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.

E. Medina (✉)
Centro de Ecología, Instituto Venezolano de Investigaciones Científicas, Caracas, Venezuela

International Institute of Tropical Forestry-US Forest Service, San Juan, Puerto Rico
e-mail: medinage@gmail.com

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.

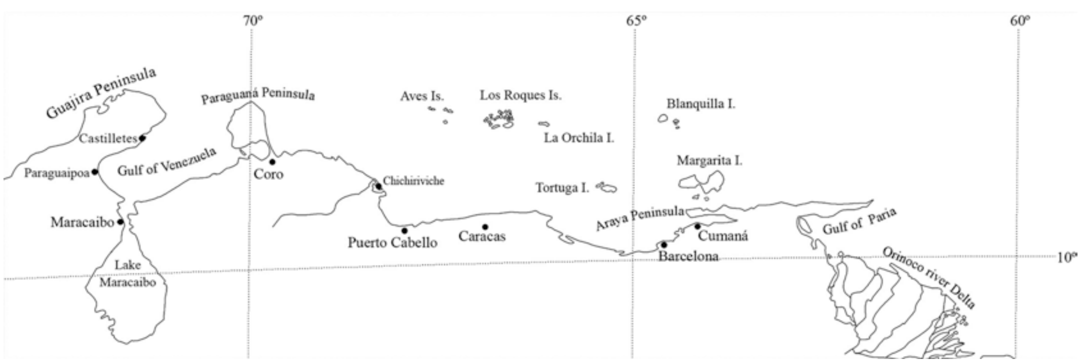

Fig. 3.1 Caribbean coastline of Colombia and Venezuela including the names of localities mentioned in the text

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)

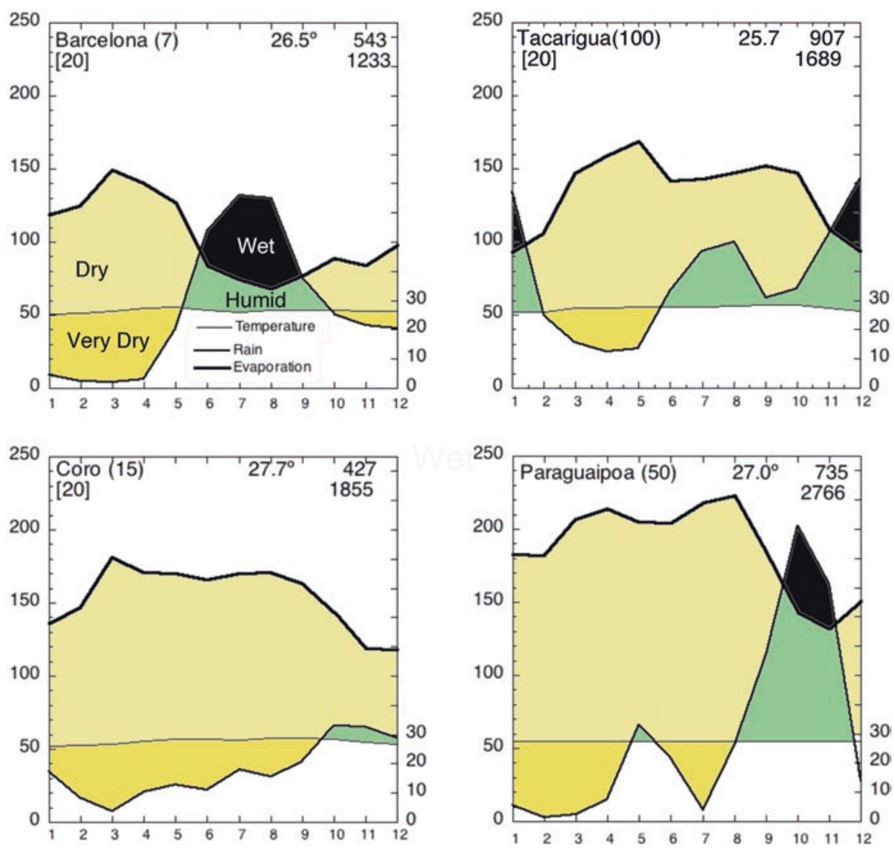

Fig. 3.2 Arid and semiarid climates in the caribbean coast of Venezuela. *Left* ordinate rainfall and evaporation (Tank A×0.812, García-Benavides and López-Díaz 1970), and temperature on the *left* ordinate. In the abscisa months from January to December. Rainfall:temperature scales 2:1. The *upper*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

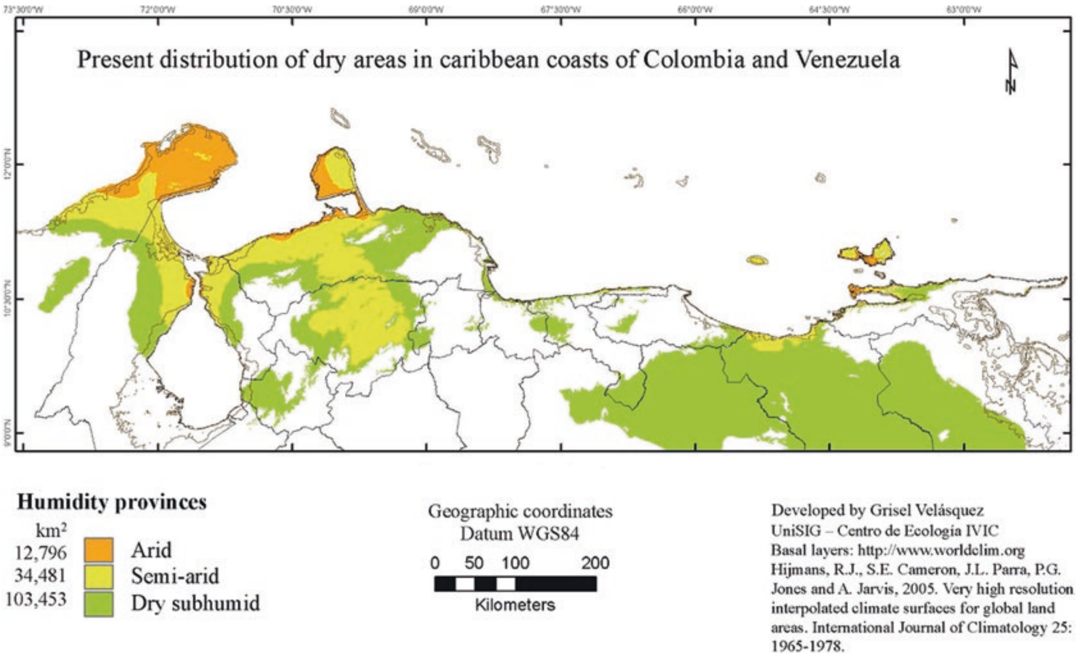

Fig. 3.3 Delimitation of dry climates in northern Venezuela and Colombia using the S index of Bayley (1979) with average annual rainfall and temperature data. Conceptual development in Nassar et al. (2013)

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-

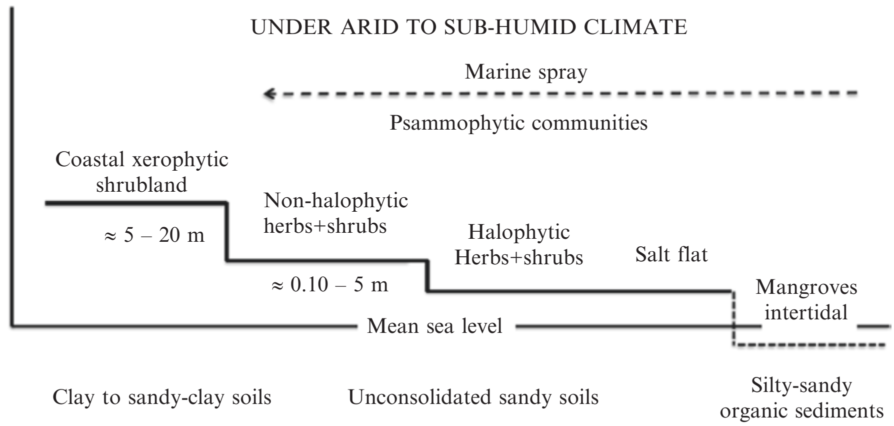

Fig. 3.4 Schematic representation of coastal vegetation types in a transect from intertidal zone to *upper* coastal xerophytic shrubland

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 semidiurnal 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-

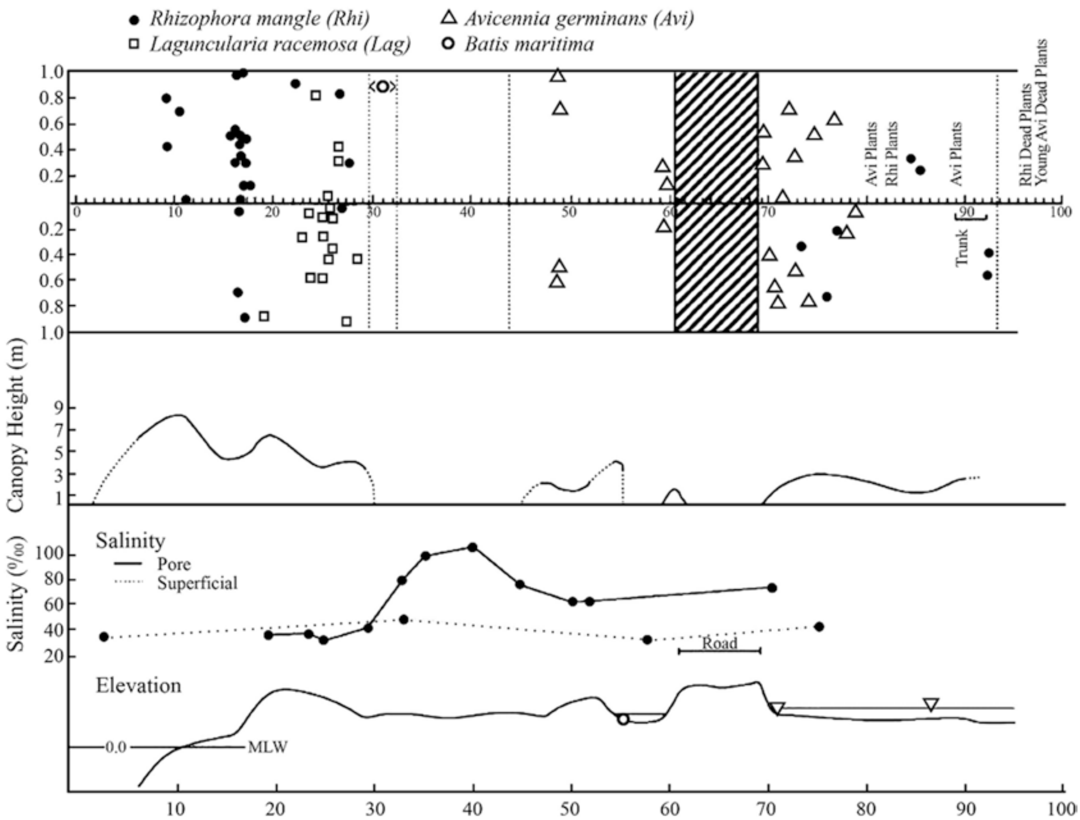

Fig. 3.5 Vegetation profile, topography, and pore salinity in an ocean fringe forest in Jobos, Puerto Rico. The *upper* panel shows the location of the 100 m × 2 m transect from the ocean (*left*) towards inland (*right*). The road is shown in the *upper* panel with dashed oblique lines. In this gradient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

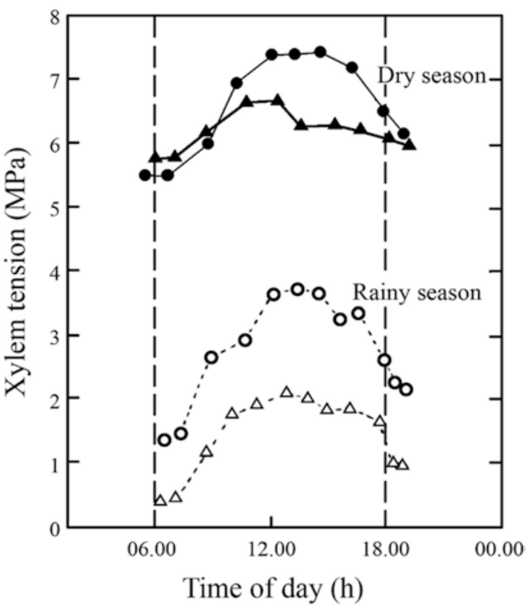

Fig. 3.6 Diurnal course of xylem tension measured with a pressure bomb during rainy and dry season in *Avicennia germinans* (*circles*) and *Conocarpus erectus* (*triangles*) (From Smith et al. 1989)

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 of 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_20 kg^{-1} (12 h)$^{-1}$]		
Batis maritima	n.d.	47.5
Sesuvium portulacastrum	n.d	40.8
WUE [($C0_2$:H_2O) × 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

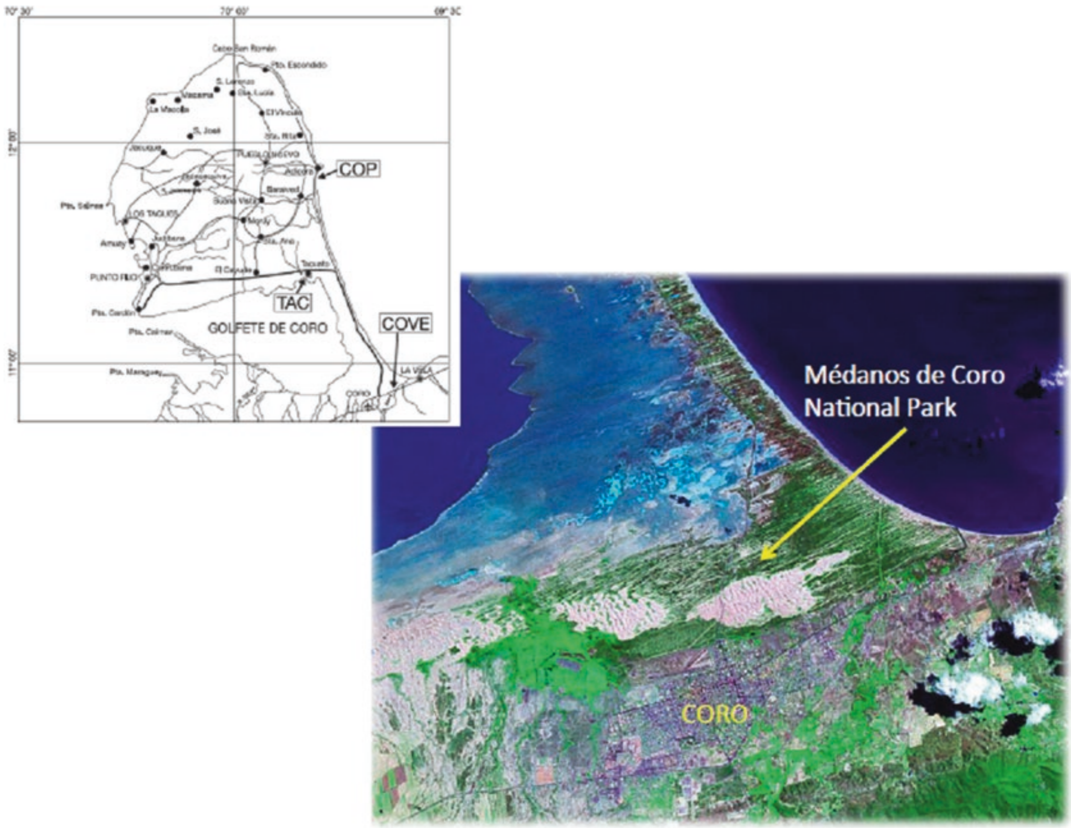

Fig. 3.7 Collection sites of psammophytes in the Paraguana peninsula in Venezuela, in north-east Coro (COVE), Tacuato bay (TAC) and eastern coast south of Adicora (COP). The Land Sat image (LANDSAT VENEZUELA/N-19-10_2000/) shows the extensive dune fields north of the city of Coro where many studies on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

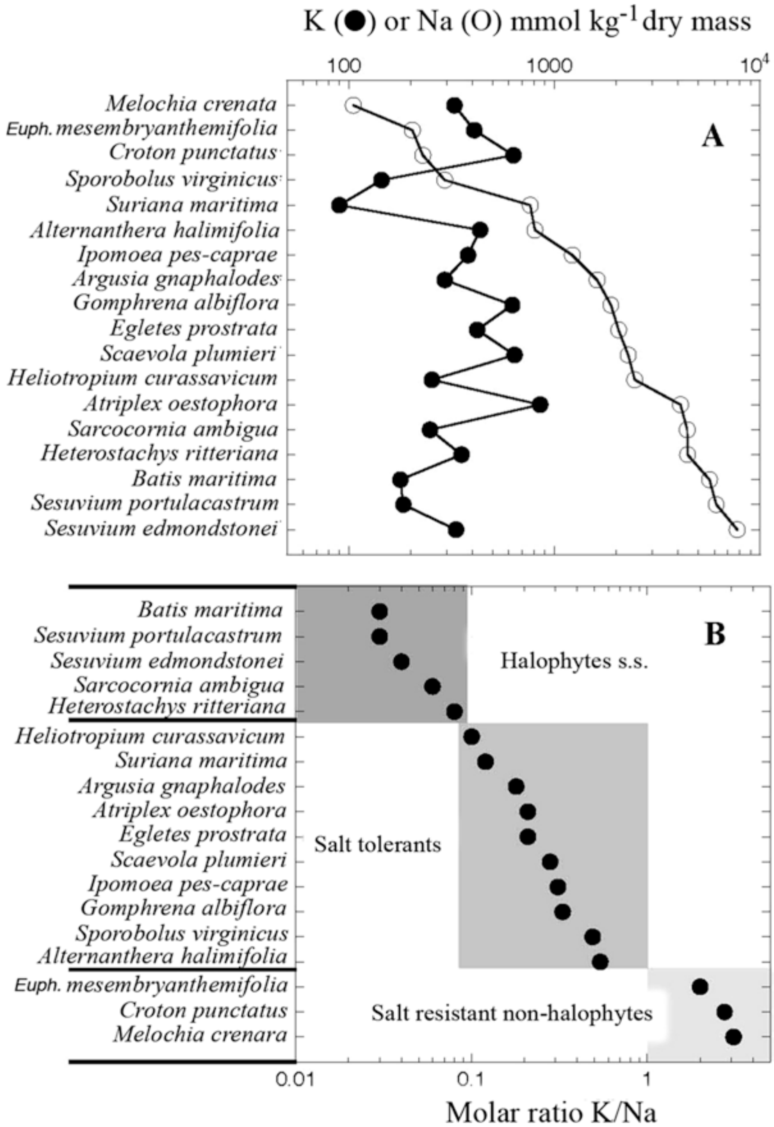

Fig. 3.8 (**a**) Distribution of the total Na and K concentrations in plant leaves; (**b**) Ordination of the species according to their halophytic character based on their K/Na ratios

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)

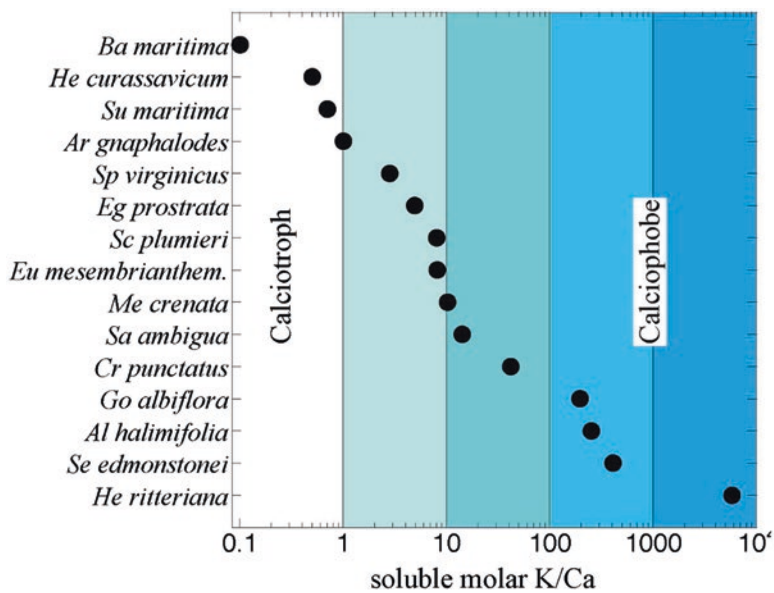

Fig. 3.9 Separation of calciotroph and calciophobs species according to soluble K/Ca ratios

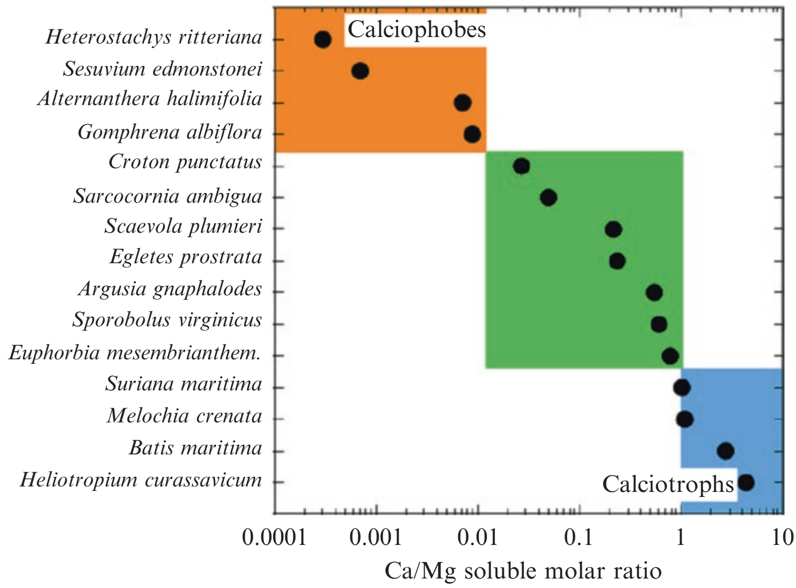

Fig. 3.10 Soluble Ca/Mg ratios as indicator of degree of calciophylly

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.

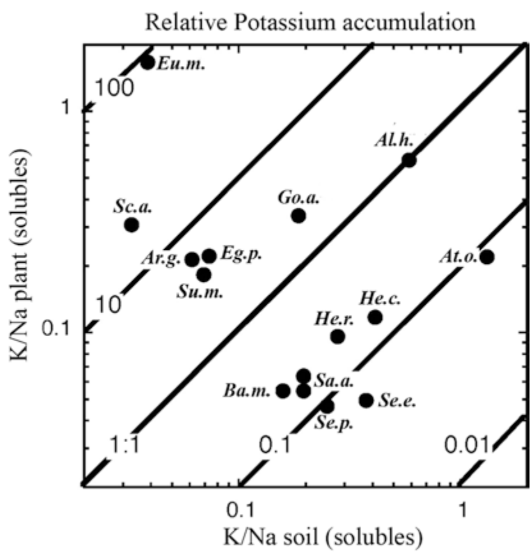

Fig. 3.11 Variation in the soluble molar K/Na ratios in photosynthetic tissues plotted agains the same ratio of the soils where the plants are growing following to Breckle (2002). The central diagonal indicates the values where relative concentrations of K related to Na are identical in plants and soils. 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-

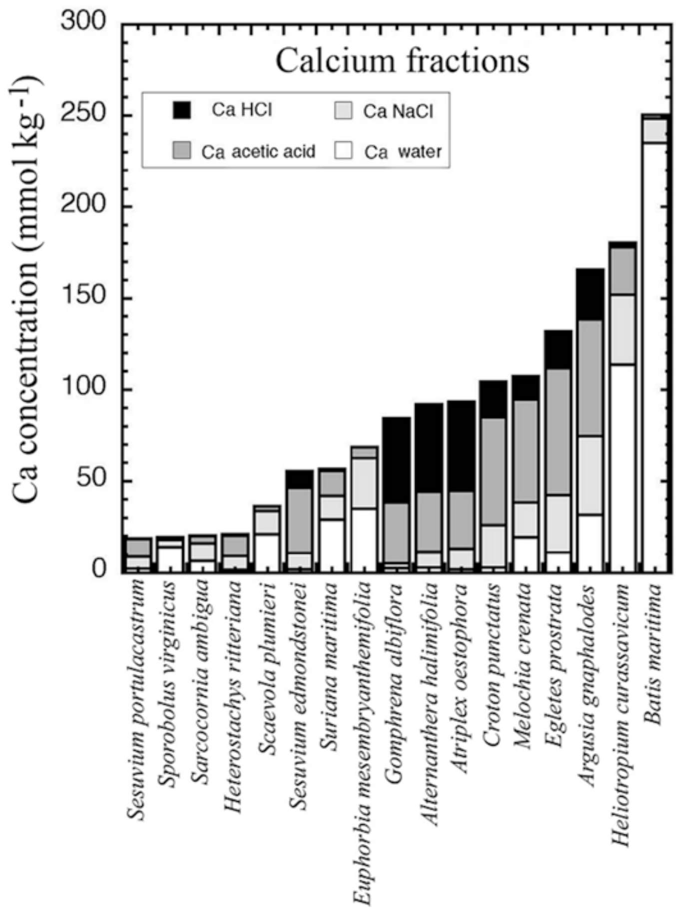

Fig. 3.12 Fractionation of Ca extracted from photosynthetic tissues of the species under analysis following the procedure described by Kinzel (1989)

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 $\delta^{13}C$ (‰) 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

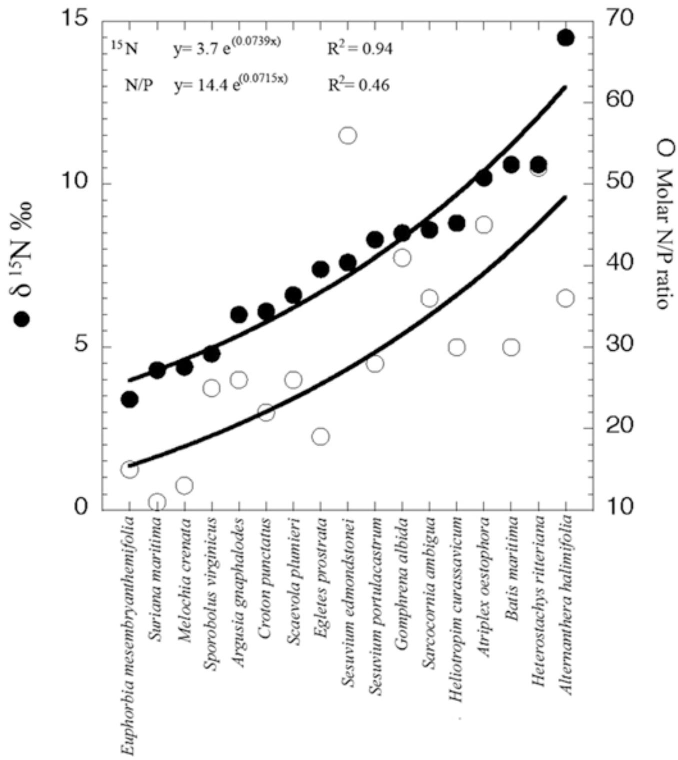

Fig. 3.13 Relationship between the natural abundance of ^{15}N (δ^{15}N) and the N/P molar ratio in photosynthetic tissues

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 $\delta^{15}N$ 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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