattle breeding in the marshlands of Chubut (Argentina).

2 Materials and Methods

2.1 Study Area

The study area includes the marshland of Malaspina Cove in the province of Chubut (Fig. 15.1), located 180 km north of Comodoro Rivadavia and 250 Km south of Trelew.

2.2 The Species *Sarcocornia neei*

Erect to decumbent small shrub. Stem robust, strongly, woody, up to 80 (–150) cm high, not creeping nor rooting at nodes (occasionally with a few adventitious, weak roots at base of branches in contact with substrate). Leaf apex rounded. Inflorescence many-flowered, medium sized (up to 60×4mm) (Alonso and Crespo 2008).

2.3 Climate

Climate data of 2014 year, was obtained from the National weather forecast service of Comodoro Rivadavia and Bahía Bustamante (http://www.accuweather.com/es/ar/bahia-bustamante/323/weather-forecast/323).

The annual average temperature is 12.8 ° C. The coldest months are June, July and August with the lowest minimum average temperature of 7.05 ° C, while the warmest months are January, February and December with the highest average temperature of 18.7 °C.

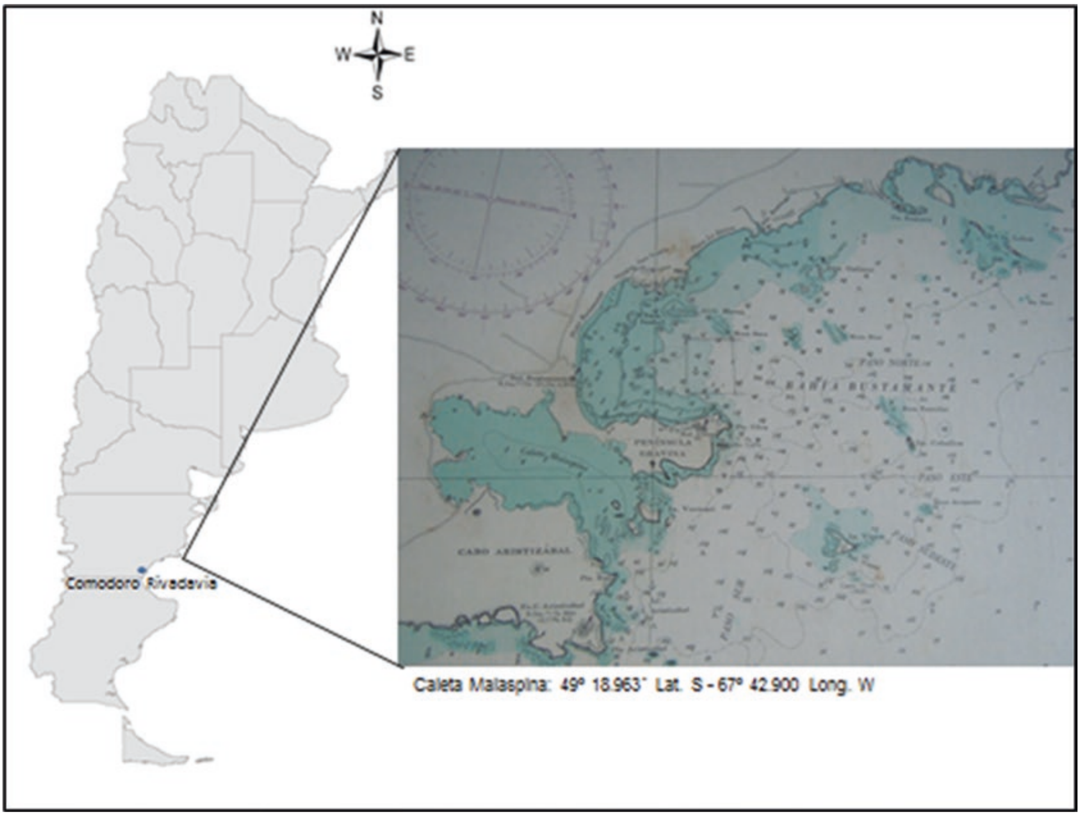

Fig. 15.1 Study area: Malaspina Cove and Comodoro Rivadavia (Chubut province-Argentina)

Rains fall in autumn and winter with an annual average of 237.43 mm. The rainiest months are March, May, June, July, and August, and in some years, September and November. The annual average wind speed was 21.71 km/h. The strong winds are more intense (100–150 km/h) in spring and autumn.

The maritime influence moderates temperatures and the location Bahía Bustamante (Malaspina Cove) ranges between 1 °C and 14 °C in winter and 12 °C to 28 °C in the summer.

2.4 Soils and Water

To characterize the physical and chemical properties of soils will be performed the following laboratory tests on soil laboratory CIEFAP-UNPSJB: textura (Bouyoucos 1927), organic matter by wet oxidation (Walkley and Black 1934), pH 1:1 and 1:5 (Bailey 1943; Peech et al. 1947) (Australian method according Piper 1944), EC (Allison et al. 1980; Blakemore et al. 1987), MO (Walkley and Black 1934); S (Anderson et al. 1992); Ca and Mg (Richter et al. 1982), Na – K (Black 1965) and CIC (Richter et al. 1982). The soils were classified as the Soil Survey Staff (1999).

Salt marsh *Sarcocornia* soil, is a loamy sand that has a 7.33 pH, 1.4 % organic matter, CE 6.64 dS/m, 0.8 % Co, S-SO_4=2 g/kg, Ca 9 meq/100 g, K 2.4 meq/100 g, Na 14.2 meq/100 g, CIC 52 meq/100 g, PSI 27 meq/100 g. Pots soil is an arid costal continental, Franco arcilloso, pH 7, 8 with carbonates and sodium, conductivity 7,7 dS/m, slightly saline

The salinity of the seawater was recorded in two points: opposite the Bahía Bustamante administration office (Ocean Atlantic Coast Bustmante Bay) and in the sector of the marshland where the tourist boat enters (Marine Chanel). The values recorded are the following (Table 15.1).

Table 15.1 Salinity of seawater

Place	mS/cm	g/l
Marine channel	45	29
Ocean Atlantic coast (Bustamante Bay)	51.6	33.1

2.5 Irrigation Water

The salinity of seawater in the port of Comodoro Rivadavia has little variation. The average value was 33, 59 g/l; pH 7, 86–8, 11, average temperature between 09 y 16 °C (Rico 2002). Freshwater had a pH de 7, 24 y electrical conductivity 4, 38 mS/cm.

2.6 Pilot Crop of *Sarcocornia neei*

The production and evaluation were carried out on the grounds of the National University of Patagonia San Juan Bosco in Comodoro Rivadavia. Cuttings with lignified sprouts approximately 10 cm long were obtained from mother plants from Malaspina Cove (Chubut). These cuttings were then potted. The potting took place in 3 litre containers with soil; using 2 irrigation treatments (n=25): (a) with sea water and (b) with fresh water. All pots were watered daily, with 300 cm^3 of water, keeping the surface always wet but avoiding flooding. Every month 10 plants of each treatment were chosen randomly to have the number and length of sprouts and branches recorded. At the end of spring, 10 plants were chosen again at random and the aboveground parts were cut leaving just a few cm for regrowth in order to determine the biomass per weight dried in a stove 60 ° C until constant weight.

2.7 Sheep Production Pilot Run in the Community of *S. neei* of Malaspina Cove (Chubut)

Together with the producer (M. Soriano), a corral of 74 × 118 m was built using a 1 m high diamond wire fence. It consisted of a patch of pure marshland of *Sarcocornia neei* subjected to tides, and other interspersed patches of *Suaeda* spp. Plants and *S. neei.* A fresh water trough was also placed inside.

In order to measure the weight gain and quality of meat of the treated animals, 10 weaning lambs of multipurpose Merino breed were introduced into the corral. They were kept for 21 days. The control animals ($n=2$) came from nearby fields with holistic pasture management of *Festuca* spp. The small number of animals does not allow statistical comparison of results. Five of these animals were slaughtered in order to obtain the *Longissimusdorsi* cut to analyze chemical quality. The weights were recorded and within 24 h and the meat was delivered in cold containers to the INTI (National Institute of Industrial Technology) for analyses of salts (K-Mg), cholesterol and essential fatty acids.

2.8 Production of *Sarcocornia neei* in Malaspina Cove Marshland

In order to determine the biomass at the starting and end of the experiment, 4 sample units of 0.25 m^2 were taken in and out of the corral. For each sample unit, lignified and green material was separated. Determination was done by dry weight (oven at 60 °C until constant weight).

2.9 Tasting

Sample meat was grilled without salt and tasted by 20 people (INTI tasting in Bianciotto et al. 2004). A survey was carried out to evaluate taste, colour, overall flavour and tenderness.

2.10 Statistical Analyse

Data was analysed ANOVA SPSS statistical package ($\alpha \leq 0{,}05$).

3 Results

This paper presents preliminary results of the project “Halophyte communities of *Sarcocornia* sp.: fodder production and human consumption”. The community of the Malaspina Cove marshland consists of a dominant *Sarcocornia neei,* covering 90 % of the meso-littoral zone with a lower presence of *Limonium brasiliense* (Boissier) Kuntze, *Atriplex* sp., *Suaeda* sp. and *Spartina densiflora* Borngniart (Fig. 15.2). There are also tall shrubs of *Suaeda divaricate* Moquin and *Frankenia patagonica* Spegazzini.

Sarcocornia neei is a robust evergreen sub shrub (Fig. 15.3b), with woody stems at the base and the apex succulent that grows up to 15–50 cm high. It presents a profusely branched underground stem system with adventitious roots and aerial stems developing from them (Fig. 15.3a). In edges of gullies or heavily eroded areas was observed large specimens. In the plains of marsh form a tapestry of succulent stems, a few centimeter tall (10 cm to 15 cm) from a network of prostrate stems covered by sediments (Fig. 15.2a). This defines a modular structure. Its veg-

Fig. 15.2 (**a**) *Sarcocornia neei- Spartina densiflora* marshland (**b**) S. *neei* flowering (Stamens with exposed anthers)

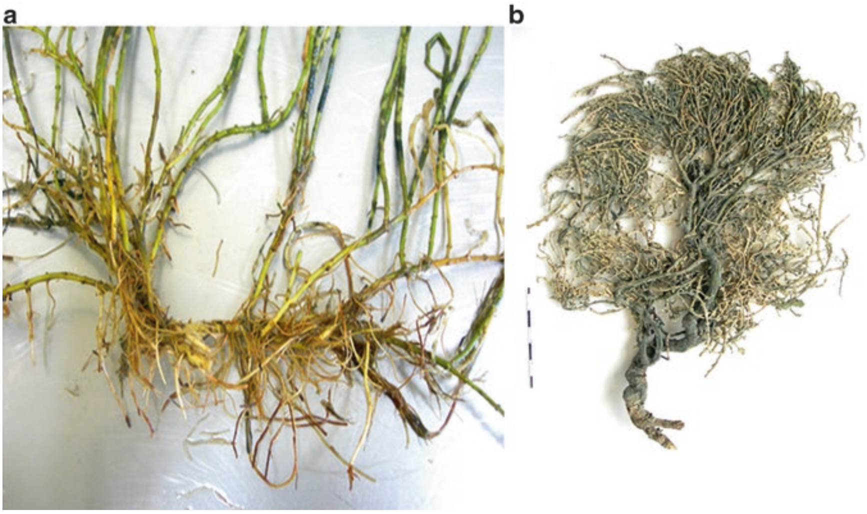

Fig. 15.3 (**a, b**) *S. neei,* (**a**) with prostrate stems and adventitious roots (**b**) shrubs

etative development is a key factor in the formation of the marshland. Growth begins during late autumn and the greatest growth of sprouts takes place in winter. Branches grow in spring and at the end of the season the flowers start to blossom. March and April are the months when fruits grow and the dissemination process begins.

3.1 *Sarcocornia neei* Crop Using Seawater

A 100 % of the plants grown from stem cuttings survived. In the three readings, the number of new shoots and branches was greater in the plants irrigated with seawater, with a positive tendency in branch growth, and negative tendency in sprout growth at the final summer, because a processing branches out breaks (Fig. 15.4a, b).

Two groups or length ranges differ because of the great variability in the measurement data recorded in the growth of shoots and branches. At the end of spring it was observed that the sprouts and ramifications irrigated with seawater grew longer, with a positive tendency in sprout and higher branch (Figs. 15.5a, b, 15.6, and 15.7).

There were no significant differences in the average dry biomass of the plants observed. A great variability between the units of 0.7–2.3 g per container (35–115 g/m^2) is observed in this preliminary sample.

3.2 Meat Production in the *S. neei* Community of Malaspina Cove (Chubut)

Weaning Merino multipurpose lambs were weighed at the beginning and end of the trial (Table 15.2). The lambs did not eat during the first three days; they only drank water. At the fifth day, they first browsed the community of *S. neei* and *Suaeda divaricata*, and finally *Sarcocornia* pure community (Fig. 15.8). No health problems were observed.

At the end of the trial it was observed that the lambs made consumed 45 % DM biomass of *S. neei* (Table 15.2). After the 21-day trial, sheep remained at their initial level weight (Table 15.2) and then were slaughtered, to take samples of *Longissimus dorsi*cuts, which were recorded for the analysis by INTI (Table 15.3).

In general, meat from lambs fed with *S. neei* showed lower values of saturated and trans fatty acids in their profiles compared to meat from lambs fed on natural pastures without *Sarcocornia*. Likewise, cholesterol was 12.8 % lower.

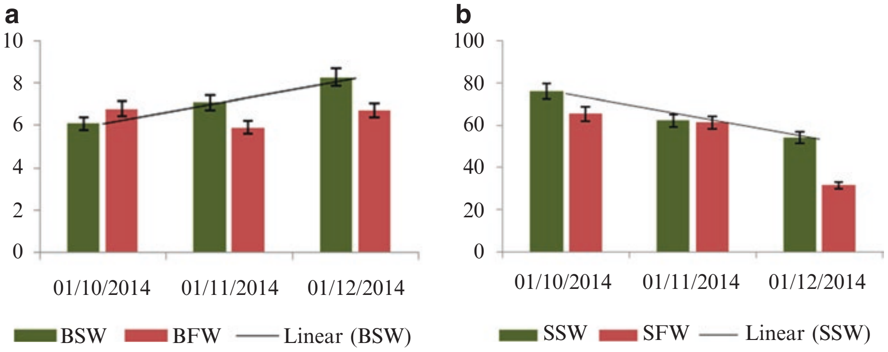

Fig. 15.4 (**a, b**) *S. neei* number of branches (**a**) and sprouts (**b**). Ref.: *BSW* brunch seawater, *BFW* brunch seawater, *SSW* sprout seawater, *SFW* sprout fresh water

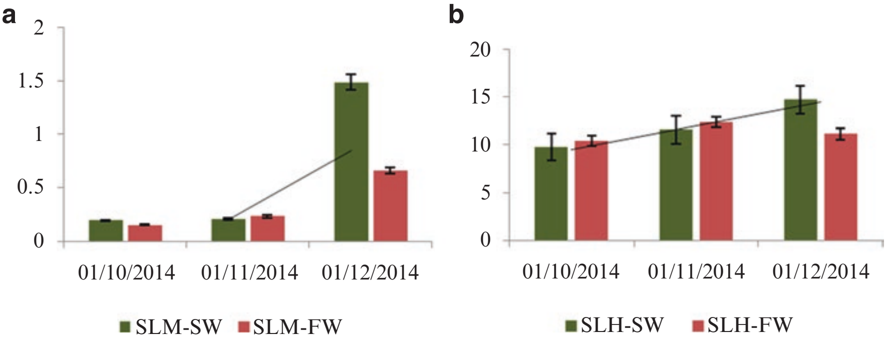

Fig. 15.5 (**a, b**) *S. neei* sprout length range (**a**) minor and (**b**) higher distribution. References: *SLM* sprouts length interval minor, *SLH* sprouts length interval higher, *SW* seawater, *FW* fresh water

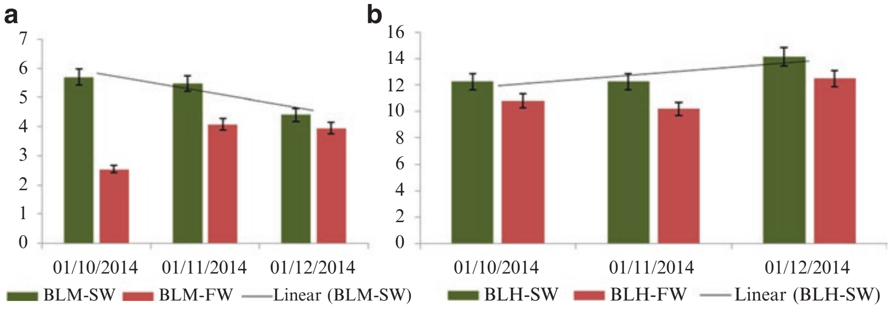

Fig. 15.6 (**a, b**) *S. neei* branches length ranges (**a**) minor and (**b**) higher (cm). References *BLM* branch length interval minor, *BLH* branch length interval higher, *SW* seawater, *FW* fresh water

Fig. 15.7 *S. neei* culture seawater (*left*) and freshwater (*right*). November 2014

Table 15.2 Live weight (Kg/lamb) of control lambs (grazing *Festuca* Pasture) and lambs fed with *S. neei.* Biomass production (DM) of *S. Neei*pasture

Biomass and lamb mean weight	Beginning trial (17/02/2014)	End trial (19/03/2014)	Observ.
Dry green biomass (g/m^2)	347.8	223.96	45 % consumed
Grazing with *S. neei* (n=4)	33,2 (starting)	32,21 (slaughtering)	Without changes (NS)[a]
Control Grazing without *S. neei* (*Festuca* pasture) (n=2)	31	31,6	Without changes (NS)

[a] Statistical difference no found

Fig. 15.8 Merino lambs grazing saline pasture

Table 15.3 Proximal Analysis of lamb meat

Determination	Unit	Grazing with /*S.neei*	Grazing without/*S. neei*
CLA (Fatty acids profile)	g/100 g	<0.1	0.1
Cholesterol	Mg/100 g	75	86
Monounsaturated fats	g/100 g	2.3	6.0
Unsaturated fats	g/100 g	2.6	6.5
Polyunsaturated fats	g/100 g	0.3	0.5
Saturated fats	g/100 g	3.5	11.0
Trans fats	g/100 g	0.1	0.4
Oleic (C18:1n C)	g/100 g	2.1	5.2
OMEGA 3	g/100 g	0.1	0.1
OMEGA 6	g/100 g	0.2	0.3
OMEGA 9	g/100 g	2.2	5.5

Table 15.4 Tasting of lamb fed with and without *Sarcocornia*

Parameters	Grazing without/*S. neei*	Grazing with/*S. neei*
Taste	Less tasty	Tastier
Colour	Light fresh	Light fresh
General flavour	Tasty	Tastier
Tenderness	Yes	Yes
Fatty aspect	Less visible fat	Visible fat

N = 20 people

3.3 Tasting of Sheep Meat

Meat without the addition of table salt was grilled and offered for tasting to people that does not know which treatment they were eating. Results of people surveyed are described in Table 15.4. In general, they found that meat from sheep that grazed in *Sarcocornia* tasted better than control sheep.

4 Discussion and Conclusions

The Malespina Cove (MC) marshland is a wetland that is flooded during exceptional tides, two or three times per month, and has loamy to clay-loamy soils with 7–8 pH, high values of S-Ca-K and Na salts. MC is a high salinity fertile ecosystem suitable for growing halophytes. *Sarcocornia* community develops into folders with a profusely branched subsurface stems system and adventitious roots.

Given its biomass production in terms of dry matter (DM), between 2200 and 3500 kg/ha, it becomes a highly productive natural grassland that can receive a load of 4–10 animals/ha, over 30–100-day periods without affecting productivity. It is also suitable for animals requiring high energetic values such as milking sheep or weaning lambs in the transition from fattening to slaughtering (Matías Soriano pers.com.)

In the cases studied, the lambs in the corral consumed approximately 1200 kg/ha of DM during the 21 day study, i.e. 40–45 % of the initial biomass.

These results match those found by Bianciotto et al. (2014), which showed that for a load of 6–7 animals/ha during 24 days, weight gained was 15 kg/ animal. Quality of meat shows low levels of cholesterol (12–14 % lower in animals fed with *Sarcocornia*).

Sarcocornia neei grown in pots, showed that seawater improves the number and length of shoots and branches. No difference was found in the production of DM biomass between treatments, given their early age condition in the first year. Similar results were found to Costa et al. (2006). The variability of the data suggests the need for continuity testing. It would require validation of the studied biological parameters and the incorporation of new biological indicators of productivity.

These preliminary results have turned the marshlands of the province of Chubut into a valuable resource for producing meat with a differential nutrient value, but not weight gain. It also gives producers new production alternatives on fields with a presence of salt flats.

Acknowledgments This work was supported by University National de la Patagonia S.J.B. and Lic. Hector Zaixso (Director of the Institute of Coastal Development). Thanks to Lic. Adolfo Genini (Rector – mandate fulfilled-of the National University of Patagonia S.J.B.), Matías Soriano (owner) and the field staff of Soriano S.A. Farm.

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16

Germination and Growth of *Panicum virgatum* Cultivars in a NaCl Gradient

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and Amy N. Morris

Abstract

Increased levels of soil salinity are common in the plains of North America, frequently the result of agricultural practices. The use of *Panicum virgatum* (Switchgrass) is common in grassland restorationas well as a biofuel crop, both of which are typically performed on former agricultural lands. Knowledge of germination and growth are thus critical for successful establishment of switchgrass especially in saline soils, still fundamental knowledge is lacking. In this study we used a NaCl gradient to determine the effects of increasing salinity on germination and growth of four cultivars of switchgrass (Trailblazer, Cave-in-Rock, Blackwell, and Kanlow). Two-way analysis of variance indicated a significant ($p<0.05$) interaction of cultivar type and salinity, where germination rates decreased with increasing salinity for all cultivars. Germination rate was highest for Trailblazer with a maximum of 93 % at 0.0 M while Blackwell had the lowest of 0 % at 0.15 M. Growth measured as shoot height was also significant for the interaction of cultivar x salinity, and a similar pattern of decreasing height with increasing salinity was seen. In general shoot length of Blackwell and Trailblazer was higher and had no negative effects of salinity on height up to 0.05 M NaCl concentration. Taken together, this work identifies switchgrass cultivars that are well suited for establishment and growth in saline lands, while also indicating that germination rate alone is not always good predictor of survival and growth.

1 Introduction

Agricultural systems are critical for contemporary society, however as lands become too degraded for adequate production other uses must be considered and restoration becomes a logical and sometimes necessary choice.

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M.A. Khan et al. (eds.), *Sabkha Ecosystems Volume V: The Americas*,
Tasks for Vegetation Science 48, DOI 10.1007/978-3-319-27093-7_16

Although lands are taken out of agricultural production, other economic avenues may be just as viable especially with government incentives for restored lands and potential for growth of biofuel crops. In addition to potential economic benefits, many ecosystem processes are enhanced when ceasing agricultural production and returning to native perennial grasses (Baer et al. 2012). These include rebuilding of soil organic matter (SOM) lost during cultivation (Anderson and Coleman 1985), rebuilding of soil structure and reduced soil losses due to erosion (Euliss et al. 2008), and providing habitat for wildlife (Hipple and Duffy 2002; Samson et al. 2008).

Coincidental with the rise in agricultural expansion is the increase of fossil fuel combustion, adding a tremendous amount of CO_2 into the atmosphere. One strategy being pursued on a large scale to help offset emissions is biofuel production (Adler et al. 2007). According to Dornburg and colleagues (2004) bio-based polymers saved the most energy per hectare compared to those of non-natural polymers for fossil fuel emissions. Ethanol is the main product of current production methods primarily from such crops as corn, where about 25 % of the total crop acreage is currently used in biofuel production (Mumm et al. 2014). Future technologies promise a cellulose based process yielding methanol (Pimentel et al. 2002; Frigon et al. 2008; Blanco-Canqui 2010) and increased potential for other raw plant material sources. In this process, any material high in cellulose (a structural component of plants) could be used to great effect. In addition to replacing fossil fuels, biofuel production reduced emissions in other ways. Namely the fossil fuels that were used to perform traditional growing techniques such as annual tilling, planting, and watering would be greatly reduced in a perennial system (Samson 2007). Even on a large-scale production of bio-fuels from agricultural lands, petroleum based fuel production is reduced (Nabity et al. 2011). Aside from reduction of emissions there is also evidence of other benefits including the economic enhancement of rural communities (Schmer et al. 2008).

In many respects switchgrass is an ideal candidate for both restoration purposes as well as biofuel usage. Switchgrass is a tall, warm season (C_4) perennial grass native to most of the North American prairie; spanning a range from Northern Mexico through the United States and into Southern Canada going east from the Rocky Mountains (Wolf and Fiske 1995; Samson 2007; Murphy 2008; Blanco-Canqui 2010; NRCS 2011; Schaeffer et al. 2011). It is commonly used in habitat restoration projects, filter strips, livestock feed, phytoremediation of petroleum-contaminated soils, and more recently as a biofuel crop (Rankins et al. 2001). As a perennial grass, switchgrass has an extensive root system (Samson 2007; Euliss et al. 2008) that reaches to 1.5 m deep, greatly improving the soil and surrounding environment by reducing water and wind erosion and facilitating a healthy belowground environment (Blanco-Canqui 2010). The perennial growth and extensive root system also means that there is less need for active management on an annual basis in a restoration or biofuel production context (Escamilla-Trevino et al. 2010), because the plant is more capable of seeking out water and nutrients and more tolerant to environmental and anthropogenic stressors (Wolf and Fiske 1995; Rankins et al. 2001; Grassini et al. 2009).

In addition to general species traits, individual cultivars have unique attributes and have been adapted and selected for specific applications. For the purposes of this study four unique cultivars were used. Trailblazer, developed by the University of Nebraska from another cultivar called Pathfinder, is primarily used as a fodder crop, matures later in its growth cycle, and requires less water than typical switchgrass; around 13 in of precipitation minimum (NRCS 2011). Cave-in-Rock comes from near Cave-In-Rock, Illinois and is commonly used for restoration purposes (habitat and erosion control) as well as biofuel production. It is less drought tolerant and requires a minimum precipitation around 24 in. (NRCS 2011). Blackwell was originally collected from Blackwell, Oklahoma in 1934. Its main use has been coverage, pasture, and restoration (Buffalo Brand Seed 2013) and requires a moderate level of precipitation at 18 in. (NRCS 2011). The University of Kansas developed the Kanlow cultivar in 1963. Its main uses include pasture and soil conservation (Seed Land 2013) but it is also a prime candidate along with the Alamo cultivar for biofuel production in the Unites States, but has high water requirements, around 30 in. annually (NRCS 2011). The large amount of aboveground biomass for some cultivars has given rise to interest in using switchgrass as a biofuel crop, while the general species characteristics are favorable for a broad range of restoration efforts.

Contemporary biofuel production is centered on corn based ethanol, though as Samson (2007) makes clear, the use of switchgrass in biofuel production can produce a net gain of 73 % higher than corn based systems. Additionally, there is now scientific evidence that suggests that a switchgrass based ethanol facility, if managed properly, has the potential to reduce greenhouse gas emissions from biofuel production by 90 % (Samson 2007; Samson et al. 2008). Should cellulose based methanol production become a reality the benefits of switchgrass and even food crop residue will greatly increase the efficiency of biofuel production; however this technology is not currently available for large scale production. Taken together it is easy to imagine a switchgrass based restoration effort coinciding with biofuel production.

While the benefits of restoration and conversion of plant materials into biofuel have received substantial attention, the establishment of vegetation in saline areas has received less consideration. However, agricultural practices, namely irrigation, common in the Midwest tend to concentrate salts in soils (Metternicht and Zinck 2009; Poss et al. 2010). In the Unites States alone some 16 million ha of soils are salt-affected (Beek et al. 1980) and on a global basis some 20 % of the worlds land is salt affected (Ghassemi et al. 1995). Coincidentally, lands with increased levels of soil salinity are often prime candidates for both restoration as well as conversion to biofuel crop production. Therefore, an understanding of how *P. virgatum,* a good candidate for both applications, responds in terms of germination and initial establishment is key for successful land reclamation, conversion, and biofuel production.

This study builds upon prior research by Carson and Morris (2012, data re-presented here) that looked at germination of *P.virgatum* cultivars and investigates the possibilities of establishing switchgrass in soils with increased salinity using growth as a proxy. Other research has supported decreased germination rates with increasing salinity for an annual salt adapted species (*Atriplexpatula*,Ungar 1996) but studies looking at subsequent establishment rates are less common. Our research has looked to address this fundamental gap by first identifying cultivars with high germination rates with increased salinity and then seeing if differences in growth persist beyond germination. We hypothesize that (1) as salinity increases response variables: biomass, root and shoot length will decrease, and (2) that cultivars known to have higher germination rates (i.e. Trailblazer and Cave-in-Rock) will have higher biomass and root/shoot length with increased salinity than cultivars with lower germination rates.

2 Methods

Four cultivars of *Panicum virgatum* (Trailblazer, Cave-in-Rock, Blackwell, and Kanlow; Stock Seed Farms, Murdock, Nebraska) were tested for their growth (root/shoot length and biomass) in a NaCl gradient. For the first two trials, four concentrations (0.0, 0.05, 0.1, and 0.15 M NaCl) were made using Sigma reagent grade (>99.5 %) sodium chloride (Gulzar et al. 2007). These concentrations were based on past experiments that utilized salt salinity testing for germination of three of the same cultivars (Carson and Morris 2012) originally defined to fit within constraints of other literature. Trays were washed, air dried, and filled with Perlite (SUN GRO Horticulture). Five seeds were then placed on top of the Perlite in each well and were watered with their corresponding solution. Trays were placed in a greenhouse at 25 °C and incubated for 3 weeks. Each combination of cultivar and salinity was replicated 24 times and the average of all germinated seeds was calculated for each well. Aboveground (shoot) height (cm) was measured weekly, and at the conclusion of 3 weeks switchgrass was removed and allowed to air dry for 1 week. Each sample was measured for both root and shoot length and total biomass. The third trial followed the same methods but used a finer NaCl gradient that included 0, 0.0125, 0.025, and 0.05 M concentrations. Data was tested for normality, analyzed, and plots made using R version 3.1.2 (R 2014). A two-way analysis of variance (ANOVA) using type 3 sum of squares for unbalanced data was used (car package) to determine the relationship between each cultivars and salinity on above ground height. When significant ($p \leq 0.05$) differences were detected, Tukey's HSD was used to find differences. Mean values for root length, biomass and percent germination were calculated, however records of well location were lost for these data and more rigorous statistical analyses could not be done without pseudo replication issues; these overall mean values should be interpreted accordingly and while close to the true replicated means do not represent the actual mean values. See Carson and Morris (2012) for methods specific to collection of those data on seed germination alone.

3 Results

Germination rates from Carson and Morris (2012) showed similar patterns for all three trials run (Fig. 16.1) where percent germination decreased for each cultivar with increasing salinity and cultivar differences were observed among different salinity treatments. In all three trials the interaction of salinity and cultivar was highly significant ($p < 0.001$). In general, the Trailblazer cultivar had a significantly ($p \leq 0.05$) higher germination rate especially when NaCl concentrations were higher than 0.05 M, with a maximum value in trial 2 of 93.3 % at 0.0 M concentration (Fig. 16.1b). Trailblazer and Cave-in-Rock had similar germination rates at the 0.0 and 0.05 M concentrations for the first two trials with a difference of ca. 11 % (Fig. 16.1a, b). However, significant differences between these concentrations and cultivars did occur in trial 3, although this difference was minimal with a reduction in germination of only 27.9 % (Fig. 16.1c). Consistently significant differences between Trailblazer and Cave-in-Rock were seen at the 0.1 M concentra-

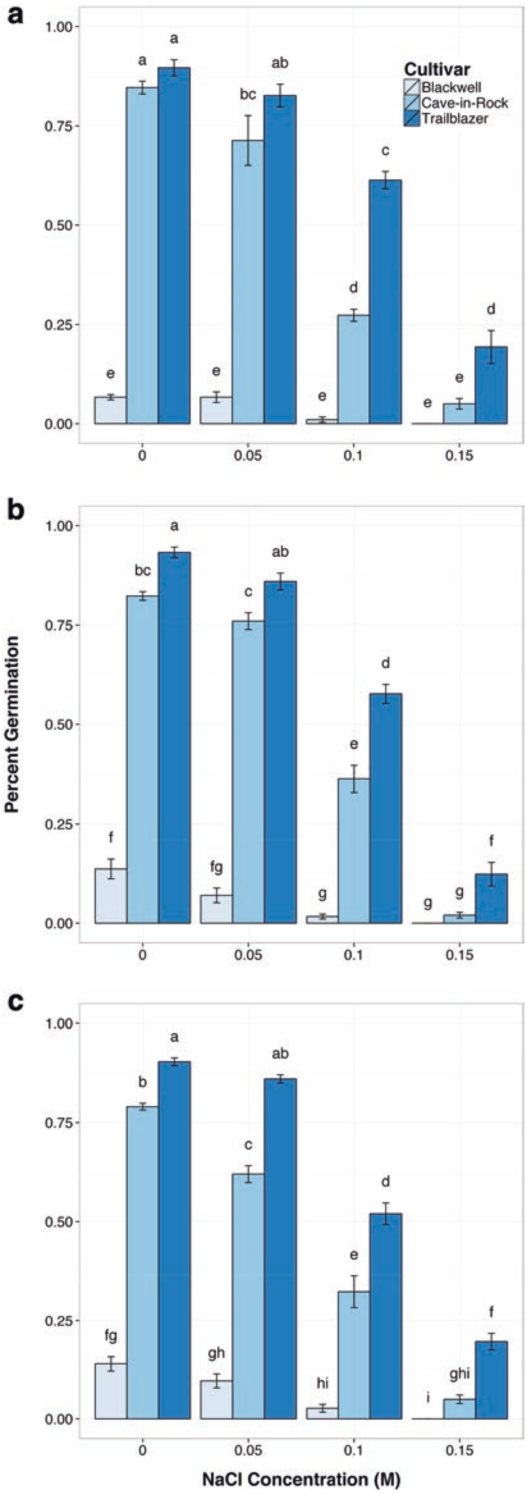

Fig. 16.1 Germination rate mean values ± se ($n = 6$) from Carson and Morris (2012) of three cultivars of *P. virgatum* in four NaCl concentrations. The experiment was repeated in three trials (A, trial 1; B, trial 2, and C, trial 3). *Letters* indicate significant interaction effects ($p \leq 0.05$) of cultivar and NaCl concentration within each trial

tion for all three trials, with a decrease in Cave-in-Rock's germination rate ranging from 55.4 to 37 % below that of Trailblazer in trials 1 and 2 respectively (trial 3 was 37.8 %). Blackwell performed poorly overall with a maximum germination rate of 14 % in trial 3, 0.0 M (Fig. 16.1c) and a minimum of 0 % in all three trials at the 0.15 M treatment. Overall mean germination rates (Tables 16.1 and 16.2) were also calculated for the growth study and while direct statistical analyses could not be done, trends also showed decreased germination rate with increasing salinity. Compared to the previous study germination rates were lower for all cultivars except Blackwell, and in general less variation within each NaCl concentration was seen for all four cultivars.

The shoot height for all three trials was influenced by the interaction of cultivar type and NaCl concentration with p-values <0.001 for all trials. Comparisons within each trial (Fig. 16.2) revealed differences ($p \leq 0.05$) within and between cultivars and salinity concentration. Shoot height tended to decrease within each cultivar type as NaCl concentration increased (Fig. 16.2a, b). Conversely, a slight but significant within cultivar increase in trial 3 (Fig. 16.2c) was seen for Blackwell, Cave-in-Rock, and Trailblazer at the 0.025 M and 0.0125 M concentrations. This trend disappeared in the 0.05 M treatment with all three cultivar's shoot height becoming significantly shorter. Kanlow was unique in that it was the only cultivar to show a negative shoot height response in relation to increasing salinity across all salinity levels. Additionally, significant differences for Kanlow between neighboring salinity levels only occurred once (trial 1, 0.0 and 0.05 M). Maximum shoot height in all trials was 6.3 cm (Blackwell 0.05 M, trial 2), and minimum height was Cave-in-Rock which failed to grow at all in trial 2 at a concentration of 0.15 M. Differences between cultivar types within each salinity level tended to be minimal, however exemptions to this generality can be found (e.g. Fig. 16.2a, 0.05 M) but were typically driven by only one poorly preforming cultivar.

Data for biomass and root length could only be expressed as the overall means (Tables 16.1 and 16.2) without direct statistical tests (see methods). Still it is prudent to discuss general patterns observed in these data. In general biomass was highest below NaCl concentrations of 0.05 M for all trials. There was high variability

Table 16.1 Meanbiomass, root length and germination rate for four cultivars of *P. virgatum* in varied NaCl concentrations from first and second trials

Molarity	Cultivar	Trial 1			Trial 2		
		Biomass (mg)	Root length (cm)	Germ. rate	Biomass (mg)	Root length (cm)	Germ. rate
0.00	Blackwell	6.95	11.36	0.35	11.61	13.69	0.66
	Cave-in-Rock	6.25	10.09	0.20	6.66	11.80	0.54
	Kanlow	4.84	14.25	0.43	9.83	10.28	0.55
	Trailblazer	6.66	13.32	0.75	18.04	15.85	0.63
0.05	Blackwell	4.79	2.47	0.28	10.02	11.27	0.54
	Cave-in-Rock	4.09	2.06	0.09	5.50	2.50	0.18
	Kanlow	3.00	4.20	0.33	6.33	5.24	0.28
	Trailblazer	3.52	0.97	0.43	6.42	2.70	0.36
0.10	Blackwell	3.22	1.43	0.27	5.25	2.16	0.37
	Cave-in-Rock	2.60	0.26	0.04	3.81	1.52	0.18
	Kanlow	1.06	0.79	0.13	3.00	3.74	0.18
	Trailblazer	3.90	0.59	0.26	5.03	1.76	0.31
0.15	Blackwell	2.07	0.54	0.13	3.00	0.79	0.09
	Cave-in-Rock	2.60	0.25	0.08	0.00	0.00	0.00
	Kanlow	2.00	0.41	0.17	1.00	0.19	0.16
	Trailblazer	2.26	0.26	0.35	1.72	0.21	0.15

Table 16.2 Mean biomass, root length and germination rate for four cultivars of *P. virgatum* in varied NaCl concentrations from the third trial

		Trial 3		
Molarity	Cultivar	Biomass (mg)	Root length (cm)	Germ. rate
0.0000	Blackwell	3.31	5.51	0.24
	Cave-in-Rock	3.86	4.50	0.24
	Kanlow	3.77	8.20	0.37
	Trailblazer	5.57	6.37	0.50
0.0125	Blackwell	5.16	9.72	0.31
	Cave-in-Rock	5.67	8.06	0.43
	Kanlow	2.74	4.61	0.23
	Trailblazer	5.76	4.79	0.42
0.0250	Blackwell	6.00	8.20	0.24
	Cave-in-Rock	3.85	3.51	0.22
	Kanlow	2.60	2.58	0.21
	Trailblazer	5.61	4.30	0.32
0.0500	Blackwell	2.00	2.87	0.03
	Cave-in-Rock	2.00	2.36	0.04
	Kanlow	2.00	1.10	0.03
	Trailblazer	4.00	2.37	0.10

between cultivar types, but Blackwell and Trailblazer often had the highest biomass regardless of salinity concentration or trial. Root length was increased slightly with low salinity (0.0125 M, Table 16.2) for Blackwell and Cave-in-Rock. In general root length was dramatically reduced with increased salinity, with one exception in trial 2 where Blackwell maintained a high mean root length at 0.05 M (Table 16.1), however values from this same concentration in trial 1 (Table 16.1) and trial 3 (Table 16.2) suggest a lower true value. No consistent root length differences were seen between cultivars when comparing within a salinity concentration regardless of trial. Although care must be taken when interpreting these data, patterns of reduced biomass and root length with increasing salinity are likely real and significant effects, while comparisons between cultivars within concentrations are likely too close to confidently conclude differences.

4 Discussion

During the settlement of the Midwest, large portions of prairie were replaced with cool season grasses and agricultural crops (Wolf and Fiske 1995). For example, land use conversion to cropland or industrialization has left North America with less than 4 % of its original 66 million hectares of tallgrass prairie (Samson and Knopf 1994; DeLuca and Zabinski 2011). This pattern is not unique to North American grasslands (Ellis and Ramankutty 2008) and widespread grassland ecosystem conversion to agricultural lands is common on a global scale (Samson and Knopf 1994). The resulting impacts range from increased erosion from wind and water, to decreased stores of soil carbon (Kern 1994; Conant et al. 2001) and increased soil salinity. In particular, the effects of salinity on germination have received increased attention in recent years, as soil salinization is a common problem globally and remediation efforts are dependent on successful establishment of vegetation.

The practicality of using switchgrass in restoration of saline lands was realized early and pioneering work in 1962 by Sautter found that as salinity increased germination rates decreased (Sautter 1962). Since that time a number of additional cultivars have been developed and so far the consensus is that germination rates of *P. virgatum* cultivars express a negative relationship with increasing salinity (Kim et al. 2012; Schmer et al. 2012; Liu et al. 2014a). This supports our findings from Carson and Morris (2012) and the germination data from this study. However it has been noted that while a negative relationship exits, germination rates can vary widely between cultivars (Carson and Morris 2012; Schmer et al. 2012; Liu et al. 2014a). This may be due to methodological, cultivar specific difference. For example this study found higher rates of germination for the Blackwell cultivar (ca. 32 % at 0.10 M) compared to past work which used cold wet stratification and had a germination rate below 2 %(Carson and Morris 2012, Fig. 16.1). Indeed Blackwell has been show elsewhere to have high germination rates

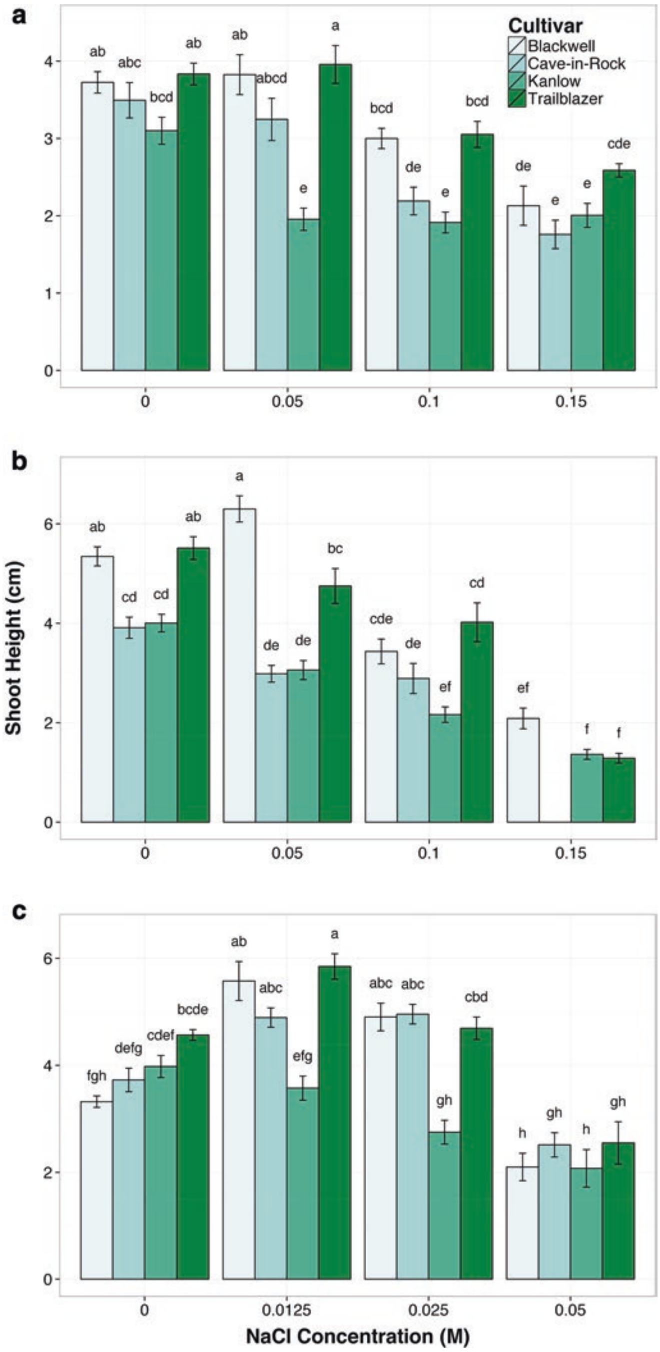

Fig. 16.2 Mean values of height ± se of four cultivars of *P. virgatum* in four NaCl concentrations. The experiment was repeated in three trials (A, trial 1; B, trial 2, and C, trial 3). Letters indicate significant interaction effects ($p \leq 0.05$) of cultivar and NaCl concentration within each trial (Note the scale difference for NaCl concentration in trial 3; C)

comparable to those of Cave-in-Rock (Liu et al. 2014a) ca. 70 % at moderate (0.01–0.11 M) salinity levels without stratification. Germination rates are not influenced by salinity alone and have also been shown to be negatively impacted by increasing pH (>8.3) especially when salinities are over 0.01 M where sharp declines in germination rate are seen (Liu et al. 2014a). Other potential factors such as physiological differences in seed coat are also known to exist and affect germination rates for switchgrass cultivars (Duclos et al. 2013).

There are multiple mechanisms that affect germination of seeds but in saline lands it is thought that a main controlling factor is differences in osmotic potential, where high solute concentration outside of the seed reduces water availability to the germinating seed (e.g. Kaydan and Yagmur 2008; Garg 2010; Zhang et al. 2010). This effectively means that less water is available to the seed, limiting imbibition and ultimately causing failure to germinate. Interestingly it is thought that differences in seed coats doesn't affect water uptake and that ions are relatively impermeable to switchgrass' seed coat (Duclos et al. 2013), lending merit to solute availability and osmotic stress being the main cause behind these experimental differences.

In addition to salinity affecting germination, there is also evidence that increasing salinity negatively affects plant growth (Kaydan and Yagmur 2008) and physiological processes such as reducing the activity of photosystems I and II (Mirshad et al. 2014). Our research supports these broad findings, where all four cultivars experienced negative growth reactions in response to increasing salinity. The only exception to this was at very low salinity levels in trial 3 (0.0125 and 0.025 M) where slight increases in shoot and root length, and biomass were seen. Other studies have supported our conclusions. For example, Kim et al. (2012) compared the Cave-in-Rock cultivar to prairie cordgrass and found that as NaCl concentration increased to 0.4 M height, number of tillers, and dry biomass all decreased for both grasses. While they tested a broader range of salinity, significant decreases were seen in salinity levels equivalent to this research. Despite these negative relationships, it has been found that plant shoots can adjust to increased osmotic stress, likely by concentrating ions within the plant (Pujol et al. 2001), although this may be an adaptation specific to halophytes and not the broader plant community at large. Few studies have looked explicitly at growth of numerous switchgrass cultivars, however in one of the most comprehensive study to date, Liu et al.(2014b)used 33 cultivars under salt stress to evaluate physiological responses, finding negative reactions to a salinity level of 0.25 M using a salt tolerant trait index for electrolyte leakage, chlorophyll, leaf photochemical efficiency, photosynthetic rate, stomatal conductance, and transpiration. Additionally these traits were linked to genetic diversity using sequence-related amplified polymorphism (SRAP) finding that two main clusters formed for lowland and upland populations. More to the point the lowland cultivars preformed better under salt stress than the upland cultivars, suggesting that genetic factors may lead to advantageous adaptations under salt stress (Liu et al. 2014b). Despite these findings, studies like ours that look specifically at growth between multiple cultivars of switchgrass are uncommon, but as evidenced here cultivar specific differences likely play a significant role in the growth of switchgrass cultivars in saline environments and research linking the interaction of cultivar types, physiology, and salinity are needed to parse out these differences.

When remediating any contaminated ecosystem establishment of new species is critical, both from an ecological context but also an economic one. Switchgrass is a broadly distributed species with diverse cultivars, and intended application as well as regional climate must be considered when thinking of establishing switchgrass. One easy consideration is seeding rate and time of seeding as both of these factors have been found to affect seedling density and/or dry matter yield (Foster et al. 2013). Additionally, timing is also critical for upland and lowland species, with upland cultivars doing better when planted in the fall and lowland cultivars fairing better when planted in the spring to avoid frosts. Seeding rate and timing considerations are even more important in saline environments as we and other researchers have shown that cultivar specific differences exist that may be critical to achieving successful establishment. An essential consideration is that it is neither practical nor economical to plant a cultivar in an environment where it will not be able to establish, regardless of whether or not it is the most ideal cultivar for an intended use. For example if biomass production is the intended goal, it may be more sensible to establish a cultivar with a moderate biomass yield that will be successful in establishing on degraded land over one with a high yield that would fail. Similarly, seeding rates may be adjusted to account for an expected low germination rate under specific local soil conditions especially when a specific cultivar's establishment is preferred or critical to intended goals. Finally a multi-species approach must be considered. Whether for restoration purposes or biofuel production (Gonzalez-Hernandez et al. 2009), a multi-species approach ensures a diverse ecosystem facilitating ecosystem resilience to stress as well as a more heterogeneous habitat for wildlife. Taken together there are multiple factors that must be considered when establishing switchgrass, especially in the context of remediation of saline lands with the intent for economic or ecological benefit.

While we are beginning to establish an understanding of cultivar specific differences in terms of germination rates under saline and non-saline conditions there are still many avenues of research that need addressing. Our study and a number of recent publications have begun to look at growth and survivability of switchgrass cultivars in saline environments, but further work at the plot level scale must be conducted. Most growth studies are only carried out for 3–4 weeks but these may not reflect true growth characteristics of a mature plant. It is possible and likely that mature plants could be either delayed or stunted in growth, both important factors to know. It is also suggested that future studies use as many cultivars as possible when comparing survivability and growth and in the context of saline environments focus should be directed towards lowland species (Foster et al. 2013; Liu et al. 2014b).

5 Conclusions

Switchgrass has been used in studies for more than 70 years, with prairie restoration and biofuel production studies being the dominant focus (Farm Energy 2013). The potential for switchgrass to be used in marginal soils has a high likelihood of success for the future; with other nutrients available (other than water and NaCl) the growth of these cultivars will increase drastically. We have shown that switchgrass germination and growth are both susceptible to increasing levels of salinity commonly seen across North America. In addition, the magnitude of susceptibility is affected significantly by cultivar type. As interest in both biofuel production and prairie restoration mature, a fundamental understanding of the effects of salinity on switchgrass will be critical to successful establishment and production of biomass and/or habitat. Current knowledge on germination is well established and future research should focus more on survivability through maturity to ensure that desirable traits of individual cultivars (e.g. high biomass) persist under high salt conditions and over multiple growing seasons.

Acknowledgements We would like to thank the editors of Sabkha Ecosystems Vol. V, The Americas for inviting us to contribute this work. Additionally, we thank the Hastings College Biology Department, the Hastings College Student Research Initiative, and the Hastings College Excelsior Scholarship for support. Funding also was provided through two TriBeta undergraduate student research grants and we would like to thank BIOS for permission to republish select germination data.

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Floristic Diversity of Halophytic Plants of Mexico

17

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Abstract

Along the Mexican coasts of the Pacific, the Atlantic and the Caribbean, diverse plant communities affected by seawater and breeze, support salt tolerant species here considered as halophilic. Moreover, the intercontinental semiarid and arid regions, and the Transmexican Volcanic Belt are characterized by ecosystems such as endorheic basins, with species also living in salty soils. In the Chihuahuan Desert saline and saline-gypseous soils occur, supporting gypsohalophilic plants. After many years of search in literature, herbaria and fieldwork, we can provide a floristic list of 647 species of angiosperms growing in these harsh environments. In absence of a summary on the halophyte flora of Mexico we deliver a list of angiosperms distributed in saline or saline-gypseous habitats. Those species living also in other soil types are considered as non restrictive to distinguish them from those living only in these environments (restricted). The floristic diversity include endemic species of several lineages, but specially of Poaceae, Asteraceae, Euphorbiaceae, Chenopodiaceae, Amaranthaceae, Boraginaceae, Fabaceae, Cyperaceae, Brasicaceae and Cactaceae.

1 Introduction

Because of its geographic position, geological history and large extension in North America, Mexico includes a high variety of climates and a

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M.A. Khan et al. (eds.), *Sabkha Ecosystems Volume V: The Americas*,
Tasks for Vegetation Science 48, DOI 10.1007/978-3-319-27093-7_17

complex topography. Consequently, the country shows a large number of soil types distributed in different regions. Knowledge and investigation of soil is extensive and has a long history in Mexico, beginning long before the arrival of the Spaniards. Ancient cultures such as the Aztecs and Mayan had sophisticated soil classifications and taxonomy (Tovar 1986). With the introduction of modern agriculture in the late nineteenth century a modern applied soil science began in Mexico (Krasilnikov et al. 2013). The most comprehensive research on soils in Mexico has recently been published by Krasilnikov et al. (2013), which includes compiled extensive information on soils distribution, classification and a complete history of soil research.

There are different ways of defining saline soils, but the value mostly usedworldwide was proposed by Richards (1954). Thus, saline soils have more than 4 dS m^{-1} at 25 °C electrical conductivity of the saturation soil extract. From this value the growth of non-halophytic plants is adversely affected. Chlorides and sulphates of sodium and calcium are the most common soluble salts in these soil profiles (Abrol et al. 1988). Krasilnikov et al. (2013) divided the soils of Mexico into a new, provisional system with the following 14 groups;

1. Volcanic soils.
2. Texturally differentiated soils, or soils having clay-enriched subsurface horizons.
3. Soils with a brownish poorly differentiated profile.
4. Soils with a developed humus-enriched topsoil.
5. Shallow soils derived from silicate consolidated rock.
6. Shallow soils derived from limestone.
7. Saline and alkaline soils.
8. Expanding and shrinking soils: Vertisols and similarsoils.
9. Soils with carbonate and gypsum accumulation.
10. Hydromorphic soils, both organic and mineral.
11. Strongly weathered soils.
12. Poorly developed soils in unconsolidated sediments.
13. Anthropogenic soils (Anthrosols and Technosols)
14. Less abundant and less studied soils.

However, the distinction among saline and gypsum soils in the field can cause considerable problems. Especially in the north of the country, under arid climate conditions in the Chihuahuan Desert, a complex mixture of the two soil types occurs, including saline, gypsum and saline-gypsum outcrops. Frequently, only the halophyte and gypsophyte remain to be differentiated. These soils are characterized by plant communities that contain species of diverse ecological affinities, named halophilic, gypsophilic, and gypsohalophilic, which are either endemic to one of those soils or widespread (Table 17.1).

Saline soils mainly occur in Mexico in coastal areas (due to seawater intrusion) and in inland regions of the country with arid climate. While saline soils near the littorals are small in terms of area, the arid northern parts of the country with its extensive intermontane valleys and endorheic basins contain large areas of salt affected soils. One of the greatest regions (116,000 km^2) with saline soils in the northern part of Mexico is Laguna Mayrán in the state of Coahuila (Krasilnikov et al. 2013). This enormous lagoon was a huge Pleistocene lake that dried up during the Holocene (Czaja et al. 2014a). Numerous smaller endorheic basins surrounded the Laguna Mayrán. This geographic complex of saline environments is a hotspot for halophytes and gypsophytes diversity. These saline soil profiles, remains of ancient sabkhas, contain mainly chlorides and sodium sulphates that come from Permian, Jurassic and Cretaceous powerful strata due to evaporation (Czaja et al. 2014b).

As mentioned, the coastal areas with salt affected soils in Mexico are relatively small but, nevertheless, the halophyte plant diversity is high in these regions (Table 17.1). This could be explained by the long extention of the coasts of Mexico, being the Atlantic coast the most studied part (see for example, Moreno-Casasola 1988).

Table 17.1 Plant species tolerant to salty environments

Family	Genus and species	Saline habitat	Distribution
Acanthaceae	*Avicennia germinans* (L.) L.	Salt marsh, mangroves	HNR; native, A, C, P
Aizoaceae	*Carpobrotus chilensis* (Molina) N.E. Br.	Coastal beach and dunes, salt shrub communities	HNR; introduced (?), P
Aizoaceae	*Carpobrotus edulis* (L.) N.E. Br.	Coastal beaches and dunes, salt shrub communities	HNR; introduced, P
Aizoaceae	*Drosanthemum floribundum* (Haw.) Schwantes	Coastal beaches and dunes, salt shrub communities	HNR; introduced, P
Aizoaceae	*Mesembryanthemum crystallinum* L.	Coastal beaches and dunes, salt shrub communities	HNR; introduced, P
Aizoaceae	*Mesembryanthemum nodiflorum* L.	Coastal beaches and dunes, salt shrub communities	HNR; introduced, P
Aizoaceae	*Sesuvium maritimum* (Walt.) Britt.	Coastal beaches and dunes, salt marshes, salt shrub communities	HR; native, A, P
Aizoaceae	*Sesuvium portulacastrum* (L.) L.	Coastal dunes, salt marshes, salt shrub communities, salty plains	HR; native, A, C, P, I
Aizoaceae	*Sesuvium verrucosum* Raf.	Coastal wetlands, salty-gypseous soils	H/GHNR; native, A, P, I
Aizoaceae	*Tetragonia tetragonioides* (Pall.) Kuntze	Coastal dunes, salt marshes	HNR; introduced, P
Amaranthaceae	*Alternanthera caracasana* Humb., Bonpl. & Kunth	Salt shrub communities	HNR; native, I
Amaranthaceae	*Alternanthera flava* (L.) Mears	Coastal dunes	HNR; native, A
Amaranthaceae	*Alternanthera flavescens* Kunth	Coastal beach and dunes	HNR; native, C
Amaranthaceae	*Alternanthera paronychioides* St. Hil.	Salt shrub communities	HNR; native, A, P, I
Amaranthaceae	*Amaranthus arenicola* I.M. Johnst.	Coastal dunes	HNR; native, A, C
Amaranthaceae	*Amaranthus australis* (A. Gray) J.D. Sauer	Coastal salt marshes, swamps, brackish wetland habitats,	HNR; native, A, C, P,
Amaranthaceae	*Amaranthus dubius* Mart. ex Thell.	Coastal dunes	HNR; native, C
Amaranthaceae	*Amaranthus polygonoides* L.	Coastal areas, salt shrub communities	HNR; native, C, P, I
Amaranthaceae	*Amaranthus fimbriatus* (Torr.) Benth. ex S. Watson	Coastal dunes	HNR; native, P
Amaranthaceae	*Amaranthus greggii* S. Watson	Coastal beaches and dunes, salt shrub communities	HNR; native, A, C
Amaranthaceae	*Amaranthus hybridus* L.	Coastal sand and dunes, salt shrub communities	HNR; native, C, I
Amaranthaceae	*Amaranthus lepturus* S.F. Blake	Salt shrub communities	HNR; endemic to Baja California
Amaranthaceae	*Amaranthus myrianthus* Standl.	Coastal beach and dunes	HNR; endemic to Tamaulipas
Amaranthaceae	*Amaranthus palmeri* S. Watson	Coastal dunes	HNR; native, P, I
Amaranthaceae	*Amaranthus powellii* S. Watson	Saline plains	HNR; native, I
Amaranthaceae	*Amaranthus* scariosus Benth.	Coastal dunes	HNR; native, P
Amaranthaceae	*Amaranthus scleropoides* Uline & W.L. Bray	Coastal dunes	HNR; native, A, P,
Amaranthaceae	*Amaranthus spinosus* L.	Coastal dunes	HNR; native, A, C, P, I
Amaranthaceae	*Amaranthus venulosus* S. Watson	Salt shrub communities	HNR; native, P

(continued)

Table 17.1 (continued)

Family	Genus and species	Saline habitat	Distribution
Amaranthaceae	*Amaranthus watsonii* Standl.	Coastal dunes, salt shrub communities	HNR; native, P
Amaranthaceae	*Blutaparon vermiculare* (L.) Mears	Coastal beaches and dunes, salt marshes, mangroves saline soils	HNR; native, A, C, P
Amaranthaceae	*Celosia floribunda* A. Gray	Salt shrub communities	HNR; native, P
Amaranthaceae	*Chamissoa acuminata* Mart.	Coastal dunes	HNR; native, P
Amaranthaceae	*Chamissoa altissima* (Jacq.) Kunth	Coastal dunes	HNR; native, A, C, P
Amaranthaceae	*Froelichia drummondii* Moq.	Coastal dunes	HNR; native, A
Amaranthaceae	*Froelichia interrupta* (L.) Moq.	Coastal dunes, salt shrub communities	HNR; native, P, I
Amaranthaceae	*Gomphrena palmeri* Standl.	Coastal dunes	HNR; native, P
Amaranthaceae	*Gomphrena parviceps* Standl.	Saline soils	HNR; endemic to D.F., Mexico, Jalisco, Guanajuato, Michoacán
Amaranthaceae	*Gomphrena serrata* L.	Coastal dunes	HNR; native, A, P
Amaranthaceae	*Gomphrena sonorae* Torr.	Coastal dunes	HNR; native, P
Amaranthaceae	*Guilleminea densa* (Humb. & Bonpl. ex Schult.) Moq.	Saline soils	HNR; native, I
Amaranthaceae	*Iresine angustifolia* Euphrasén	Coastal dunes, salt shrub communities	HNR; native, P
Amaranthaceae	*Iresine diffusa* Humb. & Bonpl. ex Willd.	Coastal dunes, salt shrub communities	HNR; native, A, C, P
Amaranthaceae	*Iresine heterophylla* Standl.	Coastal dunes, salt shrub communities	HNR; native, A
Amaranthaceae	*Iresine leptoclada* (Hook. f.) Henrickson & S.D. Sundb.	Saline flats	HNR; native, I
Amaranthaceae	*Tidestromia carnosa* (Steyerm.) I.M. Johnst.	Saline flats, salty-gypseous shales	H/GHNR; native, I
Amaranthaceae	*Tidestromia lanuginosa* (Nutt.) Standl.	Coastal dunes, saline soils, salt shrub communities	HNR; native, A, I
Amaranthaceae	*Tidestromia rhizomatosa* I.M. Johnst.	Saline and salty-gypseous flats	H/GHNR; endemic to Coahuila
Amaryllidaceae	*Hymenocallis littoralis* (Jacq.) Salisb.	Coastal beaches and dunes, salt marshes	HNR; native, C
Anacardiaceae	*Cyrtocarpa edulis* (Brandegee) Standl.	Coastal dunes	HNR; endemic to Baja California Sur
Anacardiaceae	*Metopium brownei* (Jacq.) Urb.	Coastal dunes	HNR; native, C
Annonaceae	*Annona glabra* L.	Coastal dunes, mangroves	HNR; native, A, C
Annonaceae	*Cascabela gaumeri* (Hemsl.) Lippold.	Coastal dunes	HNR; native, C
Apocynaceae	*Catharanthus roseus* (L.) G. Don	Coastal dunes	HNR; native, A
Apocynaceae	*Echites umbellatus* Jacq.	Coastal beaches and dunes	HNR; native, A, C
Apocynaceae	*Echites yucatanensis* Millsp. ex Standl.	Coastal dunes	HNR; native, C
Apocynaceae	*Plumeria rubra* L.	Coastal dunes	HNR; native, A, C
Apocynaceae	*Rhabdadenia biflora* (Jacq.) Müller Argoviensis	Coastal dunes, mangroves, salt marshes	HNR; native, A, C
Apocynaceae	*Tabernaemontana citrifolia* L.	Coastal dunes	HNR; native, A

(continued)

Table 17.1 (continued)

Family	Genus and species	Saline habitat	Distribution
Apocynaceae	*Thevetia ahouai* (L.) A. DC.	Coastal dunes	HNR; native, A, C
Apocynaceae	*Vallesia antillana* Woodson	Coastal dunes	HNR; native, C
Apocynaceae	*Asclepias curassavica* L.	Coastal dunes	HNR; native, C
Apocynaceae	*Asclepias mexicana* Cav.	Edges of saline lakes	HNR; endemic to Mexico
Apocynaceae	*Asclepias oenotheroides* Schltdl. & Cham.	Coastal dunes, salt marshes	HNR; native, A, C
Apocynaceae	*Asclepias* subulata Decne.	Coastal dunes	HNR; native, P
Apocynaceae	*Asclepias subverticillata* (A. Gray) Vail	Subsaline flats	HNR; native, I
Apocynaceae	*Marsdenia edulis* S. Watson	Saline plains	HNR; endemic, P
Apocynaceae	*Metastelma schlechtendalii* Decne.	Coastal dunes	HNR; native, A, C
Apocynaceae	*Metastelma yucatanense* W.D. Stevens	Coastal dunes	HNR; native, C
Asteraceae	*Ageratum maritimum* Kunth.	Coastal dunes and cliffs	HNR; native, C
Asteraceae	*Amblyopappus pusillus* Hook. & Arn.	Coastal bluffs and dunes, salt shrub communities	HNR; native, P
Asteraceae	*Ambrosia chamissonis (Less.) Greene*	Coastal dunes, salt shrub communities	HNR; native, A, P
Asteraceae	*Ambrosia dumosa* (A. Gray) W.W. Payne	Coastal dunes, brackish flats	HNR; native, C
Asteraceae	*Ambrosia hispida* Pursh.	Coastal beaches, bluffs and dunes, mangroves	HNR; native, C
Asteraceae	*Ambrosia peruviana* Willd.	Coastal dunes	HNR; native, A
Asteraceae	*Ambrosia psilostachya* DC.	Saline plains	HNR; native, I
Asteraceae	*Aphanostephus ramosissimus* DC.	Saline plains	HNR; native, I
Asteraceae	*Artemisia klotzchiana* Besser	Saline plains	HNR; endemic to N of Mexico
Asteraceae	*Bebbia juncea* (Benth.) Greene	Salt shrub communities	HNR; native, P
Asteraceae	*Berlandiera lyrata* Benth.	Saline plains	HNR; native, I
Asteraceae	*Boeberastrum anthemidifolium* (Benth.) Rydb.	Coastal bluffs and dunes	HNR; endemic to Baja California Sur
Asteraceae	*Borrichia arborescens* (L.) DC.	Coastal dunes, mangroves, salt marshes, salt shrub communities	HNR; native, A, C
Asteraceae	*Chaenactis lacera* Greene	Salt shrub communities	HNR; endemic to Baja California
Asteraceae	*Clappia suaedifolia*A. Gray	Coastal dunes, saline soils, brackish flats	HNR; native, A, I
Asteraceae	*Chromolaena sagittata* (A. Gray) R.M. King & H. Rob.	Saline flats near the beach	HNR; endemic to Sinaloa and Sonora
Asteraceae	*Coulterella capitata* Vasey & L. Rose	Coastal beaches	HNR; endemic to Baja California Sur
Asteraceae	*Encelia farinosa* A. Gray ex Torr.	Brackish plains, salt shrub communities	HNR; native, P
Asteraceae	*Encelia ventorum* Brandegee	Coastal bluffs dunes, and brackish plains	HNR; endemic to Baja California and Baja California Sur
Asteraceae	*Erigeron longipes* DC.	Saline plains	HNR; native, I

(continued)

Table 17.1 (continued)

Family	Genus and species	Saline habitat	Distribution
Asteraceae	*Erigeron procumbens* (Houst. ex Mill.) G.L. Nesom	Coastal dunes, salt marshes	HNR; native, A
Asteraceae	*Euphrosyne partheniifolia* DC.	Saline plains	HNR; endemic to DF, Mexico, Jalisco
Asteraceae	*Flaveria chlorifolia* A. Gray	Saline and salty-gypseous soils	H/GHNR; native, I
Asteraceae	*Flaveria linearis* Lag.	Coastal dunes, mangrove, salt marshes	HNR; native, C,
Asteraceae	*Flaveria oppositifolia* (DC.) Rydb.	Saline andbrackish plains	HNR, native, I
Asteraceae	*Flaveria palmeri* J.R. Johnst.	Salty-gypseous soils	GHNR; endemic to Coahuila
Asteraceae	*Flaveria trinervia* (Spreng.) C. Mohr	Coastal dunes, saline and salty-gypseous soils	H/GHNR; native, C, A, I
Asteraceae	*Flourensia cernua* DC.	Saline plains	HNR; native, I
Asteraceae	*Gaillardia comosa* A. Gray	Saline plains	HNR; endemic to Chihuahua, Coahuila, Nuevo León, San Luis Potosí, Tamaulipas, Zacatecas
Asteraceae	*Gaillardia pulchella* Foug.	Coastal beaches and dunes, saline plains	HNR; native, A
Asteraceae	*Geissolepis suaedifolia* B.L. Rob.	Salt shrub communities	HR; endemic to San Luis Potosí
Asteraceae	*Haploësthes robusta* I.M. Johnst.	Saline and salty-gypseous flats	H/GHNR; endemic to Coahuila
Asteraceae	*Haplopappus phyllocephalus* DC.	Saline plains	HNR; native, A
Asteraceae	*Helianthus niveus* (Benth.) Brandegee	Coastal beach hills and dunes	HNR; native, P
Asteraceae	*Heterotheca latifolia* Buckley	Coastal dunes, salt marsh	HNR; native, A
Asteraceae	*Hofmeisteria crassifolia* S. Watson	Cliffs near sea and rock crevices near ocean	HNR; endemic to Sonora
Asteraceae	*Hofmeisteria fasciculata* (Benth.) Walp.	Coastal beach, cliffs facing sea in reach of saline sea spray	HNR; endemic to Baja California, Baja California Sur, Sonora
Asteraceae	*Hymenoxys odorata* DC.	Salty flats	HNR; native, I
Asteraceae	*Isocoma acradenia* (Greene) Greene	Salt shrub communities, saline flats	HNR; native, P
Asteraceae	*Isocoma felgeri* G.L. Nesom	Coastal beach and dunes, saline flats	HNR; endemic to Sonora
Asteraceae	*Isocoma pluriflora* (Torr. & A. Gray) Greene	Saline soils	HNR; native, I
Asteraceae	*Isocoma menziesii* (Hook. & Arn.) G.L. Nesom	Coastal bluffs, and dunes, borders of salt marshes, edges of saline ponds	HNR; native, P
Asteraceae	*Isocoma veneta* (Kunth) Greene	Saline flats	HNR; endemic to Mexico
Asteraceae	*Iva asperifolia* Less.	Coastal dunes	HNR; native, A
Asteraceae	*Iva hayesiana* A. Gray	Coastal beaches	HNR; native, P
Asteraceae	*Jaumea carnosa* (Less.) A. Gray	Coastal dunes, salt marshes	HNR; native, P
Asteraceae	*Laennecia coulteri* (A. Gray) G.L. Nesom	Salty flats	HNR; native, I

(continued)

Table 17.1 (continued)

Family	Genus and species	Saline habitat	Distribution
Asteraceae	*Machaeranthera arenaria* (Benth.) Shinners	Coastal bluffs and dunes	HNR; endemic to Baja California
Asteraceae	*Machaeranthera coulteri* (A. Gray) B.L. Turner & D.B. Horne	Coastal saline soils	HNR; native, P
Asteraceae	*Melanthera nivea* (L.) Small	Coastal beach and dunes	HNR; native, A, C
Asteraceae	*Palafoxia lindenii* A. Gray	Coastal beach and dunes	HNR; endemic to Veracruz
Asteraceae	*Palafoxia linearis* (Cav.) Lag.	Coastal beach and dunes	HNR; native, P
Asteraceae	*Palafoxia texana* DC.	Coastal beach dunes	HNR; native, A
Asteraceae	*Parthenium confertum* A. Gray	Salty flats	HNR; native, I
Asteraceae	*Parthenium hysterophorus* L.	Salty flats	HNR; introduced, A
Asteraceae	*Parthenium incanum* Kunth	Salty flats	HNR; native, I
Asteraceae	*Pectis multiflosculosa* (DC.) Sch. Bip.	Coastal beach and dunes	HNR; native, P
Asteraceae	*Pectis prostrata* Cav.	Coastal dunes	HNR; native, P
Asteraceae	*Perityle crassifolia* var. *robusta* (Rydb.) Everly	Coastal beach and dunes	HNR; endemic to Baja California Sur, Sinaloa and Sonora
Asteraceae	*Perityle socorrosensis* Rose	Coastal beach, sea cliffs	HR; endemic to Colima
Asteraceae	*Pluchea camphorata* (L.) DC.	Coastal brackish areas, salt marsh	HNR; native, C
Asteraceae	*Pluchea carolinensis* (Jacq.) G. Don	Coastal dunes	HNR; native, C
Asteraceae	*Pluchea odorata* (L.) Cass.	Coastal dunes, salt marsh	HNR; native, C
Asteraceae	*Pluchea rosea* R.K. Godfrey	Coastal dunes	HNR; native, C
Asteraceae	*Porophyllum crassifolium* S. Watson	Coastal beach, salt shrub communities	HNR; endemic to Baja California
Asteraceae	*Pseudoclappia arenaria* Rydb.	Salty-gypseous plains	GHNR; native, I
Asteraceae	*Pseudoclappia watsonii* A.M. Powell & B.L. Turner	Salty-gypseous plains	GHNR; native, I
Asteraceae	*Psilostrophe gnaphalodes* DC.	Salty flats	HNR; native, I
Asteraceae	*Psilostrophe tagetina* (Nutt.) Greene	Salt shrub communities	HNR; native, I
Asteraceae	*Sartwellia flaveriae* A. Gray	Salty-gypseous plains	GHNR; native, I
Asteraceae	*Sartwellia humilis* I.M. Johnst.	Salt shrub communities	HNR; endemic to Coahuila, Nuevo León, San Luis Potosí, Zacatecas
Asteraceae	*Solidago sempervirens* L.	Salty and brackish marsh	HNR; native, A
Asteraceae	*Sonchus asper* (L.) Hill	Salty flats	HNR; introduced, I
Asteraceae	*Sonchus oleraceus* L.	Salty flats	HNR; introduced, I
Asteraceae	*Spilanthes urens* Jacq.	Coastal beach	HNR; native, C
Asteraceae	*Strotheria gypsophila* B.L. Turner	Salty-gypseous flats	GHNR; endemic to Nuevo León
Asteraceae	*Symphyotrichum subulatum* (Michx.) G.L. Nesom	Salt marsh, salty falts	HNR; native, A, P
Asteraceae	*Varilla texana* A. Gray	Salty soils	HNR; native, I
Asteraceae	*Viguiera dentata* (Cav.) Spreng.	Salty soils	HNR; native, I
Asteraceae	*Xanthisma spinulosum* (Pursh) D.R. Morgan & R.L. Hartm.	Salty soils	HNR; native, I

(continued)

Table 17.1 (continued)

Family	Genus and species	Saline habitat	Distribution
Asteraceae	*Xanthium strumarium* L.	Coastal dunes, salty soils	HNR; native; A
Asteraceae	*Xanthocephalum centauroides* Willd.	Salty soils	HNR; endemic to Durango, Guanajuato, D.F., Mexico
Asteraceae	*Xanthocephalum humile* (Kunth) Benth. & Hook. f.	Salty soils	HNR; endemic to D.F., Mexico, Puebla, Tlaxcala
Asteraceae	*Xylothamia diffusa* (Benth.) G.L. Nesom	Coastal dunes and scrub, salty flats	HNR; endemic to Baja California, Baja California Sur, Sonora
Asteraceae	*Xylothamia palmeri* (A. Gray) G.L. Nesom	Coastal dunes, salty flats	HNR; native, A, I
Asteraceae	*Xylothamia triantha* (S.F. Blake) G.L. Nesom	Salty flats	HNR; native, I
Bataceae	*Batis maritima* L.	Coastal dunes and scrub, salty flats, salt marsh, mangrove	HNR; native, A, C, P
Bignoniaceae	*Amphitecna latifolia* (Mill.) A.H. Gentry	Coastal beach	HNR; native, A
Boraginaceae	*Amsinckia intermedia Fisch. & C.A. Mey.*	Coastal dunes	HNR; native, P
Boraginaceae	*Bourreria sonorae S. Wats.*	Saline soils, rocks washed by the sea	HNR; endemic to Baja California, Baja California Sur
Boraginaceae	*Cordia boissieri* A. DC.	Coastal dunes	HNR; native, A
Boraginaceae	*Cordia curassavica* (Jacq.) Roem. & Schult.	Coastal beaches, mangroves	HNR; native, A, C, P
Boraginaceae	*Cordia dentata* Poir.	Coastal beaches and dunes	HNR; native, A, C, P
Boraginaceae	*Cordia dodecandra* DC.	Coastal beaches	HNR; native, C, A
Boraginaceae	*Cordia globosa* (Jacq.) Kunth	Coastal dunes	HNR; native, C, P
Boraginaceae	*Cordia parvifolia* A. DC.	Saline soils	HNR; endemic to Baja California, Sonora, Sinaloa, Coahuila, Durango, Zacatecas
Boraginaceae	*Cordia sebestena* L.	Coastal beach and dunes, mangroves	HNR; native, C
Boraginaceae	*Cordia seleriana* Fernald	Mangroves	HNR; endemic to Colima, Jalisco, Michoacán, Guerrero, Oaxaca
Boraginaceae	*Cordia stellifera*I.M. Johnst.	Coastal dunes	HNR; native, A, C
Boraginaceae	*Cryptantha albida* (Kunth) I.M. Johnst.	Saline flats	HNR; native, I
Boraginaceae	*Cryptantha grayi* (Vasey & Rose) J.F. Macbr.	Coastal dunes	HNR; native, P
Boraginaceae	*Cryptantha intermedia* (A. Gray) Greene	Coastal cliffs, dunes and slopes	HNR; native, P
Boraginaceae	*Cryptantha maritima* (Greene) Greene	Coastal cliffs and dunes, mangroves	HNR; native, P
Boraginaceae	*Ehretia tinifolia* L.	Coastal dunes, mangroves, salt shrub communities	HNR; native, A, C,

(continued)

Table 17.1 (continued)

Family	Genus and species	Saline habitat	Distribution
Boraginaceae	*Heliotropium angiospermum* Murray	Coastal beach and dunes, mangroves, salt shrub communities	HNR; native, C, A, P
Boraginaceae	*Heliotropium convolvulaceum* (Nutt.) A. Gray	Coastal beach and dunes, salt shrub communities	HNR; native, P
Boraginaceae	*Heliotropium curassavicum* L.	Coastal beach and dunes, salt marsh, mangroves, salt shrub communities	HNR; native, A, C, I, P
Boraginaceae	*Heliotropium fruticosum* L.	Coastal dunes	HNR; native, A, C, I, P,
Boraginaceae	*Heliotropium glabriusculum* (Torr.) A. Gray	Gypseous-saline areas	GHNR; native, I
Boraginaceae	*Heliotropium greggii* Torr.	Saline plains	HNR; native, I
Boraginaceae	*Heliotropium indicum* L.	Coastal dunes	HNR; native, A, C, P
Boraginaceae	*Heliotropium molle* (Torr.) I.M. Johnst.	Saline plains	HNR; native, I
Boraginaceae	*Heliotropium procumbens* Mill.	Coastal beach, saline plains	HNR; native, A, C, P
Boraginaceae	*Heliotropium racemosum* I.M. Johnst.	Coastal dunes	HNR; native, A
Boraginaceae	*Tiquilia cuspidata* (I.M. Johnst.) A.T. Richardson	Coastal beach	HNR; endemic to Baja California, Baja California Sur, Sonora
Boraginaceae	*Tiquilia mexicana* (S. Watson) A.T. Richardson	Saline-gypsum, saline soils	H/GHNR; native, I
Boraginaceae	*Tiquilia palmeri* (A. Gray) A.T. Richardson	Coastal beaches and dunes	HNR; native, P
Boraginaceae	*Tiquilia plicata* (Torr.) A.T. Richardson	Coastal dunes	HNR; native, P
Boraginaceae	*Tournefortia bicolor* Sw.	Coastal beaches and dunes, mangroves	HNR; native, A, C, P
Boraginaceae	*Tournefortia glabra* L.	Mangroves	HNR; native, A, P
Boraginaceae	*Tournefortia gnaphalodes* (L.) R. Br. ex Roem. & Schult.	Coastal beaches and dunes	HR; native, A, C
Boraginaceae	*Tournefortia hirsutissima* L.	Coastal beaches and dunes	HNR; native, A, C, P
Boraginaceae	*Tournefortia mutabilis* Vent.	Coastal beaches	HNR; native, P
Boraginaceae	*Tournefortia volubilis* L.	Coastal beaches and dunes	HNR; native, A, C, P
Brassicaceae	*Brassica rapa* L.	Saline soils	HNR; introduced, I
Brassicaceae	*Brassica tournefortii* Gouan	Edge of salty lakes	HNR; introduced, P
Brassicaceae	*Cakile edentula* (Bigelow) Hook.	Coastal beaches and dunes	HNR; native, A, C, P
Brassicaceae	*Cakile geniculata* (B.L. Rob.) Millsp.	Coastal beaches and dunes	HR; native, A
Brassicaceae	*Cakile lanceolata* (Willd.) O.E. Schulz	Coastal beaches and dunes, salt marshes, salt shrub communities	HR; native, A, C,
Brassicaceae	*Cakile maritima* Scop.	Coastal beaches and dunes, salt marshes	HR; native, A, P
Brassicaceae	*Dithyrea californica* Harv.	Coastal beaches and dunes	HNR; native, P
Brassicaceae	*Eruca vesicaria* (L.) Cav.	Saline soils, salt shrub communities	HNR; introduced, I
Brassicaceae	*Hutchinsia procumbens* (L.) Desv.	Coastal cliffs, saline flats	HNR; native, P

(continued)

Table 17.1 (continued)

Family	Genus and species	Saline habitat	Distribution
Brassicaceae	*Lepidium montanum* Nutt.	Saline plains, salty-gypseous plains	H/GHNR; native, I
Brassicaceae	*Lepidium oblongum* Small	Saline lake beds, mangroves	HNR; native, I, P
Brassicaceae	*Lepidium perfoliatum* L.	Saline plains	HNR; introduced, P
Brassicaceae	*Lepidium sordidum* A. Gray	Saline plains	HNR; native, I
Brassicaceae	*Lepidium virginicum* L.	Saline plains	HNR; native, I
Brassicaceae	*Nerisyrenia incana* Rollins	Salty-gypseous soils	GHNR; endemic to Coahuila
Brassicaceae	*Physaria rosei* (Rollins) O'Kane &Al-Shehbaz	Salty flats	HNR; endemic to D.F., Hidalgo, Puebla, Veracruz
Brassicaceae	*Physaria schaffneri* (S. Watson) O'Kane & Al-Shehbaz	Salty flats	HNR; endemic to Durango, Hidalgo, San Luis Potosí, Zacatecas
Brassicaceae	*Rorippa* pinnata (Sessé & Moc.) Rollins	Salty flats	HNR; native, I
Brassicaceae	*Sibara brandegeana* (Rose) Greene	Salty soils	HNR; endemic to Baja California
Brassicaceae	*Sisymbrium auriculatum* A. Gray	Salty flats	HNR; native, I
Brassicaceae	*Sisymbrium irio* L.	Salty soils	HNR; introduced, I
Brassicaceae	*Synthlipsis greggii* A. Gray	Salt shrub communities	HNR; native, I
Burseraceae	*Bursera microphylla* A. Gray	Coastal beaches and dunes	HNR; native, P
Cactaceae	*Acanthocereus occidentalis* Britton & Rose	Coastal dunes and rocks washed by the sea water	HNR; endemic to Sonora, Nayarit, Jalisco, Michoacan, Guerrero
Cactaceae	*Acanthocereus pentagonus* (L.) Britton & Rose	Coastal dunes and rocks washed by the sea water	HNR; native, A, C
Cactaceae	*Ariocarpus kotschoubeyanus* (Lem.) K. Schum.	Saline flats	HNR; endemic to Tamaulipas, San Luis Potos
Cactaceae	*Cochemiea poselgeri* (Hildm.) Britton & Rose	Rocky cliffs along the sea	HNR; endemic to Baja California Sur
Cactaceae	*Coryphantha macromeris* (Engelm.) Lem.	Saline plains	HNR; native, I
Cactaceae	*Cylindropuntia imbricata* (Haw.) F.M. Knuth	Saline plains	HNR; native, I
Cactaceae	*Echinocactus texensis* Hopffer	Saline plains	HNR; native, I
Cactaceae	*Echinocereus conglomeratus* C.F. Först.	Saline plains	HNR; endemic to Chihuahua, Coahuila
Cactaceae	*Echinocereus maritimus* (M.E. Jones) K. Schum.	Coastal dunes	HNR; endemic to Baja California, Baja California Sur
Cactaceae	*Echinocereus merkeri* Hildmann in Schumann	Saline plains	HNR; endemic to Zacatecas
Cactaceae	*Grusonia bradtiana* (J.M. Coult.) Britton & Rose	Saline plains	HNR; endemic to Coahuila
Cactaceae	*Mammillaria dioica* K. Brandegee	Coastal beach and dunes	HNR; native, P
Cactaceae	*Melocactus curvispinus* subsp. *dawsonii* (Bravo) N.P. Taylor	Coastal beach and dunes	HNR; endemic to Jalisco

(continued)

Table 17.1 (continued)

Family	Genus and species	Saline habitat	Distribution
Cactaceae	*Neomammillaria gaumeri* Britton & Rose	Coastal beach and dunes	HNR; endemic to Yucatán, Quintana Roo
Cactaceae	*Opuntia engelmannii* Salm-Dyck ex Engelm.	Saline plains	HNR; native, I
Cactaceae	*Opuntia kleiniae* DC.	Saline plains	HNR; native, I
Cactaceae	*Opuntia leptocaulis* DC.	Saline plains	HNR; native
Cactaceae	*Opuntia macrocentra* Engelm.	Saline plains	HNR; native, I
Cactaceae	*Opuntia stricta* (Haw.) Haw.	Coastal beach and dunes	HNR; native, A, C
Cactaceae	*Selenicereus hondurensis* (K. Schum.) Britton & Rose	Coastal dunes	HNR; native, C
Cactaceae	*Stenocereus standleyi* (J.G. Ortega) Buxb.	Coastal dunes	HNR; endemic from Sinaloa to Guerrero
Caesalpiniaceae	*Caesalpinia crista* L.	Coastal beaches and dunes	HNR; native, A
Caesalpiniaceae	*Caesalpinia vesicaria* L.	Coastal dunes	HNR; native, A, C
Caesalpiniaceae	*Chamaecrista chamaecristoides* (Collad.) Greene	Coastal dunes	HNR; native, A, C, P
Capparaceae	*Capparis cynophallophora* L.	Coastal dunes, mangroves	HNR; native, P
Capparaceae	*Capparis flexuosa* (L.) L.	Coastal beaches and dunes	HNR; native, C
Capparaceae	*Capparis odoratissima* Jacq.	Mangroves	HNR; native, P
Capparaceae	*Quadrella incana* (Kunth) Iltis & Cornejo	Coastal dunes, mangroves	HNR; native, A, C, P
Cleomaceae	*Cleomella longipes* Torr.	Saline soils	HNR; native, I
Cleomaceae	*Cleomella mexicana* DC.	Saline plains	HNR; endemic to D.F., Mexico, Puebla, Veracruz
Cleomaceae	*Cleomella perennis* Iltis	Saline plains	HR; endemic to Durango, Coahuila, San Luis Potosí, Zacatecas, Guanajuato
Cleomaceae	*Wislizenia refracta* Engelm.	Coastal dunes, mangroves	HNR; native, P
Caryophyllaceae	*Drymaria holosteoides* Benth.	Coastal beach and dunes, mangroves	HNR; endemic to Baja California Sur
Caryophyllaceae	*Drymaria viscosa* S. Watson	Coastal beach	HNR; endemic to Baja California, Baja California Sur
Caryophyllaceae	*Spergularia macrotheca* (Hornem. ex Cham. & Schltdl.) Heynh.	Saline soils	HR; native, P
Caryophyllaceae	*Spergularia marina* (L.) Griseb.	Salt marshes	HNR; native, P
Casuarinaceae	*Casuarina equisetifolia* L.	Coastal dunes	HNR; introduced, A, C
Celastraceae	*Crossopetalum gaumeri* (Loes.) Lundell.	Coastal dunes	HNR; native, C
Celastraceae	*Crossopetalum parviflorum* (Hemsl.) Lundell.	Coastal dunes	HNR; native, A, C
Celastraceae	*Crossopetalum rhacoma* Crantz.	Coastal dunes	HNR; native, C
Celastraceae	*Maytenus phyllanthoides* Benth.	Coastal beaches, mangroves, salt marshes, saline soils	HR; native, A, C, I, P
Chenopodiaceae	*Allenrolfea occidentalis* (S. Watson) Kuntze	Coastal beach and dunes, mangrove, salt marshes, salty flats	HR; native, I, P

(continued)

Table 17.1 (continued)

Family	Genus and species	Saline habitat	Distribution
Chenopodiaceae	*Aphanisma blitoides* Nutt. ex Moq.	Coastal bluffs and dunes	HR; native, P
Chenopodiaceae	*Arthrocnemum subterminale* (Parish) Standl.	Salt marshes	HR; native, P
Chenopodiaceae	*Atriplex abata* I.M. Johnst.	Salty plains	HR; endemic to Chihuahua, Coahuila, San Luis Potosí, Zacatecas
Chenopodiaceae	*Atriplex acanthocarpa* (Torr.) S. Watson	Saline and saline-gypsum plains	H/GHNR; native, I
Chenopodiaceae	*Atriplex argentea* Nutt.	Saline soils	HNR; native, I
Chenopodiaceae	*Atriplex barclayana* (Benth.) D. Dietr.	Coastal beaches and dunes, salty soils	HNR; endemic to Baja California, Sinaloa, Sonora
Chenopodiaceae	*Atriplex californica* Moq.	Coastal bluffs and dunes, salt marshes	HNR; native, P
Chenopodiaceae	*Atriplex canescens* (Pursh) Nutt.	Coastal dunes, saline flats, salty-gypsum soils	H/GHNR; native, I, P
Chenopodiaceae	*Atriplex confertifolia* (Torr. & Frém.) S. Watson	Salt desert shrub	HNR; native, I
Chenopodiaceae	*Atriplex coulteri* (Moq.) D. Dietr.	Coastal bluffs	HNR; native, P
Chenopodiaceae	*Atriplex elegans* (Moq.) D. Dietr.	Saline flats	HNR; native, I
Chenopodiaceae	*Atriplex julacea* S. Watson	Coastal dunes, salt marshes	HR; endemic to Baja California
Chenopodiaceae	*Atriplex lentiformis* (Torr.) S. Watson	Salt marshes	HR; native, P
Chenopodiaceae	*Atriplex leucophylla* (Moq.) D. Dietr.	Coastal beaches and dunes, saline flats	HR; native, P
Chenopodiaceae	*Atriplex linifolia* Humb. & Bonpl. ex Willd.	Saline flats	HR; endemic to D.F., Mexico, Durango
Chenopodiaceae	*Atriplex matamorensis* A. Nelson	Coastal dunes, salt shrub communities	HNR; native, A, I
Chenopodiaceae	*Atriplex muricata* Humb. & Bonpl. ex Willd.	Salty flats	HNR; native, I
Chenopodiaceae	*Atriplex obovata* Moq.	Salty-gypseous soils, salty flats, salt shrub communities	H/GHNR; native, I
Chenopodiaceae	*Atriplex pacifica* A. Nelson	Sea bluffs, salty soils close the coast	HNR; native, P
Chenopodiaceae	*Atriplex parishii* S. Watson	Salty soils	HNR; native, I
Chenopodiaceae	*Atriplex patula* L.	Salt marshes, saline flats	HNR; introduced, I, P
Chenopodiaceae	*Atriplex pentandra* (Jacq.) Standl.	Coastal beaches and dunes, mangrove, salt marshes, saline flats	HR; native, A, C
Chenopodiaceae	*Atriplex polycarpa* (Torr.) S. Watson	Saline soils, salt shrub communities	HNR; native, P
Chenopodiaceae	*Atriplex prosopidum* I.M. Johnst.	Edges of salty lakes, salty-gypseous plains	H/GHNR; endemic to Coahuila, Nuevo León, Zacatecas
Chenopodiaceae	*Atriplex reptans* I.M. Johnst.	Salty-gypseous plains	GHNR; endemic to Coahuila, Nuevo León, Zacatecas
Chenopodiaceae	*Atriplex semibaccata* R. Br.	Salty flats	HNR; introduced, I

(continued)

Table 17.1 (continued)

Family	Genus and species	Saline habitat	Distribution
Chenopodiaceae	*Atriplex suberecta* I. Verd.	Salty flats	HNR; introduced, I
Chenopodiaceae	*Atriplex texana* S. Watson	Saline plains	HNR; native, I
Chenopodiaceae	*Atriplex valdesii* Flores Olv.	Saline plains	HR; endemic to San Luis Potosí, Zacatecas
Chenopodiaceae	*Atriplex watsonii* A. Nelson ex Abrams	Coastal beaches, bluffs and dunes, salt marshes	HNR; native, P
Chenopodiaceae	*Bassia hyssopifolia* (Pall.) Kuntze	Coastal dunes, salt marshes	HNR; introduced, I
Chenopodiaceae	*Chenopodium album* L.	Salty flats, edges of salty lakes, salt marshes	HNR; introduced, I, P
Chenopodiaceae	*Chenopodium berlandieri* Moq.	Salty soils, salt shrub communities	HNR; native, I
Chenopodiaceae	*Chenopodium fremontii* S. Watson	Salt marshes, edges of salty lakes	HNR; native, I, P
Chenopodiaceae	*Chenopodium glaucum* L.	Brackish and saline plains	HNR; native, I
Chenopodiaceae	*Chenopodium macrospermum* Hook. f.	Brackish soils	HNR; introduced, I
Chenopodiaceae	*Chenopodium mexicanum* Moq.	Brackish soils, saline plains, borders of salty lakes	HNR; endemic to D.F., Mexico
Chenopodiaceae	*Chenopodium murale* L.	Saline plains	HNR; introduced, I
Chenopodiaceae	*Dysphania ambrosioides* (L.) Mosyakin & Clemants	Saline plains	HNR; native, I
Chenopodiaceae	*Meiomeria stellata* (S. Watson) Standl.	Saline and salty-gypseous plains	H/GHNR; endemic to Coahuila
Chenopodiaceae	*Nitrophila occidentalis* (Moq.) S. Watson	Saline soils	HNR; native, I, P
Chenopodiaceae	*Salicornia bigelovii* Torr.	Coastal beaches, salt marshes, mangroves, saline plains	HR; native, P
Chenopodiaceae	*Salicornia depressa* Standl.	Salt marshes	HR; native, P
Chenopodiaceae	*Salsola tragus* L.	Brackish and saline plains	HNR; introduced, I
Chenopodiaceae	*Salsola kali* L.	Coastal beach, saline plains, seashores, salt marshes, salt shrub communities	HNR; introduced, I, P
Chenopodiaceae	*Sarcoconia pacifica* (Standl.) A.J. Scott	Coastal dunes, mangroves, salt marshes, tidal flats	HR; native, P
Chenopodiaceae	*Sarcocornia utahensis* (Tidestr.) A.J. Scott	Salt marshes, saline flats	HR; native, I
Chenopodiaceae	*Suaeda californica* S. Watson	Coastal dunes, salt marshes	HR; native, P
Chenopodiaceae	*Suaeda edulis*Flores Olv. & Noguez	Salty flats	HR; endemic to Guanajuato, Jalisco, Michoacan, Mexico, D.F., Tlaxcala, Puebla
Chenopodiaceae	*Suaeda pulvinata* Alvarado Reyes & Flores Olv.	Edges of salty lakes	HR; endemic to D.F., Mexico, Puebla, Tlaxcala
Chenopodiaceae	*Suaeda taxifolia* (Standl.) Standl.	Coastal bluffs	HR; native, P
Chenopodiaceae	*Suaeda conferta* (Small) I.M. Johnst.	Coastal beaches and dunes, saline flats, salt shrub communities	HR; native, A
Chenopodiaceae	*Suaeda esteroa* Ferren & S.A. Whitmore	Salt marshes	HR; native, P

(continued)

Table 17.1 (continued)

Family	Genus and species	Saline habitat	Distribution
Chenopodiaceae	*Suaeda jacoensis* I.M. Johnst.	Salty-gypseous flats	GHR; endemic to Coahuila, Nuevo León
Chenopodiaceae	*Suaeda linearis* (Elliott) Moq.	Coastal beaches, salt marshes, salt shrub communities	HR; native, A
Chenopodiaceae	*Suaeda mexicana* (Standl.) Standl.	Salty-gypseous plains	GHR; endemic to Coahuila, San Luis Potosí
Chenopodiaceae	*Suaeda nigra* (Raf.) J.F. Macbr.	Coastal beaches and dunes, salt marshes, saline and salty-gypseous plains, mangroves, salt shrub communities	H/GHNR; native, I, A
Chenopodiaceae	*Suaeda palmeri* (Standl.) Standl.	Salty soils	HNR; endemic to Coahuila, Nuevo León, Zacatecas
Chenopodiaceae	*Suaeda tampicensis* (Standl.) Standl.	Salty soils	HNR; native, A
Chenopodiaceae	*Suaeda taxifolia* (Standl.) Standl.	Coastal bluffs, margins of salt marshes	HR; native, P
Chrysobalanaceae	*Chrysobalanus icaco* L.	Coastal dunes, mangroves	HNR; native, A, C, P
Convolvulaceae	*Cressa truxillensis* Kunth	Coastal dunes, salt marsh, saline plains, salt shrub communities	HNR; native, P
Convolvulaceae	*Cuscuta salina* Engelm.	Parasitic on plants growing on inland salt flats	HR; native, P
Convolvulaceae	*Cuscuta umbellata* Kunth	Parasitic on plants growing in saline soils	HNR; native, A, C, I
Convolvulaceae	*Dudleya brittonii* D.A. Johans.	Edge of salt marshes	HNR; endemic to Baja California
Convolvulaceae	*Ipomoea halierca* I.M. Johnst.	Climbing over brush along coastal beaches	HR; endemic to Colima
Convolvulaceae	*Ipomoea pes-caprae* (L.) R. Br.	Coastal beaches and dunes, salt shrub communities	HR; native, A, C, P
Convolvulaceae	*Ipomoea sagittata* Poir.	Coastal beaches and dunes	HNR; native, A, C
Convolvulaceae	*Ipomoea stolonifera* (Cirillo) J.F. Gmel.	Coastal beach and dunes	HNR; native, A, C, P
Convolvulaceae	*Ipomoea violacea* L.	Coastal beaches and dunes, mangroves	HNR; native, A, C
Convolvulaceae	*Jacquemontia havanensis* (Jacq.) Urb.	Coastal dunes	HNR; native, C
Combretaceae	*Conocarpus erectus* L.	Coastal dunes, salt marsh, mangroves, brackish plains	HNR; native, A, C, P
Combretaceae	*Laguncularia racemosa* (L.) Gaertn f.	Coastal beach and dunes, mangroves	HNR; native, A, C, P
Commelinaceae	*Commelina erecta* L.	Coastal dunes	HNR; native, A, C
Cyperaceae	*Amphiscirpus nevadensis* (S. Watson) Oteng-Yeb.	Salty flats	HNR; native, I
Cyperaceae	*Bolboschoenus maritimus* subsp. *paludosus* (A. Nelson) T. Koyama	Saline flats	HNR; native, I
Cyperaceae	*Bolboschoenus robustus* (Pursh) Soják	Salt marshes	HNR; native, A, C

(continued)

Table 17.1 (continued)

Family	Genus and species	Saline habitat	Distribution
Cyperaceae	*Carex praegracilis* W. Boott	Brackish soils	HNR; native, I
Cyperaceae	*Cladium jamaicense* Crantz	Salt marsh, mangroves	HNR; native, A, C, P
Cyperaceae	*Cyperus articulatus* L.	Coastal beach and dunes	HNR; native, A, C, P
Cyperaceae	*Cyperus compressus* L.	Coastal flats	HNR; native, C
Cyperaceae	*Cyperus planifolius* Rich.	Salt shrub communities	HNR; native, A, C, P
Cyperaceae	*Cyperus esculentus* L.	Saline flats	HNR; introduced, A, C, I, P,
Cyperaceae	*Cyperus laevigatus* L.	Saline flats	HNR; introduced, I
Cyperaceae	*Cyperus ligularis* L.	Coastal dunes, salty plains	HNR; introduced (?), A, C, P,
Cyperaceae	*Cyperus niger* Ruiz & Pav.	Saline flats	HNR; native, I
Cyperaceae	*Cyperus planifolius* Rich.	Rocks washed by the sea water, salt shrub communities	HNR; native, C
Cyperaceae	*Cyperus pycnostachyus* (Kunth) Kunth	Saline solis	HNR; native, I
Cyperaceae	*Eleocharis mutata* (L.) Roem. & Schult.	Coastal dunes, mangroves	HNR; native, A
Cyperaceae	*Fimbristylis argillicola* Kral	Saline flats	HNR; endemic to Mexico
Cyperaceae	*Fimbristylis caroliniana* (Lam.) Fernald	Coastal beach and dunes, brakish marsh, salt shrub communities	HNR; native, A, C
Cyperaceae	*Fimbristylis castanea* (Michx.) Vahl	Coastal dunes salt marshes, mangroves, salt shrub communities	HNR; native, A, C
Cyperaceae	*Fimbristylis ferruginea* (L.) Vahl	Brakish plains, places nearthe sea water	HNR; native, C
Cyperaceae	*Fimbristylis spadicea* (L.) Vahl	Coastal dunes, salt marshes, mangroves, salt shrub communities	HNR; native, A, C, P
Cyperaceae	*Fimbristylis spathacea* Roth	Coastal dunes, marshes	HNR; native, A, C, P
Cyperaceae	*Fuirena simplex* Vahl	Saline and saline-gypseous flats	H/GHNR; native, I
Cyperaceae	*Isolepis cernua* (Vahl) Roem. & Schult.	Brackish coastal marhes	HNR; native, P
Cyperaceae	*Schoenoplectus acutus* var. *occidentalis* (S. Watson) S. G. Smith	Salt marshes	HNR; native, P
Cyperaceae	*Schoenoplectus americanus* (Pers.) Volkart ex Schinz & R. Keller	Borders of brackish and saline marshes	HNR; native, P
Cyperaceae	*Schoenoplectus pungens* (Vahl) Palla	Borders of brackish and saline marshes	HNR; native, A
Cyperaceae	*Schoenoplectus tabernaemontani* (C. C. Gmel.) Palla	Salt shrub communities	HNR; native, A, C, I
Ebenacea	*Maba intricata* (A. Gray) Hiern	Coastal wet blufs along beach	HNR; endemic to Sonora
Ebenacea	*Diospyros cuneata* Standl.	Coastal dunes	HNR; native, C
Euphorbiaceae	*Acalypha arvensis* Poepp.	Coastal dunes, mangroves	HNR; native, A
Euphorbiaceae	*Acalypha californica* Benth.	Coastal bluffs and dunes	HNR; native, P
Euphorbiaceae	*Acalypha mexicana* Müll. Arg.	Brackish and saline plains	HNR; native, I

(continued)

Table 17.1 (continued)

Family	Genus and species	Saline habitat	Distribution
Euphorbiaceae	*Acalypha microphylla* Klotzsch	Coastal beach, blufs and dunes	HNR; native, P
Euphorbiaceae	*Acalypha ostryifolia* Riddell ex J.M. Coult.	Saline plains	HNR; native, I, P
Euphorbiaceae	*Acalypha phleoides* Cav.	Saline plains	HNR; native, I
Euphorbiaceae	*Acalypha radians* Torr.	Coastal dunes	HNR; native, A
Euphorbiaceae	*Acalypha umbrosa* Brandegee	Coastal bluffs, salt shrub communities	HNR; endemic to Colima
Euphorbiaceae	*Acalypha vallartae* McVaugh	Rocky cliffs near sea	HNR; endemic to Jalisco and Nayarit
Euphorbiaceae	*Astrocasia tremula* (Griseb.) G.L. Webster	Coastal dunes	HNR; native
Euphorbiaceae	*Cnidoscolus palmeri* (S. Watson) Rose	Coastal cliffs	HNR; native, P
Euphorbiaceae	*Cnidoscolus spinosus* Lundell	Hills facing the ocean	HNR; endemic to Jalisco, Colima, Nayarit, Guerrero, Oaxaca
Euphorbiaceae	*Cnidoscolus urens* (L.) Arthur	Coastal dunes, salty flats	HNR; native, A, P
Euphorbiaceae	*Croton argyranthemus* Michx.	Salty-gypseous soils	GHNR; native, I
Euphorbiaceae	*Croton californicus* Müll. Arg.	Coastal dunes, salt shrub communities	HNR; native, P
Euphorbiaceae	*Croton capitatus* Michx.	Saline soils, salt shrub communities	HNR; native, A
Euphorbiaceae	*Croton ciliatoglandulifer* Ortega	Coastal dunes	HNR; native, A, C
Euphorbiaceae	*Croton cortesianus* Kunth	Salinized lands, salt shrub communities	HNR; native, A, C,
Euphorbiaceae	*Croton culiacanensis* Croizat	Salt shrub communities	HNR; endemic to Sinaloa
Euphorbiaceae	*Croton dioicus* Cav.	Saline and salty-gypseous soils, salt shrub communities	H/GHNR; native, I
Euphorbiaceae	*Croton glandulosus* L.	Coastal dunes, mangroves, salt shrub communities	HNR; native, A, P
Euphorbiaceae	*Croton leucophyllus* Müll. Arg.	Salt shrub communities	HNR; native, A
Euphorbiaceae	*Croton lobatus* L.	Coastal dunes	HNR; introduced (?), A, P
Euphorbiaceae	*Croton magdalenae* Millsp.	Cliffs feacing the sea	HNR; endemic to Baja California, Baja California Sur, Sonora
Euphorbiaceae	*Croton ovalifolius* Vahl	Salt shrub communities	HNR; native, P
Euphorbiaceae	*Croton punctatus* Jacq.	Coastal beaches and dunes, saline soils, mangrove, salt marshes, salt shrub communities	HNR; native, A, C, P
Euphorbiaceae	*Croton reflexifolius* Kunth	Coastal dunes	HNR; native, A, P
Euphorbiaceae	*Croton suaveolens* Torr.	Salty-gypseous soils	GHNR; native, I
Euphorbiaceae	*Croton suberosus* Kunth	Coastal dunes, rocky cliffs feacing the sea	HNR; endemic from Sinaloa to Oaxaca
Euphorbiaceae	*Croton wigginsii* L.C. Wheeler	Coastal beach and dunes	HNR; native, P

(continued)

Table 17.1 (continued)

Family	Genus and species	Saline habitat	Distribution
Euphorbiaceae	*Dalechampia scandens* L.	Coastal beach and dunes mangroves	HNR; native, A, C, P
Euphorbiaceae	*Ditaxis brandegeei* (Millsp.) Rose & Standl.	Rocks along the sea beach	HNR; native, P
Euphorbiaceae	*Ditaxis lanceolata* (Benth.) Pax & K. Hoffm.	Coastal dunes, salt shrub communities	HNR; native, P
Euphorbiaceae	*Ditaxis manzanilloana* (Rose) Pax & K. Hoffm.	Coastal dunes, rocky points above sea	HNR; endemic from Sonora to Oaxaca
Euphorbiaceae	*Ditaxis neomexicana* (Müll. Arg.) A. Heller	Rocky hills at beach	HNR; native, I, P
Euphorbiaceae	*Ditaxis serrata* (Torr.) A. Heller	Salt shrub communities	HNR; native, P
Euphorbiaceae	*Euphorbia anychioides* Boiss.	Coastal dunes	HNR; native, C
Euphorbiaceae	*Euphorbia astyla* Engelm. ex Boiss.	Saline-gypseous soils	GHNR; native, I
Euphorbiaceae	*Euphorbia blodgettii* Engelm. ex Hitchc.	Coastal dunes	HNR; native, A, C
Euphorbiaceae	*Euphorbia bombensis* Jacq.	Coastal dunes, salt marshes	HNR; native, A, C
Euphorbiaceae	*Euphorbia cyathophora* Murray	Coastal dunes	HNR; native, A, C
Euphorbiaceae	*Euphorbia hypericifolia* L.	Coastal dunes	HNR; native, A, C
Euphorbiaceae	*Euphorbia incerta* Brandegee	Coastal beach and dunes	HR; endemic from Baja California to Sinaloa
Euphorbiaceae	*Euphorbia leucophylla* Benth.	Coastal beach and dunes	HR; endemic from Baja California to Sinaloa
Euphorbiaceae	*Euphorbia lomelii* V.W. Steinm.	Coastal dunes, mangroves, salt shrub communities	HNR; endemic from Baja California to Sinaloa
Euphorbiaceae	*Euphorbia mesembryanthemifolia* Jacq.	Coastal beach and dunes	HNR; native, A, C
Euphorbiaceae	*Euphorbia misera* Benth.	Coastal beach and dunes, salt marsh	HNR; native, P
Euphorbiaceae	*Euphorbia tithymaloides* L.	Salt shrub communities	HNR; native, P
Euphorbiaceae	*Enriquebeltrania crenatifolia* (Miranda) Rzed.	Coastal dunes	HNR; endemic from Yucatán to Quintana Roo
Euphorbiaceae	*Garcia nutans* Vahl	Coastal beach and dunes	HNR; native, A, P
Euphorbiaceae	*Gymnanthes lucida* Sw.	Coastal dunes	HNR; native, C
Euphorbiaceae	*Hippomane mancinella* L.	Coastal beach and dunes, mangroves	HNR; native, P
Euphorbiaceae	*Jatropha bullockii* E.J. Lott	Rocky sea cliffs	HNR; endemic to Jalisco
Euphorbiaceae	*Jatropha cinerea* (Ortega) Müll. Arg.	Coastal dunes, salt shrub communities	HNR; native, P
Euphorbiaceae	*Jatropha cuneata* Wiggins & Rollins	Coastal dunes	HNR; native, P
Euphorbiaceae	*Jatropha gossypiifolia* L.	Coastal beach, salt shrub communities	HNR; native, A
Euphorbiaceae	*Jatropha sympetala* S.F. Blake & Standl.	Coastal dunes	HNR; endemic from Nayarit to Oaxaca
Euphorbiaceae	*Manihot aesculifolia* (Kunth) Pohl	Coastal dunes	HNR; native, A, C, P

(continued)

Table 17.1 (continued)

Family	Genus and species	Saline habitat	Distribution
Euphorbiaceae	*Manihot chlorosticta* Standl. & Goldman	Coastal cliffs and dunes	HNR; endemic from Baja California to Guerrero
Euphorbiaceae	*Phyllanthus amarus* Schumach. & Thonn.	Coastal dunes	HNR; native, A, C
Euphorbiaceae	*Phyllanthus elsiae* Urb.	Mangroves, salt shrub communities	HNR; native, P
Euphorbiaceae	*Phyllanthus mocinianus* Baill.	Coastal dunes, mangroves	HNR; native, C, P
Euphorbiaceae	*Ricinus communis* L.	Coastal dunes, mangroves	HNR; introduced, A, C, I, P
Euphorbiaceae	*Stillingia linearifolia* S. Watson	Coastal dunes, mangroves, saline flats	HNR; native, P
Fabaceae	*Acacia sphaerocephala* Cham. & Schltdl.	Coastal beach and dunes	HNR; native, A
Fabaceae	*Astragalus magdalenae* Greene	Coastal hills	HNR; native, P
Fabaceae	*Astragalus mollissimus* Torr.	Saline plains	HNR; native, I
Fabaceae	*Astragalus insularis* Kellogg	Coastal beach and dunes	HNR; native, P
Fabaceae	*Caesalpinia bonduc* (L.) Roxb.	Coastal beach and dunes mangrove	HNR; native, A, C
Fabaceae	*Canavalia maritima* Thouars	Coastal beach and dunes, salt shrub communities	HNR; native, A, C, P
Fabaceae	*Chamaecrista chamaecristoides* (Collad.) Greene	Coastal beach and dunes	HNR; endemic to Mexico
Fabaceae	*Crotalaria incana* L.	Coastal dunes, mangroves, salt shrub communities	HNR; native, A
Fabaceae	*Dalbergia ecastaphyllum* (L.) Taub.	Coastal dunes, mangroves	HNR; native, A
Fabaceae	*Dalea emarginata* (Torr. & A. Gray) Shinners	Coastal dunes, salt shrub communities	HNR; native, A
Fabaceae	*Desmanthus virgatus* (L.) Willd.	Coastal dunes, salt shrub communities	HNR; native, P
Fabaceae	*Indigofera suffruticosa* Mill.	Coastal dunes	HNR; native, A
Fabaceae	*Lotus bryantii* (Brandegee) Ottley	Low coastal hills, dunes	HNR; endemic to Baja California, Baja California Sur
Fabaceae	*Lotus nuttallianus* Greene	Coastal beach and dunes	HNR; native, P
Fabaceae	*Lonchocarpus guatemalensis* Benth.	Coastal dunes	HNR; native, A
Fabaceae	*Macroptilium atropurpureum* (Moc. & Sessé ex DC.) Urb.	Coastal dunes	HNR; native, A
Fabaceae	*Marina divaricata* (Benth.) Barneby	Coastal dunes	HNR; endemic to Baja California Sur
Fabaceae	*Mimosa strigillosa* Torr. & A. Gray	Coastal dunes, salt shrub communities	HNR; native, A
Fabaceae	*Muellera frutescens* (Aubl.) Standl.	Mangroves	HNR; native, A
Fabaceae	*Phaseolus filiformis* Benth.	Coastal beach and dunes	HNR; native, P
Fabaceae	*Pithecellobium dulce* (Roxb.) Benth.	Coastal dunes	HNR; native, A
Fabaceae	*Pithecellobium keyense* Britton	Coastal dunes, mangroves	HNR; native, C
Fabaceae	*Pithecellobium lanceolatum* (Humb. & Bonpl. ex Willd.) Benth.	Coastal dunes, mangroves	HNR; native, A, C
Fabaceae	*Prosopis glandulosa* Torr.	Coastal dunes, salty plains	HNR; native, I

(continued)

Table 17.1 (continued)

Family	Genus and species	Saline habitat	Distribution
Fabaceae	*Prosopis juliflora* (Sw.) DC.	Coastal dunes, saline plains, mangroves	HNR; native, I
Fabaceae	*Prosopis laevigata* (Humb. & Bonpl. ex Willd.) M.C. Johnst.	Salty plains	HNR; native, I
Fabaceae	*Prosopis reptans* var. *cinerascens* (A. Gray) Burkart	Coastal dunes, salt marshes, saline plains, salt shrub communities	HNR; native, I
Fabaceae	*Prosopis velutina* Wooton	Saline plains	HNR; native, I
Fabaceae	*Psorothamnus emoryi* (A. Gray) Rydb.	Coastal dunes	HNR; native, P
Fabaceae	*Rhynchosia americana* (Mill.) Metz	Coastal beach and dunes, salt shrub communities	HNR; native, A
Fabaceae	*Sophora tomentosa* L.	Coastal beach and dunes, salt flats, mangroves	HNR; native, A, C
Fabaceae	*Tephrosia cinerea* (L.) Pers.	Coastal beach and dunes, mangroves	HNR; native, A, C
Frankeniaceae	*Frankenia grandifolia* Cham. & Schltdl.	Coastal beach and dunes, salt marshes	HR; native, P
Frankeniaceae	*Frankenia johnstonii* Correll	Saline-gypseous soils	GHR; native, I
Frankeniaceae	*Frankenia margaritae* González Medrano	Saline and salty-gypseous flat, salt shrub communities	H/GHNR; endemic to Nuevo Leon
Frankeniaceae	*Frankenia palmeri* S. Watson	Coastal dunes, marshes, subsaline soils	HR; native, P
Gentianaceae	*Eustoma exaltatum* (L.) Salisb. ex G. Don	Coastal dunes, mangroves, saline soils	HNR; native, A, C
Gentianaceae	*Sabatia arenicola* Greenm.	Coastal beaches and dunes, salt flats	HNR; native, A
Gentianaceae	*Sabatia tuberculata* J. E. Williams	Gypseous-saline soils	GHNR; endemic to Coahuila
Goodeniaceae	*Scaevola plumieri* (L.) Vahl	Coastal beaches and dunes, mangroves	HNR; native, A, C, P
Hydrophyllaceae	*Nama hispida* A. Gray	Saline plains	HNR; native, I
Hydrophyllaceae	*Nama rzedowskii* J.D. Bacon	Alluvial saline palins	HR; endemic to San Luis Potosi
Hydrophyllaceae	*Nama serpylloides* var. *velutina* C.L. Hitchc.	Salty and salty-gypseous flats	H/GHNR; endemic from Coahuila to San Luis Potosí
Hydrophyllaceae	*Nama stenophylla* A. Gray ex Hemsl.	Salty flats	HNR; endemic to Chihuahua, Coahuila, Nuevo Leon
Hydrophyllaceae	*Phacelia distans* Benth.	Coastal dunes	HNR; native, P
Juncaceae	*Juncus acutus* L.	Salt marshes	HNR; introduced, P
Juncaceae	*Juncus arcticus* var. *mexicanus* (Willd. ex Schult. & Schult. f.) Balslev	Brackish and saline plains	HNR; native, I
Juncaginaceae	*Triglochin concinna* Burtt Davy	Salt marshes	HNR; native, P
Juncaginaceae	*Triglochin maritima* L.	Salt marshes	HNR; native, P
Juncaginaceae	*Triglochin striata* Ruiz & Pav.	Saline plains	HNR; native, I
Lamiaceae	*Teucrium townsendii* Vasey & Rose	Coastal cliffs	HNR; endemic to Colima

(continued)

Table 17.1 (continued)

Family	Genus and species	Saline habitat	Distribution
Lauraceae	*Cassytha filiformis* L.	Coastal dunes, mangroves	HNR; native, C
Lauraceae	*Nectandra salicifolia* (Kunth) Nees	Coastal dunes, sea cliffs	HNR; native, A
Lythraceae	*Lythrum californicum* Torr. & A. Gray	Saline plains	HNR; native, P
Malvaceae	*Gossypium hirsutum* L.	Coastal dunes	HNR; native (?), C
Malvaceae	*Malvaviscus arboreus* Cav.	Coastal dunes	HNR; native, A, C
Malvaceae	*Malvella leprosa* (Ortega) Krapov.	Brackish flats	HNR; native, I
Malvaceae	*Thespesia populnea* (L.) Sol. ex Corrêa	Coastal dunes, mangrove	HNR; native, A, C
Malvaceae	*Waltheria indica* L.	Coastal cliffs and dunes	HNR; native, A, C, P
Martyniaceae	*Proboscidea altheifolia* (Benth.) Decne.	Coastal dunes	HNR; native, P
Menispermaceae	*Hyperbaena winzerlingii* Standl.	Coastal dunes	HNR; native, C
Nyctaginaceae	*Abronia gracilis* Benth.	Coastal dunes	HNR; native, P
Nyctaginaceae	*Abronia latifolia* Eschsch.	Coastal dunes	HNR; native, P
Nyctaginaceae	*Abronia maritima* Nutt. ex S. Watson	Coastal beach and dunes	HNR; native, P
Nyctaginaceae	*Abronia umbellata* Lam.	Coastal beach and dunes	HNR; native, P
Nyctaginaceae	*Allionia incarnata* L.	Saline plains	HNR; native, I
Nyctaginaceae	*Boerhavia erecta* L.	Coastal dunes, mangroves	HNR; native, A
Nyctaginaceae	*Commicarpus scandens* (L.) Standl.	Coastal dunes	HNR; native, P
Nyctaginaceae	*Okenia hypogaea* Schltdl. & Cham.	Coastal beach and dunes	HR; native, A, C
Nyctaginaceae	*Pisonia calafia* León de la Luz et Levin	Coastal strand	HR; endemic to Baja California Sur
Onagraceae	*Camissonia crassifolia* (Greene) P.H. Raven	Coastal beach, dunes, and slopes	HNR; endemic to Baja California, Baja California Sur
Onagraceae	*Oenothera drummondii* Hook.	Coastal dunes, salty plains	HNR; native, A
Orobanchaceae	*Agalinis maritima* (Raf.) Raf.	Coastal dunes, salt marshes	HNR; native, C
Orobanchaceae	*Cordylanthus maritimus* Nutt. ex Benth.	Coastal beach, salt marshes	HR; native, P
Orobanchaceae	*Gerardia maritima* Raf.	Salt marsh	HR; native, A
Orobanchaceae	*Silvia serpyllifolia* (Kunth) Benth.	Brackish plains	HNR; endemic to DF, Hidalgo, Puebla, San Luis Potosì, Tlaxcala, Veracruz
Passifloraceae	*Passiflora ciliata* Aiton	Coastal dunes	HNR; native, C
Passifloraceae	*Passiflora foetida* L.	Coastal dunes	HNR; native, A, C
Passifloraceae	*Turnera ulmifolia* L.	Coastal dunes	HNR; native, A
Plantaginaceae	*Bacopa monnieri* (L.) Wettst.	Coastal dunes, saline flats	HNR; native, I
Plantaginaceae	*Maurandya antirrhiniflora* Humb. & Bonpl. ex Willd.	Saline flats	HNR; native, A
Plantaginaceae	*Stemodia maritima* L.	Coastal dunes, mangroves	HNR; native, C
Plumbaginaceae	*Limonium californicum* (Boiss.) A. Heller	Salt marshes	HR; native, P
Plumbaginaceae	*Limonium carolinianum* (Walter) Britton	Coastal dunes, salt marshes	HR; native, A
Plumbaginaceae	*Limonium limbatum* Small	Saline and salty-gypsum plains	H/GHNR; native, I

(continued)

Table 17.1 (continued)

Family	Genus and species	Saline habitat	Distribution
Poaceae	*Achnatherum editorum* (E. Fourn.) Valdés-Reyna & Barkworth	Salt shrub communities	HNR; endemic to Mexico
Poaceae	*Agrostis hyemalis* (Walter) Britton, Sterns & Poggenb.	Salt shrub communities	HNR; native, A
Poaceae	*Andropogon glomeratus* (Walter) Britton, Sterns & Poggenb.	Coastal beach and dunes	HNR; native, A, C
Poaceae	*Anthephora hermaphrodita* (L.) Kuntze	Coastal cliffs, beach, and dunes	HNR; native, P
Poaceae	*Aristida adscensionis* L.	Coastal beach, saline flats	HNR; native, A, I
Poaceae	*Aristida californica* Thurb.	Coastal beach and dunes	HNR; native, P
Poaceae	*Aristida curvifolia* E. Fourn.	Saline and salty-gypseous soils	H/GHNR; endemic to Mexico
Poaceae	*Aristida havardii* Vasey	Saline soils	HNR; native, I
Poaceae	*Aristida pansa* Wooton & Standley f. *contracta* Allred & Valdés-Reyna	Salt shrub communities	HNR; endemic to Mexico
Poaceae	*Aristida purpurea* var. *wrightii* (Nash) Allred	Coastal dunes	HNR; native, A
Poaceae	*Arundo donax* L.	Coastal dunes, mangroves	HNR; introduced, A, C
Poaceae	*Avena fatua* L.	Salty soils	HNR; introduced, I
Poaceae	*Avena sativa* L.	Brackish and salty soils	HNR; introduced, I
Poaceae	*Bothriochloa barbinodis* (Lag.) Herter	Salty soils	HNR; native, I
Poaceae	*Bouteloua aristidoides* (Kunth) Griseb.	Coastal dunes, salty soils	HNR; native, P
Poaceae	*Bouteloua barbata* Lag.	Coastal beach, salty flats	HNR; native, I, P
Poaceae	*Bouteloua curtipendula* (Michx.) Torr.	Salty soils, salt shrub communities	HNR; native, I
Poaceae	*Bouteloua dactyloides* (Nutt.) Columbus	Saline and salty-gypseous flats	H/GHNR; native, I
Poaceae	*Bouteloua erecta* (Vasey & Hack.) Columbus	Soft saline shales	HNR; native, I
Poaceae	*Bouteloua gracilis* (Kunth) Lag. ex Griffiths	Salty flats, salt shrub communities	HNR; native, I
Poaceae	*Bouteloua karwinskii* (E. Fourn.) Griffiths	Saline and salty-gypseous soils	H/GHNR; endemic to Coahuila, Durango, Nuevo León, San Luis Potosí, Zacatecas
Poaceae	*Bouteloua repens* (Kunth) Scribn. & Merr.	Coastal dunes	HNR; native, C
Poaceae	*Bouteloua simplex* Lag.	Saline soils	HNR; native, I
Poaceae	*Bouteloua trifida* Thurb.	Saline soils	HNR; native, I
Poaceae	*Cenchrus ciliaris* L.	Salt shrub communities, salinized lands	HNR; introduced, A
Poaceae	*Cenchrus echinatus* L.	Coastal dunes	HNR; native, A
Poaceae	*Cenchrus incertus* M.A. Curtis	Salty flats	HNR; native, A, C
Poaceae	*Cenchrus myosuroides* Kunth	Salty flats	HNR; native, I,
Poaceae	*Cenchrus tribuloides* L.	Coastal dunes	HNR; native, A
Poaceae	*Chloris barbata* Sw.	Salty flats	HNR; native, A
Poaceae	*Chloris virgata* Sw.	Coastal dunes, salty flats, salt shrub communities	HNR; native, A, I

(continued)

Table 17.1 (continued)

Family	Genus and species	Saline habitat	Distribution
Poaceae	*Cynodon dactylon* (L.) Pers.	Salty flats	HNR; introduced, A, I
Poaceae	*Dactyloctenium aegyptium* (L.) Willd.	Coastal dunes, mangroves, salt shrub communities	HNR; introduced, A, C
Poaceae	*Dasyochloa pulchella* (Kunth) Willd. ex Rydb.	Coastal dunes	HNR; native, A, I
Poaceae	*Digitaria bicornis* (Lam.) Roem. & Schult.	Coastal dunes	HNR; introduced, A, C, P
Poaceae	*Distichlis eludens* (Soderstr. & H.F. Decker) H.L. Bell & Columbus	Saline alluvial flats	HNR; endemic to Durango, San Luis Potosí, Zacatecas
Poaceae	*Distichlis palmeri* (Vasey) Fassett	Salt marshes, salt shrub communities	HR; endemic to Baja California, Sonora
Poaceae	*Distichlis spicata* (L.) Greene	Coastal beach and dunes, salt marshes	HNR; native, A, I, P,
Poaceae	*Echinochloa colona* (L.) Link	Saline flats, salinized lands	HNR; introduced, I
Poaceae	*Echinochloa crus-galli* (L.) P. Beauv	Saline flats	HNR; native, A
Poaceae	*Eleusine indica* (L.) Gaertn.	Salt shrub communities	HNR; introduced, A, C, I, P
Poaceae	*Eragrostis mexicana* (Hornem.) Link	Saline flats, salinized lands	HNR; native, I
Poaceae	*Eragrostis obtusiflora* (E. Fourn.) Scribn.	Saline flats	HNR; native, I
Poaceae	*Eragrostis prolifera* (Sw.) Steud.	Coastal dunes, mangroves, saline flats	HNR; native, A, C
Poaceae	*Eragrostis secundiflora* J. Presl	Coastal dunes, saline flats, salt shrub communities	HNR; native, A, C
Poaceae	*Eriochloa aristata* var. *boxiana* (Hitchc.) R.B. Shaw	Coastal dunes, mangroves	HNR; native, C
Poaceae	*Erioneuron pilosum* (Buckley) Nash	Salt shrub communities	HNR; native, I
Poaceae	*Eustachys petraea* (Sw.) Desv.	Coastal dunes, mangroves	HNR; introduced, A
Poaceae	*Hopia obtusa* (Kunth) Zuloaga & Morrone	Saline flats	HNR; native, I
Poaceae	*Hordeum jubatum* L.	Saline flats	HNR; introduced, I
Poaceae	*Jouvea pilosa* (J. Presl) Scribn.	Coastal becahes and dunes	HNR; native, P
Poaceae	*Leptochloa fascicularis* (Lam.) A. Gray	Salt or brackish marshes	HNR; native, P
Poaceae	*Leptochloa nealleyi* Vasey	Salt marshes	HNR; native, A
Poaceae	*Monanthochloe littoralis* Engelm.	Costal beach and dunes, mangroves, salt marshes, salt shrub communities	HR; native, A, C, P
Poaceae	*Muhlenbergia arenicola* Buckley	Saline flats	HNR; native, I
Poaceae	*Muhlenbergia asperifolia* (Nees & Meyen ex Trin.) Parodi	Saline and brackish soils	HNR; native, I
Poaceae	*Muhlenbergia repens* (J. Presl) Hitchc.	Saline flats	HNR; native, I
Poaceae	*Muhlenbergia utilis* (Torr.) Hitchc.	Saline flats	HNR; native, I
Poaceae	*Muhlenbergia villiflora* Hitchc.	Saline flats	HNR; native, I
Poaceae	*Nassella tenuissima* (Trin.) Barkworth	Saline flat	HNR; native, I
Poaceae	*Panicum amarum* var. *amarulum* (Hitchc. & Chase) P. Palmer	Coastal dunes, salt shrub communities	HNR; native, A, C

(continued)

Table 17.1 (continued)

Family	Genus and species	Saline habitat	Distribution
Poaceae	*Panicum hallii* Vasey	Salt shrub communities	HNR; native, I
Poaceae	*Panicum hirticaule* J. Presl	Saline flats	HNR; native, A, C
Poaceae	*Parapholis incurva* (L.) C.E. Hubb.	Salt marshes	HNR; introduced, P
Poaceae	*Paspalidium geminatum* (Forssk.) Stapf	Salt marshes	HNR; introduced, P
Poaceae	*Paspalum monostachyum* Vasey	Saline flats	HNR; native, A
Poaceae	*Paspalum vaginatum* Sw.	Salt marshes, mangroves	HNR; native
Poaceae	*Phragmites australis* (Cav.) Trin. ex Steud.	Saline depressions, salt marshes	HNR; native, A, C, P
Poaceae	*Pleuraphis mutica* Buckley	Saline flat	HNR; native, I
Poaceae	*Polypogon elongatus* Kunth	Salt marshes	HNR; native, P
Poaceae	*Polypogon viridis* (Gouan) Breistr.	Saline flat	HNR; introduced, I
Poaceae	*Schizachyrium scoparium* (Michx.) Nash	Coastal beach and dunes	HNR; native, A
Poaceae	*Scleropogon brevifolius* Phil.	Salt shrub communities	HNR; native, I
Poaceae	*Setaria macrostachya* Kunth	Salt shrub communities	HNR; native, A
Poaceae	*Sporobolus airoides* (Torr.) Torr.	Saline, salty-gypseous soils	H/GHNR; native, I
Poaceae	*Sporobolus alterniflorus* (Loisel.) P.M. Peterson & Saarela	Saline plains, salt shrub communities	HNR; native, I
Poaceae	*Sporobolus contractus* Hitchc.	Saline plains	HNR; native, I
Poaceae	*Sporobolus cryptandrus* (Torr.) A. Gray	Saline plains	HNR; native, I
Poaceae	*Sporobolus cynosuroides* (L.) P.M. Peterson & Saarela	Coastal dunes, salt shrub communities	HNR; native, A
Poaceae	*Sporobolus domingensis* (Trin.) Kunth	Coastal dunes	HNR; native, C
Poaceae	*Sporobolus flexuosus* (Thurb. ex Vasey) Rydb.	Saline plains	HNR; native, I
Poaceae	*Sporobolus foliosus* (Trin.) P.M. Peterson & Saarela	Coastal beach, saline flats	HNR; native, P
Poaceae	*Sporobolus jacquemontii* Kunth	Mangroves, salt shrub communities	HNR; native, A
Poaceae	*Sporobolus nealleyi* Vasey	Saline plains	HNR; native, I
Poaceae	*Sporobolus pumilus* (Roth) P.M. Peterson & Saarela	Saline plains, salt shrub communities	HR; native, A, C
Poaceae	*Sporobolus pyramidatus* (Lam.) Hitchc.	Coastal dunes	HNR; native, A, C, I,
Poaceae	*Sporobolus spartinus* (Trin.) P.M. Peterson & Saarela	Saline plains, salt shrub communities	HR; native, A, C, I,
Poaceae	*Sporobolus spiciformis* Swallen	Salty-gypseous plains	GHNR; endemic to Chihuahua, Coahuila, and Durango
Poaceae	*Sporobolus splendens* Swallen	Coastal dunes, mangroves, tidal marsh, saline soils	HNR; endemic to Nayarit, Jalisco, Oaxaca, Chiapas
Poaceae	*Sporobolus virginicus* (L.) Kunth	Coastal beach and dunes, salt marshes, mangrove	HR; native, A, C, P
Poaceae	*Sporobolus wrightii* Munro ex Scribn.	Salt shrub communities	HNR; native, I

(continued)

Table 17.1 (continued)

Family	Genus and species	Saline habitat	Distribution
Poaceae	*Uniola paniculata* L.	Costal beach and dunes, edges of salt marshes, salt shrub communities	HNR; native, A, C
Poaceae	*Urochloa maxima* (Jacq.) R.D. Webster	Costal beach and dunes	HNR; introduced, A, C
Poaceae	*Urochloa mutica* (Forssk.) T.Q. Nguyen	Mangroves, salt shrub communities	HNR; introduced, A, C
Polygonaceae	*Coccoloba humboldtii* Meisn.	Coastal dunes	HNR; native, A. C, P
Polygonaceae	*Coccoloba uvifera* (L.) L.	Coastal beaches and dunes	HR; native, A, C
Polygonaceae	*Rumex flexicaulis* Rech. f.	Salty soils	HNR; endemic to DF, Mexico
Portulacaceae	*Portulaca oleracea* L.	Coastal dunes, mangrove,	HNR; native, A, C, I
Portulacaceae	*Portulaca pilosa* L.	Coastal dunes	HNR; native, A, C, P
Primulaceae	*Bonellia macrocarpa* (Cav.) B. Ståhl & Källersjö	Coastal dunes, mangrove	HNR; native, A, C, P
Primulaceae	*Jacquinia armillaris* Jacq.	Coastal dunes	HNR; native, C
Primulaceae	*Jacquinia aurantiaca* W.T. Aiton	Coastal dunes, mangrove	HNR; native, A, C
Primulaceae	*Samolus ebracteatus* Kunth	Coastal dunes, saly marshes, salty plains	HNR; native, A, I, P
Ranunculaceae	*Ranunculus cymbalaria* Pursh	Salinized plains	HNR; native, I
Resedaceae	*Oligomeris linifolia* (Vahl) J.F. Macbr.	Salty flats	HNR; native, I
Rubiaceae	*Chiococca alba* (L.) Hitchc.	Coastal dunes, mangroves	HNR; native, A, C
Rubiaceae	*Erithalis fruticosa* L.	Coastal dunes	HNR; native, C
Rubiaceae	*Ernodea littoralis* Sw.	Coastal dunes	HNR; native, C
Rubiaceae	*Hedyotis mucronata* Benth.	Coastal beach	HR; endemic to Campeche, Tabasco
Rubiaceae	*Rachicallis americana* (Jacq.) Hitchc.	Coastal dunes	HR; native, C
Rubiaceae	*Randia aculeata* L.	Coastal dunes, mangroves	HNR; native, A, C
Rubiaceae	*Randia laetevirens* Standl.	Coastal dunes	HNR; native, A
Rubiaceae	*Strumpfia maritima* Jacq.	Coastal dunes and rocks	HR; native, C
Ruppiaceae	*Ruppia maritima* L.	Brackish pools	HNR; native, A, C, I
Rhizophoraceae	*Rhizophora mangle* L.	Muddy shores of esteros and bays of the coast	HNR; native, A, C, P
Sapotaceae	*Sideroxylon americanum* (Mill.) T.D. Penn.	Coastal dunes	HNR; native, C
Saururaceae	*Anemopsis californica* Hook. & Arn.	Salt marsh	HNR; native, I, P
Solanaceae	*Lycium brevipes* Benth.	Coastal dunes, salt marsh	HNR; native, P
Solanaceae	*Lycium californicum* Nutt. ex A. Gray	Coastal blufs, salt marshes, saline flats	HNR; native, P
Solanaceae	*Lycium carolinianum* Walter	Coastal dunes, salt marshes	HNR; native, A, C
Solanaceae	*Lycium leiospermum* I.M. Johnst.	Salty and brackish flats	HNR; endemic to Coahuila, San Luis Potosi, Zacatecas
Solanaceae	*Nierembergia angustifolia* Kunth	Brackish flats, edges of salty lakes	HNR; endemic to D.F., Mexico
Solanaceae	*Petunia parviflora* Juss.	Salty flats	HNR; native, I
Stegnospermataceae	*Stegnosperma halimifolium* Benth.	Costal dunes	HNR; native, A, C

(continued)

Table 17.1 (continued)

Family	Genus and species	Saline habitat	Distribution
Stegnospermataceae	*Stegnosperma watsonii* D.J. Rogers	Seacoast, saline swales	HNR; endemic to Sinaloa, Sonora
Surianaceae	*Suriana maritima* L.	Costal dunes	HNR; native, C
Tamaricaceae	*Tamarix ramosissima* Ledeb.	Subsaline wet places	HNR; introduced, I, P
Verbenaceae	*Citharexylum ellipticum* D. Don	Costal dunes	HNR; native, A
Verbenaceae	*Lantana camara* L.	Costal dunes, mangroves	HNR; introduced, A, C
Verbenaceae	*Lantana involucrata* L.	Costal dunes, mangroves	HNR; native, C
Verbenaceae	*Phyla nodiflora* (L.) Greene	Coastal dunes, mangroves, salty and brackish flats	HNR; native, A, C
Vitaceae	*Cissus trifoliata* (L.) L.	Coastal dunes, mangroves	HNR; native, A, C
Zygophyllaceae	*Larrea tridentata* (Sessé & Moc. ex DC.) Coville	Saline soils	HNR; native, I
Zygophyllaceae	*Tribulus cistoides* L.	Coastal beach and dunes, mangroves	HNR; introduced, C
Zygophyllaceae	*Viscainoa geniculata* (Kellogg) Greene	Coastal beach and dunes	HNR; endemic to Baja California Sur, Sonora
Zosteraceae	*Phyllospadix torreyi* S. Watson	On wave-washed rocks below sea level at low tide	HNR; native, P
Zosteraceae	*Zostera marina* L.	Saline and brackish mud	HNR; native, P

HNR halophyte non restricted, *HR* halophyte restricted, *GHNR* gypsohalophyte non restricted, *GHR* gypsohalophyte restricted, *A* atlantic coast, *P* pacific coast, *C* caribbean coast, *I* in inland saline areas of Mexico

Also worth mentioning are the former saline lakes of the Transmexican Volcanic Belt in non arid climate regions such as the large Texcoco Lake, in the Valley of Mexico, with soils that show extreme values of salinity (Krasilnikov et al. 2013).

However, compared with other countries such as USA or Pakistan with wide areas of similar arid and semiarid climate conditions, salt affected areas in Mexico are surprisingly relatively small (Szabolcs 1974; Krasilnikov et al. 2013). Nonetheless the flora of Mexico contains a diversity of halophytes and gypsohalophytes which is certainly related to the peculiar distribution of soils. Unlike other countries, in Mexico there are no large enclosed areas of saline soils but a mosaic pattern of small areas called by some authors "soil islands" (Mota et al. 2009) (Fig. 17.1). These "edaphic islands" are isolated from each other and often contain a large numbers of endemic halophyte species. This mosaic pattern of soils could be the basis for adaptive radiation of the halophytes plants and, finally, one of the reasons for the great diversity of Mexican halophytic flora.

2 Floristic Diversity in Salty Soils of Mexico

As previous authors have pointed out, the term halophyte is controversial. Salt tolerance of plants is rare and estimations of halophytes vary from 2 % (Glenn and Brown 1999) to only 0.25 % of all flowering plants (Saslis-Lagoudakis et al. 2014). To know which species could be considered "halophyte" in terms of their ability to grow, reproduce and germinate in the presence of either periodic sea water inundation, or the clear presence of a salt surface crust (Böer et al. 2002), ecological studies are still required for species growing on saline or saline-gypseous soilsof Mexico. Here we aim to provide a list of the species that have been reported or collected in such habitats in Mexico. Halophytic plant communities are found both along the Atlantic (Gulf of Mexico), the Pacific, and the Caribbean coasts; and inland. The habitats influenced by sea water or its spray, include cliffs, rocks, beaches, sand dunes, salt marshes, mangroves and the intertidal zones characterized by saline mud inundated by sea water at high tide in several localities of the

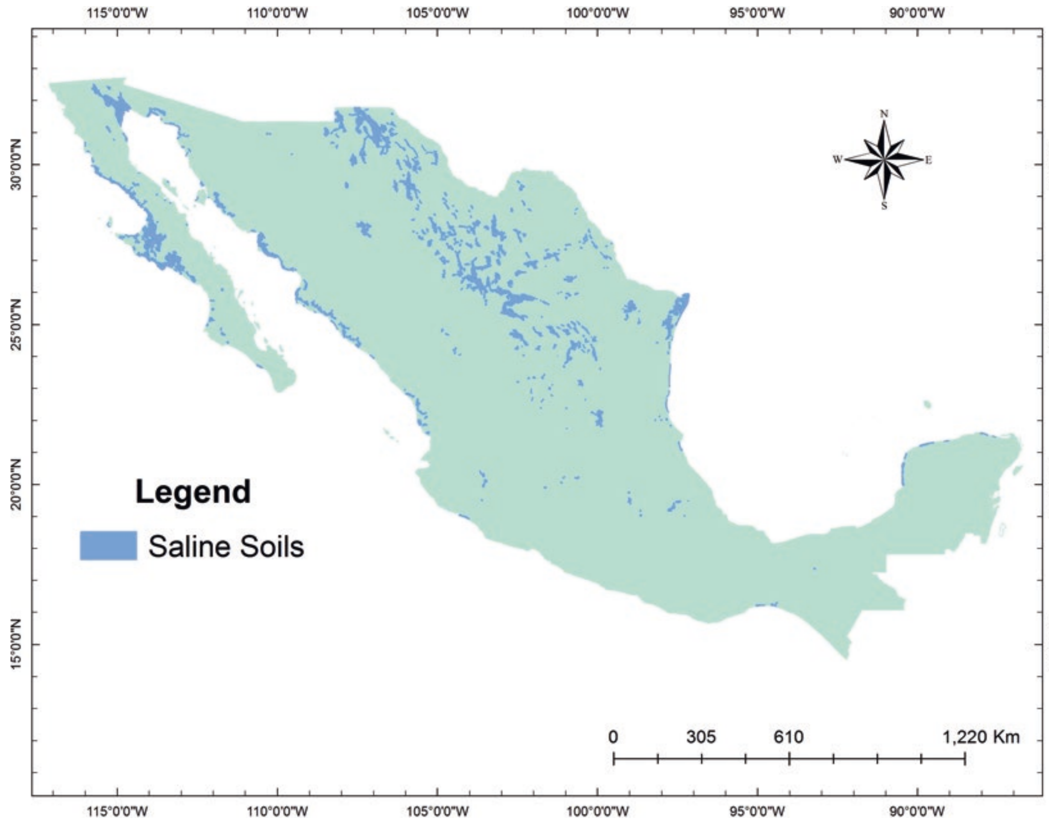

Fig. 17.1 Distribution of saline soils in Mexico (Modified after CONABIO, 1999)

Pacific coast. Inland habitats include endorheic basins or plains with saline or saline-gypseous soils. The presented list is based on field work within the project "Halophytic and gipsophytic Flora of Mexico" headed by Javier Valdés Gutiérrez (╬), revision of Mexican Herbaria, and literature (Náder García 1992; Fuentes Soriano 1995; Sánchez-Del Pino et al. 1999; Cervantes Maldonado et al. 2001), including the more comprehensive treatments for the Flora of Mexico for NW (Shreve 1964), NE and Chihuahuan Desert (Correll and Johnston 1979; Pinkava 1984; Valdés and Allred 2003), Valley of Mexico (Calderón de Rzedowski and Rzedowski 2001), SE (Carnevali Fernández-Concha et al. 2010). The actualization of the nomenclature for the list was done using Tropicos.org.; Espejo Serna et al. (2000); González Elizondo et al. (2008); Herrera Arrieta and Cortés Ortiz (2010); Herbario CICY (2010 onwards).

Table 17.1 sumarizes the information of 647 species of angiosperms living in salty environments and their distribution in Mexico. Those species restricted to live only in salty environments are marked as HR (halophytes restricted); those restricted to saline-gypseous soils are marked as GHR (gypsohalophytes restricted), and the tolerant to these kind of environments but also living in non saline environmets are marked as NR (non restricted). The variation in the degree of salt tolerance of the diverse group of species halophytes achieves through differenttraits and life forms were recently emphatizes by Saslis-Lagoudakis et al. (2014).

Edaphic endemism in Mexico, determined by ecological factors, includes plants growing on saline, gypseous and saline-gypseous soils of the endorheic basins of the arid lands (Rzedowski 1991b; Henrickson 1977). For the Chihuahuan Desert, Henrickson (1977) proposed three genera and 25 endemic halophytic species. *Geissolepis* is a monotypic genus growing only in halophytic conditions; and *Strotheria* and *Pseudoclappia* are endemic to saline-gypseous flats of the Chihuahuan Desert. An important number of taxa of restricted distribution are considered as paleo-endemic in Pleistocene refuges (Rzedowski 1991a), and Moore et al. (2014) proposed that most gypsophile lineages first appeared no earlier than the latest Miocene.

Plants found in saline environments of Mexico are extremely diverse, including 10 species of Pteridophytes (Valdés and Flores 1987b), 10 gymnosperms (Valdés and Flores 1987a), and 647 angiosperms (Table 17.1). The families with more diversity in saline soils of Mexico are Poaceae (94), Asteraceae (86), Euphorbiaceae (64), Chenopodiaceae (61), Amaranthaceae (38), Boraginaceae (36), Fabaceae (32), Cyperaceae (27), Brasicaceae (22) and Cactaceae (21). The genera with more species in saline soils of Mexico are *Atriplex* (28), *Sporobolus* (17), *Croton* (17), *Amaranthus* (16), *Suaeda* (13), *Euphorbia* (12), *Bouteloua* (10), and *Heliotropium* (10). The wide range of angiosperm lineages of halophytes suggested that the adaptations involved in salt tolerance arised repeatedly in angiosperm evolution (Flowers et al. 2010).

The halophytes of Mexico include species of wide distribution, or endemic, restricted to salty habitats or not (Table 17.1). For example, *Sporobolus virginicus* has pantropical distribution in salt marshes and seacoasts;in Mexico it is found along both, the Gulf of Mexico and the Pacific coast in Baja California and Sonora. *Distichlis spicata* is found from USA to South America and survives in areas of fresh and salt waters. Other species of wide distribution not restricted to saline habitats are for example: *Aristida adscensionis*, *Croton leucophyllus*, *Lepidium perfoliatum*, *Sisymbrium irio*, *Viguiera dentate*, *Xanthium strumarium*. Examples of invasive weeds in interior saline soils are*Brassica rapa*, *Parthenium confertum*, *Parthenium incanum*. Introduced species native of Eurasia or Africa are amongst others, *Carpobrotus edulis*, *Mesembryanthemum crystallinum*, *Sonchus asper*, *Sonchus oleraceus*, etc. We include species commonly growing in coastal dunes, mangroves and/or salt marshes, but also in non saline habitats. For example, *Lonchocarpus guatemalensis*usually grows in tropical forest, but it is common in coastal dunes, near the sealine. Some species such as *Dalbergia brownei* (Jacq.) Schinz present in the borders of mangroves are not included, because they grow mostly in nonsaline environments. *Schoenoplectus acutus* var. *occidentalis* and *S. tabernaemontani*live along the Pacific coast of North America in fresh marsh communities, but also in saline marshes.

The list also includes parasitic species such as *Cuscuta salina* and *C. umbellata* growing on plants which occur in saline soils, such as *Atriplex*, *Polygonum*, *Portulaca*, *Sesuvium*, *Suaeda*, *Trianthema*, etc. An obligate parasite *Cassytha filiformis*, is found living in coastal dunes, mangrove, etc. This species has a pantropical distribution encompassing the Americas, Indomalaya, Australasia, Polynesia and East Africa.

The biogeographic relation of the halophytic flora of Mexico, to North America, Canada, the Caribbean, Central or South America is shown by some species. For example, *Gerardia maritima* occurs in salt marshes of W USA and Canada; the hemiparasitic *Cordylanthus maritimus*which grows in salt marshes and salt flats, is native to the SW USA and north of Baja California (Mexico). *Rachicallis americana* is known from the Caribbean and SE of Mexico on rocks and dunes near the sealine. *Ernodea littoralis*occurs on coastal dunes and other non saline habitats in Florida, the Caribbean region, Central America and South America. *Batis maritima* occurs on both Atlantic and Pacific coast, and the Caribbean.

Natural disturbed halophytic grasslands are invaded by species such as *Aristida adscensionis*, *Echinochloa crus-galli*, *Eleusine indica*or*Eragrostis mexicana*. Cultivated salinized lands in Tamaulipas are invaded by weeds such as *Avena fatua*, *Avena sativa*, *Cenchrus ciliaris*, *Croton cortesianus*, *Echinochloa colona*, etc.

3 Conclusions

In Mexico saline soils are found in coastal areas and inland either in arid or semiarid climates, but also along the volcanic belt. Besides the saline soils and other environments with sea water influence, there are saline-gypseuos soils supporting species edaphically restricted. We recorded 647 species of Angiorperms living in salty environmets of Mexico. The halophytic flora of Mexico has diverse geographical affinities to North America and Canada, the Caribbean, Central or South America, but also endemism. Halophytes include aquatic and parasitic species. Disturbed halophytic grasslands are invaded by weeds which also support saline soils. Further ecological research will provide understanding of the ability of the enlisted species to be considered as halophytes.

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Soil-Plant Relationships in the Sabkhat of America

18

Marcos S. Karlin

Abstract

In Sabkhat, plant ecology will depend on the soil characteristics, according to the type and dynamics of sediments and to water movement, dynamized by salt concentration and climate. Soil profile defines the ability of species to develop under its influence, according to critical variables such as soil salinity, water table depth and granulometry. Also, plant growth and development will depend on special physiological and morphological characteristics that are suited to extreme conditions in sabkhat. In America, sabkhat are the habitat of halophytic species, dwelling characteristic genera that can be found from the Columbia Basin to the Monte ecoregion. In this review soil conditions, plant characteristics and their interactions in saline basins of America will be discussed. Hydrology controls the sediment and solute chemistry, forming a dynamic cycle with halophyte vegetation. When the water table is depressed, deflation is enabled and medium-coarse particles are deposited over small hummocks, usually by the form of dunes or over tussocks, forming nabkhat. Aeolian dust may be responsible for the development and maintenance of plant communities along a salinity gradient towards the adjacent dunes in the periphery. Sabkhat hold an important pool of plant functional groups according mainly to soil salinity and water table depth. Such functional groups perform important ecological functions in the soil-plant-climate triad, such as soil formation, facilitation and zonation. These processes have a dynamic behaviour according to seasonality and climate interannual and decadal variability, assisted by anthropic impacts such as fire, overgrazing or even climatic change.

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M.A. Khan et al. (eds.), *Sabkha Ecosystems Volume V: The Americas*,
Tasks for Vegetation Science 48, DOI 10.1007/978-3-319-27093-7_18

1 Introduction

Evaporites receive different names according to their origin and many definitions have been made depending on their hydrogeological origin. Briere (2000) has compiled most of the used definitions around the world. In his paper he defines the concepts of *playa*, *playa lake* and *sabkha*. The difference between *playa* and *playa lake* is basically the amount of time the basin remains dry, defining more than 75 % of the time for playas and less of 75 % for playa lakes. Regarding sabkhat, he uses this definition for "*marginal marine mudflats*", with gypsum dissolutions dominating over halite dissolutions.

However, Barth (2001) disagrees in part with these definitions, including the inland features in the sabkha definition, differentiating playas and sabkhat according to their geological origin. What distinguishes inland sabkhat from playas, according to Barth, is that the first is exclusively aeolian in nature. These are "*located in large desert plains within unconsolidated sediments. They are not catchments of internal drainage like playas and flooding occurs only episodically and exclusively by precipitation*" (Barth 2001). According to this, playas are formed by both aeolian and water runoff particles, developed in more humid areas than sabkhat, characteristic of Middle East desert conditions.

Why is it so important to find the best definition of saline basins? From the biological viewpoint, the hydrogeological origin, and therefore the definition, is quite important to identify the main mechanisms that enable vegetation to install and develop on these geomorphic features.

Perhaps a better title for this chapter should be "Soil-plant relationships in the *playas* of America", considering that the term *sabkha* can be reserved for Middle East features, with specific climatic and hydrogeological dynamics, more suitable for hyperarid conditions. In terms of practicality, in this chapter both local (playa and salina) and foreign terms (sabkha) will be considered as synonyms, referring specifically to inland saline basins with no current marine influence, but considering hydrogeomorphic origins for each case, and differentiating them from the playa lakes.

In all cases, plant ecology will depend on the soil characteristics, according to the type and dynamics of sediments and to water movement, dynamized by salt concentration and climate.

Basically, the main variable that controls plant distribution and zonation is soil salinity (Richards 1954; Barbour 1970; Ozturk et al. 2006; Chedly et al. 2008; Karlin et al. 2012; Khan et al. 2014); nevertheless, other factors appear in the equation: depth of water table (Karlin 2013), pH (Reitemeier 1946; Richards 1954; Karlin et al. 2012), ions speciation (Reitemeier 1946; Richards 1954), granulometry (Karlin et al. 2012), apparent density (Karlin 2013), osmotic pressure (Sívori and Ragonese 1952; Richards 1954), nutriments (Blank et al. 1999), soil salinity spatial heterogeneity (Bazihizina et al. 2012), among others.

In America, sabkhat (or playas) ecosystems are the habitat of halophytic species, dwelling characteristic genera that can be found from the Columbia Basin (in the US) to the Monte ecoregion (in Argentina). The most commonly distributed genera along saline basins in America are *Heterostachys* (from South America), *Allenrolfea* (mostly in Mexico and Argentina), *Sarcobatus* (exclusive from US), *Atriplex* (also distributed in Middle East, Australia, western Europe, southern and eastern Africa,), *Suaeda* (also in eastern Africa and western Europe), *Sarcocornia* (also in southern Africa, south-western Europe and southern Australia), *Distichlis* (also in southern Australia) and *Sporobolus* (also in central Africa, eastern Australia and southern Asia).

In this review soil conditions, plant characteristics and their interactions in saline basins of America is discussed. First, hydrogeological characteristics are analyzed for the understanding of the dynamic behaviour of geoforms and soils, in order to understand the second part of this review, of why specialized plants evolved and adapted to such conditions. The last part of the review describes soil-plant (and climate) relationships in several sabkhat of the American continent, for the understanding of these ecosystems from the structural and dynamic point of view, as sources of important natural resources for local dwellers' social reproduction.

2 Hydrogeological Behaviour

Topographically, all these features are essentially endorreic basins, with flat surfaces, with (e.g. Mono Lake; Great Salt Lake, US) or without (e.g. playas of western Texas, US; Salar de Uyuni, Bolivia; Salinas Grandes; Argentina) permanent water deposits (Williams 2002; Yechieli and Wood 2002; Karlin 2010). Hydrology controls the sediment and solute chemistry, forming a dynamic cycle with halophyte vegetation. Water level usually varies seasonally, annually (Yechieli and Wood 2002) or pluriannually, but in playas, water table usually allows soluble salts to crystallize, forming a layer of salts of variable thickness (Ragonese 1951). Water regulates both physical and chemical dynamics.

2.1 Physical Dynamics

Sediment movement and deposition depends both on aeolian and runoff processes. There is often a dynamic equilibrium between the surface of the ground-water table and wind occurrence. Wind will remove soil particles and minerals depending on direction, velocity and water table depth. When water table rises and intersects the surface, wind cannot remove particles and deposition by runoff is enabled, predominating fine particles such as clay and line silt. When the water table is depressed, deflation is enabled and medium-coarse particles such as fine sands or coarse silt is deposited over small hummocks, usually in the form of dunes (Shaw and Bryant 2011) or over tussocks, forming nabkhat (Gutiérrez Elorza 2008). The evidence of nabkhat (another Middle East term that can be replaced by the term "vegetated dune") means that tussocky vegetation plays an important role in the formation of these features.

Such dynamics may produce heterogeneous salinity patterns, both horizontally and vertically, conducting to areas with more or less saline concentration in the surface and in depth, where plants will develop their rooting system according to water availability and quality, and mechanical resistance (Bazihizina et al. 2012).

Aeolian dust may be responsible for the development and maintenance of plant communities along a salinity gradient towards the adjacent dunes in the periphery. Blank et al. (1999) studied the dust flux in Eagle Valley playa (Nevada, US) and found an important flow of nutriments from deflation processes. Depending on the year and month, nitrate-N, sulphates, sodium, potassium and boron levels are usually higher in playas than in beaches and dunes, forming a negative gradient; ammonium-N and oxalate (this last blown from halophyte tissues, and carrying calcium) levels present a positive gradient towards dunes. According to these authors, possible changes in the playa hydrology might have produced a depression in the water table, enabling a greater entrainment of salt efflorescences, and these might have triggered a rising in the dust and nutriment fluxes, allowing the species *Salsola paulsenii* to invade, probably due to an increase in concentration of nitrates. Dust and mineral fluxes modify soil conditions along a salinity gradient, depending on the depositions and according to plant's soil adaptations and competition ability (Blank et al. 1999; Karlin 2013).

2.2 Chemical Dynamics

The most important solute input is that of deep ground water. Depending on the ionic composition of the sediment and brine waters, different salt depositions can occur and therefore, it can affect the development of different kinds of plants. Salt movement along the capillary layer depends on the solubility of salts. Capillary water movement lifts the ions towards the surface, triggered by evaporation and transpiration, incrementing ion concentration and causing precipitation according to salt solubility.

Carbonates usually precipitate first, followed by sulphates and chlorides at last, depending on the brine temperature. It is expected that during summer time, gypsum, anhydrite and calcite will precipitate in the capillary zone because high temperatures decrease solubility of these minerals. On the opposite, during winter time sodium salts and magnesium chlorides can precipitate as they become supersaturated (Yechieli and Wood 2002).

If the capillary fringe reaches the surface, a sodium chloride layer of variable depth is usually seen, acting as a barrier for aeolian soil erosion.

When rain occurs, salt crusts are dissolved, elevating electrical conductivity and reducing water activity. This reduction in the water activity drastically reduces evapotranspiration rates, and in hypersaline basins there might be "negative evaporation". According to Yechieli and Wood (2002), if water activity were lower than the relative humidity of the atmosphere, water would be transported from the atmosphere to the brine. This phenomenon is commonly seen as a sector of clear skies over the basin when the surroundings are covered by clouds.

Soil pH on dilution is well known. It is very common that pH values are increased by water inputs, enabling mineral hydrolysis when the exchangeable base complex is sodium rich. pH may increase over one pH point when this happens, affecting biochemical processes in soil and in plant. If soils are gypsum or calcite/dolomite rich, these minerals might repress hydrolysis by replacing Na^+ for Ca^{++} into the exchangeable base complex (Reitemeier 1946) through Gapon's Dilution Effect; OH^- concentrations in the soil solution does not increase notably by this effect.

It is also well known that ion concentrations are usually increased by the dissolution of minerals in saline/arid soils, depending on the dominant mineral (Reitemeier 1946).

As said before, high salt concentrations produce a reduction of the water activity and an increase of osmotic pressures. Knowing the relation between osmotic pressure (OP) and electrical conductivity (EC) is useful for agronomic purposes. The osmotic pressure of the soil solution is closely related to the rate of water uptake and growth of plants in saline soils. The osmotic pressure (OP) of solutions expressed in atmospheres is usually calculated from the freezing-point depression (ΔT) in °C (Richards 1954).

The relation between the electrical conductivity and the salt content of various solutions depends on the solubility of the salts and the amount of chemical equivalents per mole. For the chloride salts and Na_2SO_4, the relation between OP and EC is mainly the same, but $MgSO_4$, $CaSO_4$, and $NaHCO_3$ have lower conductivities than the other salts at equivalent concentrations. This means that for the same EC, soils with higher concentrations of alkaline earth salts (except for chlorides and nitrates) present less osmotic pressure than those rich in soluble salts such as chlorides (Figs. 18.1 and 18.2) (Richards 1954).

The relation between OP and EC for salt mixtures, determined in different saline soils in the US, is indicated in Fig. 18.2 (Campbell et al. 1948). The relation $OP = -0.36\ EC$; where OP is measured in bars or atmospheres (approximately, since 1 bar = 0.987 atm), (EC is measured in mmhos/cm or dS/m); can be used for estimating the osmotic pressure of soil solutions from conductivity measurements (Richards 1954). This means, for example, that a saline soil that gives an EC value of 20 dS/m, present −7.2 atm of suction. However, this function is useful for low values of EC; for larger values the function should be adjusted by an exponential factor of approximately 1.055, as shown in Fig. 18.2.

3 Plant Behaviour

Obligate halophytes, facultative halophytes, succulents and glycophytes are terms applied to plants more or less suited to grow under different saline conditions; nevertheless the definitions for these terms are not quite clear.

Usually, obligate halophytes are defined as plants that live normally in saline habitats by accumulating high amounts of ions in their tissues. Barbour (1970) defines a threshold of 0.1 % concentration of NaCl in soil extract (about 2 dS/m of electrical conductivity), above which halophytes can grow successfully with no apparent reduction of growth, until they reach a superior threshold depending on the species. For obligate halophytes, mechanisms for salt

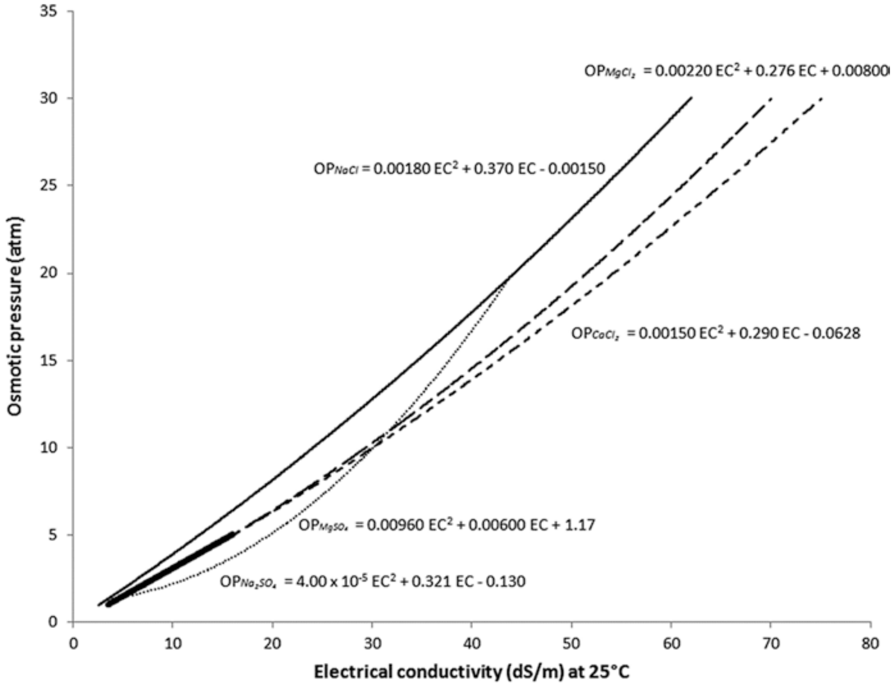


Fig. 18.1 Osmotic pressure of single-salt solutions as related to the electrical conductivity (Modified from Richards 1954)

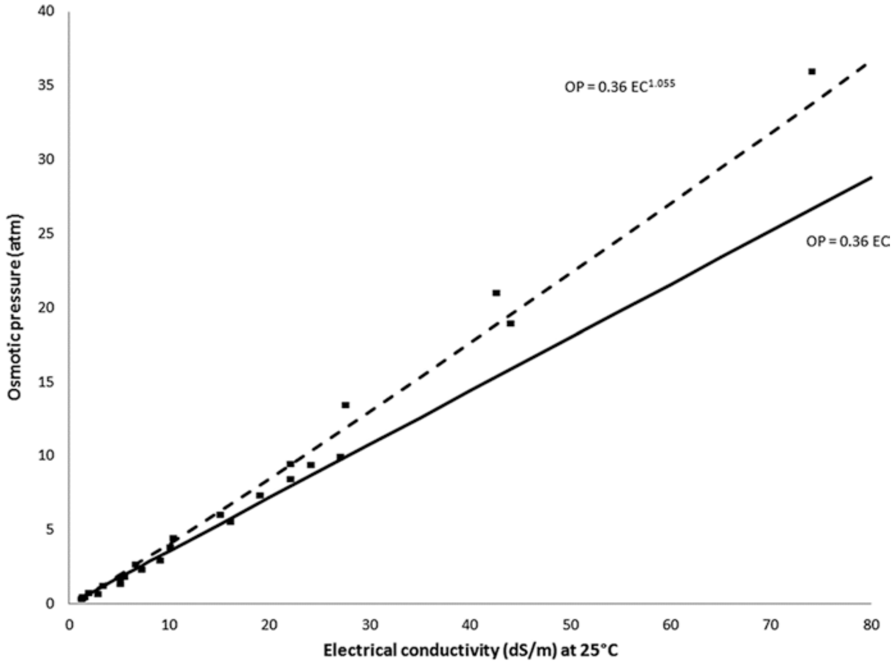


Fig. 18.2 Osmotic pressure of saturation extracts of soils as related to the electrical conductivity (Modified from Richards 1954)

tolerance are twofold: those minimizing the entry of salt into the plant, and those minimizing the concentration of salt in the cytoplasm (Munns 2002).

Facultative halophytes are usually defined as plants that cannot accumulate high amounts of salts in their tissues, but they are able to adapt through other physiological strategies such as salt extrusion (e.g. *Distichlis spp.*).

Glycophytes are those plants that usually grow under fresh water environments and do not have the ability to exclude salt, concentrating to toxic levels in the transpiring leaves (Munns 2002). Such species can develop under saline conditions up to a certain threshold (Porter 1982; Barbour 1970) by producing polysaccharides or amino acids that may, in part, elevate the osmotic pressure. Mesophytes and non-halophytes are included into this definition.

Available soil water can be expressed in terms of water potential which is a measure of the retention force of water by the soil and therefore, the pressure the plant should apply to extract water from the soil. The osmotic potential is the force that soluble salts make over water, and therefore, high ionic concentrations mean high water pressure (Ayers and Westcot 1985). Osmotic potential is added to soil moisture tension (matric potential), which is increased by the desiccation of the soil. Both (jointly with the gravitational potential which, in saline basins, turns to be null by the water table raising) represent the total water potential that plants should beat for water absorption. According to Abrol et al. (1988), in very strongly saline soils (EC above 16 dS/m), with a superficial water table, the soil moisture tension turns to be negligible compared to osmotic potential.

Salts entering the plant with the transpiration stream will be left behind in the leaf intercellular fluids as water evaporates from the leaf. Salts entering the cytoplasm in high concentrations may disrupt the enzymatic functioning (Comstock and Ehleringer 1992).

In order to develop and survive, plants have to apply some morphological and physiological strategies for the success in the water absorption.

3.1 Obligate Halophytism

Under very strong salinities, some plants can develop physiological strategies that may counteract the high osmotic pressures produced by soluble salts in soil. One of these strategies is the elevation of the plant osmotic pressure in the cellular juices, surpassing those values obtained by mesophytes. Mesophytes usually present osmotic pressure values lesser than 25 atm, while the highest values have been obtained for the genera *Sarcocornia*, *Batis* (Scholander et al. 1966) and *Atriplex* (Sívori and Ragonese 1952) with 105, 102 and >130 atm, respectively.

Halophytes are characterized by the strategy of compartmentalization in vacuoles of salts (usually NaCl) that inevitably get into the plant, complementing mechanisms of prevention in the entrance of soluble salts through the root system (Munns 2002). However, Barbour (1970) concludes in his paper that there is no real "obligate halophyte" because such species may be able also to grow under fresh water conditions and behave as glycophytes, but only if competition with other plants is not deleterious. Medina et al. (2008) define the obligate halophytes or halophytes *sensu stricto* as those species which present a *K*/*Na* ratio in tissues lesser than 0.1, positively correlated with those species with succulent photosynthetic organs. Succulent species of the saline coasts of Venezuela as *Heterostachys ritteriana*, *Batis maritime*, *Sarcocornia perennis* and *Sesuvium spp.* are considered by these authors as obligate halophytes, presenting the highest Na concentrations, superior to 4000 mmol/kg (92 g Na/kg).

In Salinas Grandes, Central Argentina, some "halophyte-supposed" species, such as *H. ritteriana* and *Allenrolfea patagonica*, have presented intermediate values of osmotic pressures measured over vegetable saps (between 38 and 58 atm the first, 66–76 atm the second) as measured by Sívori and Ragonese (1952). These values are by far, lower than those in *Atriplex argentina* (growing under less saline condition in the same region), despite the fact that *H. ritteriana* and *A. patagonica* grow under hypersaline conditions and they are the first visible species observed in the core of Salinas Grandes. These differences have been explained by the fact that in the "pickleweed" or "jume" communities (*Heterostachys*, *Allenrolfea*, *Sarcocornia*), soils are usually saturated with water and this is permanently available in the rooting zone. As a consequence, plant water potentials do not reach the extreme low values of the saltbush (*Atriplex*) communities (Comstock and Ehleringer 1992).

In Salinas Grandes, pickleweeds grow in calcic Aquisalids and gypsic Haplosalids, with soil ECs between 20 and 85 dS/m, measured in a soil/water ratio of 1:1 (Karlin et al. 2012). This means that EC in a saturated paste should be between 45 and 200 dS/m (applying a 2.3 factor of conversion), and therefore, should mean approximate osmotic values between −17 and −70 atm of osmotic potential in the soil. Evidently, osmotic pressures in plant tissues should not be enough for water absorption in some cases, and these species might present other physiological strategies to do so, such as the production of organic osmolites.

Succulence is correlated with the total water potential in halophytes; however, according to Gul et al. (2001), succulence might increase by the rising of matric potential, when there is low availability of water, better than an increase of salinity in soil, studied over communities of *Allenrolfea occidentalis* in Utah. Soil osmotic pressures oscillate through wide limits depending on climatic conditions along the seasons. Soil salinity is usually higher after the rainy season because soluble salts are dissolved in the soil, increasing salt concentrations, while it is lower during the dry season when salts precipitate in the form of crystals.

Plants transpire 30–70 times more water that they use for cell expansion, depending on environmental conditions. Such transpiring concentrates the salts into the cells, increasing osmotic pressure. Halophytes have the ability to filter salts by the root system (e.g. *Krascheninnikovia lanata*), allowing the entrance of only 2 % of the total amount of salts in the soil solution, avoiding the excessive concentration of salts in the plant cells. Over time, older leaves have higher salt concentrations, killing it (Munns 2002) and destining photoassimilates to new tissues.

Soils with high concentrations of alkaline earth metals help the plants to counteract the accumulation of Na in tissues, allowing the plant growth under higher salinities (Medina et al. 2008).

3.2 Facultative Halophytism

The most important physiological strategies in these species are the K^+/Na^+ exchange mechanism.

The genus *Distichlis* is mentioned by Chapman (1936) and Hansen et al. (1976) as a plant with salt-excreting glands. Sodium, potassium and chloride are the main ion compounds in their tissues. Concentrations of these ions are parallel to the concentration of the same ions in the subsurface layer of the soil (Hansen et al. 1976). Such concentrations are related by the changes produced by leaching effects over soil, thus, when soil is washed out, ion concentrations are reduced, and plants copy this behaviour by reducing the salt concentration in tissues. Nevertheless, as seen in the analysis by Reitemeier (1946) in "*chemical dynamics*" subsection, such concentrations will depend on the reposition by the dynamics of the soil exchange complex.

As tissues begin to decline, concentrations of Na^+ and Cl^- tend to increase and K^+ declines as a response of the reduction of the functioning of the salt excreting glands (Hansen et al. 1976).

A way for identifying species with this mechanism is comparing the *K*/*Na* relation in tissues with the *K*/*Na* relation in soil, as studied by Medina et al. (2008; Fig. 18.3). Species with ratios superior to 10 might indicate Na excreting or exclusion mechanisms.

According to Fig. 18.3, *Chamaesyce mesembryanthemifolia* and *Scaevola plumieri* should have extrusion mechanisms for sodium or mechanisms for sodium and potassium selection through the roots.

Organic osmolites are usually produced by facultative halophytes as a strategy of exclusion

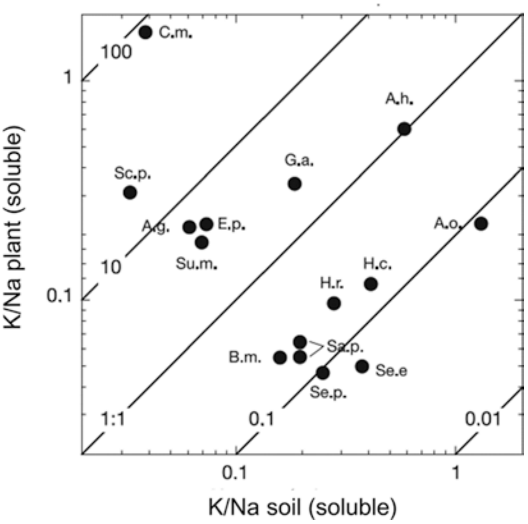


Fig. 18.3 Variation in the relative concentration of K with respect to the total availability of K and Na in soil. *Diagonals above* indicate accumulation factors of 10 and 100; *diagonals below* indicate a reduction in *K* regardless to *Na*. A.g. *Argusia gnaphalodes*, A.h. *Althernanthera halimifolia*, A.o. *Atriplex oestophora*, B.m. *Batis maritima*, C.m. *Chamaesyce mesembryanthemifolia*, E.p. *Egletes prostrata*, G.a. *Gomphrena albiflora*, H.c. *Heliotropium curassavicum*, H.r. *Heterostachys ritteriana*, Sa.p. *Sarcocornia perennis*, Sc.p. *Scaevola plumieri*, Se.p. *Sesuvium portulacastrum*, Se.e. *Sesuvium edmondstonii*, Su.m. *Suriana maritima* (Extracted from Medina et al. 2008)

of Na^+ and Cl^- into the vacuoles, balancing (jointly with K^+) the osmotic pressure of such cells. According to Munns (2002) the most common organic osmolites are proline, glycine betaine and sucrose. Apparently, this mechanism may occur in all three kinds of life forms (obligate and facultative halophytes, and glicophytes).

There are also contributory mechanisms that promote low rates of salt accumulation in leaves: high shoot:root ratios and high intrinsic growth rates, reducing the rate at which salt enters the transpiration stream and accumulates in the shoot (Pitman 1984; Munns 2002).

Another mechanism is the exclusion of Na^+ and Cl^- from the phloem sap, reducing retranslocation of salts into the plant (Munns 2002) and avoiding the "contamination" of younger tissues.

3.3 Glycophitism

Low osmotic pressures in vegetable saps are found in Cactaceae, presenting similar values to those of mesophytic species (Sívori and Ragonese 1952). The resistance of these plants to the lack of water lies in the imbibition pressure due to mucilages, and this physiological mechanism has nothing to do with the halophytic succulence mechanism (Ogburn and Edwards 2010). Another compound founded in cacti under water and salt stress is; as happens in facultative halophytes; proline (Silva-Ortega et al. 2008), acting as an osmoprotector, and as a protein and a cell membrane stabilizer. Under this category it is also possible to find calcium-phobic species if the soils contain important concentrations of this ion. Apparently, roots can select Ca^{++} over Na^+ from soils, avoiding the accumulation of Na in the tissues at toxic levels (Medina et al. 2008).

3.4 Other Strategies

3.4.1 C$_4$ Pathway

The C$_4$ metabolic pathway is often associated with plants from saline soils. Such pathway overcomes photorespiration, has higher temperature thresholds for photosynthesis and presents greater water-use efficiency under high salinity conditions reducing salt flux into the tissues. There are some halophytic genera with the C$_4$ mechanism such as many *Atriplex* species, some *Suaeda* bushes (Chenopodiaceae) (Sage et al. 2011) and grasses like *Distichlis* and *Sporobolus* (Poaceae), growing in moderate and highly saline soils. Species such as *Alternanthera* and *Heliotropium*; both with species growing under saline conditions; present intermediate C$_3$–C$_4$ metabolic pathway (Vogan and Sage 2012).

Photorespiration is strongly induced by salt stress in C$_3$ but not in C$_4$ and CAM plants. It has been estimated that photorespiration produces an important reactive oxygen species (ROS) such as H_2O_2, produced under osmotic stress. This means that photorespiration is expected to be the major source of ROS under salt stress. ROS is responsible for causing oxidative damage to various components of living cells including lipids, proteins and nucleic acids. C_4 plants should produce less ROS under salt stress as compared to C_3 plants; however, studies have not been conclusive (Abogadallah 2010).

3.4.2 Polyploidy and Genetic Variability

Polyploid species of *Atriplex* are reported as drought resistant in clayey, saline soils. Some adapted polyploids may suggest adaptive edaphic differences among cytotypes, which is due, at least in part, to their differences in xylem water transport efficiency and resistance to drought-induced hydraulic failure. Polyploid cytotypes can produce larger leaves, but are ephemeral, and maintain lower water conductivities rates, far below their capacity during most periods of the year, and only reaches high values during rainfall pulses (Hao et al. 2013).

Spartina species in salt marshes can also develop polyploid cytotypes. Duplication of genes may improve transcription factors, heat shock protein and cytochrome *c* oxidase that have been found to respond to salt and oxidative stress (under waterlogged conditions) by balancing ion concentrations in the species (de Carvahlo et al. 2012).

Plants developing under hypersaline conditions may reproduce either by seeds or clonally. Some species have the ability to recombine genetically, e.g. *Atriplex spp*., obtaining a heterogeneous genetic pool through seed recruiting in order to produce heteromorphism that allow species to widen the survival spectra. However, a genetic line; proved to be successful under determined environment conditions; may be able to make copies of the best suited genotype (Gul et al. 2013), e.g. the stoloniferous *Lippia salsa* in saline basins of Argentina.

3.4.3 Phenological Adjustments

It appears that some halophyte species have adapted their phenological phases according to salinity dynamics and climate conditions. Seeds of halophytes in the temperate environment usually mature during the late fall and undergo a period of dormancy. Seeds will be activated when soil saline concentrations are below certain threshold and temperatures are adequate for the appearance and survival of seedlings (Gul et al. 2013).

It has been found that Chenopodiaceae in Salinas Grandes (Argentina) produces flowers and fruits in autumn (end of the rainy season, after the precipitation of 330 mm of rainwater), differentiating from the rest of the botanical families (which flowered in spring and early summer). All considered Chenopodiaceae species were halophytes and it was observed that these set back flowering and fruiting according to the development of the species regarding soil salinity. Flowering is inversely related to soil salinity; i.e. *Heterostachys ritteriana*, growing in the centre of the saline basin, is the species with the latest flowering, followed by *Allenrolfea patagonica*, *Suaeda divaricata* and *Atriplex argentina*, this last growing under intermediate salinity.

It can be suggested that halophyte species might set back flowering as response to the amount of water accumulated in the profile, freeing the fruits when soil saline concentration is lower after the rainy season, soil salinity is reduced from an average value of 65 dS/m (1:1) to an average value of 50 dS/m (1:1) (Karlin et al. 2010).

Other studies by Gul and Weber (2001), regarding *Allenrolfea occidentalis* in colder and dryer saline inlands, in the Great Basin, also report that this species produces fruits during autumn after the second annually peak of precipitations. Nevertheless, seeds have the ability to remain dormant in the seed bank until soil conditions are adequate, i.e. soil is leached or salinity is reduced down to 800 mM of NaCl (around 73 dS/m over saturated paste).

3.4.4 Morphological Mechanisms

Apart from physiological and genetic mechanisms, it is possible to find some morphological characteristics between saline-growing plants that help such species to grow under high saline conditions and under saturated soils.

Atriplex spp. have specialized hair-bladders on the leaf surface into which salts are excluded from the plant saps. Hairs eventually rupture excreting salts to the exterior of the leaves, and they may be washed out from the leaves by rainfall adding salts to the soil surface, or even added by leaf abscission (Comstock and Ehleringer 1992).

Distichlis genus has aerenchymatous tissues in roots, allowing gas exchange through the plant-atmosphere interface during brief periods of partial inundation by water. This species can grow marginally in soils with low water saturation, producing a root network that permits the expansion of the species by rhizomes of the species towards saturated soils. This behaviour also permits the plant to extract nutrients and less saline water and to retranslocate these to extreme portions of the network, avoiding high osmotic pressures (Hansen et al. 1976; Young et al. 1986). In addition, the accumulation of silica cells in the tip of the rhizome, allows salt grass to penetrate heavy clays and shales as a natural subsoiler (Hansen et al. 1976).

The expansion by rhizomes allows the colonization of saline and inundated playa soils, and the production of aerial shoots form a natural barrier for sediment particles, forming saline hummocks which accumulate salts on the top by capillarity, reducing salinity in subsurface layers. New roots may be able to grow under these new soil conditions, repeating the process (Hansen et al. 1976; Karlin et al. 2011).

Similar processes occur through "mutualism" actions. The installation of halophyte species in very strongly saline soils, form a physical barrier against sedimentary particles, forming a silty-sandy layer of variable depth which cuts capillarity, avoiding the ascent of soluble salts to the surface. After the formation of a sandy topsoil layer, superior to 6 cm (Karlin et al. 2012; Karlin 2013) some tree-like cacti such as *Stetsonia coryne*, can grow with lesser concentrations of salts by the development of a superficial root system (Fig. 18.4). Rainfall can leach the topsoil, reducing soil salinity and enabling cacti to develop. This species can use the rainfall's fresh water without absorbing salty water from the subsoil.

High water potentials throughout the xylematic system usually reduce hydraulic conductivity per unit cross-sectional area. This problem may be ameliorated by increased cross-sectional area of the xylem by increased allocation to wood growth (Comstock and Ehleringer 1992), i.e. stem length is reduced at the expense of diametric growth.

Fig. 18.4 Sand "step" from a very strongly saline soil (in the *front* of the image). On the back, a community of *Stetsonia coryne* on a thin layer of fine sand and silt

3.4.5 Life Forms

Hypersaline halophyte communities are often dominated by hemicryptophytes and succulent chamephytes, and generally lack therophytes due to high soil osmotic potentials, therefore it is very rare to see annual species in these communities. Some bulb geophytes (e.g. *Zephyranthes spp*.) may act as annual species, with sporadic appearances in highly saline soils. Nanophanerophytes are also rare in these communities, perhaps due to their low tolerance to salinity as seen in the Salar of Ascotán (northern Chile) by Teillier and Becerra (2003). Nevertheless, phanerophytic vegetation is common in zones with intermediate salinity (~5 to ~35 dS/m 1:1 soil-water ratio) (Karlin 2013). Therophytes appear in the dunes with sufficient low salinity levels in soil and plant cover, in order to germinate during warm and rainy season.

4 Soil-Plant Interactions

Soil profile defines the ability of species to develop under its influence, according to critical variables. Those variables are mainly soil salinity, water table depth and granulometry of soil horizons. Also, plant growth and development will depend on special physiological and morphological characteristics that are suited to extreme conditions in sabkhat.

In saline systems, plants must use high energy (energy of high quality) reserves to equate the soil osmotic potential in order to absorb water. In these cases, soluble salts constitute an impediment to plant biomass formation, increasing the system's entropy (energy of low quality) (Karlin et al. 2011).

The presence of soluble salts in soils generates adverse conditions for unadapted species, reducing the total amount of biomass in the sub-system and, therefore, its energy. This biomass reduction is related to a decrease in richness and biodiversity.

Spatial changes in sabkhat are correlated to geomorphological processes (Méndez 1993). It is common to find gradients of salinity, water table depth and granulometry according to topographic changes from the centre of the basins towards peripheral non-halophyte vegetation belts. Dunes, tussocks of coppice mounds are characteristic features included into the saline matrix, conforming biodiversity islands that are important as flora and fauna habitats, and result in critical products for the local dwellers through the exploitation of grass, wood or non-timber forest products (Karlin et al. 2009).

Chenopods are the most common species in high saline salt pans, forming clumps where litter-fall enhances seedbeds that support germination and seedling establishment. The recruitment of seedlings may be conditioned by episodic climatic events and changes in saline concentrations in the supporting mounds (Young et al. 1986). Such mounds or hummocks may reach extremely high saline concentrations like 400 (Young et al. 1986) to 550 dS/m (Karlin 2013) in the saturated paste.

Karlin et al. (2012) studied in Salinas Grandes (central Argentina) that the accumulation of coarser particles above the capillary fringe, with the consequent dominant macroporosity, breaks capillary rise, reducing the evaporation rate and maintaining the profile with higher amounts of sub-superficial water. Water migrates through the superficial layer as vapour during the day, followed by night condensation, producing a wetter environment with less salt concentration due to a process of natural distilling (Ruiz Posse et al. 2007). This process enables the growth of few halophyte species, increasing plant cover (Fig. 18.5), biodiversity (Fig. 18.6) and minimum rangeland requirement (Fig. 18.7).

The species found over dunes may depend on its depth and local climate. In semiarid regions it might be possible to find woody species, while in arid or hyperarid regions these might be occupied by xerophytes.

Dunes may not only be fixed by plant cover, but by biocrusts that can develop in the upper few centimetres of the soil, healing uncovered areas. Such biotic crusts formed by cyanobacteria, algae, bryophytes, fungi and lichens (Comstock and Ehleringer 1992; States and Christensen 2001), might even improve the soil by nitrogen fixation (Barger et al. 2013), carbon fixation and

Fig. 18.5 Box plot graph for plant cover (Cov) ($m\ m^{-1}$) in the zones. ANOVA test. Different letters indicate significant differences ($n = 24$; LSD Fisher $p < 0.05$). *Dots* represent mean values; *solid lines*, medians; *boxes* extremes, 25th and 75th percentiles; *whiskers*, 5th and 95th percentiles. *VS* Vegetated Salinas, *WP* Waterlogged plains, *SAF* Saline Affected Forests, *SSAF* Slightly Saline Affected Forests, *D* Dunes (Taken from Karlin et al. 2012)

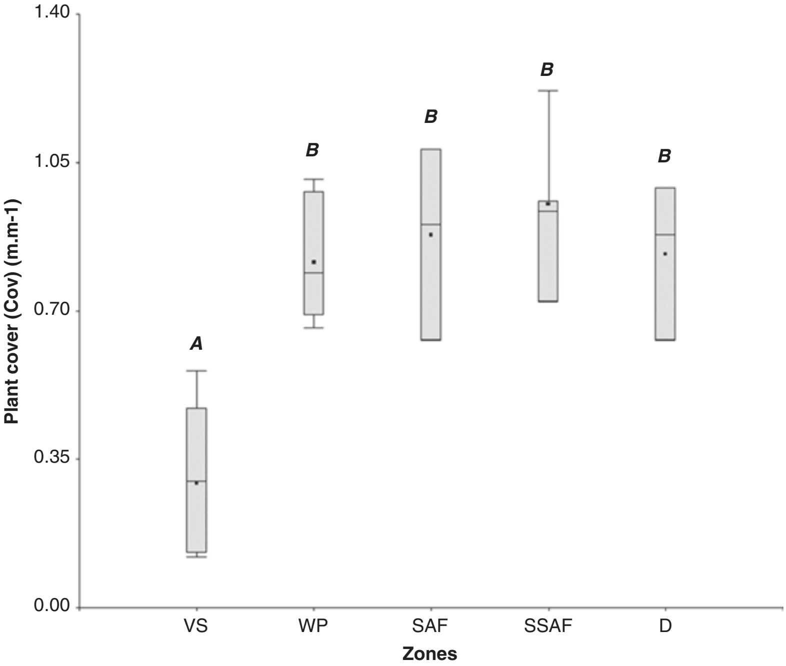
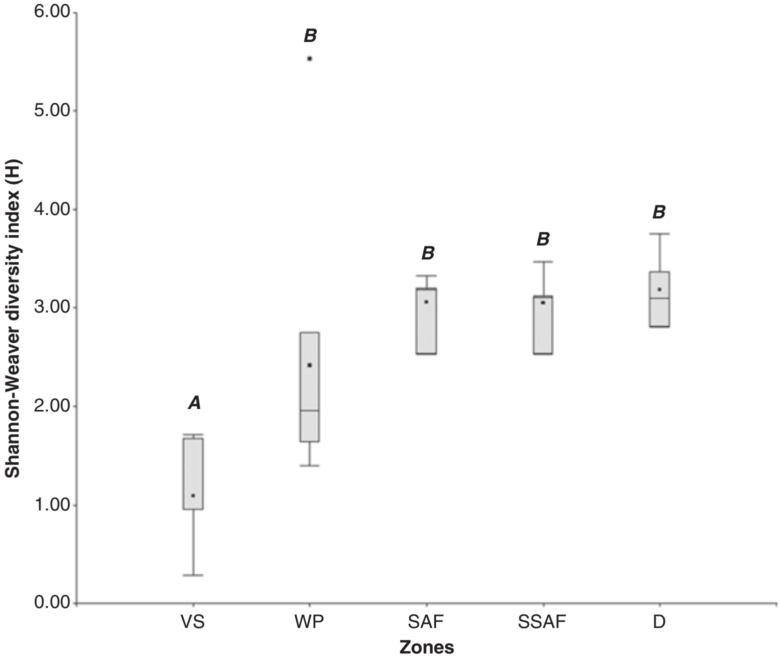


Fig. 18.6 Box plot graph for Shannon-Weaver diversity index (H) in the zones. ANOVA test. Different letters indicate significant differences ($n = 26$; LSD Fisher $p < 0.05$). *Dots* represent mean values; *solid lines*, medians; *boxes* extremes, 25th and 75th percentiles; *whiskers*, 5th and 95th percentiles. *VS* Vegetated Salinas, *WP* Waterlogged plains, *SAF* Saline Affected Forests, *SSAF* Slightly Saline Affected Forests, *D* Dunes (Taken from Karlin et al. 2012)



may reduce water evaporation (Coe et al. 2012), preparing soil for the colonization of vascular plants.

The colonization of dunes and saline areas can be enabled by nursing of specialized species or through dispersion and facilitation by animals. The first mechanism can perform beneficial effects by shading, soil construction (as a barrier to soil particles; Fig. 18.8), moister conditions in the surface layers or litter accumulation

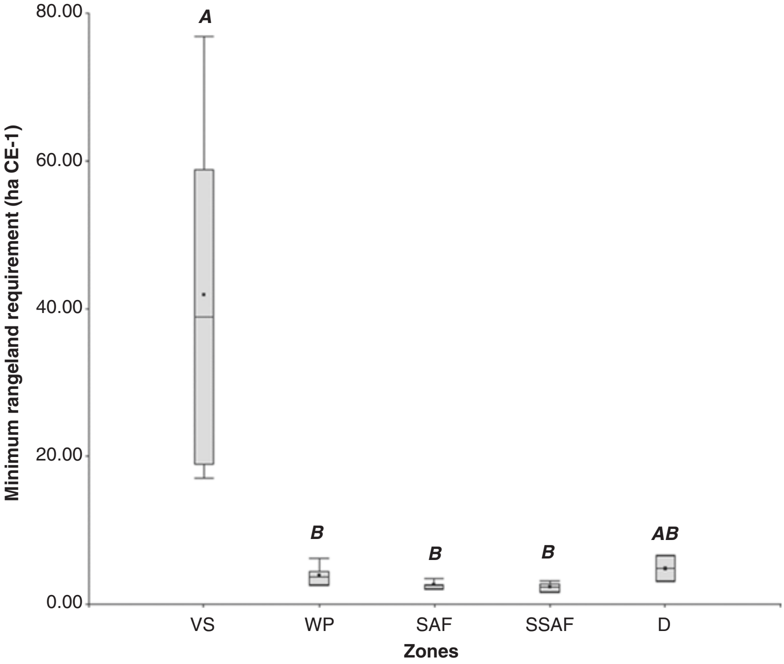


Fig. 18.7 Box plot graph for minimum rangeland requirement (MRR) (ha CE^{-1}) by sub-environment. Kruskal-Wallis test. Different letters indicate significant differences (n = 24; pair comparison, $p < 0.05$). *Dots* represent mean values; *solid lines*, medians; *boxes* extremes, 25th and 75th percentiles; *whiskers*, 5th and 95th percentiles. *VS* Vegetated Salinas, *WP* Waterlogged Plains, *SAF* Saline Affected Forests, *SSAF* Slightly Saline Affected Forests, *D* Dunes (Taken from Karlin et al. 2012)

Fig. 18.8 Tussock acting as runoff barrier (Salinas Grandes, central Argentina). The species shown in the figure are *Heterostachys ritteriana*, *Plectocarpa tetracantha*, *Prosopis reptans*, *Tephrocactus articulatus*

(Comstock and Ehleringer 1992). The second mechanism will enable the conditioning (e.g. tegument softening by the digestive tract flow) and dispersion of seeds to wider areas, and these can be deposited in different zones protected with dung, offering the seed adequate moisture conditions and available nutriments; this way, the seeds may avoid direct contact with salts and can imbibe more easily (Fig. 18.9).

Although nursing helps some species to establish under adverse conditions, it does not always produce a positive effect over other species.

Fig. 18.9 Emergence of *Prosopis reptans* seedlings in cow dung, over hypersaline soil conditions (Salinas Grandes, central Argentina)

Rickard (1965, in Young et al. 1986) demonstrated that the litter of *Sarcobatus vermiculatus* in saline mounds increases salinity on the surface to the point of excluding reproduction of *Artemisia tridentata* in the Columbia Basin (US).

According to biodiversity data (Fig. 18.6); despite that only very highly saline zones (VS in the figure) differentiate from other zones; higher values are observed for dunes probably because these zones appear as patches inside the saline basin, but present forest physiognomy, with larger floristic richness. This allows a higher potential forage and forest use, making them very important zones for silvopastoral use (Karlin et al. 2009) and function as buffer areas for forestry and grazing activities.

Biodiversity (*H*) and minimum rangeland requirement (*MRR*) in Salinas Grandes are strongly related to total salinity, represented exponentially by average electrical conductivity (EC_{av}) between humid and dry seasons, as shown in Eqs. (18.1) and (18.2) (Karlin et al. 2012).

$$H = 3.22 * \exp\left(-0.0213 * EC_{av}\right)\left(\mathrm{R}^2 = 0.66\right) \quad (18.1)$$

$$MRR = 2.23 * \exp\left(0.0471 * EC_{av}\right)\left(\mathrm{R}^2 = 0.89\right) \quad (18.2)$$

Predominant salinity in a saline patch enables the development of more or less halophyte communities. Such species can be classified as decreasers, increasers and invaders, according to its behaviour depending on soil electrical conductivity (Dyksterhuis 1949).

In Fig. 18.10, Karlin et al. (2011) have classified and defined different dominant populations in Salinas Grandes, in relation to a growing salinity gradient as communities. These are "increasers" (communities of *Heterostachys ritteriana*), "intermediate" (communities of *Cyclolepis genistoides*, *Atriplex argentina* and *Stetsonia coryne*) or "decreasers" (communities of *Mimozyganthus carinatus*, *Larrea divaricata* and *Aspidosperma quebracho-blanco*).

Accompanying species of *H. ritteriana* are *Allenronfea patagonica* and *Distichlis acerosa*; *Atriplex argentina* may be accompanied (among other species) by *Suaeda divaricata*. The distribution of halophyte species in Salinas Grandes shows remarkable similarities with those reported by Comstock and Ehleringer (1992), who also found species of *Distichlis* and *Allenrolfea* (*D. spicata* and *A. occidentalis*) in hypersaline zones of the Great Basin, and *Atriplex* (*A. confertifolia*) and *Suaeda* (*S. suffrutescens*) in moderately saline soils. The last two genera are usually found in areas where soils are notably saline in the lower half of the rooting zone, but less in the upper soil layers, and lack of long term flooding

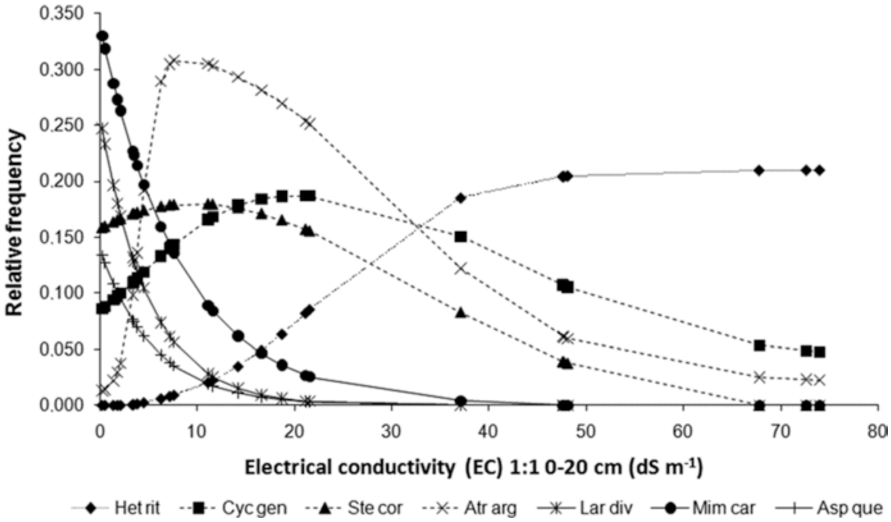


Fig. 18.10 Relative frequency curves in relation to soil electrical conductivity (EC). *Heterostachys ritteriana*: Het rit, *Cyclolepis genistoides*: Cyc gen, *Stetsonia coryne*: Ste cor, *Atriplex argentina*: Atr arg, *Larrea divaricata*: Lar div, *Mimozyganthus carinatus*: Mim car, *Aspidosperma quebracho-blanco*: Asp que (Taken from Karlin et al. 2011)

(Comstock and Ehleringer 1992; Karlin 2013). Outside saline areas, Comstock and Ehleringer (1992) also found species of *Larrea tridentata*, closely related phylogenetically to *L. divaricata* in the south, and both characteristic features from arid and semiarid regions in US, Mexico in the north, and Argentina, Bolivia and Peru in the south. This analogy shows the specialization of some genera distributed along the hypersaline and desert areas of the Americas.

4.1 Climate Change and Sabkhat Dynamics

Sabkhat, playas, pans or salinas have suffered the ups and downs of climate change all through the history. Playas in the American continent are not the exception and the study of changes in vegetation due to climate changes can be interesting antecedents for future climate modifications.

Saline basins alternate through history between the condition of playa lakes and dry playas, modifying zonation of plant communities depending on saline concentrations in soil water and water table depth. An example is the 12,000 km^2 Salar de Uyuni in Bolivia, the world's largest saltpan. It is a modern saltpan, and in the past, a series of paleolakes have been reported through increased precipitation, decreased evaporation and reduced overflow from Lake Titicaca towards southern salars (Chepstow-Lusty et al. 2005). According to these authors, wetter conditions in the salar may be related to cold periods in the North Atlantic Ocean. The rise in water level in the lake reduces salinity levels, these together with the colder conditions lead to the development of non-saline species nearer to the lake (*Polylepis*/*Acaena*). Hotter conditions transform the lake into a salar, increasing soil saline concentrations, leading to a retraction of *Polylepis*, sensitive to salinity and high temperatures.

The correlation between the reduction in temperature and dryer conditions is consistent with the observations made by Rojo et al. (2012) for the Salar del Bebedero in Argentina during the last 12,600 years. A reduction in the lake water levels is related to a reduction in the clastic materials, an increment of the evaporitic facies, the reduction of Chenopodiaceae and the increment of non-halophytic desert species.

In the Salar de Atacama (Chile) there has been an abrupt appearance of the species *Atriplex imbricata* after the Younger Dryas; the last cool phase occurred 12,000 years ago; related to hotter and drier conditions (Latorre et al. 2002).

Although this species is not an obligate halophyte and the increment in the frequency in central Atacama does not necessarily mean an increment on soil salinity.

Anthropic effects over these ecosystems can be severe and might affect the dynamics of soil-plant relations (Méndez 1993). The severity of changes is closely related to local climate change. Anthropic degradation is caused by overgrazing, fire and deforestation.

Méndez (1993) identified in Pampa Amarilla (western Argentina) the dynamics of degradation over this saline ecosystem. He divides the area into three functional environments: salt marshes, salinas and sand fields. The periodic burning of *Cortaderia rudiuscula*, for the improvement of rangelands, and subsequent overgrazing in salt marshes, produces the incorporation of ashes into the soil, increasing salt content and exposing the degraded surface to erosive processes which decapitate the soil until the water table is reached. This species is replaced first by *Baccharis spartoides* and then by the grass *Distichlis scoparia* and other halophytes, which by the progressive salinization of the lands are then replaced by obligate halophytes of low capacity for soil coverage (*Heterostachys ritteriana* and *Sarcocornia ambigua*). Adjacent communities of *Chuquiraga erinacea*, growing over silty-sands as relicts are also affected if water erodes the sand fields. The effects of sand deposition by wind over *Chuquiraga* communities are highly degradative. Such species cannot endure the saline sands inputs. If new dunes are created, the psammophyte species *Sporobolus rigens* can develop if soluble salts are leached by rainfall (Fig. 18.11). Following the same logic as Karlin et al. (2011), *C. rudiuscula*, *B. spartoides* and *D. scoparia* can be classified as intermediate species; *H. ritteriana* and *S. ambigua* as increasing species, and *C. erinacea* and *S. rigens* as decreasing species, according to a positive salinity gradient.

It is assumed that if rainfall over successive years is above the historical average, and plant cover is low due to anthropic degradation, runoff and deposition may occur in the lowlands, leading to the accumulation of a thin layer of saline sand and/or silt. This ends up with the development of intermediate species (Méndez 1993; Karlin et al. 2011). If rainfalls occur below the historical average over successive years, water erosion is reduced and the reactivation of the dunes would be possible through deflation of the basin and the accumulation of sand. Aeolian erosion is activated due to a drop of the water table. However, dune stabilization requires biomass production, which obviously needs water. Therefore, during this dry succession, annual fluctuation between dry and wet seasons is necessary for this process to occur, with long dry seasons (autumn, winter, and spring) and major concentration of rain in summer, when plants are phenotypically more active (Karlin et al. 2010).

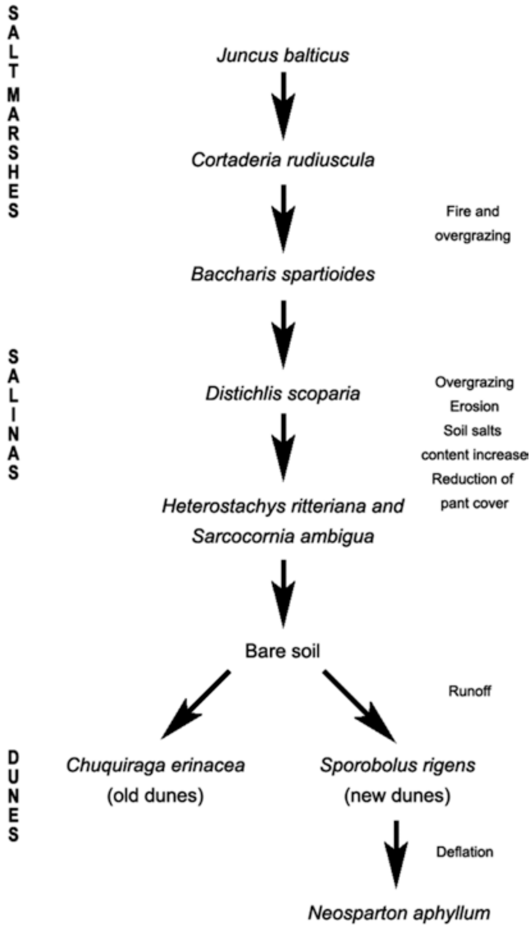


Fig. 18.11 Dynamism in Pampa Amarilla (western Argentina). Each community is identified by the dominant species (After from Méndez 1993)

To prevent the dunes from being destroyed by rain, installation of rapid-growing species (r type) is required to reduce run-off erosion effects and backward primary succession. Low intensity and high frequency precipitations would favour dune stabilization (Karlin et al. 2011).

Zones evolve toward a stationary state through erosion/deposition processes depending on the predominant climate (climatic quasi-equilibrium).

5 Conclusions

Sabkhat, playas, salt pans or salinas, whichever the name is best suited for saline basins in America, hold an important pool of plant functional groups according mainly to soil salinity and water table depth. Such functional groups perform important ecological functions in the soil-plant-climate triad, such as soil formation, facilitation and zonation. These processes have a dynamic behaviour according to seasonality and climate interannual and decadal variability, assisted by anthropic impacts such as fire, overgrazing or even climatic change.

Along the continent some specific halophyte species are found, represented by common genera such as *Allenrolfea*, *Atriplex*, *Suaeda*, *Sarcocornia* or *Distichlis*. These genera and other local halophytes and glycophytes perform an important role in biodiversity and the development of local (marginal or not) economies. Hypersaline zones, together with other geomorphological features such as dunes, tussocks, mounds or even peripheral non-saline belts, form an intricate network of vegetation patches that prove to be very important for diversification and reduction of climatic and economic risks for local dwellers.

In order to understand best the behaviour of American sabkhat, technicians should encompass the whole structure and dynamic of the triad for a better use or conservation of saline basins, learning from local experiences and traditional knowledge in the management and use of natural resources.

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19

Effects of Competition, Salinity and Disturbance on the Growth of *Poa pratensis* (Kentucky Bluegrass) and *Puccinellia nuttalliana* (Nuttall's Alkaligrass)

Ashleigh Anne Gilbert and Lauchlan Hugh Fraser

Abstract

Saline wetland and ponds in Canada can be found in arid and semi-arid regions where evaporation exceeds precipitation. An increase in salinity can reduce plant growth and affect competitive interactions between plants. A field experiment and a greenhouse experiment tested the effects of salinity and competition on the growth of two wetland plants, *Poa pratensis* (a glycophyte) and *Puccinellia nuttalliana* (a halophyte). For the field experiment, seedlings of *Poa pratensis* and *Puccinellia nuttalliana* were transplanted to six sites (two highly saline, two moderate, and two at low salinity) with and without plant neighbours. All sites were affected by high mortality and poor growth of the transplants. Survivorship was greater for plants grown alone. Biomass of plants grown alone was greatest at one of the moderate saline sites. The greenhouse experiment tested the response of *P. nuttalliana* and *P. pratensis* in a factorial design with 70 combinations (2 species × 7 salinity × 5 competition) replicated 6 times. Both of the species' biomass was greatest when grown alone without salt. Species, salt type and competition had greatest effect on survivorship. *Puccinellia nuttalliana* displayed a greater degree of salt tolerance than *P. pratensis*. Re-growth after clipping was suppressed at higher salinities. Our results indicate that the interactions between plant species, salinity and clipping (or grazing) can affect the potential quality and quantity of forage for livestock and wildlife.

1 Introduction

Salt occurs naturally in many of the world's wetland systems, whether it is from the ocean in estuaries and tidal marshes or from the ground and atmosphere in inland potholes and playas. Coastal wetlands are dominated by NaCl salts derived

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M.A. Khan et al. (eds.), *Sabkha Ecosystems Volume V: The Americas*,
Tasks for Vegetation Science 48, DOI 10.1007/978-3-319-27093-7_19

from the oceans, whereas inland wetlands may contain various salt combinations leached from bedrock and surface material, deposited from atmospheric salts and agricultural run-off. In addition to salt composition, inland wetlands may vary in salt concentration (Topping and Scudder 1977), which is influenced by local climatic trends (McKinstry et al. 2004). Arid and semi-arid climates where evaporation is greater than precipitation can often lead to saline water bodies.

British Columbia's southern interior is a prime example of a semi-arid environment possessing numerous saline alkali lakes and wetlands. Salinity in this region can be attributed to the composition of underlying volcanic bedrock and overlying glacial till and a semi-arid climate. Interior depressional or intermountain wetlands, like those in the southern interior, are considered to be very susceptible to climate change (Winter 2000; McCarty 2001; Mitsch and Gosselink 2007). Small catchment areas and locations within semi-arid or arid regions make these systems sensitive to increasing temperatures and shifting precipitation patterns (Mitsch and Gosselink 2007). Furthermore, even a slight increase in temperature may drastically alter the recharge and discharge rates of groundwater in the southern interior (Walker and Sydneysmith 2008). In some predicted climate change models, British Columbia's southern interior may experience warmer temperatures, drier summers and reduced snowpack which may lead to as high as a 65 % of a reduction in the annual surface water supplies (Merritt et al. 2005; Spittlehouse 2008; Walker and Sydneysmith 2008). Less surface water and greater rates of evaporation may lead to reduced water volume in many of the southern interiors' lakes and wetlands; with less water, there will be a higher concentration of ions and salts. Higher salinities can generate more stress for vegetation and create toxic environments for many plants and animals. A shift in vegetation towards more salt-tolerant species will result.

In the following chapter, we present two experiments to explore the relationship between salinity, plant growth and plant competition of halophytic and glyophytic plants in the southern interior of British Columbia, Canada. A transplant experiment determined the growth (aboveground biomass) of two transplanted wet meadow species, *Poa pratensis* and *Puccinellia nuttalliana*, with and without neighbours in six wetland systems with varying salinities. A greenhouse experiment determined the effects of two salt types (NaCl and Na_2SO_4) along artificially manipulated salinity gradients, competition and clipping (to simulate grazing) on two wet meadow species *P. nuttalliana* (Schult.) Hitchc. and *P. pratensis*L.

The transplant and greenhouse experiments are closely related and were designed to complement each other. *Poa pratensis* and *Puccinellia nuttalliana* were selected based on their presence in and around the study area and were used in both studies.

2 The Effects of Competition on Two Grass Species Along a Salinity Gradient

A species' competitive ability and adaptations to environmental stress will determine its range (Silvertown 2004; Brooker 2006). Wetlands are excellent arenas to study the effects of plant competition and environmental stress gradients in the field because of their rich biodiversity and wide range of topographical, hydrological and chemical characteristics (Keddy 2001; Mitsch and Gosselink 2007). The effects of environmental stresses can be observed in the field by manipulating a natural stress gradient (Wilson and Keddy 1988; Grosshans and Kenkel 1997) or utilizing a natural stress gradient (Crain et al. 2004; Sanderson et al. 2008). In wetlands, interactions between competition and sea inundation (Disraeli and Fonda 1979; Ewing 1983; Bertness and Ellison 1987; Greiner La Peyre et al. 2001), competition and water level (Grosshans and Kenkel 1997; Fraser and Karnezis 2005; Fraser and Miletti 2008) and competition and soil-water chemistry (Barbour 1970, 1978; Sanderson et al. 2008) have been used to understand plant community composition.

In North America, saline wetlands can be found in arid and semi-arid regions of the prairies and mountain ranges where evaporation exceeds precipitation (Cumming and Smol 1993; Wilson et al. 1994; Chhabra 1996; Fraser and Keddy 2005). Intermountain wetlands have a range of salinities dependent on bedrock and substrate composition, hydrologic regime and microclimate (Topping and Scudder 1977; Chhabra 1996). Differences in salinity can lead to a variety of plant communities by influencing plant-plant competitive interactions and restricting the range of salt-intolerant plants (Cheeseman 1987; Kenkel et al. 1991). Global climate change is predicted to increase warming and alter precipitation patterns which could lead to altered hydrology (Poiani and Johnson 1991). Such changes to intermountain hydrologic patterns might impact wetland salinity and therefore plant community composition.

Within the semi-arid grasslands of the southern interior of British Columbia, Canada, the rugged topography, limited precipitation and extreme temperatures have resulted in numerous, often isolated, wetlands and lakes. Forming in valleys and depressions, these water bodies are largely spring run-off and groundwater fed (Topping and Scudder 1977; Renaut 1990). Groundwater leaches minerals from the bedrock and overlain glacial till and accumulates in these wetlands and lakes causing many of them to be saline (Renaut 1990; Chhabra 1996), often characterized as athalassic alkaline wetlands (Topping and Scudder 1997). Throughout the growing season, water volume generally decreases due to evaporation and groundwater drawdown in many of the small or shallow wetlands. Declining water levels or complete loss of surface water can lead to a higher concentration of solutes and therefore salinity of the remaining water and soil (Topping and Scudder 1977; Wilson et al. 1994). Intermountain wetlands are used as water sources and their vegetation provides forage for grazing cattle and wildlife (El Shaer 2010).

Here we focused on the effects of salinity on aboveground biomass and competitive abilities of two grass species, *Puccinellia nuttalliana* (Schult.) Hitchc. (Nuttall's alkaligrass) and *Poa pratensis*L. (Kentucky bluegrass). Both species are commonly found in the southern interior of British Columbia (Gilbert and Fraser 2013). *Puccinellia nuttalliana* is often limited to wetlands and areas with alkali soils in mid to low elevations (Kenkel et al. 1991; Tarasoff 2007). *Poa pratensis*, commonly used as lawn and pasture seed (Tarasoff et al. 2007), can be found in a wider range of habitats including meadows, open forests and areas of disturbance from low to high elevation (USDA 2004). The species differ in their salt tolerances; *P. nuttalliana* is a facultative halophyte and grows in and around alkali and saline wetlands, but can flourish in fresh water conditions (Kenkel et al. 1991; Tarasoff et al. 2007). *Poa pratensis* has a relatively low tolerance to salt (Kenkel et al. 1991). Both species are flood tolerant and can survive in saturated soils, but *P. nuttalliana* is better adapted to drought conditions (Tarasoff et al. 2009). While *P. pratensis*and *P. nuttalliana* may be restricted by different abiotic and biotic stresses they can overlap in their distribution (Tarasoff et al. 2007), making them good species for competition studies.

We examined the effects of salinity and competition on these two grass species in intermountain ponds in British Columbia, Canada. We tested the following hypotheses: (1) Survivalship of *P. nuttalliana* and *P. pratensis* will be greatest at the freshwater sites and least at the saline sites, with *P. nuttalliana* being less affected by salinity than *P. pratensis*; (2) survivalship of *P. nuttalliana* and *P. pratensis* will be greater when neighbouring vegetation is removed than with neighbours present; (3) aboveground biomass of both species will be greater when neighbouring vegetation is removed; (4) aboveground biomass of *P. pratensis* will be less effected than *P. nuttalliana* when neighbours are present.

3 Materials and Methods

3.1 Field Experiment

3.1.1 Study Site

Six intermountain ponds were selected within Lac du Bois Provincial Park, located approximately 10 km north of Kamloops, British Columbia, Canada. During May to October the upper grasslands received 145 mm rain and had a mean temperature of 15.7 °C in 2007, less than 145 mm rain (uncertain value due to missing data) and had a mean temperature of 15.0 °C in 2008 and 179 mm of rain and a mean temperature of 14.4 °C in 2009. The ponds are depressional wetlands surrounded by grasslands matrix. All ponds were athalassic alkaline, but differed in salinity concentration: two were relatively fresh (≤5 ppt or oligosaline), two moderately saline (5–18 ppt or mesosaline) and two saline (30–40 ppt or eusaline) (Cowardin et al. 1979). Water input is from precipitation, run-off and ground water inflow. Evapotranspiration and ground water outflow were the main processes for water output. Fresh 1, Fresh 2, Saline 1 and Saline 2 dried out during the course of the 2009 growing season. Each pond contained a wet meadow section where transplantation occurred. *Juncus balticus, Lactuca serriola* and *Poa compressa* dominated the wet meadow of the fresh sites and Mid 1 (moderately saline site). The wet meadow of Mid 2 (moderately saline site) was dominated by *P. nuttalliana* and *Suaeda depressa*, while *P. nuttalliana, Elymus elymoides* and *Distichlis stricta* were the dominant species at the saline sites. Upland grassland vegetation occupied the area surrounding the wet meadow.

3.1.2 Experimental Design

We performed a factorial experiment that included two wet meadow species (*Puccinellia nuttalliana* and *Poa pratensis*), two levels of competition (with neighbours and neighbouring vegetation removed) at six sites varying in salinity. Treatment combinations contained only one transplant. Each treatment had six replicates at each pond for a total of 144 transplanted individuals.

Ponds were selected based on their salinity, presence of a wet meadow zone, and accessibility. Water conductivity readings were done using a Palintest waterproof 800 pH/conductivity/TDS meter on May 11, 2009, where a relative range was determined and each pond was designated its position along the respective salinity/conductivity gradient.

We established six 2.5×2.5 m blocks, each block contained four 50×50 cm quadrats that were randomly assigned one of the four treatment combinations (*P. nuttalliana* with neighbours, *P. nuttalliana* without neighbours, *P. pratensis* with neighbours or *P. pratensis* without neighbours) randomly assigned. Blocks and quadrats were orientated so that there was at least 50 cm separating each block and 50 cm between each quadrat within a block.

Transplants were cultivated in the greenhouse. Seeds of *P. nuttalliana* and *P. pratensis* were sown March 7, 2009 onto a distilled water saturated peat medium (peat pellet) placed in large trays. Distilled water was supplied as needed to the bottom of the trays to ensure the peat remained saturated during the germination and establishment process and to prevent seedling desiccation. On May 6, 2009 the transplants were moved outside to a protected area with high sun exposure to acclimate and test for temperature shock. Prior to transfer and planting in the field, a single dose of 200 ml of Rorison's nutrient solution was added to each tray containing the transplants to help reduce transplant shock.

The neighbouring vegetation was manually removed by clipping at the soil surface in half of the randomly selected quadrats. Quadrat selection and above ground biomass removal was conducted May 14 and 15, 2009 and transplanting occurred May 15, 2009. Transplanted individuals were planted in the centre of each 50×50 cm quadrat. Above ground biomass was continually removed by clipping and discarded throughout the season, weekly for the first 10 weeks then biweekly for the remaining 4 weeks.

Transplants were examined on Day 3, Day 6 and Day 13 following planting for signs of shock, herbivory and desiccation. Within this time period any individuals that had died were replaced. Individuals that died after Day 13 were not replaced and considered a mortality. Transplants severely damaged by herbivory were also removed from the analysis. In all plots that the transplant survived, the transplants aboveground biomass was harvested on August 3 and 4, 2009. Percent cover estimates of the other species in the ‘with neighbours’ plots were collected in addition to their aboveground biomass. Aboveground biomass was identified and separated to species in the field. Biomass was dried in a drying oven at 65 °C for 48 h and weighed with a Fisher Scientific analytical balance accu-225D (d = 0.01/0.1 mg) or Fisher Scientific analytical balance accu-4102 (d = 0.01 g) on August 7–9, 2009.

Soil samples were collected on August 3 and 4, 2009. Small soil plugs were removed from the uppermost 6 cm of each plot by a 2.5 cm diameter soil corer. The individual plot soil samples were then combined by block within each site. Individual block soil samples were mixed for uniformity and sieved through a 0.2 mm mesh sieve for soil nutrient analysis. Block soil samples were combined into site samples for further analysis conducted outside of the lab. Site soil samples were sent to Bodycote Exova Testing Group, Edmonton, Alberta, Canada for soil nutrient and soil quality analysis.

3.1.3 Statistical Analysis

A 3-way ANOVA was conducted on the transplant biomass to test the effect of site, transplant species and presence/absence of neighbours. Biomass data were log transformed to satisfy assumptions of a normal distribution. Mortality among the transplants almost 50 %; therefore, all transplants were analyzed for survivorship and only site Mid 2 was analyzed for the effects of neighbours on each species.

A 3-way Generalized Linear Model was conducted on the survivorship data of all the transplants by transplant species, neighbours presence or absence and site, with survivorship as a binomial response variable. Site Mid 2 surviving transplant biomass was transformed using a natural log function to satisfy assumptions of a normal distribution. A 2-way ANOVA was conducted by transplant species and presence/absence of neighbours. The transplants were separated and ANOVAs were conducted on both species individually by presence/absence of neighbours. Post-Hoc Tukey tests were run to determine statistical differences between sites or between treatments.

Total species community biomass was analyzed by using both biomass and percent cover value estimates. Results of both analyses were compared for consistency. Total species biomass values were selected to be used for further analysis including richness, diversity and total species biomass. A 1-way ANOVA was conducted on species richness, Shannon’s diversity, Simpson’s diversity, Inverse Simpson’s diversity, community biomass and litter by site with a Post-Hoc Tukey test to determine statistical difference between sites. Shannon’s diversity was selected and a Post-Hoc Tukey test was conducted to determine statistical difference between sites. Community biomass was transformed with a natural log function. All ANOVAs and the Post-Hoc Tukey tests were conducted using R version 2.9.1 (2009).

3.2 Greenhouse Experiment

Our experiment tested the interacting effects of salt concentration, salt type, competition and clipping on *Puccinellia nuttalliana* and *Poa pratensis*. The factorial combination included the 2 wet meadow grass species (*P. nuttalliana* and *P. pratensis*) at 7 salt type-concentration combinations (3 levels of Na_2SO_4, 3 levels of NaCl and 1 control) × 5 competition (*P. nuttalliana* alone, *P. pratensis* alone, and three pair wise interactions) × 2 clipping (clipped or not) × 6 replicates for a total of 672 plants in 420 pots. The factorial design was unbalanced due to the seven salinity levels.

3.2.1 Greenhouse Conditions

The greenhouse climate was set with a 16:8 hday:night cycle with light in each greenhouse room supplemented with three 1000 W halogen sulfide lamps, temperature was maintained at 22:15 C and relative humidity at 65:80 day: night cycle for 90 days. Pots were evenly divided between two greenhouse rooms containing three blocks each. Each block contained 70 pots, one of each treatment combination. Pots were randomly arranged within each block. Due to the large number of pots, experiment room 1 was planted a day later than room 2 allowing staggered treatment applications.

3.2.2 Germination

Approximately 400 seeds of *P. nuttalliana* and *P. pratensis* were placed in separate plastic Petri dishes filled with a sand medium saturated in distilled water. An initial germination experiment indicated that the *P. nuttalliana* seeds required approximately 12 days to germinate, whereas *P. pratensis* germinated in approximately 7 days; therefore seed sowing was staggered. *Puccinellia nuttalliana* seeds were sown on September 11 and 14, 2009 and *P. pratensis* seeds were sown on September 16 and 18, 2009 to ensure germination of both species occurred within days of each other. Seeds received distilled water while in the Petri dishes because germination results are best when initially grown under freshwater conditions (Flowers et al. 1986; Kenkel et al. 1991).

3.2.3 Treatments

Seedlings were removed from Petri dishes on September 30 and October 1 2009 (Week 1) and transplanted into 900 ml plastic pots (12.5 cm tall, 7.5 × 7.5 cm base and 11 × 11 cm top) containing a sand medium. Each pot received one or two transplants: *Puccinellianuttalliana alone, P. pratensis alone, P. nuttalliana* with *P. nuttalliana, P. pratensis* with *P. pratensis* or *P. nuttalliana* with *P. nuttalliana*.

The sand medium was saturated with 270 ml of Rorison's nutrient solution (see Hendry and Grime 1993) immediately prior to transplantation. One week after planting (Day 7) the pots were flushed by adding 270 ml of Rorison's nutrient solution (270 ml was found to be sufficient in flushing old salt-nutrient medium from the pots) to the top of the pots (Kenkel et al. 1991). By Week 2, Na_2SO_4 or NaCl was added to the Rorison's solution at low levels (0 for the control or 2.5 g/L for all the others) and flushed through the pots. Salt concentrations were gradually increased by 2.5 g/L per week until the desired final concentrations were achieved (5, 10, 15 g/L Na_2SO_4 and 5, 10, 15 g/L NaCl). Flushing occurred once a week. The control of no salt addition remained at 0 g/L and only received Rorison's nutrient solution. Distilled water was added to the pots from the bottom to keep the sand medium saturated and reduce the potential of flushing the salts and nutrients. Plants that had died within 2 weeks were replaced. Mortalities consisted of only those plants that had died after the 2 week replacement period. If only one plant had died within a pot of 2 plants, a single mortality was recorded and the other plant was removed from all analyses.

To simulate cattle grazing, half of all treatment combinations were clipped. Pots were randomly selected so their plants underwent manual clipping on Day 44. Clipping removed 75 % of the plants' photosynthetic material, so that only 25 % remained; this process was repeated on Day 63 (Hendry and Grime 1993).

3.2.4 Harvesting

Harvesting occurred on day 90 (December 29 and 30, 2009). Individuals were separated to species and then into above-ground and below-ground biomass. Biomass was dried in the drying oven at 65 °C for 10 days and weighed with Fisher Scientific analytical balance accu-225D (d = 0.01/0.1 mg).

3.2.5 Statistical Analysis

To analyze mean total biomass we used only the plant grown alone data. All biomass data were log transformed and R:S rations were arcsine transformed to meet the assumptions of normality. A 4-way unbalanced ANOVA with a blocking factor was conducted to test the effects of species, salt concentration, salt type and clipping on the total plant biomass, above ground biomass, below ground biomass and R:S ratio. Competitive importance was calculated using the equation:

$$C_{imp} = (P_{-N} - P_{+N}) / (MaxP_{-N} - y)$$

where P_{-N} is plant grown without neighbours (alone) and P_{+N} is plant grown with neighbours (both inter and intraspecific competition), and $MaxP_{-N}$ is the maximum value of P_{-N} and y is the lesser of P_{-N} or P_{+N} (Brooker et al. 2005). The equation was slightly modified from the original used by Brooker et al. (2005) to show C_{imp} as a positive value instead of a negative. A 5-way unbalanced ANOVA with a blocking factor was conducted to test the effects of species, salt concentration, salt type, competition type and clipping. P values <0.05 were considered significant. All ANOVA's and the Post-Hoc Tukey test were done using R version 2.9.1 (2009).

4 Results

4.1 Field Experiment

4.1.1 Abiotic

All six study areas were identified as alkaline with soil pH values ranging from 9.2 to 7.8 (Table 19.1). The Saline sites had the highest soil and water electrical conductivity, substantially greater than the Mid and Fresh sites. Nitrogen levels were relatively low for all sites except Mid 2, while phosphorus levels were relatively low at both Fresh sites and Mid 1. Potassium, sulphate, calcium and magnesium levels were high and considered in excess for farm soil (farm soil is a standard the samples were compared to by Bodycote Exova Testing Group) (Table 19.1). Saline 1 showed extremely high levels of calcium. Chloride was present in all the ponds and its concentration increased with salinity. Sodium was present in all ponds with the greatest concentration in the Saline and Mid 2 sites. Calcium and magnesium accounted for the majority of cations present in the soil, 78.8–95.2 % (Saline 1 and Fresh 1).

The size of the ponds ranged from just under a half hectare (Fresh 2) to just under 5 ha (Mid 2). While slope did vary by block at each site the average values were greatest at the Fresh sites and least at the Saline sites.

4.1.2 Biotic

Species richness was greatest at Mid 1 and lowest at Saline 2 (Table 19.2). Mid 1 species richness was greater than all other sites. Species richness was very similar for both fresh sites and Mid 2. Saline 1 and Saline 2 recorded on average one less species than the Fresh and Mid 2 sites. Mid 1 had the highest Shannon's Diversity value, closely followed by Fresh 1. The Saline sites reported the lowest Shannon's Diversity values. Total species biomass was not significantly different. Fresh 1 and Mid 2 had the largest amount of total species biomass. Saline1 had the smallest amount of total species biomass, almost half of Fresh 1 and Mid 2. Litter biomass covered a large range of values. Fresh 1 contained a significantly larger amount of litter biomass than the other sites. The Mid sites and Saline 2 had significantly lower amounts of litter biomass with Mid 1 containing less than 2.5 g/m^2.

Site Mid 2 Transplants

Site Mid 2 had a significantly greater amount of transplant biomass than all the other sites (Table 19.3, Fig. 19.1) because of re-growth. Therefore, further analysis was only conducted on the biomass of Mid 2. A Post-Hoc power analysis ($\alpha = 0.05$) was conducted on the transplant data and showed that there was a 35 % chance of committing a Type II error ($\Phi = 1.130462$). Power analysis results may be conservative due to the high number of treatment combinations. At Mid 2 the mean aboveground biomass of *P. nuttalli-*

Table 19.1 Soil and water analysis for each transplant site. Soil analysis on samples collected August 3 and 4, 2009, provided pH, soil EC and ionic concentrations. Water EC values were measured on May 11, 2009

Site	pH	Soil EC (ppm)	Water EC (ppm)	N (ppm)	P (ppm)	K (ppm)	S (ppm)	Ca (ppm)	Mg (ppm)	Cl (ppm)	Na (ppm)
Fresh 1	7.8	595	5070	<2	12	>600	58	3540	2050	12	40
Fresh 2	8.3	659	3110	4	34	>600	31	2610	2780	11	180
Mid 1	8.2	1421	9340	<2	10	>600	>200	2920	2260	18	180
Mid 2	9.2	1421	7550	28	>60	>600	139	2670	1960	20	1070
Saline 1	8.4	10560	35000	6	20	>600	>200	5400	2810	59.4	2830
Saline 2	8.2	7936	39700	10	29	>600	>200	26800	3120	26	1770

Table 19.2 Descriptive topographical and biological characteristics of each transplant site

Site	Location	Elevation (masl)	Area (ha)	Slope	Aspect	Richness	Shannon's diversity	Total biomass (g/0.25 m^2)	Litter (g/0.25 m^2)
Fresh 1	50°45′40″N 120°23′24″W	739	0.543	10.67°	N	$5.27 \pm 0.19_{ab}$	$1.11 \pm 0.05_{a}$	$28.60 \pm 5.25_{a}$	$27.11 \pm 0.96_{a}$
Fresh 2	50°46′58″N 120°26′22″W	861	0.432	10.08°	ENE	$5.60 \pm 0.24_{ab}$	$1.01 \pm 0.17_{abc}$	22.79 ± 0.91a	$9.54 \pm 1.37_{bd}$
Mid 1	50°46′16″N 120°25′32″W	766	3.540	9.67°	SW	$7.33 \pm 0.33_{c}$	$1.17 \pm 0.15_{ac}$	19.00 ± 2.47a	$0.62 \pm 0.03_{cd}$
Mid 2	50°47′28″N 120°27′15″W	895	4.934	7.58°	SE	$5.25 \pm 0.41_{ab}$	$1.07 \pm 0.11_{ac}$	28.39 ± 2.14a	$2.89 \pm 0.67_{cd}$
Saline1	50°46′06″N 120°23′60″W	778	1.190	5.50°	WNW	$4.17 \pm 0.31_{a}$	$0.58 \pm 0.13_{b}$	16.54 ± 2.07a	$9.52 \pm 1.23_{bd}$
Saline2	50°45′48″N 120°23′19″W	736	1.413	5.00°	SW	$4.00 \pm 0.42_{a}$	$0.64 \pm 0.19_{bc}$	$23.25 \pm 2.12_{a}$	$3.68 \pm 0.25_{bcd}$

Subscript letters represent significant differences based on a post-Hoc Tukey test ($P > 0.1$)
Standard error values are included for richness, diversity, and litter and biomass data

ana was significantly greater than the mean aboveground biomass of *P. pratensis* ($p < 0.1$, Fig. 19.1) and aboveground biomass was significantly less when transplants were grown with neighbours versus grown with neighbours (aboveground biomass) removed ($P < 0.05$).

Table 19.3 Mean total aboveground biomass 3-way ANOVA results examining the effects of site, species and competition (with or without neighbours present)

	Df	Sum of squares	F value	P value
Site	**5**	**42.356**	**27.648**	**<0.001**
Species	**1**	**1.336**	**4.361**	**0.041**
Competition	**1**	**2.525**	**8.242**	**0.006**
Site: Species	5	1.091	0.170	0.617
Site: Competition	5	2.608	1.703	0.149
Species: Competition	1	0.155	0.507	0.480
Site: Species: Competition	3	0.652	0.710	0.550
Residuals	57	17.464		

Significant values are in bold

4.1.3 Transplants Survivorship

Transplant survivorship was just over half (79 out of 144), 40 *P. pratensis* and 39 *P. nuttalliana* (Table 19.4). The presence of neighbouring vegetation did not affect survivorship. A GLM (binomial response variable) found site to have a significant reduction in survivorship at Mid 1 only. Fresh 1, Fresh 2 and Mid 1 trended towards greater *P. pratensis* survival but were not significant. Mid 2 and Saline 1 survival was equal while Saline 2 trended, but was not significant, towards greater *P. nuttalliana* survival (Table 19.4).

4.2 Greenhouse Experiment

4.2.1 Total Biomass

The mean total biomass of both *P. pratensis* and *P. nuttalliana* when grown alone (without com-

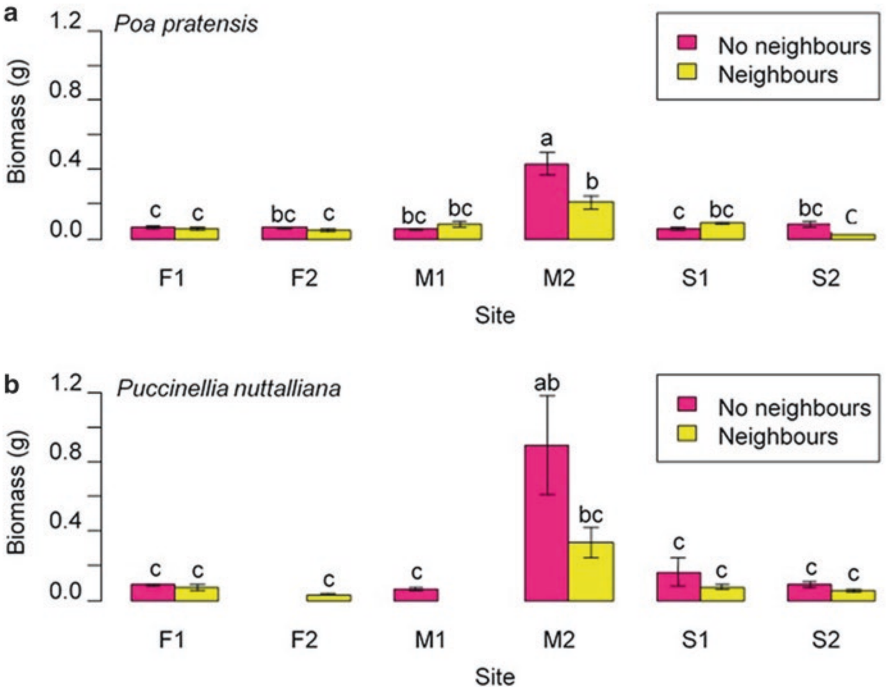

Fig. 19.1 Mean total (±1 SE) biomass of (**a**) *Poa pratensis* and (**b**) *Puccinellia nuttalliana* at six sites in Lac du Bois Provincial Park grown with neighbours and without neighbours present. 'F' is Fresh, 'M' is Mid, and 'S' is Saline. *Bars* sharing the same letter are not significantly different using Tukey HSD ($P > 0.1$)

Table 19.4 Number of transplants surviving for *Poa pratensis* and *Puccinellia nuttalliana*, with and without neighbours present, at Fresh 1, Fresh 2, Mid, 1, Mid 2, Saline 1 and Saline 2

		Fresh 1	Fresh 2	Mid 1	Mid 2	Saline 1	Saline 2	Total
Poa pratensis	**No neighbours**	6	3	2	4	4	2	21
	Neighbours	6	3	2	5	3	1	20
Puccinellia nuttalliana	**No neighbours**	5	0	2	6	4	5	22
	Neighbours	5	2	0	3	3	3	16
Total		22	8	6	18	14	11	79

petition) was significantly reduced by all the main effects (Table 19.5, Fig. 19.2). The mean total biomass of *P. pratensis* was greater than *P. nuttalliana* at the control (Table 19.5, Fig. 19.2). Salt concentration and salt type reduced the mean total biomass of both species, but the reduction was larger for *P. pratensis*(Table 19.5, Fig. 19.2). Mean total biomass of *P. pratensis*and *P. nuttalliana* was highest at 0 g/L salt (control) and lowest at 15 g/L NaCl. The NaCl treatment reduced the mean total biomass of both species to a greater degree than the Na_2SO_4 treatment. Salt concentration reduced the mean total biomass of both species. This trend was most evident in the NaCl treatment of both species and the Na_2SO_4 treatment of *P. pratensis*.

The two-way interaction between species and salt type was shown to be significant indicating that the two species are affected by salt type and concentration differently. Post-Hoc Tukey results showed a reduction in biomass in species and salt type interactions combinations involving *P. pratensis* and that 'no salt' controls for both species have greater biomass than the salt treatments (Fig. 19.2). The two-way interaction between salt and clipping was significant; Post-Hoc Tukey test indicates clipping with both salt treatments reduced the biomass of both species (Fig. 19.2). The two-way interaction between concentration and clipping was significant. Post-Hoc Tukey results show that biomass was greatest for both species at the control of 0 g/L salt with no clipping and in general showed greater reductions in biomass with clipping and increasing salt concentrations (Fig. 19.2).

Table 19.5 Results of 4-way ANOVA with blocking factor (Block) examining the effects of species, salt type (Salt), salt concentration (Conc) and clipping (Clip) on the mean total biomass of *Poa pratensis* and *Puccinellia nuttalliana*

Treatment	Df	Sum of Sq.	F value	P value
Block	**5**	**1.682**	**6.774**	**<0.001**
Species	**1**	**0.203**	**4.079**	**0.045**
Salt	**2**	**14.284**	**143.808**	**<0.001**
Conc	**2**	**1.928**	**19.407**	**<0.001**
Clip	**1**	**14.800**	**298.010**	**<0.001**
Species: Salt	**2**	**2.244**	**22.588**	**<0.001**
Species: Conc	2	0.304	3.062	0.050
Salt: Conc	2	0.301	3.027	0.052
Species: Clip	1	0.117	2.358	0.127
Salt: Clip	**2**	**0.852**	**8.580**	**<0.001**
Conc: Clip	**2**	**0.400**	**4.030**	**0.020**
Species: Salt: Conc	2	0.223	2.245	0.110
Species: Salt: Clip	2	0.065	0.659	0.519
Species: Conc: Clip	2	0.044	0.447	0.640
Salt: Conc: Clip	2	0.114	1.152	0.319
Species: Salt: Conc: Clip	2	0.088	0.886	0.414
Residuals	**120**	**5.960**		

Significant values are in bold

4.2.2 Competitive Importance

Blocking had a significant effect on competitive importance (C_{imp}) (Table 19.6). The degree of C_{imp} between species was not significantly different (Table 19.6). Salt type reduced the degree of C_{imp} of *P. pratensis* and *P. nuttalliana*. Salt

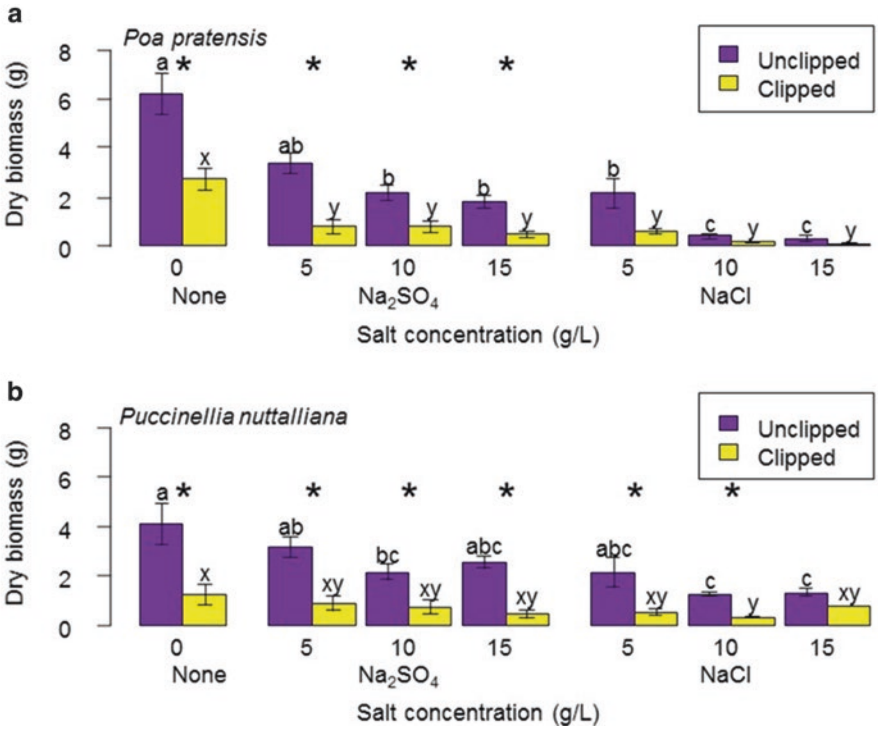

Fig. 19.2 Mean total biomass (±1 SE) of (**a**) *Poa pratensis* and (**b**) *Puccinellia nuttalliana* grown alone: clipped and unclipped at six salinities and the control. For clarity of interpretation, Tukey results have been assigned by sub-set ($P > 0.05$). The *asterisks* indicate a significant difference between the clipped and unclipped paired bars within a salt-concentration treatment. Letters a, b, c were used for the unclipped treatments and letters x, y, z were used for the clipped treatments. Bars sharing the same letter are not significantly different using Tukey HSD

concentration did not differ by treatment. Clipping was shown to significantly reduce C_{imp} of both species (Table 19.6, Fig. 19.3). The presence of competition (interspecific and intraspecific) did not have a significant effect. The 2-way interaction between salt and clipping was significant; the addition of salt and clipping always reduced C_{imp} (Fig. 19.3). The two-way interaction between clipping and competition type was significant; clipping and intraspecific competition reduced C_{imp} more than clipping and interspecific competition. When examined closer, the C_{imp} of *P. nuttalliana* was shown to be significantly affected by competition type and clipping, with intraspecific competition and clipping reducing the C_{imp} to a greater degree than interspecific competition and clipping (Fig. 19.4).

5 Discussion

5.1 Field Experiment

We found that the biomass and survivorship of transplanted *P. nuttalliana* and *P. pratensis* seedlings were affected by site and by the presence of neighbours, but those responses depended on the transplanted species as well as site. All the sites were characterized by alkali soils with some having low or deficient levels of nitrogen and phosphorus and excesses of potassium, sulphur, calcium and magnesium. Species richness, diversity, total species biomass and litter varied among sites.

5.1.1 Survivorship

Survivorship results did not support the hypothesis that the survivorship of *P. nuttalliana* and *P.*

Table 19.6 Results of 5-way ANOVA with blocking factor examining the effects of species, salt type (Salt), salt concentration (Conc), clipping (Clip) and competition (Comp) on competitive importance

Treatment	Df	Sum of Sq.	F value	P value
Block	**5**	**1.506**	**3.248**	**0.008**
Species	1	0.031	0.332	0.565
Salt	**2**	**5.700**	**30.725**	**<0.001**
Conc	2	0.075	0.406	0.667
Clip	**1**	**3.006**	**32.407**	**<0.001**
Comp	1	0.108	1.162	0.282
Species: Salt	2	0.146	0.789	0.456
Species: Conc	2	0.192	1.037	0.357
Salt: Conc	2	0.200	1.078	0.342
Species: Clip	1	0.007	0.074	0.786
Salt: Clip	**2**	**2.666**	**14.372**	**<0.001**
Conc: Clip	2	0.203	1.092	0.338
Species: Comp	1	0.067	0.727	0.395
Salt: Comp	2	0.160	0.863	0.423
Conc: Comp	2	0.162	0.876	0.418
Clip: Comp	**1**	**0.363**	**3.913**	**0.049**
Species: Salt: Conc	2	0.098	0.527	0.591
Species: Salt: Clip	2	0.073	0.394	0.675
Species: Conc: Clip	2	0.078	0.420	0.657
Salt: Conc: Clip	2	0.015	0.079	0.925
Species: Salt: Comp	2	0.081	0.434	0.649
Species: Conc: Comp	2	0.172	0.927	0.398
Salt: Conc: Comp	2	0.018	0.095	0.910
Species: Clip: Comp	2	0.167	1.800	0.181
Salt: Clip: Comp	2	0.047	0.254	0.776
Conc: Clip: Comp	1	0.081	0.439	0.646
Species: Salt: Conc: Clip	2	0.038	0.204	0.816
Species: Salt: Conc: Comp	2	0.034	0.182	0.834
Species: Salt: Clip: Comp	2	0.010	0.053	0.949
Species: Conc: Clip: Comp	2	0.062	0.334	0.716
Salt: Conc: Clip: Comp	2	0.096	0.518	0.597
Species: Salt: Conc: Clip: Comp	1	0.068	0.734	0.393
Residuals	**197**	**18.275**		

Significant values are in bold

pratensis would be greatest at the fresh sites and least at the saline sites, with *P. nuttalliana* being less affected by salinity than *P. pratensis*. While Fresh 1 did have the greatest number of surviving transplant, Fresh 2 had the lowest number of surviving transplants. Additionally, we cannot conclude from the survivorship data that *P. nuttalliana* was less affected by salinity than *P. pratensis*. Hypothesis 2 was also not supported because transplant survivorship was not significantly greater when neighbouring vegetation was removed. The low rate of survivorship and poor growth of most plants could be attributed to numerous factors such as climate, timing of transplantation, soil nutrient deficiency and herbivory.

The Kamloops growing season is generally characterized by spring rains and a hot and dry summer. Average temperature for May to August is 18.5 °C with 29.6 mm per month of rain, However in 2009 the average temperature for May to August was 20.3 °C with only 13.9 mm of rain monthly. Most of the rain fell in May (29.0 mm) and July (18.6 mm) while June (6.1 mm) and August (1.7 mm) were extremely dry (Environment Canada 2010). This warmer and drier than normal growing season likely made the environment unfavorable for the transplants to establish and grow leading to high mortality and low biomass. Abiotic stresses, like drought, can cause plants to slow or cease growth, inhibit the production of new cells, enter a dormant stage or die (Grime 2001; Zhu 2001). Re-growth may have possibly occurred if the transplants had remained in the field until the fall when precipitation generally increases (Grime 2001; Environment Canada 2010).

Facilitation may have played a greater role in the plant-plant interactions than competition at some of the ‘with neighbours’ plots. Removing biomass and litter in a semi-arid climate would have exposed the soil and plants to more direct sunlight and wind which may have led to greater rates of evaporation and thus drier soil (Facelli and Pickett 1991). Without the facilitative cover of other plants the transplants would be exposed to higher temperatures and stronger winds than

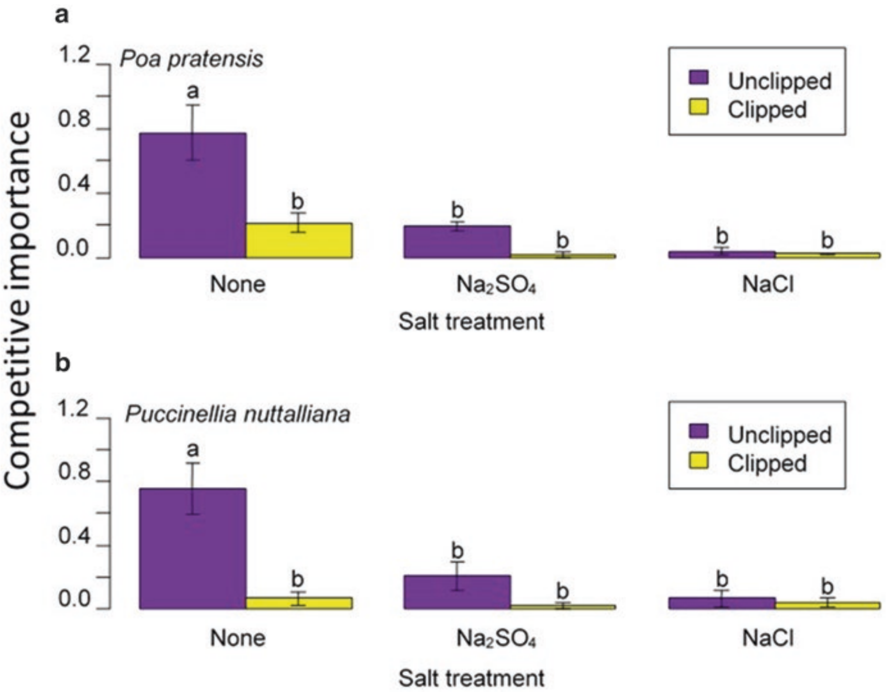

Fig. 19.3 Competitive importance (±1 SE) for (**a**) *Poa pratensis* and (**b**) *Puccinellia nuttalliana* clipped and unclipped at two salt treatment types and the control. *Bars* sharing the same letter are not significantly different using Tukey HSD (P > 0.05)

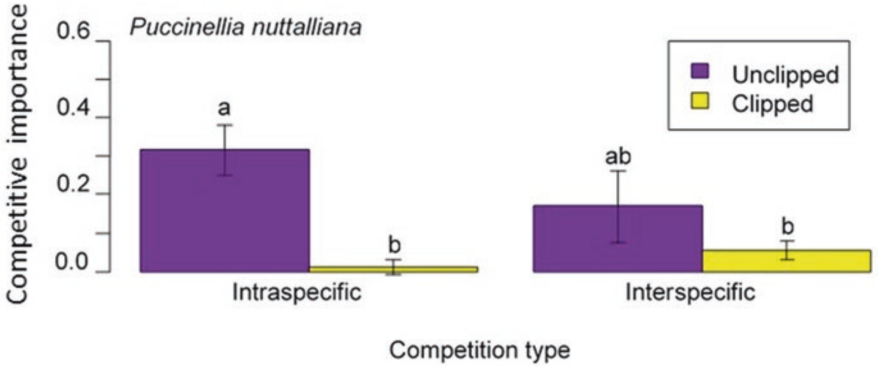

Fig. 19.4 Competitive importance (±1 SE) for *Puccinellia nuttalliana* clipped and unclipped at two competition treatments. *Bars* sharing the same letter are not significantly different using Tukey HSD (P > 0.05)

the ‘with neighbours’ transplants. In alpine environments, Callaway et al. (2002) found that as abiotic stress increased, competition shifted to facilitation; in general more facilitation is observed at high elevation or high abiotic stress locations than at the low elevation or low abiotic stress locations. The increased stress of a hotter and drier than average summer may have assisted a transplant-neighbours interaction shift towards facilitation. The possible presence of facilitation among transplants with neighbours does not support hypothesis 2.

Low levels of nutrients, especially nitrogen and phosphorus, could have contributed to the poor growth and low survivorship of the transplants. Nitrogen and phosphorus levels are consistently considered important variables when defining infertile soils (Grime 2001). According to the soil analysis, Mid 2 was the only site to have sufficient levels of nitrogen and phosphorus based on a farm soil standard (Bodycote Exova Testing Group 2010); Mid 2 was the only site where the transplants successfully established and grew. Low levels of nitrogen and likely phosphorus, can lead to less aboveground biomass because energy thus biomass is reallocated to the belowground parts of the plant (Lambers et al. 1998). Because only aboveground transplant biomass was collected, biomass reallocation to roots and increased root growth cannot be verified.

5.1.2 Abiotic and Biotic

Soil analysis of the transplant sites identified all sites as alkaline with calcium and magnesium the dominant ions. Alkali soils, ponds and lakes are common in the southern interior (Topping and Scudder 1977). High levels of calcium and magnesium can be attributed to intrusions of greenstone and igneous bedrock material (Renaut 1990). Ionic difference between sites may be the result of unconformities in bedrock material, glacial deposits or individual basin characteristics (Renaut 1990).

Species richness followed a general trend with highest richness at the mid and fresh sites, Mid 1 having significantly higher richness, and lowest richness at the saline sites. Diversity followed a similar trend with the mid and fresh sites having highest diversity and the saline sites having the lowest. Both trends show the saline sites having the least amount of species richness and diversity which would be expected in these stressed environments (Grime 2001). Total biomass varied by site; however, no definitive trends could be deduced. Litter was significantly greater at site Fresh 1 than all the other sites. Litter tended to be greatest at the fresh sites, followed by the saline sites and finally by the mid sites. The large variation in litter could be due to selective herbivory by wildlife and insects or species composition.

5.1.3 Site Mid 2 Transplants

An analysis of the mean total biomass of both transplants at all sites did not support either hypothesis 3 or 4. However, if site Mid 2 is analyzed alone the results support hypothesis 3 that aboveground biomass of both species will be greater when neighbouring vegetation is removed. Site Mid 2 was considered moderately saline based on its initial water conductivity readings with those findings reinforced by the final soil conductivity readings. However, the plant communities present at Mid 2 are indicative of an alkali-saline ecosystem and more similar to Saline 1 and Saline 2 than Mid 1. The high pH value and sodium level of Mid 2 soil may have contributed to the site containing more alkali vegetation than the other moderate salinity site (Mid 1). Mid 2 reported the highest levels of nitrogen and phosphorus, limiting nutrients that are key for plant growth (Tilman 1988; Grime 2001), which may have improved the success of the transplants.

Aboveground biomass for *P. nuttalliana* was greater than *P. pratensis* at the Mid 2 site. The high pH and moderate soil conductivity would have created soil conditions that *P. nuttalliana* is better adapted to than *P. pratensis*. These finding are supported by field observation (Tarasoff et al. 2007) and greenhouse manipulation experiments (Kenkel et al. 1991) that have observed the salinity range of *P. nuttalliana* and *P. pratensis*. Tarasoff et al. (2009) found that in the first year of a competition study *P. nuttalliana* grew at a much faster rate, obtained more biomass and was more competitive than *P. pratensis* which may explain why the biomass of *P. nuttalliana* was that much greater than *P. pratensis*. The natural presence of *P. nuttalliana* and absence of *P. compressa* at Mid 2 further supports the findings that *P. nuttalliana* is better adapted to moderate salinities than *P. pratensis*.

5.1.4 Competition Between Two Grass Species with and Without Clipping Along Two Salinity Gradients

Competition has been shown to interact with hydrology to affect plant growth (Grosshans and

Kenkel 1997; Fraser and Miletti 2008; Araya et al. 2010). There is also evidence that competition can interact with salinity to affect plant performance (Kenkel et al. 1991). The importance competition plays in determining plant community distribution along an environmental gradient is a debated topic in ecology (Tilman 1982; Grace 1991; Gough and Grace 1999; Grime 2001; Craine 2005). One view is that competition is stronger in less stressful, more productive environments and as stress increases, the role of competition decreases (Grime 2001; Keddy 2002). The other view is that competition remains constant along an environmental stress or productivity gradient, with a shift from below-ground competition in low productivity environments to above-ground in high productivity environments (Tilman 1982, 1988). Disturbance, especially herbivory, has also been shown to influence plant-plant interactions (Campbell and Grime 1992; Turkington et al. 1993; Gough and Grace 1998). Herbivores are often selective, feeding preferentially on competitive dominants (Fraser and Grime 1999). The removal of aboveground biomass by herbivores can cause a shift in root: shoot ratio; plants that invest more energy in leaf production after herbivore disturbance may experience a reduction in their root: shoot ratio (Kuijper et al. 2005). We studied the interactions between stress (productivity) and disturbance (clipping) on plant growth and plant community composition.

Here, we investigate the main and interacting effects of salt concentration, salt type, competition and clipping, as a surrogate of grazing, on two grass species, *Poa pratensis* L. and *Puccinellia nuttalliana* (Schult.) Hitchc. in a greenhouse environment. The species were selected based on salt-tolerance and recorded presence in the intermountain freshwater ponds and wetlands of the southern interior of British Columbia, Canada. *Poa pratensis* is a perennial glycophyte commonly used as a lawn and pasture species that represents a salt intolerant forage grass in this study (Kenkel et al. 1991; Tarasoff 2007). *Puccinellia nuttalliana*, a perennial halophyte associated with saline and alkaline wetlands (Tarasoff et al. 2007), represents a salt tolerant forage grass. Although a wide range of ions and salt complexes are found throughout British Columbia's lakes, ponds and wetlands, NaCl and Na_2SO_4 were chosen based on their common cation and presence in water bodies of Lac du Bois Provincial Park, Kamloops, B.C., Canada (Topping and Scudder 1977). A salt concentration gradient was used to simulate the natural range (Topping and Scudder 1977; Kenkel et al. 1991). Clipping, a disturbance, was chosen to simulate cattle grazing, a prevalent land-use practice in the southern interior of B.C. The competition treatment included plants grown alone (the control), two of the same species grown together (intraspecific competition) and one of each species grown together (interspecific competition). While numerous competition indices have been developed to better understand the role of competition in plant community structure (Weigelt and Jolliffe 2003), this study focuses on competitive importance (Brooker et al. 2005). Competitive importance indices have been identified as the best solution to determine the role of competition along a gradient (Brooker et al. 2005; Carlyle et al. 2010), but not without criticism (Freckleton et al. 2009). The inclusion of the plant's maximum biomass on the entire gradient in the equation enables the index to show the relative role of competition in different environments (or along the gradient). It must be acknowledged that the competitive importance index is thought to be biased towards supporting Grime's theory on competition along a gradient (Carlyle et al. 2010).

This study examines not only the role of competition, in the form of competitive importance, along a salt stress gradient but how competitive importance may be affected changes in a gradient's composition or the incorporation of an additional stress. Is competition affected differently by different salt complexes? How does the addition of clipping affect biomass and competitive ability along a salt stress gradient? Do different salt complexes interact with disturbance differently?

We tested the following hypotheses: (1) Biomass will decrease with increasing concentration of salt, with *Poa pratensis* experiencing a greater reduction in relative biomass than *Puccinellia nuttalliana* when subjected to the salt treatments; (2) There will be no difference in plant biomass between plants grown in NaCl and Na_2SO_4; (3) Competitive importance will decrease for *P. pratensis* and *P. nuttalliana* with increasing salt concentration.

5.2 Greenhouse Experiment

As the concentration of salt increased plant biomass decreased. As predicted, there was a greater reduction in the relative biomass of *Poa pratensis* compared to *Puccinellia nuttalliana* with an increase in salt concentration. The effect of salt type was unexpected, with NaCl causing a greater reduction in plant growth than Na_2SO_4. Because salt concentration caused a reduction in plant growth, we can assume salt concentration was a stress. We found support for Grime's hypothesis that there was an inverse relationship between C_{imp} and salt stress, with the declining role of C_{imp} for both species as salt concentration increased.

Total biomass for both species was greatest at the control salt treatment (0 g/L salt) and declined as salt concentration increased along both salt gradients (Na_2SO_4 and NaCl). These findings support the first hypothesis: biomass will decrease with increasing concentration of salt, with *Poa pratensis* experiencing a greater reduction in relative biomass than *Puccinellia nuttalliana* when subjected to the salt treatments. Previous studies examining the impacts of salinity gradients on plant biomass showed a reduction in growth, especially of glycophytes (Egan and Ungar 2001), shift in R:S ratio and increased chlorosis (Parrondo et al. 1978), reduction in water content and Na^+ ion accumulation (Glenn 1987). Salt type and concentration decreased the growth rate and biomass of both species but had a greater effect on *P. pratensis*, the glycophytic species.

While both species showed a decline in biomass along both salinity gradients, a greater reduction in biomass occurred along the NaCl gradient. Several studies have investigated the effects of salt composition on seed germination and seedling growth (Younis and Hatata 1971; Bhivare and Nimbalkar 1984), but few have examined the effects as plants mature (Ungar 1970). Younis and Hatata (1971) concluded that it was the salt cation that caused the reduction in wheat seed germination and growth. The plant community composition in the marsh systems they studied was not significantly influenced by the dominant anions and thus not as important in shaping plant communities as previously proposed. Therefore the nature of anions present was not as important as once thought (Ungar 1970). However, we show that chloride (Cl^-) anion reduced biomass to a greater degree than the sulphate (SO_4^{2-}) anion, indicating that the nature of dominant anion must also be considered an important factor in retarding and inhibiting plant growth.

5.2.1 Competitive Importance

The results supported our final third hypothesis that C_{imp} would have an inverse relationship with increasing stress (salt presence or salt type) (Grime 1979; Kenkel et al. 1991); the addition of a salt treatment or salt type decreased competitive importance. A further reduction in C_{imp} occurred with clipping. Clipping acting as another stress agent reduced the degree of C_{imp} alone and in combination with salt treatment or salt type. The degree to which C_{imp} was reduced along the salinity gradient for *P. nuttalliana* was inconsistent with our hypothesis that C_{imp} of *P. nuttalliana* will be less affected by salt concentration than *P. pratensis*. Moreover, the decline in C_{imp} for *P. nuttalliana* from the control to 5 g/L Na_2SO_4 was much greater than expected considering the biomass results.

There was no apparent difference in competitive importance between interspecific and intraspecific competition (competition type). However, intraspecific competition and clipping showed a greater reduction in the degree of competitive importance for *P. nuttalliana* than interspecific competition and clipping. These results may be attributed to the low density of this study, the morphology of *P. nuttalliana* or general competitive ability of both species. Competitive importance for *P. pratensis* and *P. nuttalliana* at the unclipped control was comparable, supporting Tarasoff et al. (2009) results, from a 2 year greenhouse pair-wise competition study that of *P. pratensis, P. nuttalliana* and *Puccinellia distans*, that *P. nuttalliana* is a stronger competitor and *P. pratensis*is a weaker competitor for the first year. Also the cultivar or origin of the *P. pratensis* seed may play a role in its competitive ability, with some cultivars producing more competitive forms of the species (Eggens 1982; Tarasoff et al. 2009). Therefore, our study suggests that the presence of stress (salt) and disturbance (clipping) has a stronger influence on the species level responses of *P. pratensis* and *P. nuttalliana* than competition.

Competition can be affected by abiotic factors in non resource stress environments. Fraser and Miletti (2008) found that competition (competitive intensity) was reduced with increased water level stress. A reduction in biomass and competitive effect was observed for all plants at the highest stress level that could be attributed to inhibited plant growth (Fraser and Miletti 2008). Similar results were found in our study, with the addition of a salt treatment or type of salt (abiotic stress) the role of competition decreased. Wilson and Keddy (1985) concluded that diffuse competition was greater at undisturbed, nutrient rich sites and lesser at disturbed, nutrient poor sites, highlighting the relationship between abiotic stress and resource stress.

Numerous indices have been devised to assess the effects of competition on plants (Weigelt and Jolliffe 2003). Absolute competition, relative competition and competitive intensity indices and analysis were conducted on the data, but competitive importance was selected as the best representation of the data due to the presence of significant values and its applicability to gradient analysis (Brooker et al. 2005; Brooker and Kikividze 2008; Carlyle et al. 2010).

5.2.2 Key Management Points

The results of our research indicate that the interactions between plant species, salinity and disturbance (clipping) can affect the potential quality and quantity of forage material for livestock and wildlife. To optimize forage potential and protect the southern interiors' essential and sensitive ponds and wetlands, we have formulated some possible management suggestions.

If possible, grazing livestock should utilize areas of low or moderate soil salinity. These areas should provide greater amounts of biomass and more palatable species. Highly saline areas should be avoided or grazed early in the season while salinity is generally at its lowest and the vegetation has time to recover from grazing disturbance. Water sources can be too saline and thus toxic to livestock so alternative water sources should be utilized in areas of high salinity. If seeding is to be done in a saline pasture that will be used for livestock, native salt-tolerant forage species such as Nuttall's alkaligrass should be considered and used in the seeding mixture. Consultation of climate change scenarios is essential for us to predict possible adaptation pathways and shifts in our grassland and wetland ecosystems. Management and policy will be more effective if we attempt to understand what our environment may hold in the future.

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Ecophysiology of Native Species from Patagonian Monte, Argentina

20

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Abstract

In the Patagonian Monte of Argentina several stresses affect the structure and function of the ecosystem, being drought the main abiotic stress. Several drought resistance strategies have been described among different plant functional types but with pour attention to physiological aspects. Indeed, differences in endogenous abscisic acid (drought stress hormone) production and changes in its metabolites (products of catabolism) may contribute to establish different patterns of plastic responses between plant functional types and may help to understand the ecological distribution of some species and their role in a given environment. In this chapter we describe several topics related to drought resistance strategies of plant functional types from Patagonian Monte, Argentina, focusing on morphological, biochemical and physiological traits and phenotypic plasticity of the main grasses inhabiting this arid shrubland.

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M.A. Khan et al. (eds.), *Sabkha Ecosystems Volume V: The Americas*,
Tasks for Vegetation Science 48, DOI 10.1007/978-3-319-27093-7_20

1 Introduction

At present, there is a great interest world-wide in the use of marginal lands for the production of crops or meat because arable lands need to be employed in meeting world food and biofuel requirements. There is the apparent danger that preservation of ecosystems plays just a minor part in these considerations. Studying the threat for ecosystems and the consequences of unbaked economic exploitation is important to visualize the future development. There is the need to take serious care of ecosystems to prevent desertification, to preserve species diversity and to protect at least the most important ones from disappearing. Therefore, it is of high relevance to demonstrate the limited bandwidth of resistance of ecosystems basing on the special strategies of existing plant functional types. The study of the arid ecosystem from Patagonia Monte, Argentina, which is characterized by the scarcity of water and nutrients whose cycling is strongly associated with the erratic and discontinuous inputs of precipitation, provides an example to demonstrate the maintenance of an "apparently nonproductive wasteland".

Drought limits plant growth and determine structure, functioning and evolution of terrestrial ecosystems (Aguiar and Sala 1998; Paruelo et al. 1998; Craine 2009; Craine et al. 2012). The main key for the maintenance of species diversity in arid lands is the way in which these species are differentiated by adaptation to exploit opportunities for growth and persist in pulsed and limited resource availability (Chesson et al. 2004).

Climatic changes alter the availability of resources and the conditions that are crucial to plant performance (Nicotra et al. 2010). Understanding of how drought affects plant species and consistently plant performance is crucial to predict global change consequences on native species as well as crop plants, and prevent this from happening (Nicotra et al. 2010; Craine et al. 2012).

The identification of plant functional types is important for characterizing vegetation dynamics at landscape and regional scales and they have been applied as modeling tools to understand the effects of global change on the Earth system (Cramer et al. 2001; Vicente-Serrano et al. 2013; Wullschleger et al. 2014). Thus, drought-response mechanisms of coexisting plant species in arid ecosystems may serve as indicators of global warming or advance of desertification and this knowledge is important for grass management (Chai et al. 2010) and conservation of these rangelands.

Recent advances in physiological and biochemical traits of drought resistance have revealed differences among grass species in their ability to survive drought, and this topic is becoming central for an ecological classification of plants (Craine et al. 2013; Cenzano et al. 2014) and for planning the conservation of Patagonian Monte.

This chapter describes fundamental topics related to drought resistance strategies of two main grasses from Patagonian Monte, Argentina (*Pappostipa speciosa* and *Poa ligularis*), focusing in morphological, biochemical and physiological traits and phenotypic plasticity. These species have different leaf life span, growth rate, resource acquisition/conservation strategy, accumulation of phenolics compounds, metabolism of abscisic acid, among other drought resistance strategies, and plasticity. In addition, both species are the main palatable grasses from native and domestic herbivorous, they integrate the patch dynamic processes preventing soil degradation processes and reducing desertification advancement in the Patagonian Monte.

1.1 Patagonian Monte Shrublands from Argentina

The Phytogeographic Province of Monte from Argentina is located from 24°15′S to 44°20′S and 64° to 68° W, occupies an area of about 42,000 km^2 and constitutes the most arid rangeland of Argentina (Soriano 1950; León et al. 1998; Fernandez and Busso 1999). Inside this Province, the Southern part of Monte is characterized by a semiarid to arid climate, with strong water deficits in spring and summer, high evaporation enhanced by westerly winds, annual rainfalls between 200 and 260 mm, mean annual temperature of 13.9 °C, and unpredictable rainfalls events (Cabrera 1976; Fernandez and Busso 1999; Campanella and Bertiller 2008, 2010). In our study, small and fluctuating precipitation events occurred along 2 years (Fig. 20.1). The total precipitation during 2008 (133.86 mm) and 2009 (190.54 mm) was lesser than 8-year average for the same study site (Campanella and Bertiller 2008). The cumulative monthly largest precipitation occurred in autumn during 2008 (May, 46.12 mm) and three precipitation events were registered during 2009 (February, 36.98 mm; May 36.37 mm and November, 37.44 mm). The smallest precipitation was registered in October 2008 (1.62 mm) and September 2009 (0.51 mm). On the other hand, the maximum/minimum temperature was 21.27/7.8 °C for 2008 and 21.18/7.94 °C for 2009. The maximum mean temperature occurred in summer (January) and the minimum mean temperature occurred in winter (June–July) (Cenzano et al. unpublished).

The precipitation events have a high intra- and inter-annual variation (Barros and Rivero 1982). Most of small rainfalls events occur during autumn and winter and only larger rainfalls events (higher than 10 mm) are correlated with annual rainfall resulting in a soil water recharge that allows plants begin life cycle (Golluscio et al. 1998). In Patagonian Monte the soil water is available in the upper soil (2.4 % soil moisture at near soil surface) during winter and early spring and it is available only in the deeper layers during summer (10.4 % soil moisture at 1.2–1.5 m depth, Bertiller et al. 1991). Soils are aridisols calcids, typic Haplocalcids and Petrocalcids (del Valle 1998), with low organic matter (0.6–0.74 % organic C) and total N contents (0.08–0.1 % N) in the upper soil (Mazzarino et al. 1996). The upper soil texture is sandy or loamy sand (Rossi and Ares 2012) and the mean soil moisture is very slow (4.5–6.0 % at 0–20 cm depth and 6.1–8.1 % at 20–40 cm depth, Mazzarino et al. 1998). The pH of soil is near to 7.9 (Prieto et al. 2011) corresponding to moderately alkaline soils (Soil Survey Staff 1999).

In Patagonian Monte several stresses affect the structure and functioning of the ecosystem, being drought the main abiotic stress (Cenzano et al. 2013, 2014).

The Patagonian Monte (Fig. 20.2) is characterized by shrublands dominated by shrubs and grasses in a patchy structure alternating with bare soil (Beeskow et al. 1987; Ares et al. 1990; Bisigato and Bertiller 1997; Ares et al. 2003; Bertiller et al. 2004). The vegetation covers 40–60 % and is distributed in three layers; the upper layer (1–2 m height) composed by scattered tall shrubs, the intermediate layer (0.5–1.2 m) composed by dwarf shrubs, and the lower layer (0.1–0.5 m) dominated by perennial grasses. The most common shrubs species in Patagonian

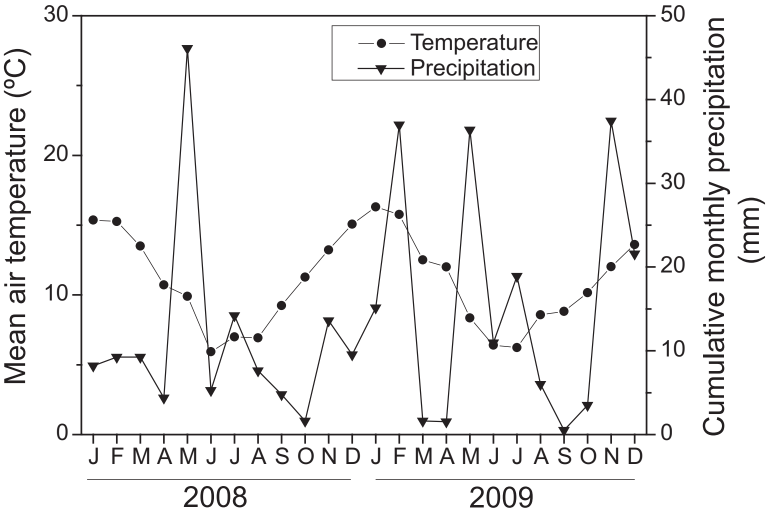


Fig. 20.1 Cumulative monthly precipitation and mean air temperature in Patagonian Monte (Estancia San Luis, 42°40′49.3″S 65°21′33.6″W) through 2008 and 2009 years

Fig. 20.2 View of Patagonian Monte in the North-East of Chubut Province, Argentina. (**a**) Estancia San Luis (42°40′49.3″S 65°21′33.6″W). (**b**) Wildlife refuge "La Esperanza" of Natural Patagonia foundation (42°7′43.92″S 64°57′40.99″W)

shrublands are *Larrea divaricata*, *Larrea nitida, Condalia microphylla*, *Schinus johnstonii, Bounganvillaea spinosa*, *Lycium chilense*, *Atriplex lampa*, *Prosopidastrum globosum*, *Prosopis alpataco*, *Chuquiraga avellanedae*, *Chuquiraga erinacea* var. *hystrix*, *Acantholyppia seriphiodes, Nasauvia fuegiana* and *Junellia seriphiodes*, among others. The most common grasses are *Poa ligularis*, *Pappostipa speciosa* and *Nasella tenuis* (Cabrera 1976; Beeskow et al. 1987; Ares et al. 1990; Bisigato and Bertiller 1997; León et al. 1998; Bertiller et al. 2004; Rossi and Ares 2012).

1.2 Plant Functional Types of Patagonian Monte

The plant functional types group species that share similar characteristics and roles in the ecosystem function (Wullschleger et al. 2014). Among grasses, an important characteristic is that they are shallow-rooted species having the ability to recover photosynthesis rapidly after small rainfall events such as 5 mm (Sala and Lauenroth 1982) conferring a high rain use efficiency (Huxman et al. 2004). However, the photosynthetic rates during interpulse period would be lower due to the lack of access to deeper soil moisture. However, deep-rooted plants such as shrubs respond more slowly and less extensively to precipitation pulses. This is because they are exposed to less water stress during dry interpulse periods than shallow-rooted plants due to draws of water from deeper reserves from previous rainy seasons (Huxman et al. 2004).

A criterion for grouping species is in terms of leaf life span as function of growing season (Kikuzawa 1991; Givnish 2002). Evergreen species retain their leaves throughout the year, thus they have longer leaf life span and longer growing season. Whilst deciduous species shed elder leaves during dry season (summer), thus they have short leaf life span and shorter growing season (Tomlinson et al. 2013). In Patagonian Monte the common evergreen species are: *Larrea divaricata*, *Chuquiraga avellanedae*, *Atriplex lampa*, *Schinus johnstonii*, and *Pappostipa speciosa*; and the common deciduous species are: *Lycium chilense*, *Bougainvillea spinosa*, *Prosopidastrum globosum*, *Prosopis alpataco*, *Nasella tenuis*, and *Poa ligularis* (Bertiller et al. 1991; Campanella and Bertiller 2008; Carrera and Bertiller 2013; Cenzano et al. 2013).

It is generally recognized that seasonal drought can benefit deciduous leaves while infertile soils can benefit long-lived evergreen leaves by increasing the cost of nutrients acquisition and depressing the maximum photosynthesis rate (Givnish 2002). Long-lived evergreen leaves offer longer photosynthetic season and lower photosynthetic rate than deciduous leaves, and reduce the amount of nutrients to be absorbed from the soil. Deciduous leaves reduce transpiration and respiration during drought and often have higher photosynthetic rate (Givnish 2002).

Thus, leaf life span is negatively associated with maximum photosynthetic rate, leaf mass per area (LMA), and leaf N concentration (Reich et al. 1992, 1997). When the water pulses are frequent, evergreen species respond relatively rapidly opening their stomata to increase carbon assimilation. However, this strategy of maintaining photosynthetic tissue has expensive cost (Reynolds et al. 1999). Thus, under large and infrequent water pulses the addition of new leaf area is necessary for optimal water use in both deciduous and evergreen species (Chesson et al. 2004).

A widespread classification in mesophytic and xerophytic species has been extensively used. Xerophytic or xeric species have low growth rates, low leaf area, low leaf turnover, low N resorption efficiency (Aerts and Van der Peijl 1993; Aerts 1996). Inside this group there are the most evergreen shrubs, among them *Larrea divaricata* and *Atriplex lampa* (Bertiller et al. 1991; Mazzarino et al. 1998; Carrera et al. 2000, 2003). In contrast, mesophytic or mesic species have high growth rates, high leaf area, high leaf turnover, high N resorption efficiency (Reich et al. 1992). Inside this group the most of perennial grasses from Patagonian Monte and the deciduous shrub *Lycium chilense* can be mentioned (Bertiller et al. 1991; Pazos et al. 2007; Cenzano et al. 2013, 2014).

Another criterion for grouping species is based on resource acquisition/conservation strategies. The resource acquisition strategy is characterized by a set of plant attributes that allow rapid acquisition of resources (acquisitive type) such as high nitrogen concentration in leaves, high leaf production/turnover, and high leaf length. This strategy is present in most mesophytic plants. While, the resource conservation strategy is characterized by attributes that allow conservation of resources within well protected tissues (conservative type) such as high physical/chemical defenses concentration (soluble phenolics and lignin) in leaves, high LMA, leaf pubescence, and high height. This strategy is present in most xerophytic plants (Westoby et al. 2002; Díaz et al. 2004). The secondary compounds such as soluble phenolics and lignin produced by conservative plants increase leaf resistance against water shortage, herbivore damage and environmental degradation (Coley 1983; Lattanzio et al. 2006).

A lower growth rate may confer a higher probability of surviving extended periods of low soil water availability (DeLucia and Schlesinger 1991). Low LMA, high photosynthetic capacity, and generally faster turnover of plant parts permit flexible response to the spatial patchiness of light and soil resources (Grime 1994). However, species with high LMA and long leaf life span have longer-term advantages (Aerts and Chapin 2000) which permit a progressively greater share of nitrogen pools in a habitat to be sequestered (Aerts and van der Peijl 1993). Additionally, species with high LMA have larger total leaf and accumulate greater total leaf mass, but have lower photosynthetic capacity than low-LMA species (Midgley and Bond 1991; Reich et al. 1992, 1999).

1.3 Importance of Vegetation Patches from Patagonian Monte

In the plant patches from Patagonian Monte, the soil has higher nutrient availability, higher water infiltration, lower soil evaporation, higher organic matter concentration, higher microbial biomass-C and enzyme activities than bare soil (Rostagno et al. 1991; Mazzarino et al. 1996; Bertiller et al. 2002; Carrera et al. 2005; Prieto et al. 2011). Additionally, the presence of mounds favours soil aggregation and water infiltration lessening erosion risk (Rostagno and del Valle 1988; Tongway et al. 1989). The mounds have been named “fertile patches” as they are refuge for a wide range of plants and animals (Tongway et al. 1989).

Shrubs are important for the conservation and restoration of soil nitrogen fertility since they have low nitrogen requirements and low N-resorption efficiency, providing more N-rich substrate (senescent leaves falling with high N concentration) for the establishment of perennial grasses in the shrub patch periphery (Aguiar and Sala 1999; Carrera et al. 2000, 2003; Bertiller et al. 2004).

In addition, seeds tend to accumulate near the vegetation patches and have low density in bare-soil areas (Bertiller and Bisigato 1998; Aguiar and Sala 1999). Thus, the emergence and establishment of perennial grasses seedlings is concentrated at the plant patches periphery (Bisigato and Bertiller 2004) which is favored by the structural (spiny, pubescent and resinous leaves, thorny stems, among others) and chemical defenses (high lignin and soluble phenolics in green leaves) of shrubs that ameliorate microenvironments around them or protect them from herbivores (Bertiller et al. 2002; Ares et al. 2007; Moreno et al. 2010). The increasing of shrub cover also favors *Poa ligularis* growth (Moreno and Bertiller 2012).

Pappostipa speciosa and *Poa ligularis* grasses integrate the patch dynamic processes and they have been extensively studied for many reasons: they are dominant perennial grasses in the arid Patagonian rangelands of Argentina and the main forage resource for domestic and native herbivores, their short life cycle respect to shrubs allows the study of short-term ecophysiological responses, and they prevent soil erosion (Aguiar and Sala 1999; Bisigato and Bertiller 1997; Chartier and Rostagno 2006; Bestelmeyer et al. 2011; Cenzano et al. 2013, 2014). Thus, the understanding of vegetation patches in these rangelands is crucial for conservation practices preventing soil degradation processes and reducing desertification advancement (Chartier and Rostagno 2006; Chartier et al. 2013).

1.4 Different Strategies of Drought Resistance

In semiarid and arid ecosystems drought is the main abiotic stress that limits plant growth, determines the structure and functioning of the ecosystems (Aguiar and Sala 1998; Bertiller et al. 2004), and together with other limited resources as nutrients are fundamental drivers of plant evolution (Paruelo et al. 1998; Craine 2009; Craine et al. 2012). In these ecosystems water availability is controlled by infrequent, discrete and largely unpredictable precipitation inputs (Noy-Meir 1973).

Plants of these ecosystems have developed different mechanisms of drought resistance: avoidance, tolerance or escape to drought (Levitt 1980). Drought avoidant plants are characterized by the maintenance of hydric status under drought without alteration of plant functions (Blum 2005). The drought stress avoidance strategy is associated with deciduous phenology, high specific leaf area (SLA), low LDMC, high stomatal conductance (Hetherington and Woodward 2003), high photosynthetic rates, low WUE, high leaf nitrogen concentration, thin leaves, low carbon investment in secondary metabolites (soluble phenolics and lignin), high relative growth rate, high potential for resource capture and may be defined as acquisitive plants with a higher survival (Díaz et al. 2004; Jones 1992; Arntz et al. 2000; Chaves et al. 2002; Westoby et al. 2002; Reddy et al. 2004; Hughes et al. 2010; Liu et al. 2011; Tomlinson et al. 2013; Cenzano et al. 2013, 2014; Pérez-Harguindeguy et al. 2013).

Otherwise, drought tolerant plants have the ability to maintain their physiological functions under low water potentials and even under long periods of drought (Lilley et al. 1996; Blum 2005; Craine et al. 2012). These species can use water over a broad range of conditions and interpulse periods (Chapin 1991; Sher et al. 2004). The drought stress tolerance strategy is associated with evergreen phenology, low specific leaf area (SLA) (Chesson et al. 2004; Campanella and Bertiller 2008), high root allocation (Lambers et al. 1998; Poorter and Nagel 2000); decrease leaf biomass (Poorter et al. 2012); high water-use efficiency (WUE) (DeLucia and Schlesinger 1991), abscisic acid accumulation (Liu et al. 2005), low stomatal conductance (Liu et al. 2005; Manzoni et al. 2011), low photosynthetic rates, low transpiration and water loss (Dolferus 2014), osmotic adjustment (Morgan 1984; Blum 2005), cell wall hardening, tough leaves, antioxidant mechanisms (Agati and Tattini 2010) such as high production of phenolics (Westoby et al. 2002; Reddy et al. 2004; Reginato et al. 2015), low relative growth rate (Cornelissen et al. 2003), high potential for resource conservation in the plant (Grime et al. 1997; Novoplansky and Goldberg 2001), low dependence on external supply, and higher survival (Díaz et al. 2004; Sinclair et al. 2008; Poorter et al. 2009; Zou et al. 2004).

Under lower water availabilities the maintenance of high WUE, defined as the ratio of net photosynthesis to stomatal conductance (Zhang et al. 1997) is beneficial because delays effects of water stress on the photosynthetic machinery (Fisher and Turner 1978). Other mechanisms associated to drought tolerance strategy are: the maintenance of membranes integrity, stability and cellular compartmentalization (Zhou et al. 2014) and changes in lipid composition (Gigon et al. 2004; Torres-Franklin et al. 2007).

In water-limited environments, avoidant plants with high stomatal conductance and good photosynthetic capacity demonstrate opportunistic and rapid growth during short periods of water availability (Hetherington and Woodward 2003). However, a reduced water uptake is reflected in higher WUE and is generally achieved by tolerant plant traits that reduce yield. Thus, an avoidant phenotype may be better adapted to a range of environments, and under selection criteria for yield under drought it would be preferred over a tolerant phenotype (Blum 2005). These plants are more sensitive to interpulse periods and more responsive to increases in water availability (Novoplansky and Goldberg 2001; Sher et al. 2004).

Drought escaping plants may complete life cycle before the drought period (short life cycle) or may have a short growing season and early reproduction (Sherrard and Maherali 2006; Franks et al. 2007).

Additionally, changes in plant growth and development under abiotic stress conditions are associated with metabolic activity to provide the energy required to establish the response (Dolferus 2014). Thus, the metabolic activity is correlated to growth rate as a strategy for stress resistance. Accelerated growth requires faster metabolism and mobilization of resources, while slowing down metabolism and growth rate saves vital resources for passive survival under abiotic stress conditions (Dolferus 2014). During stress conditions selecting for delayed foliar senescence (stay-green or evergreen) and maintenance of stomatal conductance, transpiration and photosynthesis are relatively easy phenotypes to score (Thomas and Ougham 2014). Thus, evergreen species present less active periods of growth but more extended in time (Hetherington and Woodward 2003).

The classification of species into functional types could be summarized as xerophytic, evergreen and resource-conservative species which are drought tolerant plants, and mesophytic, deciduous and resource-acquisitive species which are drought avoidant plants. A brief list of the main traits of drought resistance for both plant functional types is presented in Table 20.1.

1.5 Morphological and Functional Traits of Grasses from Patagonian Monte

Studies of phenological development of these perennial grasses revealed a vegetative growth associated with soil moisture and soil NO_3-N concentration (Bertiller et al. 1991). *Pappostipa speciosa* has vegetative growth from July (winter) to January (summer) and senescing from November (spring) to February (summer). *P. speciosa* is the only perennial grass maintaining green leaves during summer with the highest grass mass production of leaf litterfall in late spring (December) (Campanella and Bertiller 2008). This species has higher plant height, higher LMA, higher lignin concentration in green and senescent leaves, low N concentration in green and senescent leaves, largest seed length than *Poa ligularis*, and did not form a germinable soil seed bank (GSB) (Pazos et al. 2007; Campanella and Bertiller 2008; Pazos and Bertiller 2008). In addition, the roots have greater lignin content, long-lived and high phenolics concentration than *P. ligularis* roots (Semmartin et al. 2004; Rodríguez et al. 2007). Species with higher C:N ratio and secondary metabolites in leaves are less palatable and more resistant to herbivore grazing (Soriano 1956; Pazos et al. 2007).

On the other hand, *Poa ligularis* has vegetative growth from July to November followed by

Table 20.1 Main traits of drought resistance associated to drought tolerant and drought avoidant species

Drought tolerant plants	Drought avoidant plants
Morphological traits	
Low relative growth rate	High relative growth rate
Long growth duration	Short growth duration
Evergreen leaves, longer leaf life span	Deciduous leaves, short leaf life span
Low SLA (high LMA, LDMC)	High SLA (low LMA, LDMC)
High biomass allocation to roots	Low root cost during unfavorable season
Shallow and deep roots distribution	Shallow roots distribution
Presence of epicuticular was	Absence of epicuticular was
Low fecundity	High fecundity
Acquisition and conservation resources traits	
High potential for resource conservation	High potential for resource acquisition
Low capacity to capture resource	Enhanced resource capture
High WUE, reduced water use	Low WUE, high water use
Low leaf nitrogen concentration	High leaf nitrogen concentration
Physiological traits	
Low-slow metabolism	High-faster metabolism
Low-long photosynthetic rate season	High-short photosynthetic rate season
Low stomatal conductance	High stomatal conductance
High leaf ABA accumulation	Low leaf ABA accumulation
Stomatal closure	Stomatal open
Less water loss by transpiration	High water loss by transpiration
Low hydraulic root conductance	High hydraulic root conductance
Osmotic adjustment: high osmolites accumulation	Low osmolites accumulation
Maintenance integrity of membranes	
Antioxidant defense mechanisms	
Anti-herbivore defense traits	
Leaves tough	Leaves thin
High investment in secondary compounds (phenolics and lignin)	Low investment in secondary compounds
Yield	
Low yield	High yield, greater biomass production

senescence and total vegetative inactivity in summer (Bertiller et al. 1991; Campanella and Bertiller 2008). In this species late vegetative growth and flowering are associated to small precipitation events (Bertiller et al. 1991). This species has high N concentration in green leaves, high leaf turnover, small seeds and dioecy reproductive strategy (Bertiller et al. 2002; Pazos et al. 2007). Moreover, *P. ligularis* formed different GSB and most of them are located under shrub patches (Bertiller and Bisigato 1998; Pazos and Bertiller 2008).

Studies under controlled conditions revealed that *P. ligularis* plants exposed to 16 % gravimetric soil moisture (highest mean value near field capacity during autumn-winter, Coronato and Bertiller 1997; Cenzano et al. 2013, 2014) have larger number of leaves, larger number of roots, lower root dry weight, higher number of flowering tillers per bunch than *P. speciosa* plants (Cenzano et al. 2013). Previously, Leva et al. (2009) had informed lower diameter, higher specific root length and higher relative growth rate in *P. ligularis* than *P. speciosa*. *P. ligularis* also showed higher above-ground vegetative and reproductive allocation (e.g. leaves, and inflorescences), lower below-ground allocation (e.g. roots) and lower below/above-ground dry weight ratio than *P. speciosa* (Cenzano et al. 2013). These findings are in agreement with Poorter and

Remkes (1990) reporting that fast-growing species maximize shoot functioning, whereas slow-growing species maximize root allocation.

1.6 Physiological and Biochemical Traits of Grasses from Patagonian Monte

The physiological drought tolerance is assessed as the lowest plant water potential at which a species can maintain key ecological functions, such as an adequate stomatal conductance for photosynthesis (Craine et al. 2012). Most of these key responses are mediated and regulated by phytohormones.

Detailed studies on hormonal metabolite profiling of different plant functional types under natural arid conditions are still scarce; although recently, the identification of hormonal and biochemical traits that play functional roles in the adaptation to drought in Patagonian Monte grasses species has been recently reported (Cenzano et al. 2014).

The involvement of abscisic acid (ABA) as the major chemical signal that regulates the physiological responses to drought has been well documented (Srivastava 2002; Turner and Hartung 2012; Chater et al. 2014). Moreover, a suitable ABA level is necessary for successful plant growth under stress (Spollen et al. 2000; Chen et al. 2006; Tardieu et al. 2011). Under optimal water supply ABA acts promoting leaf growth by maintaining high hydraulic conductivity and high aquaporin activity, but at suboptimal water supply ABA mediates stomatal closure reducing transpiration and favouring water economy inside the plant (Chater et al. 2014). Other protective roles of ABA have been suggested, such as ROS scavenging through increasing the activity of antioxidant enzymes during drought stress (Lu et al. 2008).

ABA is synthesized in plant leaves and roots and also in the soil by rhizospheric microorganisms (Frankenberger and Arshad 1995; Xiong and Zhu 2003; Forchetti et al. 2007) and it moves from the plant to the soil and vice versa (Sauter et al. 2001). The endogenous ABA levels are dynamically regulated by the balance between synthesis, transport and degradation (Fig. 20.3). The ABA catabolic pathways are mainly 8′-hydroxylation and sugar conjugation (Nambara and Marion-Poll 2005). In higher plants, ABA catabolism is initiated by ABA 8′-hydroxylase to form 8′-hydroxy-ABA. 8′-hydroxy-ABA is then spontaneously isomerized to phaseic acid (PA) that is reduced to dihydrophaseic acid (DPA) (Cutler and Krochko 1999) which is the end-product of ABA degradation pathway (Seiler et al. 2011). The major ABA conjugation is with glucose by an ABA glucosyltransferase to produce ABA-glucose ester (ABA-GE) (Xu et al. 2002) which may function as storage form or as hormonal signal to long distance (Sauter et al. 2002). ABA-GE must be hydrolized by β-glucosidases to produce free active ABA (Lee et al. 2006; Llanes et al. 2014) (Fig. 20.3).

High ABA levels improve stress tolerance at vegetative level, but compromise at reproductive level producing less grain yield (Landi et al. 2006). However, low ABA accumulation in drought-tolerant species or cultivars of turfgrasses has been reported (Wang et al. 2003; DaCosta and Huang 2007). It has been suggested that the restriction of photosynthesis and photosynthate allocation to sink tissues induced by ABA may help in short stress periods, but under long term stresses is destructive (Dolferus 2014).

1.6.1 Abscisic Acid Metabolism

Cenzano et al. (2014) found different ABA metabolic profiles between two functional types of grasses from the Patagonian Monte that correlate with the drought-resistance strategy of each functional plant type (Cenzano et al. 2013). These authors reported that the deciduous, mesophytic, and resource-acquisitive *P. ligularis* showed the highest ABA levels due to high biosynthesis/catabolism ratio (drought avoidance strategy) while the evergreen, xerophytic, and resource-conservative *P. speciosa* showed the lowest ABA level due to low biosynthesis/catabolism ratio (drought tolerance strategy). The significance of these results will be discussed further in 2.2.

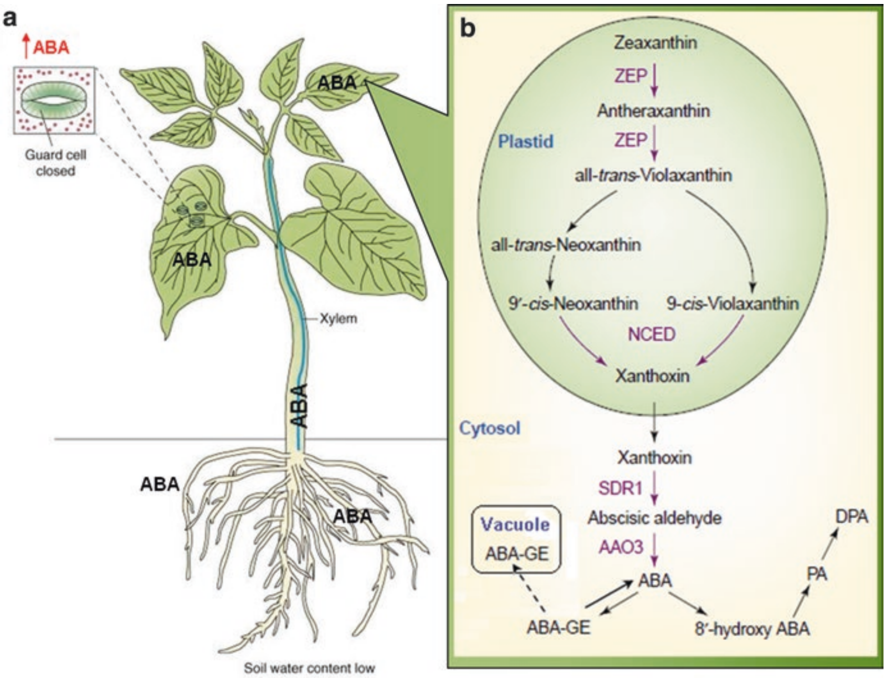


Fig. 20.3 ABA localization and changes produced by drought (**a**), adapted from Schachtman and Goodger 2008. ABA biosynthesis and catabolism (**b**), adapted from Nambara and Marion-Poll 2003; Schroeder and Nambara 2006

1.6.2 Phenolic Compounds as Non-enzymatic Antioxidants

Under drought stress stomata are closed as a rapid response to reduce water loss, but the limitation of gas exchange needed for photosynthesis conduce to reactive oxygen species (ROS) production. To protect photosynthetic membranes against photo-oxidative damage caused by excessive ROS levels, plants have two antioxidant defense mechanisms: (1) non-enzymatic antioxidants such as phenolics compounds and carotenoids among others (Agati and Tattini 2010; Reginato et al. 2015), and (2) enzymatic antioxidants (Peñuelas et al. 2004; Zhao et al. 2011; Zhou et al. 2014).

A recent study revealed that during the drought season (which coincides with high irradiance and high temperatures) the evergreen *P. speciosa* increased total phenols in its leaves in concordance with an increased antioxidant activity, suggesting a role for these compounds in protection against the oxidative stress caused by those conditions (Reginato et al. 2015). Meanwhile, *P. ligularis* increased total phenols concentration, total flavonoids and flavonols during the humid season (when this species had green leaves) in concordance with a highest antioxidant activity. In this case, phenols and principally flavonoids would play a role as protectors against UV radiation and herbivores (Reginato et al. 2015). Indeed, Patagonia receives an increased ultraviolet B (UV-B) radiation due to its close proximity to the Antarctic ozone “hole” (Helbling et al. 2005). Thus, the permanent high solar UV-B radiation and the drought climate of this area, gives flavonoids an important role in absorbing this harmful radiation and preventing ROS production mainly during summer. Thus, dissipation of excess energy under stress conditions is a major physiological process in plant photo-protection (Chaves et al. 2003).

Other compounds that help to avoid damage to the photosynthetic system are carotenoids, which collect light and dissipate the excess of energy (Wright et al. 1994; Demmig-Adams et al. 1996). Leaf photosynthetic pigments increased under drought in *P. speciosa* and *P. ligularis*, indicating the ability of both species to incorporate a large proportion of nitrogen in their molecular structures (Filella et al. 1995) and to maintain photosynthetic activity under drought in Patagonian rangelands (Cenzano et al. 2013).

2 Phenotypic Plasticity

Plants have a staggering capacity to adapt to extreme environments. They have adaptive traits constitutively present that are relevant only for that environment (Dolferus 2014). Additionally, they can adjust to novel climatic conditions through phenotypic plasticity, which is the capacity of a given genotype to render different phenotypic values for a given trait under different environmental conditions (Valladares et al. 2006). Among crucial traits that have been shown to be both under genetic and plastic control is the flowering time, which may be a maladaptive response if it occurs at a wrong time respect to species life cycle (Visser 2008).

Different plasticity types have been documented in plants such as developmental and physiological plasticity and also plasticity for structure, biochemistry and metabolic activity (Sultan 2000). The physiological plasticity is referred to traits such as stomatal aperture and photosynthetic rate that allow plants to adjust to highly temporally variable aspects of the environment such as light intensity and transpiration and it is a short-term plastic response (Sultan 2000). In this context, some plant functional traits are strongly related to the fitness and success of individuals in a given environment and provide good indicators about species ecology (Nicotra et al. 2010).

2.1 Morphological and Functional Plasticity of Grasses from the Patagonian Monte

A recent study revealed that co-existing perennial grasses contrasting in drought tolerance mechanisms display different degrees of phenotypic plasticity in underlying functional traits (Cenzano et al. 2013). These authors found highest plasticity (highest negative response to drought) in reproductive traits of both species of grasses (percentage of flowering plants, inflorescence length and number of flowering tillers). *P. speciosa* displayed high plasticity (highest negative response to drought) in vegetative traits such as total dry weight, root and senescent leaves dry weight. However, *P. ligularis* showed an intermediate plasticity in total dry weight, root, senescent leaves and inflorescence dry weight, root length and some reproductive traits (number of flowering tillers and inflorescence allocation). Green leaves dry weight and root number of *P. speciosa* showed also intermediate plasticity. A low plasticity was reported in plant height, total number of leaves, below/above-ground ratio, and root allocation of both species, green leaves dry weight, inflorescence length, and root number of *P. ligularis*, and inflorescence dry weight and root length of *P. speciosa*. However, the fractions of biomass allocation, mostly to vegetative organs, showed null or extremely low response to drought. Moreover, the highest plasticity in reproductive traits (number of flowering tillers and inflorescence allocation) of *P. ligularis* may be considered as an adaptive response to maintain fecundity conferring fitness.

Recently, it has been suggested that pre-stress memory may play the central role in new parts growth rather than final production (Xu et al. 2010). This observation is in agreement with Cenzano et al. (2013) who reported that repeated pulses of low watering at only 4 % GSM (lowest value during summer drought) induced production of new leaves in *P. ligularis*, and green leaf allocation and photosynthetic pigment concentration increase in both *P. ligularis* and *P. speciosa*. Xu and Zhou (2007) found young leaves of perennial grasses with high metabolically repairing capacity upon rewatering following a pre-water stress.

2.2 ABA Metabolic Plasticity of Patagonian Monte Grasses

Although many studies have informed plastic changes in phenology, leaf life span and seed longevity in response to abiotic stress (Nicotra et al. 2010), the identification of metabolic pathways and biochemical strategies acting as plastic response to drought is still limited. In a recent study, the ABA metabolic plasticity was evaluated in *P. ligularis* and *P. speciosa* under controlled conditions of watering (16 and 4 % GSM) during 2 years of growth, and contrasting strategies to drought resistance in both species were reported (Cenzano et al. 2014) (Fig. 20.4).

The metabolic plasticity was higher in green leaves and roots than in senescent leaves of both grass species. *P. ligularis* had higher metabolic plasticity in ABA levels of green leaves and roots than *P. speciosa* as revealed by a negative value in the plasticity index. The negative value indicates that drought increased this trait, and the high absolute value means high response to drought. However, *P. speciosa* had higher plasticity in the level of the catabolite phaseic acid (PA) in green leaves and roots than *P. ligularis* (Fig. 20.4).

The highest ABA plasticity in roots of *P. ligularis* is in agreement with the more pronounced effect of drought on root length in *P. ligularis* than in *P. speciosa* (Cenzano et al. 2013) suggesting the involvement of ABA in the root growth of the former as it has been reported in rice (Chen et al. 2006).

All products of ABA metabolism (metabolites) had lower plasticity in senescent leaves than in other organs; ABA and PA levels had higher values in 16 % GSM than in 4 % GSM for both species, resulting positive values in plasticity; while DPA and ABA-GE plasticity was positive in *P. speciosa* and negative in *P. ligularis*. This study reported for the first time the metabolic plasticity of a hormone (ABA and its metabolites) in grasses from the Patagonian Monte in response to drought. The highest ABA level was found in *P. ligularis*, a summer deciduous grass with acquisitive and mesophytic traits, and the lowest ABA level was found in *P. speciosa*, an evergreen grass with conservative and xerophytic traits. In addition, both ABA catabolic pathways, 8′-hydroxylation and ABA conjugation, were active in down regulating the ABA level. Thus, the profile of ABA metabolites of each grass species correlates with the strategy for drought-resistance for each functional plant type in Patagonian rangelands (Cenzano et al. 2014).

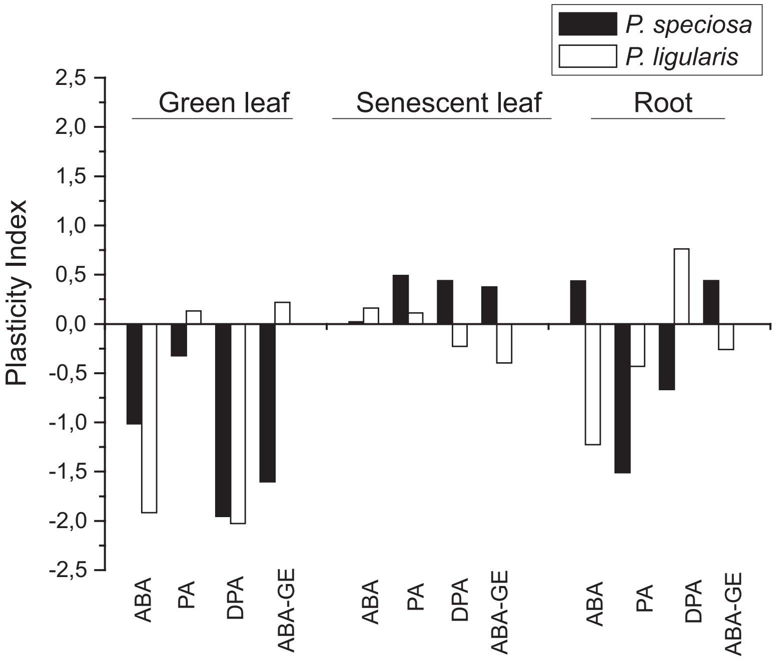
The high plasticity of metabolites found in *P. ligularis* is in agreement with the higher and faster metabolism that characterizes drought avoidant plants (Dolferus 2014). Whilst, a low phenotypic plasticity may be linked to enhanced performance under drought in agreement with the drought tolerance and a conservative resource-use strategy (Sánchez-Gómez et al. 2008; Couso and Fernández 2012). Thus, drought avoiding grasses are more sensitive to drought stress and may have a higher response range of underlying and/or functional traits resulting in higher phenotypic plasticity than drought tolerant grasses. In drought-tolerant species, the maintenance of relative water content (RWC) under drought at very slow soil moisture has been suggested to involve a physiological plasticity to drought (Maherali et al. 2010).

2.3 Adaptive Plasticity

It could be stated that the adaptive plasticity is the global capacity of an organism to function appropriately according to environmental stimulus (Sultan 2003). Phenotypic chances in plant development are all direct towards a future goal of optimal fitness or reproductive success. For any plant, the life cycle goal is to optimize fitness which operates at the whole plant level (Trewavas 2005). However, others are inevitable responses to physical processes or resource limitations (Sultan 1995; Weiner 2004; Nicotra et al. 2010). For example, the indirect influences of genotype on fitness could be exerted through growth differences such as a higher leaf mass (Arntz et al. 2000). In several herbaceous species changes in reproductive timing and allocation affect plant fitness and therefore the population persistence and response to natural selection (Sultan 2000).

Photosynthetic, morphological and phenological traits could contribute indirectly to fitness or reproductive success through their influence on plant size

Fig. 20.4 Metabolic Plasticity Index of *P. speciosa* and *P. ligularis* grasses from Patagonian Monte, Argentina



(Farris and Lechowicz 1990). In a resource-poor environment, shorter leaf life span, relative rapid growth rates, higher stomatal conductance and greater allocation to stem vs. leaves are most important in determining reproductive success. On the contrary, in a resource-rich environment, longer leaf life span, relatively slow growth rates, greater vegetative allocation, and lower stomatal conductance confer higher reproductive success (Galloway 1995; Pigliucci et al. 1995; Arntz et al. 2000). Thus, adaptive plasticity in functional traits is likely to assist rapid adaptation to new conditions and requires a signal perception-transduction system allowing plants to change their development (Nicotra et al. 2010). Adaptive plasticity reduces the chances of extinction in a novel environment setting for subsequent evolution and the non adaptive plasticity can provide sources of novel phenotypes (Ghalambor et al. 2007).

For drought avoidant species, high metabolic activity, high stomatal conductance and rapid growth confer a fitness advantage (Sherrard and Maherali 2006). Moreover, an increased allocation to reproductive tissues is a way to maintain a given level of reproductive output despite reduced total biomass (Sultan 2003).

Determining whether plastic response is functionally adaptive can be difficult and specifically the involvement of ABA in adaptive processes is not yet fully understood.

3 Conclusion

The identification of species groupings into ecological functional types according to morphological, hormonal and biochemical traits, phenology, acquisition and conservation of resources (water and nutrients), preference for herbivorous, drought resistance mechanisms, among others, is very useful for planification and maintenance of the structure and diversity of plant communities to prevent desertification advance in arid regions.

The knowledge of complex interactions between elevated [CO_2], increase of temperature, drought, changing rainfall patterns and soil salinization should remain as main research topics inside a context of global climate change. A better understanding at molecular, biochemical, physiological and ecological levels of drought response mechanisms is needed for arid ecosystems.

Acknowledgements We thank to Mr. F. Sarasa who allowed us to harvest mother plants in his Estancia San Luis, Wildlife refuge "La Esperanza" of Natural Patagonia Foundation, to Dr. Mónica Bertiller and Dr. Analía Carrera for providing climate data, and to the anonymous reviewer for his helpful comments that improved the chapter. This research was funded by the National Research Council of Argentina (CONICET) and the Ministry of Science, Technology and Innovation of Chubut Province, Argentina.

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Distichlis palmeri: An Endemic Grass in the Coastal Sabkhas of the Northern Gulf of California and a Potential New Grain Crop for Saltwater Agriculture

21

Cylphine Bresdin and Edward P. Glenn

Abstract

Extensive coastal sabkhas in the northern Gulf of California in North America are colonized by *Distichlis palmeri*, an endemic grass that produces a grain that was harvested as a staple food by native Cocopah people. It has been considered as a potential perennial grain crop for salt water agriculture. Previous short-term trials have shown good vegetative growth but low percentage of flowering stems resulted in low grain yields. In these trials, we grew *D. palmeri* outdoors in paddy-style (flooded) conditions in 26–34 g L^{-1} sea salt solutions. Reproductive maturity was reached 4 years after initial establishment of plants from seed, with nearly all stems producing male or female flowers. Mixtures of male and female plants (1:3) produced 231–310 g m^{-2} of grain, with nutritional content similar to domesticated grains. These yields are within the range of other grain crops and demonstrate the potential for further developing *D. palmeri* as a global crop for salinized soils and water supplies.

1 Introduction

While sabkhas are usually associated with North Africa and the Middle East, they occur on all continents except Antarctica (Yechieli and Wood 2002). An extensive set of coastal salt flats occurs in the Northern Gulf of California, Briere (2000) where they are called esteros or negative estuaries (Briere 2000; Brusca et al. 2006; Glenn et al. 2006). In this extreme desert environment (less than 100 mm $year^{-1}$ of rainfall) and with a tidal range of up to 7–9 m, esteros typically form at the mouths of rivers that are no longer connected to the sea. They are flooded and drained twice a day with hypersaline seawater (36–42 g L^{-1}) through a network of tidal creeks bringing seawater as much as 10 km inland at high tide and exposing vast mudflats and saltflats at low tide (Fig. 21.1). Occurring mainly along the Sonoran (eastern) coastline above 28° N, esteros extend from the

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M.A. Khan et al. (eds.), *Sabkha Ecosystems Volume V: The Americas*,
Tasks for Vegetation Science 48, DOI 10.1007/978-3-319-27093-7_21

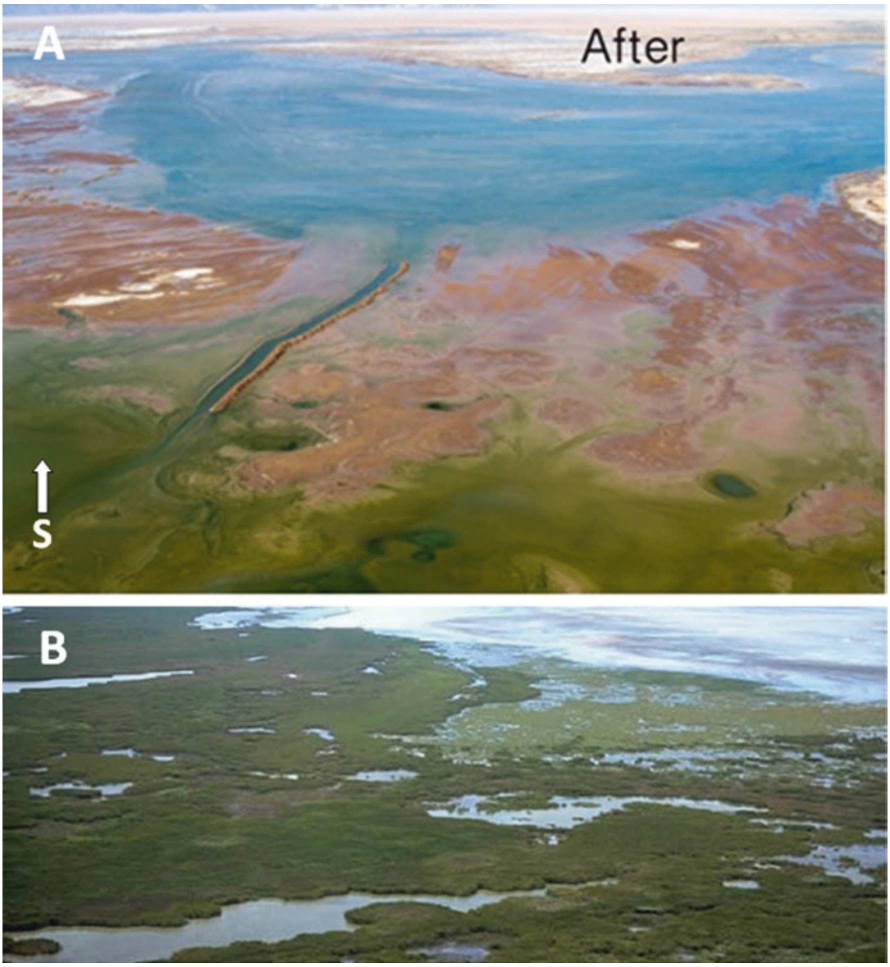

Fig. 21.1 (**a**) Esteros of the Colorado River Delta, U.S.A. are crucial areas where freshwater mingles with tidal saltwater. The image was taken in 2012, after a pilot channel had been dug to reunite the river and ocean after the 2010 earthquake had shifted topography. credit: Sonoran Institute/LightHawk. http://www.lighthawk.org/what-we-do/blog/happy-accidents-and-restoring-colorado-river-delta. (**b**) Esteros at high tide. Source: http://sonoranjv.org/wp-content/uploads/2014/01/610x250-delta-osvel-hinojosa.jpg

city of Guaymas to the mouth of the Colorado River and occupy over 114,000 ha. Unlike normal estuaries with active river systems, these esteros often contain extensive salt flats and are saltier at their heads than at their mouths (Fig. 21.1a), with vegetation confined to the margins of the tidal creeks.

The southernmost esteros, below 29° N, contain mangroves (*Avicennia germinans*, *Rhizophora mangle*, *Laguncularia racemosa* and *Conocarpus erectus*) as well as 17 low-growing, halophytic shrubs, succulent forbs, and grasses (Glenn et al. 2006; Castetter and Bell 1951). Above 29° N, 14 halophytes are commonly found in the esteros, four of which are endemic to the Sonoran Desert. The dominant species in the low zone of these esteros is an endemic grass, *Distichlis palmeri* (Palmer's salt grass) known only from the northern Gulf of California (Felger 2000, 2007). It was named nipa (nee-pah) by the indigenous Cocopah people, who harvested its grain as a major food staple in summer (Castetter and Bell 1951). Distichlis is a genus of dioecious perennials with Kranz anatomy that predicts C4 photosynthesis. The leaves have bicellular microhairs that excrete salts, which commonly are seen

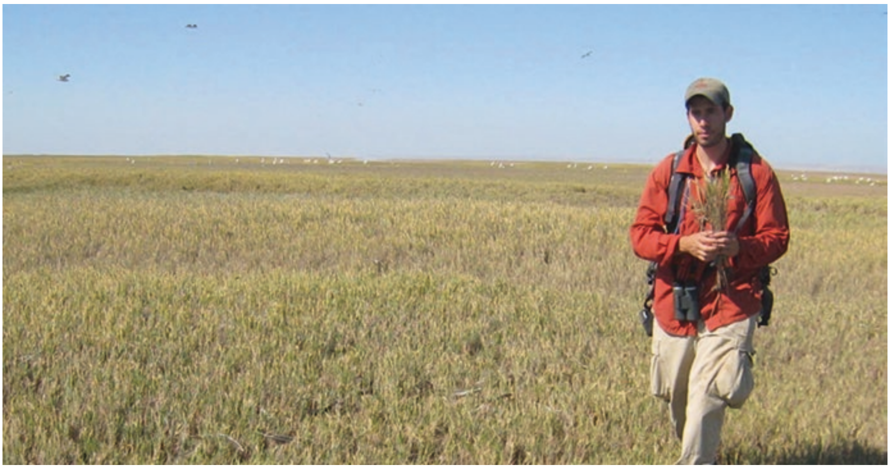

Fig. 21.2 Large monoculture stands of *D. palmeri* at the Colorado River delta. Ben Wilder collecting specimens on Montague Island. Photo by Richard Felger, May 13, 2009

on the leaf surfaces (e.g., Bell and Columbus 2008). The stems (culms) of *D. palmeri* produce terminal panicles. Female panicles are usually 5–13.5 cm long; the spikelets break apart above the glumes and between the florets, and are 6–9-flowered, with the terminal one often a sterile rudiment. As with other grasses, the fruit of *D. palmeri* is called a caryopsis and at maturity it is called a grain. In naturally occurring populations most or often nearly all stems become synchronously reproductive, with flowering occurring in March and April and grain ripening in May (Pearlstein et al. 2012). In the esteros, male and female plants grow in mixed stands with approximately equal numbers of males and females (Fig. 21.2).

D. palmeri is distinguished from common saltgrass (*D. spicata*) by the large size of its grain. While *D. spicata* caryopses are minute, the caryopsis of *D. palmeri* weighs about 10 mg and is the size of a rice grain (Pearlstein et al. 2012). Because they are borne on terminal panicles like wheat, the grains are easily harvested and processed, which is why they were a major food source for the Cocopah. *D. palmeri* might have evolved from *D. spicata* in response to the annual summer floods, from snow melt in the Rocky Mountains that entered the northern Gulf of California in the Colorado River. *D. palmeri* grain germinates readily in brackish water and it was able to colonize large areas of shifting mudflats in the Colorado River delta, formed from sediments carried in the river. These floods were curtailed by construction of upstream dams and diversions of water for agriculture, and the river only occasionally reaches the sea today. Nevertheless, *D. palmeri* has persisted as the dominant halophyte in the Colorado River delta, forming clonal stands covering several thousand hectares along the banks of the river in its intertidal reach and on Montague Island at the mouth of the river (Glenn et al. 2006). It is also the dominant halophyte in the low intertidal zone of the esteros south of the Colorado River delta, but above the mangrove line.

Interest in *D. palmeri* as a modern grain crop for saltwater agriculture began in the 1970s when the idea emerged of developing new crops for saline soils and waters from wild halophytes (Felger 1979, 2000, 2007). All our major grain crops are annual grasses, but a case has been made for developing energy-efficient non-tillage perennial grain crops (Glover et al. 2010; Van Tassel and DeHaan 2013). Not only is *D. palmeri* perennial but it also can be grown paddy-style like rice, as it has aerenchyma tissues that allow it to grow in permanently flooded conditions (Pearlstein et al. 2012). Furthermore, it is extremely salt tolerant, growing on seawater with salinities of 38–42 g L^{-1} under natural conditions.

Dense stands of *D. palmeri* on Montague Island yield an estimated 1250 kg ha^{-1} of grain (Pearlstein et al. 2012), overlapping the low end of cultivated grain crops. Several attempts have been made to introduce *D. palmeri* into cultivation as a grain crop. Yensen and Weber (1986, 1987) showed that *D. palmeri* grain had nutritional qualities similar to wheat and other grains. Yensen (2006) patented several selected lines of *D. palmeri* and *D. spicata* for forage and grain production. However, in 2 years of large-scale field trials in Australia, Leake (2004) reported vegetative growth but very low seed production.

Pearlstein et al. (2012) revived interest in *D. palmeri* by collecting new germplasm from the Colorado River delta and conducting greenhouse trials. The high salt tolerance, high biomass production under anaerobic soil conditions, and high nutritional value of the grains were confirmed. However, in 2 years of trials, grain production was very low. After 2 years, only 2 % of stems of female plants became reproductive, compared to nearly 100 % each year in the natural stands from which the grain was collected. It was speculated that *D. palmeri* might require several years of vegetative growth before reaching its full reproductive potential. The longest growth trials had only continued for 2 years. The present study reports grain yields and nutritional value of *D. palmeri* grown for 6 years in tubs flooded with saline water, simulating a paddy-style agronomic system. During outdoor trials, plants reached full reproductive potential and produced high yields of grain with high nutritional content, confirming the feasibility of developing *D. palmeri* as a perennial grain crop for salinized soils and water supplies.

2 Materials and Methods

Plant material originally sown by Pearlstein et al. (2012) in November 2009 was allowed to mature in a greenhouse under flooded conditions at 10 g L^{-1} TDS until March 2012 when the plants were relocated outdoors (Environmental Research Laboratory, Tucson, AZ). Plant stock was divided and planted into seven, 60 cm diameter, 60 cm deep pots (with drainage holes) containing a 2:1 ratio of sand to potting soil. Pots were set into a larger diameter, 60 cm deep tub filled with flood irrigation water of 10 g L^{-1} synthetic sea salt (Crystal Sea® Marinemix, Marine Enterprises International, Baltimore, MD) consisting of 83 % NaCl, 10 % $MgSO_4$, 3.5 % $CaCl_2$, 3.1 % KCl and trace amounts of other salts (Fig. 21.4f). Consumed and evaporated water was replenished with 10 g L^{-1} irrigation water for the first 9 months. This allowed time for soil moisture and salinity to stabilize. Irrigation was then changed to city water, approximately 0.7 g L^{-1}, to make up for water lost to evaporation and consumption. After 1 year outdoors a small sample of plants were transplanted and moved back into the greenhouse and continued to receive the same irrigation regime. TDS concentration (g L^{-1}) was measured in 2014 with a Traceable probe (VWR® Traceable® Portable Conductivity Meter, model: 23226-505) during the flowering season from mid-February to harvest in May. Probe calibration was with synthetic sea salt mix and NaCl solutions. Stem density was counted in two, 10 cm^2 areas per pot, averaged and translated to total stems.

D. palmeri grain was harvested over two crop cycles in 2013 and 2014. Crop 1 was harvested in May, 2013 by cutting all stems in each pot at the base. Total female and male stems per pot were counted. The number of caryopses per spikelet and number of spikelets per stalk from five random stems from an all female pot were used to estimate grain yield. Crop 2, May 2014, was harvested by cutting only mature, grain containing panicles high on the stem. The number of caryopses per pot was calculated from the weight of spikelets per pot where grain was 66 % of spikelet weight for hand-cleaned samples. Proximate analyses of grain and stems were conducted by Litchfield Analytical Services (Litchfield, MI).

3 Results

Unlike previous trials, nearly all stems in each pot were reproductive in 2013 and 2014. One pot was 100 % male plants while others were

Table 21.1 Tabulation of number of female and male flower producing stems per pot for Crop 1

Crop 1, 2013			Crop 2, 2014	
Pot #	Female	Male	# Stems	Grain (g)
1	508	0	1416	62.082
2	0	399	1065	0
3	463	29	1766	79.440
4	279	132	1270	44.382
6	529	5	1124	55.933
7	352	42	1065	69.548
Totals	2131	607	7706	332.7

Pot #5 is not considered because it was used to resupply plant material for the greenhouse and the 35 g L^{-1} tests

Fig. 21.3 Plant material from outdoor stock grown under 26–34 g L^{-1} paddy: (**a**) panicle; (**b**) male flower; (**c**) female flower; (**d**) spikelets of panicle; (**e**) caryopses from panicle; (**f**) outdoor paddy setup showing the light green algal mat 3 months after Crop 1 harvest in May 2013. Photos by Cylphine Bresdin

dominated by female plants (Table 21.1) to give an overall male to female ratio of approximately 1:3. Male flowers (Fig. 21.3b) presented about 7 days before female flowers (Fig. 21.3c). At anthesis, versatile stamens are a greenish cream and stigmas are purple giving the outdoor stand a purple cast. Flower presentation in the greenhouse precedes outdoor presentation by about 10 days and stigmas appear before anthers form pollen. Females are less resilient than males when harvested by cutting at the base of the stem. Re-growth of females after Crop 1 harvest was slow and had not fully recovered by Crop 2 and is likely to be the reason for the lower harvest year 2. Stems with mature panicles should be cut high on the stem not at the base of the stalk as was done for Crop 1 harvest.

For crop cycle 1, five random stems averaging 1 m tall from an all female pot were used to determine number of caryopsis per flower spike (Fig. 21.3a, d, e). Number of spikelets per panicle ranged from 5 to 7 (mean = 6, Std. = 1). Number florets per spikelet ranged from 2 to 6 (mean = 4, Std. = 0.9). Number of caryopsis per floret was 1. Number of grain per panicle ranged from 18 to 30 (mean = 23, Std. = 5). We had 2131 female stems in Crop 1 which produced an estimated 49,000 mature grains or an average of 31,000 grains per square meter. Grain weight ranged from 6 to 14 mg (sample size = 42, mean = 10 mg, Std. = 2.3) A mean weight of 10 mg gives an estimated grain yield of 310 g m^{-2}. Grain size ranged from 6 to 9 mm (sample size = 42, mean size = 8 mm, Std. = 0.9). Stem density in Crop 2 was 4791 stems per m^2. The mean number of caryopses in pots containing females was estimated at 6200, equivalent to 31,000 grains per m^2 or 231 g m^{-2} including male plants.

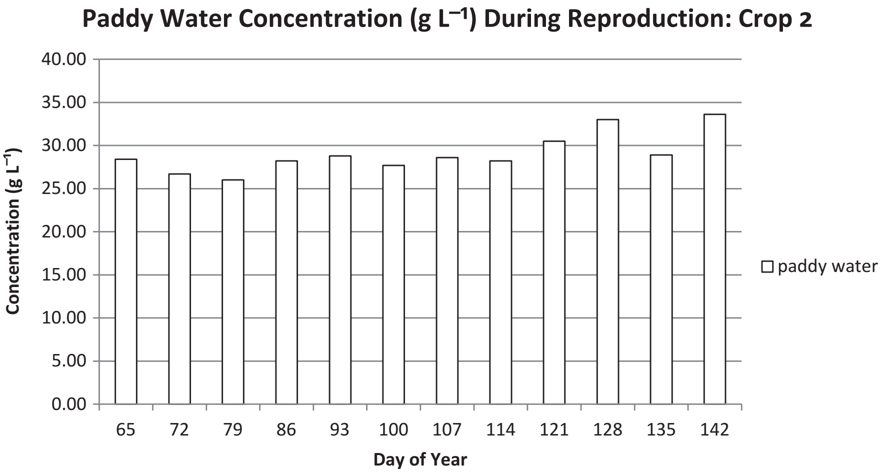

Fig. 21.4 Concentration of paddy water through the reproductive period from mid-February to harvest in mid-May 2014. The slight increase in salinity over the reproductive period may be due to decreased water volume as a result of increasing temperatures. Water volume was not measured

Proximate analysis of *D. palmeri* grain (Table 21.2) showed 7–12.5 % crude protein with an effective net energy between 60 and 75 %, with low ash and sodium content, and high iron. Digestible carbohydrates were the main constituents of both the grain and the biomass (stems). Crude fiber was 38 % of the stem material which was higher in calcium, sodium and magnesium than the grain.

Salinity of paddy water in the tub increased from 28 to 34 g L^{-1} over the flowering and grain filling season in 2014, due to consumptive water use by the plants and direct evaporation of water from the tub during high ambient spring temperature in Tucson, AZ (Fig. 21.4).

4 Discussion

D. palmeri is a perennial rhizomatous halophytic tidal marsh grass endemic to the mud flats, esteros of the Colorado River Delta. At low tide monoculture stands are left standing in pools of evaporating saltwater causing the plant available water to exceed the salinity of seawater. Pearlstein et al. (2012) reported that female stands in its natural environment were nearly all reproductive and had projected grain yields of 125 g m^{-2}. Yensen (2006) reported field yields of 200–400 g m^{-2} but did not give details, whereas Leake (2004) could not replicate those field yields within a 2 year time frame. When plants were grown paddy style in the greenhouse there was no flowering the first year and only 2 % of stems were reproductive the second year. Plants were moved outdoors when they were 2.5 year old and maintained under saline paddy style agronomic conditions. Heavy flowering was first seen mid-February 2013 and resulted in a grain yield of 310 g m^{-2} followed by a yield of 231 g m^{-2} in 2014. Our results indicate that when cultivated under saline paddy style conditions, *D. palmeri* requires 4 years to mature. Thereafter it produces high grain yields with crude protein, digestible carbohydrates and other nutritional quality similar to traditional annual crops of: rice, wheat and quinoa (Table 21.2).

The major finding of this study is that when allowed to grow for several years, *D. palmeri* reaches it full reproductive potential, a characteristic common for perennial grasses under consideration as new grain crops (Glover et al. 2010). Once established, perennial grains do not require replanting each year, offsetting the disadvantage of having to wait several years for the first grain harvest. *D. palmeri* stem material can be cut for forage until reproductive maturity is reached, but cutting too close to the ground appears to result

Table 21.2 Proximate analysis of *Distichlis palmeri* grain and biomass from crops grown outdoors under paddy style agronomic conditions with 10 g L^{-1} synthetic sea water compared to values published (USDA nutritional database, http://ndb.nal.usda.gov/ndb) for traditional grains

	2013	2014		USDA nutritional database		
Constituent	Grain	Grain	Biomass	Quinoa	Rice	Wheat
Crude protein (%)	7.22	12.54	6.04	14.12	7.94	13.68
Acid detergent fiber (%)	4.61	5.68	37.98	–	–	–
Crude fiber	3.68	4.54	30.38	7.00	3.50	–
Digestible carbohydrates (%)	68.22	71.29	45.85	64.16	77.24	71.13
Ash (%)	1.06	2.38	4.29	–	–	–
Fat (%)	1.68	1.33	1.26	6.07	2.92	2.47
Total digestible nutrients (%)	77.88	85.75	67.33	–	–	–
Effective net energy (%)	67.27	75.11	56.81	–	–	–
Digestible energy (Mcal/kg)	0.71	0.78	0.61	0.37	0.37	0.34
Phosphorus (%)	0.26	0.36	0.15	0.46	0.33	0.51
Calcium (%)	0.04	0.06	0.33	0.05	0.23	0.03
Potassium (%)	0.68	0.79	0.47	0.56	0.22	0.43
Sodium (%)	0.09	0.1	0.49	–	–	–
Magnesium (%)	0.07	0.09	0.18	0.20	0.14	0.14
Iron ppm	116	28	107	–	–	–

in slower re-growth with a potential decrease in grain yield. The grain yields obtained here, 231–310 g m^{-2}, compare to estimates of global grain yields of 290 g m^{-2} (SD = 177) from 2000 to 2013 (Word Bank data at http://data.worldbank.org/indicator/AG.YLD.CREL.KG). The yields in this experiment cannot be extrapolated directly to potential field yields because plants were hand-harvested and were not grown in closed-canopy conditions. However, results do confirm the potential of *D. palmeri* to produce high grain yields when allowed to reach full reproductive potential under saline paddy style irrigation outdoors. Tub salinities ranged from 26 to 34 g L^{-1}, typical of global open-ocean salinities but lower than those in the esteros in the native range of *D. palmeri* indicating that this could be a true seawater crop.

In conclusion, *Distichlis palmeri* is a perennial salt water plant with high agricultural potential that flourishes under hydric soils in arid climates. It produces a large nutritious grain with yields similar to rice when cropped at a 1:3 (or less) male to female ratio. It is a prime candidate for domestication as a constructive use of waterlogged salinized lands as well as volume reduction of saline waste streams. Spikelets from both harvests have been donated to Pronatura Noroeste for their use in Colorado River Delta re-vegetation work and with our ongoing expansion of stock; we will deposit spikelets with Native Seed Search for preservation and continue to donate to esteros re-vegetation efforts.

Acknowledgements This research and manuscript partially fulfills requirements for the Degree of Doctor of Philosophy, University of Arizona.

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Effect by Plant Growth Promoting Bacteria (*Azospirillum halopraeferens* and *Klebsiella pneumoniae*) on Lipid Value in Seed of the Halophyte *Salicornia bigelovii* Torr.

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Abstract

Halophytes species appears on great scale as an alternative for the essential fatty acid production in human nutrition, for that reason, the fatty acid composition receives special importance. *Salicornia bigelovii* is a halophyte that developed in arid and coastal zones like Sonora State and the peninsula of South Baja California, Mexico. *Salicornia* could be an alternate species in the edible oil production. The similar fixation of N_2 by bacteria associated with roots of *Salicornia bigelovii* and halophyte are an important nitrogen source available in coastal ecosystems. The inoculation of *Klebsiellapneumoniae* and *Azospirillumhalopraeferens* was evaluated

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M.A. Khan et al. (eds.), *Sabkha Ecosystems Volume V: The Americas*,
Tasks for Vegetation Science 48, DOI 10.1007/978-3-319-27093-7_22

during the vegetative development of *Salicornia bigelovii* under field conditions in two ecotypes (Cerro Prieto = CP and Santa Rosa = SR), having affected positively variable as weight, yields of production and biochemical characteristics and contained total of ashes, protein and total lipids in seed produced. Our results suggest that both ecotypes of *S. bigelovii*, under the conditions field used, can be improved with the application of *K. pneumoniae* and *A. halopraeferens*, showing a potential utility for agricultural producers of coastal semi-arid zones.

1 Introduction

Sustainable agricultural productivity in arid regions includes selection, evaluation and development of salt-tolerant plants, focusing on the desirable crops adapted to dry saline and desert areas (Chatrath et al. 2000; Ungar 2000). Increasing interest on the range of salt levels in soils to enhance the salt-tolerant crops (Stove 1997). Halophytes, *Salicornia bigelovii* particularly (Chenopodiaceae), promise to be a resource in arid coastal areas because they tolerate highly saline conditions (Glenn et al. 1991). *Salicornia bigelovii* was identified among many halophytic species tested for possible domestication, because it is considered as a new promising economical resource of oilseed production (Glenn et al. 1991). *Salicornia bigelovii* is a leafless, jointed and succulent stems that form terminal fruit-bearing spikes, in which seeds are borne (Gallawa 1996). The produced seeds by *S. bigelovii* has a high proportion of unsaturated fatty acid where linoleic acid proportion is 50 %. These important plants could be incorporated into traditional agriculture to help the agricultural economy (Glenn et al. 1995). The state of Sonora and Baja California Sur are two of the driest states of Mexico, with 60 mm average annual rainfall, in addition to lack of water resources. Agricultural activities are dependent on wells. Unfortunately, the extraction of too much water, and inappropriate use of fertilizers has promoted agricultural soil salinization (SARH 1981). Production alternatives include the development of salt tolerant crops and selection and evaluation of salt tolerant plants (Ungar 2000). In the states of Sonora and Baja California Sur, *S. bigelovii* is widely distributed along the coasts. It is possible that this halophyte has commercial value. However, in both states, their productivity is limited by the lack of available nitrogen, a condition that affects the growth and reproduction (Jefferies 1981). The nitrogen-fixing bacteria are endemic ecological-organic alternative for the delivery of this nutrient. Bacteria capable of promoting growth and development in plants; one of the most studied are *Azospirillum halopraeferens,* having halotolerant properties and promote positive outcomes in crop production (Reinhold et al. 1987; Bashan and Holguin 1997). The use of endemic bacteria associated with rhizosphere of plants such as *S. bigelovii* is needed to evaluate its effectiveness as a resource in the vegetative development (Hamdi 1999). For above mention the goal of this investigation was to evaluate the effect of inoculation of *Klebsiella pneumonia* and *Azospirillum halopraeferens* in two ecotypes of *Salicornia bigelovii* (Cerro Prieto = CP and SR = Santa Rosa), recording performance and physiological variables and production of fatty acids in seed, in order to be able to propose (*S. bigelovii* with the interaction of Plant Growth Promoting Bacteria) as an alternative agricultural production in the agricultural sector of dry arid zones.

2 Materials and Methods

2.1 Evaluation of *Salicornia bigelovii* Inoculated with *Azospirillum halopraeferens* and *Klebsiellap neumoniae* Under Field Conditions Establishment

The treatments evaluated in this study were two ecotypes of *Salicornia bigelovii* seeds (ecotype Cerro Prieto = CP and SR = Santa Rosa), from two areas with pure populations of Salicornia. Area 1 is located between Lat coordinates. 31°21′18.82″ N and Long. 113°35′29.41″ W, area 2 is located between Lat. 29°9′26.62″ N and Long. 112°14′40.66″ W, respectively. In both ecotypes the effect of inoculation of the root zone with nitrogen-fixing bacteria was assessed: *Klebsiella pneumoniae* and *Azospirillum halopraeferens* under field conditions. Prior to planting, wild seed was cleaned manually in order to separate the mature seed by wiping dry vegetative material to select larger seeds, uniform color without apparent damage. Subsequently both ecotypes underwent disinfection, performing an immersion in sodium hypochlorite for 30 s at a concentration of 3 % (v/v). They were then washed three times with sterile distilled water. The seeds were then dried on sterile paper towel.

2.2 Inoculation of *S. bigelovii* Seed (Ecotype Cerro Prieto = CP and SR = Santa Rosa) with the Bacteria *Klebsiellap neumoniae* and *Azospirillum halopraeferens*

Bacteria *K. pneumoniae* and *A. haloprefaerens* were independently developed in liquid medium OAB with 0.5 M NaCl. Incubation conditions were continuously stirred (120 rpm) at a temperature of 30 °C, based on recommended by Reinhold et al. (1987). Between 14 and 16 h elapsed (log phase), the culture concentration of each bacteria, according to the following procedure was determined: 1 mL of the culture was poured into a cell for spectrophotometer (master spectrum FISHER SCIENTIFIC 415) taking the reading absorbance at a wavelength of 540 nm against a control medium with liquid OAB without 0.5 M NaCl bacteria. The bacterial suspension was diluted to 1.00 absorbance unit, corresponding to a concentration of 1×10^9 CFU/mL. To each of the crops 0.5 g (590 seeds) were added to each of the ecotypes a Kitazato 50 mL flask were evacuated to 600 mmHg for 5 min in the expression are given by (Carrillo et al. 1998). After this time, the seeds inoculated vacuum infiltration or *Klebsiella pneumoniae* or *Azospirillum halopraeferens* were deposited on 1 m^2 germinating plates containing 7 cm sandy substrate. Then the seed was covered with a thin layer (3 mm ± 1) substrate type peat -moss (Sunshine, Sun Gro Horticulture Canada, Ltd.). The germinating plates were placed in the open (open sky). For 1 month was carried out irrigation with potable water saturation daily. A month after obtaining the corresponding germinated seedlings to each of the treatments were transplanted in field conditions in micro of an area of 1 m^2, in order to avoid mechanical damage to the root system and a possible entry of soil pathogens. Plants (60) were established in each watershed at a distance of 10 cm between plants and 15 cm between rows.

2.3 Inoculation of *Klebsiella pneumoniae* and *Azospirillum halopraeferens*, Solid Route in Alginate Beads in Two Different Vegetative Stages (Seedling, and Flowering-Inoculation of Solid Root System Pathway in Calcium Alginate Beads)

The fertilization program by inoculation via solid in the form of calcium alginate beads during the vegetative growth of *S. bigelovii* was performed by depositing with a spatula, a gram of spheres containing *K. pneumoniae* or *A. halopraeferens*, according to the study treatments in seedling and flowering stages. During the first month of vegetative plant development, (germination and seedling development) seedlings were irrigated with potable water and then saltwater. The frequency of irrigation at this stage was every other day, applying 55 ± 5 L/m^2; in these period stages, the irrigation system used was that of flooding. The properties of the fresh water used: electrical conductivity: 1.194 w dS/m; the properties of salt water used: electrical conductivity of 11,230 w dS/m. A week before transplanting, seedlings were adapted to saline water, gradually increasing salinity. After transplantation, the irrigation system that was used in the micro sprinkler type, applying irrigation depth of 65 ± 5 L 30 μm. When finish the growth of *Salicornia* (11 months), 10 plants per treatment were randomly selected to quantify the variable seed production per plant (g/plant). For the variable seed production per m^2 (g/m^2 seed production) of each treatment was determined by multiplying the value obtained from the average seed production per plant by the total number of plants to be planted by watershed. Dry matter produced by watershed (g/m^2 dry matter) was evaluated. In addition, samples of seeds produced in each treatment were analyzed for the quantification of protein, moisture, ash and total lipids. The absolute percentage of fatty acids (palmitic, stearic, oleic, linoleic and linolenic), was analyzed by the technique suggested by Bligh and Dyer (1959) and amended by Arredondo et al. (1997) and Sato and Murata (1988). Analyses of variance were performed as proposed by Snedecor (1956). The least significant difference test was performed by Duncan's Multiple Range ($p > 0.05$ %). Analyses were performed using SAS (SAS 1996).

3 Results and Discussion

Salicornia bigelovii is a halophyte that is emerging for the immediate future as an option to contribute to the agricultural economy with a possible positive impact on the regional development of the agricultural sector of northwestern Mexico (Mota 1980). In addition, the microorganisms with beneficial effects on plantsplay a significant role as potential agents of bio-fertilizers. However, investigations into growth-promoting bacteria and halophyte plants are scarce. Therefore, it is necessary to conduct studies on halophytes and the environment around them in order to extend the range of endemic nitrogen fixing bacteria, to enlarge the knowledge of inoculum density, physiology promoter strains, inoculation into different cultures and ecology rhizosphere level among others. According our study, inoculating *Klebsiella pneumonia* and *Azospirillum halopraeferens* in two ecotypes of *Salicornia bigelovii* (Cerro Prieto = CP and SR = Santa Rosa), the ecotype Cerro Prieto (CP) with *K. pneumoniae* and *A. halopraeferens* was significantly with $p > 0.05$, favored in bloom, fresh and dry weight, root length and content of nitrates (NO_3) in flowering stage. Although *A. halopraeferens* stimulated a greater percentage of flowering in CP ecotype with $p < 0.05$, followed by *K. pneumoniae* compared with uninoculated controls of both ecotypes.

With respect to fresh samples obtained in the flowering stage weight, the results showed significant differences ($p < 0.05$) between treatments under field conditions (SR = 1700 g/plant; CP + *Azospirillum halopraeferens* = 2430 g/plant; CP + *Klebsiella pneumoniae* = 2427 g/plant; SR = 1.428 g/plant; SR + *Azospirillumhalopraeferens* = 1728 g/plant; *Klebsiella pneumoniae* + SR = 1.693 g/plant). In this sense, SR ecotype inoculated with *K. pneumoniae* was stimulated by 200 % while with *A. halopraeferens* the effect was 94 %. However, the CP ecotype inoculated with *A. halopraeferens* and *K. pneumoniae* were stimulated by 900 and 150 %, respectively. In dry weight reached at the flowering stage, the results show that both ecotypes were stimulated by the inoculants, showing *A. halopraeferens* the highest values for both ecotypes (CP = 267 g/plant, CP + *Azospirillum halopraeferens* = 1120.0 g/plant; *Klebsiella pneumoniae* + CP = 673 g/plant; SR = 320 g/plant; SR + *Azospirillum halopraeferens* = 487 g/plant; *Klebsiella pneumoniae* + SR = 865 g/plant).

Regarding the root length in the flowering stage, performing variance analysis significant differences between treatments. The highest values of growth was CP ecotype inoculated with *A. halopraeferens*, followed by SR with *K. pneumoniae* (CP = 14.23 cm; CP + *Azospirillum halopraeferens* = 26 cm; *Klebsiella pneumoniae* + CP = 15.23 cm; SR = 17.32 cm, SR + *Azospirillum halopraeferens* = 14.45 cm; *Klebsiella pneumoniae* + SR = 20.34 cm).

The nitrate content in control plants of both genotypes showed high values compared with those plants inoculated with N_2-fixing bacteria (CP = 1.3 mg/mL of NO_3/plant, CP + *Azospirillum halopraeferens* = 0.32 mg/mL NO_3/plant; *Klebsiella pneumoniae* + CP = 0.45 mg/mL of NO_3/plant, SR = 1.1 mg/mL of NO_3/plant, SR + *Azospirillum halopraeferens* = 0.35 mg/mL of NO_3/plant, SR + *Klebsiella pneumoniae* = 0.49 mg/mL NO_3/plant). This apparent inhibition in the uptake or nitrate accumulation appear to be controversial. Similar results have been found in studies in maize (Zea mays) (Blackmer and Scheppers 1995; Pérez-Silva 1989), where different levels of fertilizers were applied from N_2, low NO_3 concentrations detected in the sap were being directed towards the formation of biomass. With regard to biomass production, the phenological Salicornia bigelovii response by effect of *Azospirillum halopraeferens* and *Klebsiella pneumoniae* shows that inoculation Cerro Prieto ecotype (CP) with *A. halopraeferens* and *K. pneumoniae* was favored significantly with 718.0 and 677.0 kg/ha respectively. Meanwhile ecotype Santa Rosa (SR) showed values of 549.0 and 576.0 kg/ha as a result of *A. halopraeferens* and *K. pneumoniae*, respectively. The not inoculated control treatments reduced production by up to 50 % less; (CP) with 310.0.0 kg/ha, and ecotype (SR) showed values of 225.0 kg/ha. According the analysis of variance for the proportion of lipid, protein, moisture and ash the treatments showed significant differences. It was found that plants inoculated with N_2-fixing bacteria (Table 22.1), showed higher values compared with controls plants treatments. The higher lipid values were obtained consecutively showing a statistical equality for *K. pneumoniae* + SR treatments , CP + *K. pneumoniae*, *A. halopraeferens* CP + and CP + *A. halopraeferens*. For proteins, CP + *A. halopraeferens* showed higher values followed by the same ecotype inoculated with *K. pneumoniae*. For moisture and ash variable, CP ecotype inoculated with *K. pneumonia* was statistically higher compared to other treatments.

Regarding the proportions of fatty acids, Table 22.2, showed significant differences ($p > 0.05$) between treatments with the content of palmitic fatty acid, when the treatments were inoculated with *K. pneumonia*; however the CP + *A. halopraeferens* ecotype, was the most affected with this acid. Concerning the stearic acid there was not statistical significances between treatments inoculated in both ecotypes of seed, compared with oleic acid. With linoleic acid, CP ecotype and *A. halopraeferens* showed statistically significant. Relative to linoleic acid between treatments there was no significant improvement except without inoculant who proved to lower values ecotypes. This implies the possibility of the possible introduction of beneficial bacteria like *K. pneumoniae* and *A. halopraeferens* as a halotolerant bacteria to be improved with the *S.*

Table 22.1 Effect of N_2-fixing bacteria on the content of lipid, protein, moisture and ash seed present in two ecotypes of *Salicornia bigelovii* under field conditions

Ecotype	Inoculant (Bacteria)	Seed			
		Lipid (mg/g)	*Protein (%)	Moisture (%)	*Ash (%)
Santa Rosa	Control	53.0^c	23.3^c	4.68^c	20.0^d
Santa Rosa	*K. pneumoniae*	95.4^a	22.4^e	4.79^c	24.1^b
Santa Rosa	*A. halopraeferens*	96.4^a	23.0^d	4.77^c	21.4^c
Cerro Prieto	Control	77.0^b	20.1^f	4.80^c	14.0^f
Cerro Prieto	*K. pneumoniae*	90.2^a	24.1^b	6.48^a	25.2^a
Cerro Prieto	*A. halopraeferens*	99.1^a	30.0^a	5.85^b	16.1^e

Means with same literal column indicate no significant differences ($P > 0.05$)
*Results expressed on a dry basis

Table 22.2 Effect of N_2-fixing bacteria on the percentage of fatty acids in seed produced two ecotypes of *Salicornia bigelovii* under field conditions

		Fatty acids (%)				
Ecotype	Inoculant (Bacteria)	Palmitic	Estearic	Oleic	Linoleic	Linolenic
Santa Rosa	Control	16.44^{ab}	0.69^{c}	19.36^{ab}	64.02^{bc}	2.56^{a}
Santa Rosa	*K. pneumonia*	16.44^{ab}	1.18^{b}	16.48^{bc}	66.71^{b}	2.29^{ab}
Santa Rosa	*A. halopraeferens*	10.74^{c}	0.45^{c}	14.30^{c}	75.03^{a}	2.56^{a}
Cerro Prieto	Control	18.85^{a}	2.43^{a}	16.32^{bc}	63.98^{bc}	1.51^{c}
Cerro Prieto	*K. pneumonia*	12.18^{bc}	0.59^{c}	21.59^{a}	66.37^{b}	2.35^{ab}
Cerro Prieto	*A. halopraeferens*	17.78^{a}	0.63^{c}	14.20^{c}	68.12^{b}	2.35^{ab}

bigelovii as a potential halophyte to be introduced in semi-arid areas (Bashan et al. 2000). However, further research is needed on the fate of the inoculations in the rhizosphere of *Salicornia bigelovii* halophyte.

4 Conclusion

The results related with the inoculation of plant growth promoting bacteria's (*K. pneumoniae* and *A. halopraeferens*) with *Salicornia* plants, suggest the feasibility of replacing nitrogen fertilizers, where biomass and seed production values were significant compared with the controls no inoculated. Finally, it is worth mentioning that this type of experimental work contributes to enhancing knowledge in agricultural production alternatives and effects on the application of biofertilizers in new plant materials with productive potential of socio-economic interest to States with problems of water availability good quality, as is the Northwest Mexico.

Acknowledgments We are thankfully with Consejo Nacional de Ciencia y Tecnología-Mexico to support project number 245853, awarded to Dr. Murillo – Amador by modality national program of short visits within the framework of the national call stays sabbatical , sabbatical abroad and short stays for consolidation research groups (Call 2014 second phase).

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Factors Affecting Buttonwood (*Conocarpus erectus* L.) Germination

23

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Abstract

This study examined the effects of seasonal temperature regimes on Buttonwood *Conocarpus erectus* L. (Combretaceae) seed germination and how well seeds store under refrigeration vs. ambient temperature. There was no difference in imbibition between scarified and non-scarified seeds, so non-scarified seeds were used for the germination experiments. Seeds were growth chamber germinated to determine which season is most conducive to Buttonwood germination. The growth chamber was set at a day/night (12 h day/12 h night) temperature regime for 3 trials at 28 °C/14 °C, 31 °C/16 °C, and 33 °C/20 °C representing the months of January, April, and July, respectively, on San Salvador Island, The Bahamas. Germination ranged from 0 to 0.12 %, while Timson's values ranged from 0 to 1.43 out of a possible score of 50. Seeds germinated best at 28 °C/14 °C (January, the coolest month) with 0.12 % germination and a 1.1 Timson's value. Seeds stored at ambient temperature and refrigerated at 4 °C were germinated at the 28 °C/14 °C regime, and it was found that refrigerated seeds had the best germination.

1 Introduction

Buttonwood, *Conocarpus erectus* L. (Combretaceae) is a tropical shrub native to the New World tropics and subtropics and West Africa (Francis 2007). It is salt tolerant (Tomlinson 1994) and grows landward of true mangroves above the high tide mark and along beaches. Buttonwood grows in the open or in co-dominant stands of plants of similar size; however, it will not grow in the understory because it is shade intolerant (Francis 2007). Although

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M.A. Khan et al. (eds.), *Sabkha Ecosystems Volume V: The Americas*,
Tasks for Vegetation Science 48, DOI 10.1007/978-3-319-27093-7_23

Buttonwood is sometimes called Button Mangrove (Francis 2007), it lacks specialized structures such as pneumatophores and prop roots (Tomlinson 1994). For these and other reasons it is often not considered a “true” mangrove species (Tomlinson 1994).

Buttonwood is native to the Florida region of North America and is important for a variety of reasons. It is an ecologically important species as it helps prevent erosion, stabilizes dunes, and can withstand heat. It grows on the margins of salt flats and can grow in low nutrient soils, but is itself a source of food for wildlife. Buttonwood is economically important as saw timber and fuel as charcoal. It is planted as an ornamental, and its soft tissue is used as animal fodder. It is therefore being studies as a plant that can be used to revegetate saline ecosystems (Asif et al. 2014).

In Florida, Buttonwood blooms begin in March and end in September; in contrast, in Mexico and The Bahamas, Buttonwood blooms throughout the year (Francis 2007; Kass et al. 2007). Buttonwood flowers are green to white (Francis 2007), 2 mm long (Kass et al. 2007) in clusters of 25 or more (Tomlinson 1994), and are likely wind-pollinated (Kass et al. 2007). The sexual system of Buttonwood has only recently been studied in any detail. It was originally thought that Buttonwood was dioecious (plants with either staminate or pistillate flowers); however, a study by Kass et al. (2007) examined over 1840 flowering Buttonwood plants on San Salvador Island, The Bahamas, and found that 11 % of morphological males produced some fruit. They termed such “male” flowers cryptically andromonoecious, therefore rendering the Buttonwood population on San Salvador polygamous (Kass et al. 2007).

Buttonwood produces small winged drupes arranged in globular, button-like cones (Kass et al. 2007) that are about 1 cm in diameter (Tomlinson 1994). *Conocarpus erectus* derives the common name Buttonwood from these button-like infructescences (Guppy 1917) that shatter when fruits are mature (Kass et al. 2007). Although observed to be a copious seed producer, Buttonwood seedlings are rare in comparison with associated mangrove species (Tomlinson 1994).

There have been very few studies on Buttonwood germination (Kass et al. 2007). Guppy (1917) found that on Turks Island, The Bahamas only 3–4 % of fruits produced by Buttonwood had seeds in them, and in Jamaica only 10 % of the fruits contained seeds. Francis and Rodriguez (1993) reported 12 % germination from a Puerto Rican population. Experimental studies by Kass et al. (2007) found seed germination to be almost 10 % lower than previous studies. In these studies, seeds were germinated at ambient temperature and there was no attempt to account for day/night temperature changes or seasonal variation. In addition, seeds produced by cryptically andromonoecious flowers germinated at the same rate as seeds produced by plants with only pistillate flowers (1.3–1.7 %) (Kass et al. 2007).

This paper presents quantitative data on Buttonwood seed germination in four related experiments, and may be one of the first detailed studies on the germination of this species. We tested seasonal variation with day/night temperature regimes, the potential for seed coat dormancy, the effects of seasonal temperature on germination, and how seed storage may affect seed germination.

1.1 Hypotheses

This study tested three separate hypotheses related to Buttonwood germination with four different tests. The first hypothesis was that a broken seed coat will allow scarified seeds to take up more water and at a faster rate than unscarified seeds. The second hypothesis was that seeds germinated at the lowest temperature will have the highest percent germination and fastest germination rate because this is when heat stress and salinity would be at their lowest in a tropical saline environment like San Salvador Island, The Bahamas where our seeds were collected. And lastly, storing Buttonwood under refrigeration will reduce percent germination as well as germination rate because the cool temperature may damage this tropical species.

2 Materials and Methods

This study entailed four experiments. The first experiment tested seed coat dormancy of Buttonwood. The second experiment examined germination in response to seasonal temperatures. The third study compared germination of seeds that were stored unrefrigerated at room temperature to seeds that were stored refrigerated at 4 °C. In all three studies, seeds were placed in 15 × 100 mm Petri dishes on 9 mm no. P5 Fisherbrand© filter paper moistened with 10 ml of de-ionized water. The water layer just covered the top of the seeds. Seeds were germinated in an Environmental Growth Chamber Model G10 chamber (2001). The fourth study used tetrazolium to test seed viability.

Seeds for the first two experiments were collected along the Fresh Lake causeway (N. 24° 6.011′; W. 74° 26.844′) from several Buttonwood shrubs with ripe infructescences on 1 May 2005. Seeds for the third experiment were collected on the access road to the AV pond (N. 23° 59′ 4.5″, W. 74° 29′ 8.7″) from a single female tree on 26 June 2005. Seeds for the tetrazolium test used the above groups of seeds as well as freshly collected seeds (23 June 2007) from the Fresh Lake causeway.

2.1 Seed Coat Dormancy

Baskin and Baskin (1998) found that when studying the germination biology of a species for which little is known, it is best to determine if an unscarified seed will imbibe water. Francis and Rodriguez (1993) state in their germination study of several tropical species that many of the hard coated seeds were nicked with a knife or file prior to germination; however, they do not specify if Buttonwood received this treatment in their germination trial.

To determine if the seed coat was inhibiting germination, an experiment comparing scarified seeds with unscarified seeds was performed. The experimental group of Buttonwood seeds was scarified between 2 pieces of 150 grit aloxite sand paper and were abraded just enough to break the seed coat. The control group contained unabraded seeds. Seeds were weighed dry, then placed in 10 ml of reverse osmosis water on filter paper in a Petri dish. Seeds were allowed to soak for 1, 2, 19, and 32 h, then blotted dry on paper towels and weighed. There were three sets of 50 seeds for the control group and each experimental group. Data are presented as 1-(mass @ time n/original dry weight) vs. time (hours) (Fig. 23.1). Data were graphed in this manner to represent imbibition as an increase in a type II graph. Scarification did not increase imbibition, and may have slightly hindered it; therefore, non-scarified seeds were used for the temperature and seed storage studies.

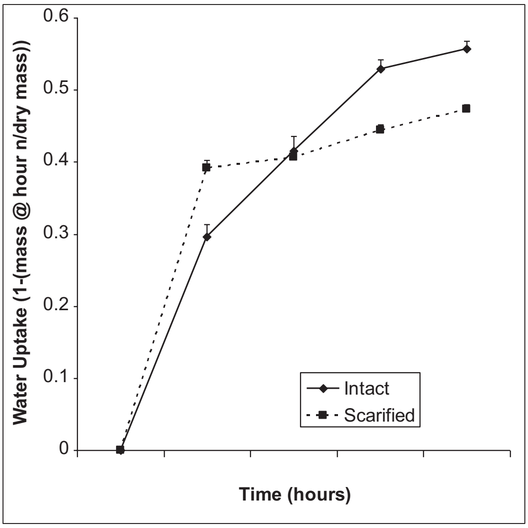


Fig. 23.1 Mean (± S.E.) water uptake (g) by scarified and non-scarified *Conocarpus erectus* seeds over time (0–32 h)

2.2 Temperature Effect

Very little is known about the effects of temperature on Buttonwood germination, therefore one goal of this study was to determine if seed germination was influenced by seasonal temperature regimes. To represent the full range of seasonal temperature fluctuations on San Salvador Island, mean documented day/night temperatures at 28 °C/14 °C (January), 31 °C/16 °C (April), and 33 °C/20 °C (July) (Gamble 2003) were programmed into a single growth chamber (EGC 2001) with a 12 h day/night light regime. Five Petri dishes containing 50 seeds per dish on moist filter paper were monitored. De-ionized water was replenished every 3–4 days, as needed. Each temperature trial ran until seeds stopped germinating (approximately 28 days).

Percent germination as well as relative germination rates for each treatment were calculated using a modified Timson's Index (Timson 1965; Khan and Ungar 1984) in which the sum of germinated seeds for each day at the end of the germination period was divided by the total number of seeds. Because each replicate contained 50 seeds, the highest possible Timson's Index value would be 50 if all of the seeds germinated after 1 day.

2.3 Seed Storage

The temperature effect study indicated that the best germination temperature regime for Buttonwood was 28 °C/14 °C (January). This regime was therefore used to determine if seeds were best stored at 21 °C (room temperature) or refrigerated at 4 °C.

Five Petri dishes (n = 5) containing 50 seeds per dish were germinated on moist filter paper. Each Petri dish contained 10 ml of de-ionized water. Water was replenished every 3–4 days, as needed. The trial ran approximately 28 days, until seeds stopped germinating. Germination percent and relative rates were calculated. Relative germination rates of each treatment were calculated using a modified Timson's Index (Timson 1965; Khan and Ungar 1984) as previously described. Because each replicate contained 50 seeds, the highest possible Timson's Index value would be 50 if all of the seeds germinated after 1 day.

2.4 Tetrazolium Test for Viability

Seeds collected on 1 May 2005 were stored at 4 °C. Seeds collected on 26 June 2005 and 23 June 2007 were stored at ambient temperature. Ten seeds from each of the above groups were tested for viable embryos via a tetrazolium test. A 2,3,5-triphenyltetrazolium chloride solution was used to test for dehydrogenase (respiratory) enzymes. In live seeds these enzymes reduce tetrazolium to a red color (Bonner 1974; Baskin and Baskin 1998). Seeds were soaked in reverse osmosis water overnight then dissected from their achene and placed in a solution of 0.5 % solution tetrazolium for 6 days. Field corn seeds cut in half were used as a control for solution concentration.

3 Results and Discussion

With such extremely low germination, many Petri dishes did not have any seeds that germinated, and it would require counting several thousand seeds in order to have meaningful statistical analyses. Basáñez-Muáñoz et al. (2011) used 500 Buttonwood seeds per treatment in a germination study and found few significant differences. Although statistical analyses could not be performed for the present study, it is never the less important because there are now documented germination conditions that are favorable to Buttonwood.

3.1 Seed Coat Dormancy

Both scarified and unscarified seeds took up water at about the same rate (Fig. 23.1). Interestingly, the seeds with their seed coats intact took up slightly more water than scarified seeds, but these differences were minimal. The mean seed weight (n = 3 for Petri dishes of 50 seeds each) before imbibition for unscarified seeds was 0.12 g, and mean weight for scarified seeds was 0.14 g. Although scarified seeds were slightly heavier, these differences may reflect natural variation, and are unlikely to be statistically significant. After 32 h, unscarified seeds weighed 0.28 g, while scarified seeds weighed 0.26 g. This represents a 225 % increase in weight for unscarified seeds, but only a 190 % increase for the scarified seeds.

Hypothesis number one was not supported because both intact and scarified seeds absorbed water at roughly the same rate, and exogenous dormancy did not occur (Baskin and Baskin 1998). Results of the tetrazolium test demonstrated that none of the seeds tested had a viable embryo, and we can rule out other reasons or dormancy mechanisms for preventing germination.

Basáñez-Muáñoz et al. (2011) studied how different temperatures or scarification techniques affect Buttonwood dormancy and germination. Techniques included refrigeration at 3 °C for 72 h, mechanical abrasion, a 25 % HCl acid bath for 5 min, and an overnight soaking in 1 % H_2O_2. There were no significant effects of scarification treatment on germination, but week two had the highest rates of germination (Basáñez-Muáñoz et al. 2011).

3.2 Temperature Effect

Timson's Index values and percent germination were much higher for the 28 °C/14 °C (January) temperature regime than the 31 °C/16 °C (April) and 33 °C/20 °C (July) temperature regimes (Figs. 23.2 and 23.3). Timson's Index values and percent germination for seeds germinated at the two warmer temperature regimes were very similar. Unfavorable environmental conditions like temperature may be what caused April and July's germination rates to be low (Baskin and Baskin 1998). Therefore, hypothesis number two was supported because the 28 °C/14 °C (January) temperature regime had the highest percent germination, Timson's Index value, and fastest germination velocity. This is consistent with Kass et al. (2007) who found a major flowering peak in December (as well as June). However, Tomlinson (1994) reports that in south Florida populations of Buttonwood have a prolonged winter dormancy.

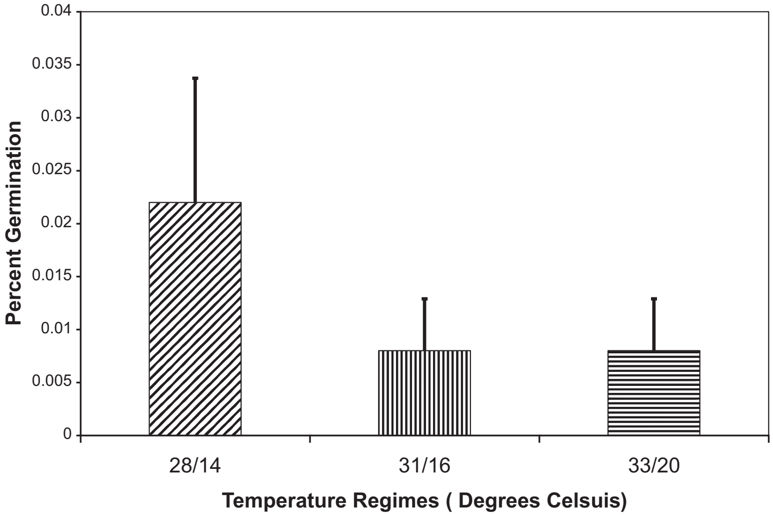
3.3 Seed Storage

The final study examined germination of refrigerated vs. unrefrigerated seeds in the best temperature regime for germination as determined by the second study (i.e., 28 °C/14 °C). The goal was to determine if the temperature regime that provided the highest germination rate for unrefrigerated seeds would also result in similar germination rates and velocities for refrigerated seeds.

Hypothesis number three was not supported because the refrigerated seeds had a higher Timson's Index (0.77 ± 0.43 vs 0.33 ± 0.20) and a higher percent germination (0.02 % ± 0.01 vs. <0.01 % ± 0.00). Therefore, storing Buttonwood seeds at 4 °C does not hinder germination.

Because both groups of seeds were collected within a month of each other, an age difference in seeds is not a likely factor in germination

Fig. 23.2 Mean (± S.E.) percent germination for *Conocarpus erectus* at three temperature regimes: 28 °C/14 °C (January), 31 °C/16 °C (April), and 33 °C/20 °C (July)



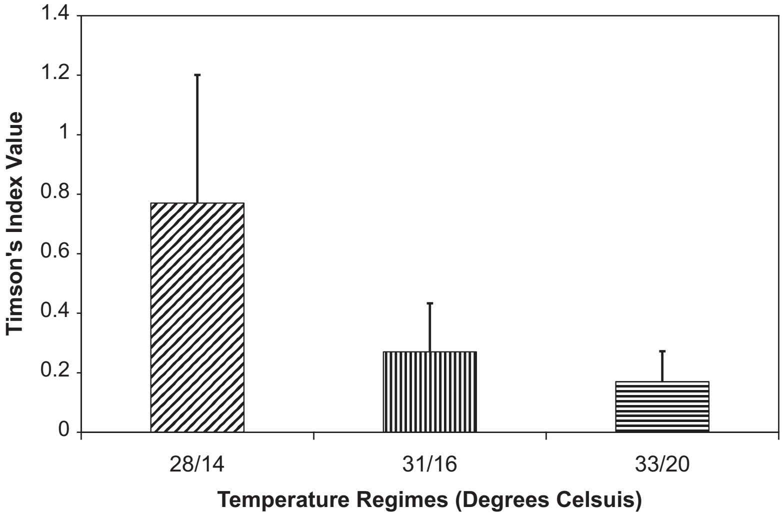


Fig. 23.3 Mean (± S.E.) Timson's Index Values for *Conocarpus erectus* seeds germinated at 28 °C/14 °C (January), 31 °C/16 °C (April), and 33 °C/20 °C (July)

variability, especially since seeds stored under refrigeration were collected sooner.

In conclusion, percent germination is very low in Buttonwood, but fortunately this species is a prolific seed producer. A seed scarification treatment has yet to be found that will increase germination, so perhaps future studies may focus on the effects of seed priming.

Acknowledgements We gratefully acknowledge the Bahamian Department of Agriculture for Permit 07-02 to collect on San Salvador Island; Vincent Voegeli and personnel of the Gerace Research Centre, San Salvador Island, The Bahamas for their help and use of field station equipment and facilities; Sarah Arrowsmith of Elmira College for assistance with the tetrazolium test; J. Forrest Meekins for helpful comments preparing the manuscript; Elmira College, Elmira, NY, USA for research funds to AES and TPE; and Lee B. Kass, Cornell University, for sharing seeds and data.

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Plant Growth Promoting Rhizobacteria Associated to Halophytes: Potential Applications in Agriculture

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Abstract

Saline soils are a major problem for agriculture, commonly salinization reduces the area for agriculture in arid and semiarid regions. On the other hand ecosystems with natural saline soils represent biotopes where the halophytes grow and develop without problems. The rhizospheres of halophytes represent excellent niches to find salt tolerant rhizobacteria with the ability to promote plant growth. Plant growth-promotion rhizobacteria (PGPR) can enhance growth in plants and protect to salt stress by several ways such as 1-Aminocyclopropane-1-carboxylate deaminase (ACC deaminase), biological nitrogen fixation, phytohormones production, exopolysaccharides, etc. The use of PGPR in agriculture as biofertilizer has greatly increased as an alternative to replace agrochemicals. In arid and semiarid areas the salt-tolerant PGPR have begun to emerge as an important alternative to recuperate abandoned farmland affected by salt, the PGPR alleviate salt stress in halophytes to some extent, but the application is more outstanding for glycophytes of agricultural interest for protection against salt stress. In this chapter, we present a vision of the salt-tolerant PGPR ability to facilitate plant growth in presence of salt, the potential of halophytes rhizosphere as reservoir of beneficial microbes and the future application as bio-inoculants as alternative in agriculture is reviewed.

1 Introduction

Soil salinization is one of the major problems affecting approximately 400 million hectares of crop land (FAO 2002; Bot et al. 2000). The productivity of agricultural crops is greatly affected by salinity; with negatives effects on germination, plant growth and crop yield (Khan and Panda 2008). Electrical conductivity (EC) of

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M.A. Khan et al. (eds.), *Sabkha Ecosystems Volume V: The Americas*,
Tasks for Vegetation Science 48, DOI 10.1007/978-3-319-27093-7_24

saline soils exceeds 4 dS m^{-1} and are distributed worldwide in arid and semiarid areas (Munns 2005; Jamil et al. 2011). In such arid and semiarid regions, soil salinity is frequently an important limiting factor for agriculture, however, in some saline soils different types of plants (halophytes) establish due to their ability to grow in such soils with high salt concentrations. However, a suitable technology not only to sustain crop productivity but also soil health through soil microflora and plant root interactions is feasible. Diverse microorganisms colonize the rhizosphere of halophytes; particularly beneficial bacteria with dual capabilities of tolerating high salinity and promoting plant growth (Dimkpa et al. 2009). It is now known that beneficial microorganisms in the rhizosphere play a significant role in stress alleviation in halophytes, glycophytes and crops grown in saline soils.

Salt-tolerant plant growth promoting rhizobacteria (PGPR) can be one of the main strategies by which crop growth and productivity in saline soil can be improved (Mayak et al. 2004; Jha et al. 2012). PGPR can promote growth either directly or indirectly. In the direct way, PGPR generally provide the compounds synthesized by bacterium such as N_2 fixation, phosphate solubilization, phytohormones: auxins, cytokinins, and gibberellin and lowering of the ethylene concentration, and compatible solutes production to the plants. In the indirect way, PGPR prevent or reduce the pathogen effects on plants by producing inhibitory substances (Glick 1995; Mayak et al. 2004). In saline conditions the protective effect from PGPR to plants is reduction of ethylene, increase of auxins, ROS protection, compatible solute production, solubilization of phosphates, exo polysaccharides production, and control of phytopathogens (Ruppel et al. 2013).

The interest in use of salt-tolerant PGPR as biofertilizer in salt affected farmland has increased, as their use allows reclamation and reuse of salt affected abandoned farmland and substantially reduce the use of agrochemicals, which contaminate terrestrial and aquatic ecosystems. The signaling mechanisms and establishment interactions between PGPR and plants are still not well understood, especially in field applications. Therefore, it is necessary to continue and increase the studies of plant-PGPR interactions, the microbe ecology in natural residents and their adaptation in stressed environment (Egamberdiyeva and Islam 2008). In this chapter, a view of the rhizosphere of halophytes as reservoir of beneficial microbes and their application as bio-inoculants as an alternative agriculture technology is presented. In addition, recent developments on our understanding of the salt-tolerant PGPR and their physiology, adaptation mechanisms, interactions with plants in natural salt environments and the applications in plants with agricultural interest are discussed.

2 Salinization

Soil salinization is the most common phenomenon of land degradation and consists in the concentration of salts in the surface or near-surface zone of soils. Human-induced salinization is the major contributor to desertification process in the world's arid and semiarid zones. Salinity and desertification cause a great disturbance to plant-microbe interactions in degraded ecosystems. The causes of salinization could be due to: poor cultivation techniques; indirect effects of irrigation schemes; vegetation changes; seawater incursion and by disposal of saline wastes (Thomas and Middleton 1993). Soil salinization has become a large problem affecting the agriculture worldwide (reducing area 1–2 % every year), it has been estimated as approximately 400 million hectares of cropland affected by salt (FAO 2002; Bot et al. 2000). It is estimated that approximately 50 % of 250 million hectares of irrigated land in the world are affected by salinization, and annually 10 million hectares are abandoned due salt problem in soil (FAO 1988; Paul and Lade 2014).

3 Halophytes

Halophytes are plants with the capacity to complete the life cycle in salt concentrations of at least 200 mM NaCl under natural saline conditions

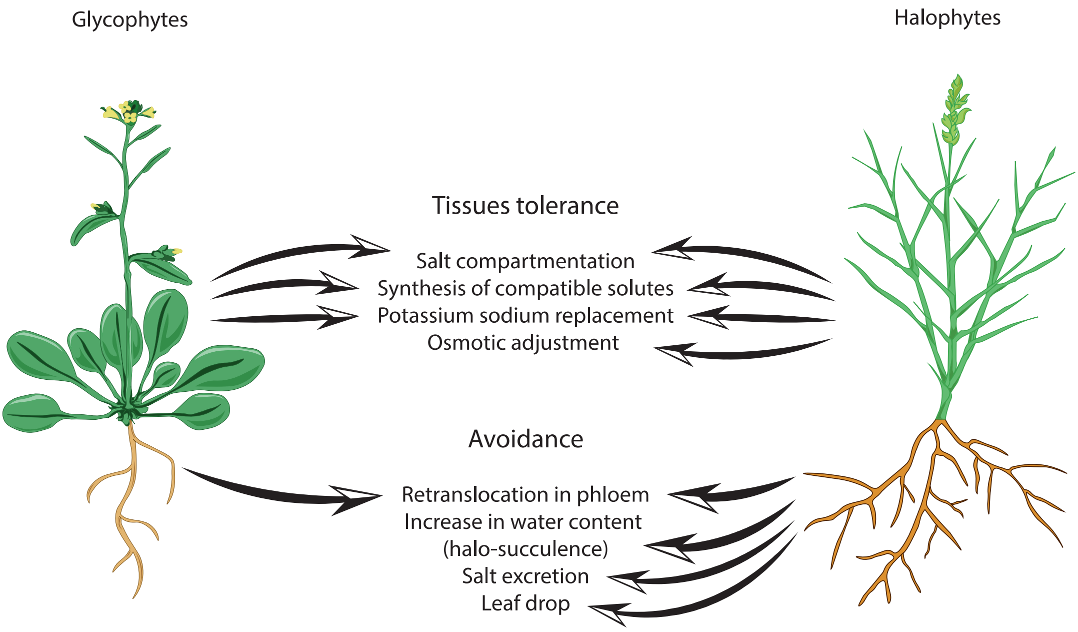

Fig. 24.1 Schematic representation of comparative mechanisms used by halophytes and glycophytes plants in saline environment. The active mechanisms to avoid salt effects are indicated by *arrows*, the halophytes mechanisms are numerous and more efficient than glycophytes implemented mechanisms

(Flowers et al. 1986; Flowers and Colmer 2008). Halophytes classification is diverse and complex depending on the authors and the physiological, morphological and ecological characteristics of plants. According to the first classification based on the response to salinity halophytes are divided in four categories: Obligatory halophytes, plants requiring salinity throughout life; preferential halophytes, plants with optimal growth in saline environment; supporting halophytes, nonaggressive plants which are capable of growing in saline habitats; accidental halophytes, plants appear in saline habitats only occasionally (Tsopa 1939). Halophytes represent approximated 1 % of the world's plants (Flowers and Colmer 2008). Halophytes are excellent resources for research of salt-tolerance mechanism in plants (Fig. 24.1). The vast majority of studies of salt tolerance in halophytes have been made in ecological, physiological, morphological and molecular regulation aspects. However, there are many ecological complex mechanisms in the rhizosphere and phyllosphere involved in salt tolerance of halophytes. The microorganisms inhabiting the rhizosphere of halophytes may contribute to salt tolerance (Ruppel et al. 2013). Currently there are few reports of how microorganisms collaborate in the halophyte resistance to salt.

Differences between halophytes and glycophytes are becoming to understand. The mechanisms of salt tolerance in halophytes are diverse (Wang et al. 2002). Although halophytes have polyphyletic origins, they evolved the same basic method of osmotic adjustment: accumulation of inorganic salts (mainly NaCl) and organic solutes. The Na^+ and Cl^- uptake in halophytes involves ions channels, transporters, and pinocytosis. The Na^+ compartamentalisation required Na^+/H^+ antiporters, which are constitutive in halophytes, whereas they must active by NaCl in salt-tolerant glycophytes and they are absent in salt-sensitive glycophytes (Hasanuzzaman et al. 2014). Several adaptatives mechanisms have halophytes, viz., osmotic adjustment, selective transport and uptake of ions, secretion, germination response, halo-succulence, enzyme responses, genetic control, and compartmentalization to reduce the cytosolic salt concentration in mesophyll cells and mechanisms to synthesize organic compatible solutes (Fig. 24.1) (Wang et al. 2002; Hasanuzzaman et al. 2014) In this book chapter we don't review in detail the morphological and physiological mechanisms of halophytes to focus on the influence of Plant Growth Promoting Rhizobacteria to salt tolerance in plants and its agriculture applications.

3.1 Halophytes in Chihuahuan Desert

Currently, there is little information about Chihuahuan desert halophytes. In arid and semiarid regions of North America, especially in West and Southwest of the USA and Northern of Mexico, Xerohalophytes dominate and over 200 halophytes are distributed in coastal and inland regions of North America. *Suaeda, Salicornia, Sesuvium, Spartina, Puccinellia* and *Baccharis* are common genera in saline regions from North America (Chapman 1974; McKell and Garcia-Moya 1989). In the Chihuahuan Desert, saline habitats (9000 km^2) occur most commonly around dry lakes, beaches, or saline as at the bottom of internally draining basins. The Chihuahuan Desert is the biggest desert in North America and the Halophytes in this area comprises 40 taxas, 25 of these are endemic or range only slightly outside the Chihuahuan Desert region (Henrickson 1974; Czaja et al. 2014). The halophytes represent a biological resource with great potential for use in agriculture, biotechnology and industrial sectors. The rhizosphere of halophytes in Chihuahuan Desert represents an important microhabitat for the establishment of beneficial microorganisms with the ability to withstand high salt concentrations but also to provide a benefit for the plant host, such as plant promoter growth rhizobacteria. It is a high priority to study the PGPR that inhabit the halophytes from the Chihuahuan Desert area as this allows developing biofertilizers that could be used in the same region, which is characterized by having large areas of cultivated land affected by salinity. Our research team has explored the PGPR of rhizosphere from diverse halophytes of *Suaeda*, *Distichlis* and *Sesuvium* genera, which are distributed throughout the Chihuahuan Desert.

4 Plant Growth Promotion Rhizobacteria

In the rhizosphere microbiome three different types of plant-bacteria interactions could be established; (1) Commensal rhizobacteria associated to plants are common in which the bacteria are innocuous interaction with the colonizing plant. (2) Plant and pathogenic bacteria interactions causing negative effects for the plant (e.g. *Erwinia* spp., *Pseudomonas* spp., *Ralstonia* spp., etc.). (3) Interaction between plant and beneficial bacteria, leading to a beneficial association and these bacteria are known as plant growth promoting rhizobacteria (PGPR) (Bhattacharyya and Jha 2012; Jha et al. 2012). Depending on their association with and/or in the plants parts, PGPR can be divided in two classes (Martínez-Viveros et al. 2010): (1) the extracellular plant growth promoting rhizobacteria (ePGPR) colonizing the rhizosphere, which comprises the immediate soil to the roots (ectorhizosphere) and the roots surface (rhizoplane), some of these bacteria have the capacity to establish between the cells of the root cortex (e.g. *Bacillus* spp., *Pseudomonas* spp., *Alcaligenes* spp., *Azospirillum* spp., *Azotobacter* spp., *Burkholderia* spp., *Caulobacter* spp., *Chromobacterium* spp., *Agrobacterium* spp., *Micrococcous* spp., *Serratia* spp., etc.); (2) intracellular plant growth promoting rhizobacteria (iPGPR) where the interaction occurs inside the root and usually results in structures known as root nodules (e.g. *Rhizobium* spp., *Sinorhizobium* spp., *Bradyrhizobium* spp., *Allorhizobium* spp., *Azorhizobium* spp., *Mesorhizobium* spp., etc.) (Soto et al. 2006; Mercado-Blanco and Bakker 2007; Bhattacharyya and Jha 2012).

PGPR promote plant growth either directly or indirectly. Indirect mechanisms include production of antibiotics, stimulation of endophytes' establishment such as mycorrhizae and rhizobium, suppression of pathogens by competitive exclusion through siderophores action, extracellular hydrolytic enzymes against fungal plants pathogens or/and removal of phytotoxic substances, allelopathy and competition with deleterious agents (Glick 1995; Swain et al. 2008; Figueiredo et al. 2008; Siddikee et al. 2010; Bhattacharyya and Jha 2012). On the other hand the direct mechanisms include improved plant nutrition through phosphate and zinc solubilization, acquisition of iron by siderophores, and nitrogen fixation. Other direct mechanisms are production of growth regulators such as indole acetic acid (IAA), cytokinin, and gibberellins; or the production of 1-aminocyclopropane-1-carboxylic acid (ACC) deaminase, an enzyme that can lower plant ethylene levels that are typically increased by a wide variety of environmental stresses such as drought and salinity among other stresses (Hayat et al. 2010; Bashan and de-Bashan 2010; Siddikee et al. 2010).

PGPRs are classified into three categories based on their mechanism of actions on crops such as biofertilizer (Increases nutrient availability for plant such as nitrogen and phosphorus), phytostimulator (with the ability to produce or stimulate the production of phytohormones such as Indole acetic acid, gibberelic acid, cytokinins and ethylene) and biopesticide (with antagonistic effect on plant pathogens microbes) (Bhattacharyya and Jha 2012). Understanding of PGPR biology and the action mechanism over the plants allow facilitate their use and application in agriculture.

4.1 Salt-Tolerant PGPRs and Halophytes

Saline natural and agriculture soils are important reservoir of halotolerant/halophytic microorganism; the halophytes rhizospheres in natural ecosystems are suitable to find bacteria with high capacities to support and promote growth of plants. The rhizobacteria of halophyte rhizosphere are well adapted to salt stress due to low water potential in a dry or saline climate to which they are exposed, it is always more pronounced as increased water uptake by plants due to transpiration (Tripathi et al. 1998; Sudhir et al. 2009). The salt tolerant rhizobacteria information is scarce, and for this reason it is necessary to continue further research on these microorganisms.

Bacteria able to grow in the presence of high concentrations of salt are classified as: (1) Halotolerant bacteria with the capacity to grow in the absence as well in the presence of salt; extremely halotolerant bacteria are able to grow above of 15 % (w/v) salt. (2) Halophiles requiring salt for growth and are classified as; slight (3 % w/v NaCl), moderate (3–15 % w/v NaCl), extreme halophiles (25 % w/v NaCl). Halotolerant and halophilic bacteria as a result of adaptation to their environment have evolved exclusive properties with considerable importance in anthropogenic activities as such agriculture, industry and biotechnology (Margesin and Schinner 2001; Ventosa et al. 2008). Halotolerant and halophilics bacteria have been isolated from a wide range of habitats, such as extreme alkali-saline soils, desert and saline soils, salt crystallizer ponds, pickled food, etc. (Ventosa et al. 2008; Ruppel et al. 2013). The halotolerant and halophilic bacteria have mechanisms that allow growth and survival in saline habitats such as; (1) specific composition of membrane or cell wall preventing the input and then high salt concentrations; (2) regulation of intracellular ionic concentration by pumping ions out of the cell through electrogenic Na^+/H^+ antiporter, ion transporters K^+/Na^+, for osmotic adjustment, etc.; (3) accumulation of compatible solutes (e.g. sucrose, trehalose, glycosyl glycerol, and glycine betaine) by endogenous biosynthesis; (4) adaptation of proteins and enzymes to high concentrations of solute ions; (5) increasing the energetic capacity; (6) production of extracellular polysaccharides (EPS) that helps the development of biofilms (Fig. 24.2) (Ruppel et al. 2013; Sandhya et al. 2010).

As mentioned earlier, the halophytes represent an ideal habitat to isolate Rhizobacteria. Some studies where the halophytes were used for the isolation of rhizobacteria are: *Salicornia brachiata*, an extreme halophyte growing in coastal areas of Gujarat, India, was used for isolation of *Brachybacterium saurashtrense* sp. nov., and *Pseudomonas* spp., which demonstrated

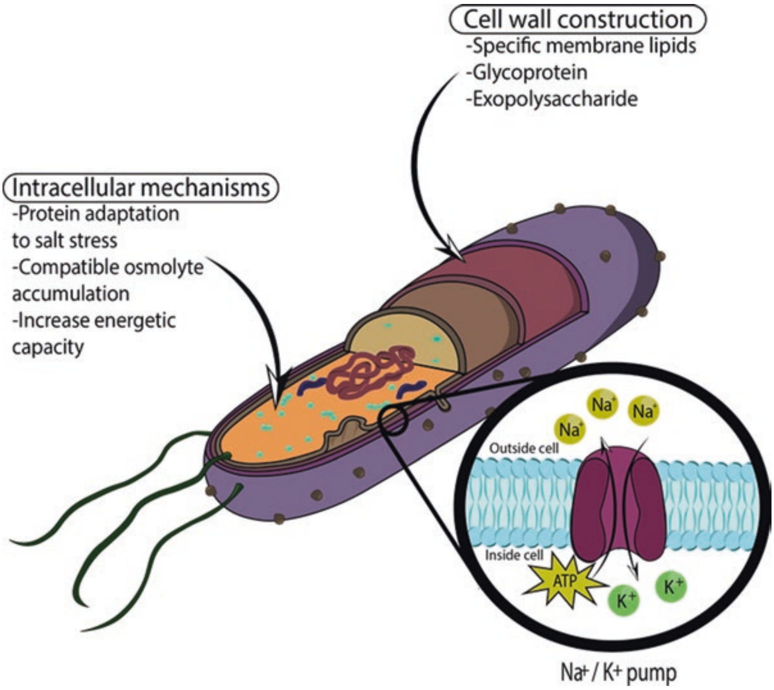

Fig. 24.2 Schematic representation of mechanisms used by bacteria to live and survive in high salt concentration ecosystems. The mechanisms are divided into intracellular and membrane mechanisms

growth-promoting activities (Jha et al. 2012); *Brevibacterium epidermidis*, *Micrococcus yunnanensis*, and *Bacillus aryabhattai* were isolated from rhizosphere of six natural halophytes from vicinity of the Yellow Sea, Incheon, Republic of Korea (Siddikee et al. 2010); *Brevibacillus borstenlensis*, *Pseudoalteromonas ruthenica* and *Halomonas sinaensis* have been isolated from *Halocnemum strobilaceum*, a halophyte inhabiting coastal Arabian Gulf sites (Al-Mailem et al. 2010); *Acacia* spp. in Australia and dry land of Algeria with high salinity demonstrated the presence of different bacteria *viz.*, *Ensifer*, *Mesorhizobium*, *Bradyrhizobium* and *Ochrobactrum* (Boukhatem et al. 2012); and *Rhizobium* spp. and *Bacillus* spp. were detected in the rhizosphere of halophyte *Salicornia bigelovii* (Rueda-Puente et al. 2010).

4.2 Salt Stress Amelioration Mechanisms of PGPRs

Growth promotion by PGPR is complex and comprises changes in the microbial balance in the rhizosphere and modification of plant physiology (Glick et al. 1999). PGPR can adapt to diverse environmental conditions and develop tolerance to stressful conditions, such as salinity and drought. The halotolerant and halophilic PGPR can provide a wide array of benefits to plants including halophytes and glycophytes to overcome salt stress (Fig. 24.3). Salinity affects plant growth, development, germination, flowering, and fruit set with negative effects such as increase ethylene production, plasmolysis, Na^+ and Cl^- toxicity, increase in the production of reactive oxygen species (ROS), and affecting photosynthesis. The water stress is the shared early negative effect under drought and salinity conditions (Sairam and Tyagi 2004; Gamalero et al. 2009). Rhizobacteria residing in halophytes are able to improve plant growth and development by increasing the germination and seedlings emergence and establishment. The above is addressed in the study of Jha et al. (2012), where germination and vigour index of *Salicornia brachiate* seeds inoculated with *Brachybacterium saurashtrense* and *Pseudomonas* sp. is evaluate at 0.25 and 0.5 mol 1^{-1} NaCl concentrations, the inoculated seeds increased percent germination to 100 % in both inoculated seeds at 0.5 mol 1^{-1} NaCl concentrations, with relation to 92 % germination of un-inoculated seeds at the same NaCl

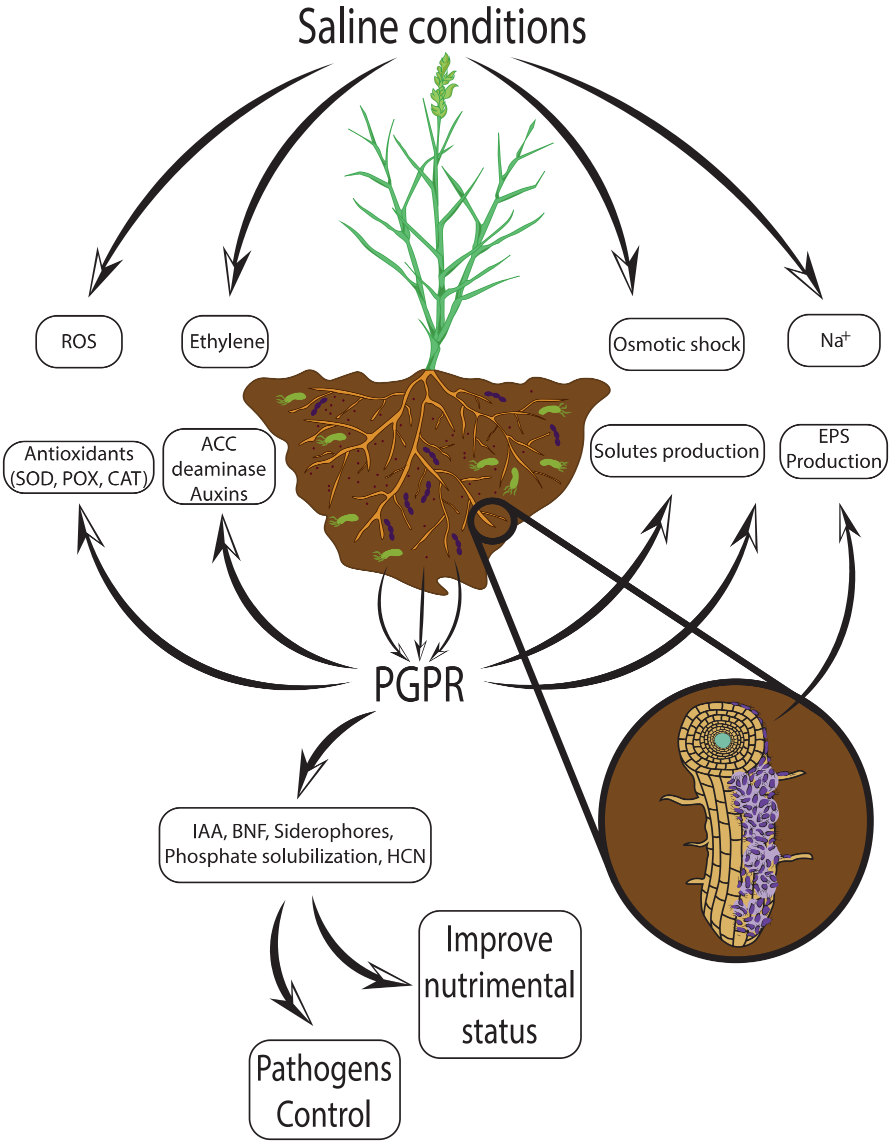

Fig. 24.3 PGPR-plant interaction in rhizosphere. PGPR colonize the rhizosphere of plants and cause growth promotion through different mechanisms that help mitigate salt stress

concentration. Some of these mechanisms are presented in Fig. 24.3.

Ethylene, the gaseous hormone is involved in a wide range of growth and development plant processes such as germination, root hair development, root elongation, leaf and petal abscission, fruit ripening and organ senescence, but is produced in response to abiotic and biotic stresses leading to inhibition of growth of the plant as a whole (Bleecker and Kende 2000; Saleem et al. 2007; Barnawal et al. 2014). The Aminocyclopropane-1-Carboxylate (ACC) deaminase regulates and reduces the ethylene levels. In numerous microbial species of Gram-negative and Gram-positive bacteria and fungi ACC deaminase has been reported. Many PGPRs contain the enzyme ACC deaminase that cleave the ethylene precursor ACC to α-ketobutyrate and ammonia, thereby reduces ethylene production which otherwise inhibits plant growth. The inoculation of plants with PGPRs capable of secreting ACC deaminase results in development of extensive roots due to lowered ethylene levels thus aiding the plants to overcome salt and drought stresses (Singh et al. 2011; Barnawal et al. 2012, 2014). The effect of PGPR contain ACC deaminase on growth promotion of maize under salinity was studied and show that there were 3.3 folds increased in root length at EC 9 dS m^{-1} when inoculated with *Pseudomonas fluorescens* biotype A (N_3), whereas shoot lengths increased by 2.3 folds by inoculation with *P. putida* biotype A (Q_7) at 12 dS m^{-1} over control uninoculated (Kausar and Shahzad 2006). Some examples of ACC deaminase producing PGPRs genera reported are; *Achromobacter*, *Agrobacterium*, *Arthrobacter*, *Azospirillum*, *Alcaligenes*, *Bacillus*, *Brachybacterium*, *Brevibacterium*, *Burkholderia*, *Cronobacter*, *Enterobacter*, *Haererehalobacter*, *Halomonas*, *Herbaspirillum*, *Methylobacterium*, *Mesorhizobium*, *Ochrabactrum*, *Pseudomonas*, *Rhizobium*, *Rhodococcus*, *Serratia*, *Sinorhizobium*, *Variovorax*, and *Vibrio* (Penrose and Glick 2003; Belimov et al. 2001, 2005; Ma et al. 2003; Hontzeas et al. 2004; Uchiumi et al. 2004; Pandey et al. 2005; Blaha et al. 2006; Jha et al. 2012; Barnawal et al. 2012, 2014)

4.2.1 Solutes Production

The solutes are important to cope with osmotic stress by cells. The compatible solutes include amino acid and its derivatives (e.g., Glutamate, proline, peptides and N-acetylated amino acid), quaternary amines (e.g., glycine, betaine and carnitine), sugars (e.g., sucrose and trehalose), etc. The bacteria may produce compatible solutes in osmotic shock and degrade them following an osmotic downshift, but the initial response is much more rapid when compatible solutes are taken up from the surrounding environment and/or released into medium via semi-conductive transport system. Accumulated compatible compound may be exported into the surrounding medium and subsequently taken up, via an active transport system, by other organisms such as plants under osmotic stress. The transports process can be subdivided into specific transport, stretch-activated channel, specific efflux system, and aqua-porins (Miller and Woods 1996; Arora et al. 2006). *Azospirillum*, *Pseudomonas*, *Bacillus*, and *Rhizobium* produce high quantity of osmolites in saline habitats (Miller and Woods 1996; Arora et al. 2006, 2012).

4.2.2 Scavenging of Reactive Oxygen Species by PGPR Antioxidants

Reactive oxygen species (ROS) are formed as a consequence of osmotic and salt stress and negatively affect the plant cells by way of oxidative damage of membrane lipids, proteins or DNA. Scavenging enzymes prevents this: including superoxide dismutase (SOD), catalase (CAT), and ascorbate peroxidase (POX) and non-enzymatic antioxidant such as ascorbate, glutathione, and tocopherol. PGPRs use similar mechanisms to cope with oxidative stress caused by generation of ROS such as superoxide radical (O_2^-), hydroxyl radical (OH^-), and hydrogen peroxide (H_2O_2) (Arora et al. 2012; Upadhyay et al. 2011). PGPR bacteria increase the tolerance of salt-sensitive plants grown under severe salt stress, through induction of antioxidant enzymes (Kohler et al. 2009a, b; Jha and Subramanian 2014). *Sesuvium portulacastrum* has a remarkable ability to survive in salinity, drought and heavy metal accumulation, the plants grown on non-sterilized saline soil containing bacteria of different genera *Bacillus*, *Aeromonas*, *Pseudomonas, Corynebacterium* and *Escherichia* recorded lower degree of oxidative stress than plants grown on sterile soil (Anburaj et al. 2012).

4.2.3 Phosphate Solubilization

The availability of phosphorous in arid saline soils is limited and hence the most appropriate approach to address this situation is use of bio-inoculants. PGPR are recognized by their ability to solubilize phosphates and mobilize iron. The solubilization of minerals by PGPR is achieved through the acidification, chelation, ion exchange reactions, and production of low molecular weight organic acids such as gluconic acid. In saline soil, higher phosphate availability by way of solubilization by PGPR to plants would improve their growth and suppress the adverse effect of salt (Giri et al. 2003). It was observed that the phosphate content of the foliage of halophyte *Salicornia bigelovii* increased when it was inoculated with various halotolerant bacteria, viz., *Azospirillum*, *Vibrio*, *Bacillus*, and *Phyllobacterium* (Bashan et al. 2000). Phosphate solubilizing rhizosphere microflora contribute significantly to the tolerance of salt stress of halophytes and glycophytes.

4.2.4 Auxins Synthesis by PGPR

Auxins play a core role increasing root growth and development. Most of PGPR are able to produce and secrete indole acetic acid (IAA). Synthesis of IAA and ethylene have a negative relation, increased ethylene level progressively blocks IAA signal transduction. Rhizobacteria producing ACC deaminase decrease the ethylene content and favors the synthesis of IAA, which aid in plant growth (Patten and Glick 1996; Glick et al. 2007; Gamalero et al. 2009). The production of auxin by rhizobacteria might be an important tool in salt tolerance of halophytes and glycophytes. *Arthrobacter* sp., *Bacillus pumilus*, *Halomonas* sp., *Nitrinicolalacis aponensis*, and *Pseudomonas mendocina* are few examples of IAA-producing salt tolerant PGPR (Tiwari et al. 2011).

4.2.5 Exo-polysaccharides Production and Biofilm Formation

Biofilms formation and exo-polysaccharide (EPS) production are common in bacteria. EPS are a complex mixture of polymers of high molecular weight ($M_W \geq 10{,}000$) secreted by bacteria in response to stresses such as heavy metals and osmotic salts (Na^+) (Nunkaew et al. 2014). Biofilm is a complex association of bacterial cells attached to surfaces such as plants root or soil particles and protects the plants of pathogens attack, retain moisture (Qurashi and Sabri 2012). EPS-producing PGPR enhance the soil structure (crumb formation) by increasing the volume of soil macropores and thus rhizosphere soil aggregation, resulting in water retention and increase in provision of nutrient for inoculated plants. EPS can also bind Na^+ therefore, decreased content of Na^+ available for plant uptake, and thereby alleviate salt stress in plants growing in saline environment. The ability of the EPS to binds cations is normally associated with the hydroxyl, sulfhydryl, carboxyl and phosphoryl groups that it contains (Watanabe et al. 2003; Nunkaew et al. 2014). Recently Nunkaew et al. (2014) identified a polysaccharide (≈18 kDa) that is constituent of EPS, mainly composed of galacturonic acid and responsible for salt removal of *Rhodopseudomonas palustris* strain PP803. Some of the rhizobacteria strains that produce EPS and facilitate biofilm formation are *Aeromonas hydrophila/caviae*, *Bacillus* sp., *Planococcus rifietoensis, Halomonas variabilis*, *Burkholderia*, *Enterobacter*, *Microbacterium* and *Paenibacillus* (Qurashi and Sabri 2012; Upadhyay et al. 2011; Ruppel et al. 2013)

4.3 Salt Tolerant PGPR and Their Application in Agriculture

With increase of the world human population, the demand for food is expected to rise by 38 % by 2015 and 57 % by 2050 if the current global food supply is to be maintained (FAO 2010). Coupled with the need for increasing crop production, and problems related to global warming, such as changes in precipitation patterns, increased temperatures, drought and flooding, and many other problems related to improper anthropogenic activities in cultivation practices, such as excessive uses of fertilizers and pesticides, poor irrigation practices, monocultures, etc., a clear sustainable strategy is needed to overcome the problems and to meet the demand. It has been estimated that nearly two thirds of the soils are prone to edaphic constraints in developing countries. Therefore in this race against time to produce more food, mitigation of abiotic stresses become imperative to increase the crop productivity by way of implementation of new agronomic technologies (Khalid et al. 2004). The use of halotolerant transgenic plants and application of salt-resistant PGPR are two of the major strategies that are being considered to improve the agriculture in saline soils (Mayak et al. 2004; Jha and Saraf 2011).

To use PGPR as a remediation strategy for saline soils further knowledge is essential for characterization of halophyte-associated rhizobacteria, and their interaction with halophytes and glycophytes in order to understand the mechanisms of their survival and protection against salt stress and to develop strategies for plant protection (Ruppel et al. 2013; Egamberdyeva and Lugtenberg 2014). The rhizobacteria isolated from a saline habitat is more efficient to improve the plant tolerance to salt than PGPR from non-saline habitats (Paul and Nair 2008). Halotolerant PGPR can be an alternative approach for mitigation of salt stress, which can eliminate or minimize the environmental pollution.

The vast majority of crops are salt susceptible (e.g. >3.0 dS/m), and in general the yield of crops are reduced by 50 % under saline conditions (EC 5.0 dS/m) (Horneck et al. 2007; Ondrasek et al. 2009). Several salt-tolerant PGPR strains have the ability to growth at least with 3 % NaCl (Shrivastava and Kumar 2014; Egamberdyeva and Lugtenberg 2014). Reports on PGPR inoculation of vegetable crops such as eggplant (Bochow et al. 2001), tomato (Mayak et al. 2004; Damodaran et al. 2013; Palaniyandi et al. 2014), bean (Yildirim and Taylor 2005; Maqshoof et al. 2012), artichoke (Saleh et al. 2005), squash (Yildirim et al. 2006), wheat (Ashraf et al. 2004; Nabti et al. 2007; Upadhyay et al. 2011), radish (Yildirim et al. 2008), maize (Hamdia et al. 2004; Nadeem et al. 2007; Bano and Fatima 2009; Rojas-Tapias et al. 2012), lettuce (Kohler et al. 2009a, b), soybean (Han and Lee 2005; Naz et al. 2009; Kasotia et al. 2015), cotton (Yao et al. 2010), canola (Cheng et al. 2007; Siddikee et al. 2010), peanut (Saravanakumar and Samiyappan 2007), red pepper (Siddikee et al. 2011), strawberry (Karlidag et al. 2011; Karlidag 2013), mung bean (Ahmad et al. 2012, 2013) sunflower (Naz and Bano 2013), potato (Gururani et al. 2013) alfalfa (Martinez et al. 2014), rice (Jha et al. 2012; Jha and Subramanian 2014), barley and oats (Chang et al. 2014) under salinity conditions are available. Although there have been many successes in crops protection test in a range of 0.5–2 % salinity (Tank and Saraf 2010; Shukla et al. 2012), is necessary continue with assays where higher levels of salinity are to be evaluated (halophyte culture).

One of the most common problems in the use of PGPR as bio-fertilizers is the decrease in the efficacy of PGPR due to the different environment conditions on cropland where the application is carried out, and which is different to the environment where the PGPR were isolated, concerning conditions such as variations in soil type, management practices, and different environment conditions (Khan et al. 2009). Due to the above is important the search for bacteria with the ability to cope the particular environmental conditions of agricultural area where the beneficial rhizobacteria are applied. The Chihuahuan Desert area host many halophytes, from which PGPR could be isolated and used on farmland, affected by salinity in the same Chihuahuan Desert area.

5 Future Directions and Conclusion

PGPR offer a friendly environment option and sustainable approach for increase of soil fertility, plant health and protection to adverse environmental conditions. Although progress has been made in understanding the rhizosphere microbial community, communication, signaling and molecular response between plant and microbes, diversity of PGPR, mechanisms of action in plants, and methods to development and use PGPR as bio-inoculants, it is necessary to continue studying the structural community and diversity microorganism's presents in the rhizosphere and how this change in relation to soil type, environmental conditions, plant species and influence of anthropogenic activities. Actually tools in molecular biology facilitate the research of microbial communities because it allows us to identify the vast majority of non-cultivable microorganisms in rhizosphere communities through metagenomics analysis. These analyses will be key in understanding the changes in rhizosphere communities when beneficial microbes are inoculates in plants. At present a great challenge to overcome is the inconsistent performance of PGPR under field conditions and under diverse environmental conditions. It is necessary to explore different rhizosphere environment (alkaline, acids, high and low temperatures, flooded) to isolate PGPR more efficient and to enable to withstand environment changes that crops are exposed today. With the advancement in the understanding of molecular mechanisms adopted by PGPR to increase growth in plants and to cope high salinity, it is possible to enhance their capacity to stimulate plant growth by genetic engineering is possible to modify or insert genes from other organisms to improve the mechanisms used by PGPR to promote growth, even feasible to transfer genetic information to plant in order to facilitate and improve interactions with beneficial microbes. Another important issue to be addressed in future research is the use of PGPR together with plants to bio-remediate farmland affected by high salt concentrations, PGPR promote shoot and roots biomass productions of halophytes that accumulate salts, which is uptake of surrounding saline soil.

Salinity is worldwide problem that increases every year. The salt-tolerant PGPR are a viable and sustainable alternative to recover agricultural areas affected by salinity, without use of chemicals that pollute soil and water. Beneficial microbes may be able to improve soil quality, soil microbial communities and agriculture yield of crops in arid and semiarid environments. Further optimization is required for application and formulation of PGPR strains to introduce in agriculture.

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ERRATUM

Sabkha Ecosystems
Volume V: The Americas

M. Ajmal Khan, Benno Boër, Münir Özturk,
Miguel Clüsener-Godt, Bilquees Gul,
Siegmar-W. Breckle

M.A. Khan et al. (eds.), *Sabkha Ecosystems Volume V: The Americas*,
Tasks for Vegetation Science 48, DOI 10.1007/978-3-319-27093-7

DOI 10.1007/978-3-319-27093-7_25

Foreword: The location "Delft, The Netherlands" had been changed to "Paris, France".

Preface: The word "North America" had been changed to "Americas" throughout the preface.

Chapter 3: Few corrections made to the chapter had been missed in the previous version. All corrections had been incorporated.

The updated original online version for this book can be found at
http://dx.doi.org/10.1007/978-3-319-27093-7

M.A. Khan et al. (eds.), *Sabkha Ecosystems Volume V: The Americas*,
Tasks for Vegetation Science 48, DOI 10.1007/978-3-319-27093-7_25

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Tasks for Vegetation Science 48, DOI 10.1007/978-3-319-27093-7

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