Chapter 14
Ecology of Inland Saline Plants

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Abstract This chapter describes the ecology and adaptive strategies of inland halophytes growing in natural saline areas, with special reference to classification, metabolic products, soil–water relationships, the role of proline in their survival, etc. Studies on eight saline plants, viz. *Aeluropus lagopoides* (Poaceae), *Cressa cretica* (Convolvulaceae), *Salsola baryosma* (Chenopodiaceae), *Sesuvium sesuvioides* (Aizoaceae), *Sporobolus helvolus* (Poaceae), *Suaeda fruticosa* (Chenopodiaceae), *Trianthema triquetra* (Aizoaceae), and *Zygophyllum simplex* (Zygophyllaceae), selected from different Indian desert sites, is described. Among these species, *S. fruticosa* is distributed widely and is highly salt tolerant. The major cations and anions in saline areas of the Indian arid zone are Na^+, K^+ and Ca^{++}, and Cl^-, respectively. The inhibition of seed germination of saline plants is controlled by both osmotic and ionic factors. Soil salinity increases especially during dry periods, which results in accumulation of more ions in leaves. The metabolic products of different plant species respond differently to higher salinity. Free proline accumulation during unfavourable conditions increases with increasing salinity, which helps in the survival of saline plants.

14.1 Introduction

Salinity problems are of great concern in arid and semi-arid regions, where soil salt contents are high and precipitation is insufficient for their leaching. In these regions, planting salt-tolerant species, particularly N_2-fixing species, is the most useful

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K.G. Ramawat (ed.), *Desert Plants*,
DOI 10.1007/978-3-642-02550-1_14,

approach to rehabilitating salt-affected degraded lands. There are a large number of plant species that are regarded as salt-tolerant, the most competitive being those that are able to become established, grow to maturity and survive until they are able to reproduce (Heidari-Sharifabad and Mirzaie-Nodoushan 2006).

Salt-affected soil is defined as soil that has been adversely affected to the extent that it is no longer suitable for normal plant growth due to presence of excess soluble salts. Such soils include both saline and sodic soils. The loss of plant productivity due to excess salinity is a worldwide problem (Evangelou 1994; Sen et al. 2002). In salt-affected soils, high electrolyte content or extreme pH conditions limit the development of the majority of plants, and such soils serve only as habitat for species that can survive or tolerate the unfavourable conditions caused by the salinity or alkalinity. Salt-affected soils can be characterised as soils formed under the dominant influence of different salts in their solid or liquid phases, which then have a decisive influence on the development, characteristics, physical, chemical and biological properties, and, eventually, the fertility of the soil. In saline soils, the high salt concentration in the solid or liquid phase results in high osmotic pressure, hindering the normal development of plants, i.e. the stress factor is the salinity, with all its disadvantageous consequences to plant life (Szabolcs 1994).

Agricultural production worldwide is greatly affected by a number of environmental hazards, one of the most important being salinity associated with aridity. Salinity is a problem not only in India, but also throughout the world. Saline lands are not only distributed in desert and semi-desert regions, but also occur frequently in fertile alluvial plains, rivers, valleys, and coastal regions close to densely populated areas and irrigation systems. Salinisation can occur in areas with arid and semi-arid climates or in coastal regions, where salts are transported by groundwater and precipitation. The direct effects of salts on plant growth can be divided into three broad categories: (1) a reduction in the osmotic potential of the soil solution, which reduces the amount of water available to plants; (2) a deterioration in the physical structure of the soil, which decreases permeability to water and gases; and (3) specific ion toxicity (Dudley 1994). Halophytes thrive under varying soil salinity conditions and may be irrigated with brackish water or with a certain percentage of seawater without any major ill effects on growth and reproduction (Parida and Das 2005).

The vegetation of saline habitats is designated as “halophytic”, as opposed to the vegetation of non-saline habitats, which is sometimes referred to as glycophytic. Phenologically, halophytic plants may be succulent or xeromorphic, having small or grass-like leaves and often also salt-secreting glands. In their saline environments, halophytes are exposed not only to salt stress, but the root system may also be exposed to osmotic water and low oxygen pressure (Palfi and Juhasz 1970). The climate of the Thar desert is one of the most important factors influencing salinity. Various climatic factors, such as low rainfall, temperature, wind direction, velocity, etc., play a key role in the formation of saline–alkali soils. Rainfall has a greater effect than temperature in determining soil salinity. In areas receiving low rainfall and high temperature, evaporation takes place, leaving behind accumulated soluble salts. High wind velocity also plays a part in evaporation of surface water as well as transporting some of the salt from salt-affected areas to adjoining areas (Poljakoff-Mayber and Gale 1975; Sen 1990; Sen and Mohammed 1994; Sen et al. 2002). The aridity caused by low rainfall and extreme high or low temperatures are very often compounded by high salinity in the soil, resulting in severe problems in absorption of water, thus curtailing productivity (Mohan Ram and Gupta 1997).

Salinity plays an important role in vegetation cover. An excess of salts in the soil inhibits plant growth in various ways. The Thar – the Indian desert – includes the arid and semi-arid portions of western India and part of Pakistan. Rajasthan State alone owns the maximum arid area, which represents 62% of the total arid area of India and 56% of the total area of the State. The salt basins of the Indian arid zone are of the inland type, and differ greatly from other saline areas in vegetation make up; they support a relatively small number of plant species, namely those capable of tolerating a high degree of salinity. The saline areas of the Indian desert can be divided into two categories: (1) salt lakes such as the Sambhar, Didwana, and Kuchaman, located in the eastern part of Rajasthan; and (2) salt basins such as Pachpadra, Thob, Sanwarla, Luni, Bap, Kaparda, Taal Chhapar, Pokran, Lunkaransar, Lanela, Sakhi, Khajuwalla, etc., located in the western half of Rajasthan (Fig. 14.1).

Fig. 14.1 Some important saline areas of western Rajasthan, India (after Mohammed 1988)

Halophytes are defined as plants that grow and complete their entire life-cycle in saline habitats. Halophytic species that live under conditions of high salinity and exhibit succulence might resort to other physiological adaptations to overcome the adverse saline environment in the soil. Their extreme tolerance to salinity is related to their ability to maintain a high salt concentration within the cells. In desert areas salinity is often very prominent, caused by the input of sodium chloride (NaCl) and other salts over long periods of time combined with lack of drainage. On such saline soils, Chenopodiaceae very often dominates typical plant associations that develop along salt gradients (Waisel 1972; Breckle 1986).

14.2 Classification of Inland Saline Vegetation in Western Rajasthan

The saline areas of the Indian arid zone have a mosaic of successive zones represented by characteristic taxa of limited distribution. These zones differ from one another in soil characteristics. Each zone supports a distinct plant grouping with its own characteristic species. The precise determination of the effect of salinity, and the sites where salinity may affect plants are not easily assessed. First, since both salt combination and salt concentration differ from one habitat to another, the term "salinity" usually has a loose meaning. In certain cases, it is not the absolute amount of a certain ion that may affect plants, but rather the composition and total concentration of salts. Certain plant species may be found in sites where the NaCl concentration is beyond their theoretical tolerance but where high concentrations of calcium, potassium, or sulfate are found as supplementary ions. These ions moderate the toxic effects of sodium and chloride, thus enabling plants to exist. In additions, contact between the salt and the plant may involve different tissues of the plant.

Sen and Rajpurohit (1978) classified the vegetation of some Indian salt basins. Later, Rajpurohit (1980) surveyed some of the salt basins and reported a total of 122 plant species, including 10 true halophytes, 48 facultative halophytes, and 64 glycophytes. According to the new classification of Mohammed and Sen (1994), plant species in this region can be divided into four groups:

1. True halophytes: plants that grow in extreme saline conditions (above 1.5% NaCl) and resist high salinity (Fig. 14.2), including *Suaeda fruticosa* (Figs. 14.3, 14.4), *Salsola baryosma* (Fig. 14.5), *Cressa cretica*, *Zygophyllum simplex* (Fig. 14.6), *Haloxylon recurvum* (Fig. 14.7), *Sporobolus helvolus* (Fig. 14.8), *Heliotropium curassavicum* (Fig. 14.9), and *Aeluropus lagopoides*.
2. Facultative halophytes: plants that grow in saline to non-saline conditions, or mainly saline, but cannot tolerate high salinity (0.5% NaCl level), such as *Sesuvium sesuvioides* (Fig. 14.10), *Trianthema triquetra* (Fig. 14.11), *Tamarix* spp. (Fig. 14.12), *Chloris virgata* (Fig. 14.13), *Eleusine compressa*, *Dipcadi erythraeum*, and *Portulaca oleracea*.

Fig. 14.2 View of salt lake at Didwana

Fig. 14.3 Field view of *Suaeda fruticosa* at Pachpadra salt basin

Fig. 14.4–14.14 Halophytes growing under different natural field conditions
Fig. 14.4 *Suaeda fruticosa* (Pachpadra)

Fig. 14.5 *Salsola baryosma* (Jodhpur)

Fig. 14.6 *Zygophyllum simplex* (Pachpadra)

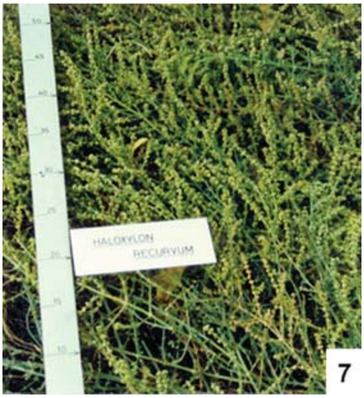

Fig. 14.7 *Haloxylon recurvum* (Jodhpur)

Fig. 14.8 *Sporobolus helvolus* (Pachpadra)

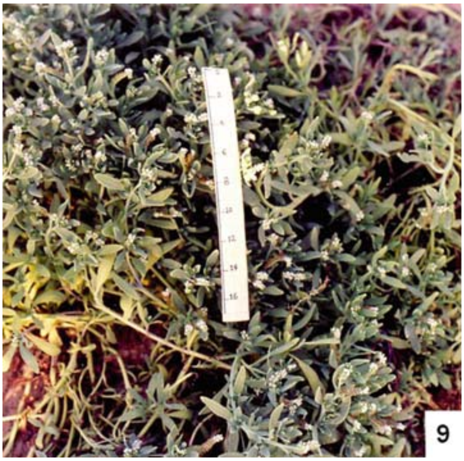

Fig. 14.9 *Heliotropium curassavicum* (Didwana)

3. Transitional halophytes: plants that grow only at the transition of saline and non-saline areas, including *Cassia italica*, *Haloxylon salicornicum*, *Fagonia cretica*, *Cyperus* spp., *Dactyloctenium aegyptium*, *Salvadora persica* (Fig. 14.14), *Tragus racemosus*, and *Boerhavia diffusa*.

Fig. 14.10 *Sesuvium sesuvioides* (Pachpadra)

Fig. 14.11 *Trianthema triquetra* (Pachpadra)

4. Glycophytes: mainly non-saline plants, but growing in saline areas only for a short duration when salinity levels are reduced, including *Brachiaria ramosa*, *Digera alternifolia*, *Eragrostis ciliaris*, *Heliotropium marifolium*, *Convolvulus microphyllus*, *Dicoma tomentosa*, *Farsetia hamiltonii*, *Gisekia pharnacioides*, *Polygala chinensis*, *Calotropis procera*, *Aerva persica*, *Oldenlandia aspera*, *Prosopis juliflora*, *Acacia jacquemonti*, etc.

These species were classified on the basis of (1) their distribution in the salt basins, and (2) their basic requirements, especially for salt and water (Mohammed 1988; Sen 1990; Mohammed and Sen 1994).

Fig. 14.12 *Tamarix troupii* (Luni)

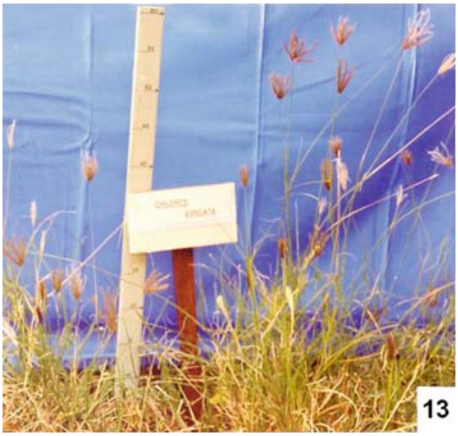

Fig. 14.13 *Chloris virgata* (Jodhpur)

The ecological limits of the distribution of plant communities depend upon the presence of soluble salts in the water or soil. The water of the habitat is the dominant ecological factor determining the distribution of species. Salinity is probably the major factor determining the characteristics of the habitat, and salts affect natural selection more than any other factor (Waisel 1972). Thus, the distribution of a halophytic community appears to be limited by salinity and the depth of the water table as well as by the competitive ability of members of the neighbouring community in the halosere (Reed 1947; Sen and Mohammed 1994; Sen et al. 1997).

Fig. 14.14 *Salvadora persica* (Luni)

14.3 Adaptive Strategies of Inland Halophytes

Plant adaptations dealing with water conservation have particular meaning in dry environments where water stress is either permanent or temporary and severely limits plant growth. Plants living in such environments get adapted by increased drought tolerance and water use efficiency. There are a number of modifications to plant structures and processes as a consequence of drought stress. These include sensitivity of stomatal response, osmotic adjustment, smaller cell volume, reduced leaf area, increased leaf thickness, hairy leaves, and increased root:shoot ratio, as well as various changes in enzyme and hormone production and activity (Pugnaire et al. 1994).

In the world where most of the water is saline, halophytic plants are examples of effective adaptation to increased salinity. Halophytic plants grow in a wide range of environmental conditions. Some grow in high moisture saline areas such as mangrove swamps; others exist in fluctuating moisture conditions in tidal zones; and still others live in inland saline areas in arid climate. In all these cases, in order to take up water halophytes must adjust their tissue water potential to a level that is lower than that of the soil water potential in the habitat where they are growing. Without sufficient moisture, halophytes can become stunted and reproduction becomes very limited (Weber 1995).

Halophytes are adapted to survive in a range of saline environments. In any environment, halophytes require water for growth and development. The key mechanism used by halophytes to obtain sufficient water for growth and development is osmotic adjustment. Halophytes take up ions to increase the osmotic level in their tissues, which permits moisture to move from the soil into the tissues. On the other hand, excess salt ions can have a toxic effect on plant cells. Some of the mechanisms used by halophytes to counter the potential toxic effect of high concentrations of ions involve exclusion of salts by the roots, dilution of ions through succulence, synthesis of organic osmotic compounds that can reduce the need for salt ions, and compartmentalisation of excess salt ions into tissues, organs, or cell vacuoles. Halophytes need to obtain sufficient ions to maintain growth, while avoiding a water deficit or an excess of ions. The net result is that halophytes grow successfully in saline environments whereas glycophytes cannot (Khan and Ungar 1995).

Sen and Rajpurohit (1982) and Sen et al. (2002) classified halophytes into two categories on the basis of salt accumulation and secretion:

1. Salt accumulating halophytes: plants growing under saline conditions maintain a high concentration of osmotically active substances in order to compete successfully with the water-retaining capacity of the surrounding medium. The increase in osmotic potential of cell sap associated with osmotic adjustment of plants to salinity is accomplished by accumulation of ions. Increased succulence has a diluting effect on the toxic ion content of cells, thus enabling plants to withstand the effects of larger quantities of salts. Examples include: *Suaeda fruticosa*, *Salsola baryosma*, *Zygophyllum simplex*, *Trianthema triquetra*, *Haloxylon recurvum*, *Heliotropium curassavicum*, etc.
2. Salt secreting halophytes: secretion of salt by salt glands is a mechanism for regulating mineral content in many non-succulent halophytic species. The salt glands act as desalination devices in halophytes and thus appear to maintain the salt balance in the leaves by secretion of excess salts, e.g. *Aeluropus lagopoides*, *Cressa cretica*, *Sporobolus helvolus*, *Chloris virgata*, *Tamarix* spp., *Atriplex* spp., etc.

A saline environment induces morphological, physiological, and phenological adaptations in plants (Waisel 1972). In saline areas, the effect of salinity on growth and salinity tolerance is temporary in glycophytes and permanent in halophytes; both try to adapt themselves accordingly. Plants that are well adapted to saline soils from various survival aspects are able to grow only in these habitats.

The resistance of plants to salinity leads to several adaptations. Most of these plants avoid salinity, some evade it, and a few others tolerate it. Most plants avoid salinity by: (1) limiting reproduction, growth, and germination during specific periods of the year; (2) limiting uptake of salt; and (3) allowing roots to penetrate into non-saline soils. Evasion of salt can be achieved through the accumulation of salts into certain specific cells and trichomes or by secretion of excess salts through special mechanised salt-secreting glands (Waisel 1972; Sen et al. 1997).

The leaves of saline plants play an important role under physiological drought conditions, developing certain xeromorphic characteristics such as succulence, reduction in surface area, thick cuticle or waxy layers on the epidermis, a hair cover, and salt glands. The hairs on leaves can accumulate salts and act as salt concentration sites although their salt storage capacity is limited (Ungar 1995). A thick cuticle and a cover of waxy layers, such as is present in *S. fruticosa*, *S. baryosma*, and *H. recurvum*, characterises xerosucculents. Cuticle and waxy layers have also been reported on the leaf surfaces of *C. cretica*, *A. lagopoides*, *S. helvolus*, and *C. virgata*. Halophytes such as *C. cretica*, *C. virgata*, *S. helvolus*, and *A. lagopoides* show an additional mode of adaptation to their habitat. The leaves and stems of these plants remain covered with hairs (trichomes), giving the plant a greyish appearance. Their effectiveness in reducing the loss of water is small, but they are able to protect the leaf surface against dust.

Halophytic cells need to have high osmotic pressure and at the same time prevent excess ions from inhibiting enzymatic processes. If excess ions are stored in the vacuole, then metabolic activity can carry on in the cytoplasm where the ion content is lower. The lower salt concentration prevents organelles such as chloroplasts from being damaged by excess ions (Khan and Ungar 1995). When a change in metabolism results in a change in the ability to resist stress conditions, anthocyanin may develop in the leaves or stems of plants. Some halophytes of the Indian region, such as *S. fruticosa*, *S. baryosma*, *T. triquetra*, and *Z. simplex*, exhibit this characteristic under osmotic stress. Thus, the development of anthocyanin is a well-known characteristic of plants exposed to drought, osmotic drought, or physiological drought.

The existence of a plant species in its natural habitat depends on its ability to reproduce under those ecological conditions. The presence of excess salt in the soil is one of the critical factors that adversely affects seed germination under such conditions, thereby preventing plant species from saline environments from becoming established successfully (Mohammed 1988; Mohammed and Sen 1990a; Ungar 1995).

Haloxylon recurvum and *H. salicornicum* are two halophytes characteristic of the Indian Thar desert. Seeds of these two species have an extremely fast seed germination time – commonly occurring within an hour – as first reported for any Indian plant species by Sharma and Sen (1989). This rapid germination serves to illustrate the adaptive strategy of these plants, as water with reduced NaCl content in soil during the rainy season is available only for a short period of time because evaporation of moisture under bright sunlight and heat results in increasing the salt content by capillary movement.

Heliotropium curassavicum is one of the rare herbaceous species of the family Boraginaceae, which has been found to flourish in inland salines of Rajasthan. This plant is a perennial herb with spreading habit. The leaves are succulent and glabrous in nature. When growing away from moist areas, the plants prefer to grow in shade and show vigorous growth. The fully grown plants appear characteristically bluish-green. Since the plants grow in a gregarious fashion, they form patches on the ground. The characteristic feature of this species is that, upon the onset of dry conditions, more and more salt is accumulated in the fleshy leaves. These salt saturated leaves dry up to maintain a balanced osmotic level in the plant. New leaves sprout, and this process continues during the whole lifespan of the plant (Sen et al. 2002).

Rajput (1992) reported that with an increase in the duration of leaching in *Atriplex* species, the amount of ions leached from the leaves also increased, with the maximum value being observed after 72 h. Maximum values of leacheable Na^+ and Cl^- were observed in young leaves of *A. halimus* and *A. nummularia*, respectively, during the summer, while a minimum Na^+ values were recorded in young leaves of *A. argentina* during the rainy season, probably due to the leaching of salts from leaves by rainwater. The young leaves and stems of *Atriplex* spp. contained quite high levels of sodium and chloride ions in comparison to mature parts, due to their fleshiness and the presence of more salt bladders in the epidermis of tender plant parts.

As mentioned above, the presence of excess salt in the soil is one of the critical factors adversely affecting seed germination under such conditions, thereby preventing plant species from inhabiting saline environments successfully. Halophytes show a reduction in germination when subjected to salinities above 1% NaCl, and increasing salt concentrations also delay germination (Chapman 1974). Information regarding the germination behaviour of Indian halophytes has been provided by various workers from the Ecology Laboratory, Department of Botany, Jai Narain Vyas University, such as Rajpurohit (1980), Sen and Rajpurohit (1982), Jhamb (1984), Jhamb and Sen (1984), Mohammed (1988), Sharma (1991), Rajput (1992), Thomas (1992), etc. Mohammed (1988) and Mohammed and Sen (1990a) collected seeds of halophytes from four different sites (Pachpadra, site-I; Didwana, site-II; Jodhpur, site-III; and Luni, site-IV) and studied the effect of various salts on seed germination behaviour. Various salts that are common in saline soils, viz. NaCl, Na_2SO_4, $MgSO_4$, KCl, and $CaCl_2$ were selected. Single salt solutions at concentrations of 100, 1,000, 5,000 and 10,000 mg l^{-1} were used. The aim of the investigation was to understand how individuals from a plant species from different localities behave with a particular salt, and whether the inhibition of germination is due to the osmotic or toxic effect of different ions. In order to make a distinction between osmotic and ionic effects, or the combined effect of these two factors on seed germination inhibition, those seeds that remained ungerminated in the saline medium at 10,000 mg l^{-1} concentration were transferred to distilled water individually to determine the additional germination per treatment. The results revealed that the germination percentage varied with different salt solutions (Mohammed and Sen 1990a, 1991). Higher concentrations of all the salts affected germination directly, thus reducing germination percentage. Seeds of *C. cretica* collected only from site-I showed dormancy, as no germination was observed in the control; no salt solution improved germination in this case. Maximum (40%) germination was recorded with 100 mg l^{-1} Na_2SO_4. Seeds of *Z. simplex* possessed extreme dormancy, because no germination was observed control. However, Mohammed and Sen (1992a) observed that one-year-old seeds of *Z. simplex* showed 50% germination when pretreated with gibberellic acid (GA_3) for 48 h. Khan and Ungar (1997a) reported that growth regulator treatments increased germination to over 80% in non-saline conditions in *Z. simplex*.

After 10 days of salt treatments, ungerminated seeds from the 10,000 mg l^{-1} concentration of the five salt solutions were transferred individually to distilled water. Mohammed and Sen (1990a) discovered that germination inhibition in saline media is due to osmotic stress or specific ion toxicity, because the germination percentage increased when seeds were transferred from salt solution to distilled water (Table 14.1). Variations in temperature appear to play an important role in the recovery of germination of halophytes from salt stress when seeds are

Table 14.1 Additional mean germination percentage of some halophytes observed after transfer of ungerminated seeds from 10,000 mg l^{-1} concentration of each salt solution to distilled water after 10 days (after Mohammed and Sen 1990a, 1991)

Species	Salt solutions					
	Site	NaCl	Na_2SO_4	$MgSO_4$	$CaCl_2$	KCl
Salsola baryosma	I	36	16	23	10	40
	III	53	13	23	20	40
Sesuvium sesuvioides	I	20	10	20	70	40
	II	10	13	16	20	50
	III	13	16	10	30	10
	IV	16	20	13	60	10
Suaeda fruticosa	I	36	26	16	20	20
	II	40	26	30	16	26
	III	40	30	10	30	26
Trianthema triquetra	I	16	30	20	13	30
	II	10	10	13	10	10
	III	13	13	10	10	10

transferred to distilled water (Khan and Ungar 1997b). Therefore, Mohammed and Sen (1990a) proved that higher concentrations of salts retarded germination because of osmotic effects, as the process of seed germination speeded up after their transfer to non-saline medium. This may be of significance under natural conditions, especially for inland desert salines, because seeds that could not germinate under extreme salinity stress may have evolved a mechanism to germinate rapidly when the salt stress is relieved. Although NaCl is the major salt in most salt-affected soils, other salts also present in the soil play a combined role in the salt tolerance of a species at the time of germination.

A significant characteristic of halophyte seeds, which distinguishes them from glycophytes, is their ability to maintain seed viability for extended periods of time during exposure to hypersaline conditions and then to initiate germination when the salinity stress is reduced (Chapman 1974; Ungar 1982). The enforced dormancy response of halophyte seeds to saline conditions is of selective advantage to plants growing in highly saline habitats. These seeds can withstand high salinity stress and provide a viable seed bank for recruitment of new individuals. However, seed germination is limited to periods when soil salinity levels are within the species tolerance limits (Ungar 1982).

Rajpurohit and Sen (1977) concluded that, under field conditions, the highest germination percentage in *C. cretica*, *S. fruticosa*, *S. baryosma*, *S. sesuvioides*, and *T. triquetra* can be achieved after rain that is heavy enough to leach out the salt from the close environment of the seeds. Several authors have shown that the increase in salinity leads to dormancy of seeds in halophytes and glycophytes (Rajpurohit and Sen 1977; Jhamb 1984; Mohammed 1988; Mohammed and Sen 1990a; Ungar 1995). Germination was inhibited or severely reduced at salinity levels above 250 mM NaCl level in *Atriplex lentiformis* (Malcolm et al. 2003). Huang et al. (2003) reported that germination of *Haloxylon ammodendron* seeds decreased with salinity, and was substantially inhibited at 1.2 mol l^{-1} NaCl; however, maximum values were seen in the non-saline control. Mohammed and Sen (1990a) thus observed that inhibition of germination of saline plants is due to both osmotic and ionic factors.

14.4 Proline Accumulation under Salt Stress

The phenomenon of free proline accumulation in plants exposed to diverse environmental stresses has considerable ecophysiological significance. Water stress produces numerous metabolic irregularities in plants (Levitt 1980). The increased proline concentration in water-stressed plants is due either to the inhibition of protein oxidation or to the breakdown of precursor proteins (Barnetts and Naylor 1966). Heidari-Sharifabad and Mirzaie-Nodoushan (2006) documented that proline accumulation is a good indicator of salinity stress. A significant increase in proline was observed under NaCl salinity stress in *Sorghum* spp. (Thakur and Sharma 2005).

Mohammed and Sen (1987) examined 65 plant species in the Indian desert for proline content; of these, 54 showed the presence of proline. Furthermore, they concluded that some of well-adapted desert plants do not accumulate proline at all. Mohammed and Sen (1990b) and Sen and Mohammed (1992) observed that proline accumulation in desert plants is not governed by the environment but rather by some innate factors.

Data on the presence of proline accumulation in the leaves of halophytes in the Indian desert revealed that plants growing in saline areas accumulated maximum proline during winter, followed by summer, with a minimum in the rainy season (Table 14.2). All plant species at site-I (Pachpadra salt basin) accumulated more proline compared to those at sites-II (Didwana salt lake) and -III (Jodhpur non-saline), which may be due to the high salinity of this former habitat. Since site-I is more saline than the latter two, it can be hypothesised that salt stress caused more accumulation of proline. Perhaps free proline content play an essential role in plant survival.

Table 14.2 Seasonal variations in proline (μg g^{-1} fresh weight) content in some halophytes growing at sites I–III (after Sen et al. 2002). R Rainy, W winter, S summer

Species	Pachpadra (site-I)			Didwana (site-II)			Jodhpur (site-III)		
	R	W	S	R	W	S	R	W	S
Aeluropus lagopoides	6.2	26.6	–[a]	24.6	–	–	–	–	–
Cressa cretica	0.5	108.0	3.8	4.8	–	–	–	–	–
Salsola baryosma	0.1	7.1	5.7	4.3	–	–	0.1	7.0	2.7
Sesuvium sesuvioides	2.0	–	–	4.3	–	–	1.8	–	–
Sporobolus helvolus	5.3	100.0	7.9	6.1	8.7	6.2	–	–	–
Suaeda fruticosa	1.4	11.9	7.0	2.7	9.9	6.6	1.9	5.8	5.0
Trianthema triquetra	3.4	74.7	–	3.7	14.3	–	5.2	15.6	8.2
Zygophyllum simplex	5.7	109.9	–	–	–	–	–	–	–

[a]Plant not seen

14.5 Soil–Plant Analyses

All desert plants and most saline plants of the Indian arid zone are totally dependent upon the availability of water in the rainy season; water controls seed germination, seedling growth, and plant survival. Rainfall leaches salts down the soil profile as far as the groundwater, with a compensating upward movement as a result of capillary action (Jackson et al. 1956). Decreases in soil moisture and the intensity of evaporation lead to increases in soil salinity.

Ion analyses of the soils of saline and non-saline areas of the Indian arid zone revealed that Na^+ and Ca^{2+} were among the major cations, and Cl^- among anions at site-I; while at sites-II and -III, Na^+ and K^+ were found as the major cations, and Cl^- among the anions. All ions in soils, such as Na^+, K^+, Ca^{2+} and Cl^-, were maximum at site-I, followed by site-II, and minimum at site-III (Table 14.3). Seasonal variations in the salt content of the soil depend on soil moisture, depth of groundwater, soil texture, habitat vegetation, the occurrence of a downward flow of water due to rainfall, flow of groundwater towards the surface in dry periods, and loss of moisture to the atmosphere (Waisel 1972; Rajpurohit and Sen 1979). Jackson et al. (1956) described the seasonal downward and upward movements of salts in the soil profile. A considerable seasonal variation in soil salinity was also observed. Higher salinity levels in the dry period have been observed as a result of the evaporative mechanism (Sharma and Tongway 1973).

Halophytes absorb salts continuously from their surrounding medium. *S. baryosma*, *S. sesuvioides*, *S. fruticosa*, *T. triquetra*, and *Z. simplex* continue to accumulate salt in their tissues. *A. lagopoides*, *C. cretica*, and *S. helvolus* secrete excess salt through the entire shoot. Fine streaks of white salt are seen on the stem and leaves throughout. On the basis of ion analyses, Na^+ and K^+ were among the major cations and Cl^- among the anions absorbed in large quantities by these halophytes (Table 14.4). Considering the habit as well as the Cl^- content of individual halophytes, it is concluded that: (1) the amount of Cl^- absorbed by the leaves of *Z. simplex* (11–18%) and *S. fruticosa* (13–19%) was nearly equal, and much higher as compared with other species; (2) the internal Cl^- content of ion-accumulating species was higher as compared to ion-secreting grass species (*A. lagopoides* and *S. helvolus*); and (3) among ion-accumulating species, *S. baryosma* (6–11%), *S. sesuvioides* (3–7%), and *T. triquetra* (3–8%) accumulated much less Cl^-. Since Cl^- is the dominant ion present in the medium at both saline sites, it can be

Table 14.3 Range of ionic contents in soil at sites I–III (after Sen and Mohammed 1994)

Site	Depth (cm)	Ion (mg 100 g^{-1} dry soil)			
		Na^+	K^+	Ca^{++}	Cl^-
I	0–5	187–4,125	39–71	93–262	0.4–4
	20–25	269–1,812	16–33	14–166	0.4–0.9
II	0–5	55–1,280	2–35	0.6–6	0.04–0.06
	20–25	105–603	15–62	0.7–3	0.1–1.2
III	0–5	41–219	2–87	0.7–5	0.03–0.1
	20–25	35–176	2–76	0.7–19	0.03–0.1

Table 14.4 Range of ionic content (mg g^{-1}) accumulated by leaves of some halophytes growing at sites I–III (after Sen and Mohammed 1994)

Species	I				II				III			
	Na^+	K^+	Ca^{++}	Cl^-	Na^+	K^+	Ca^{++}	Cl^-	Na^+	K^+	Ca^{++}	Cl^-
Aeluropus lagopoides	55–100	5–14	1–22	5.8–6.3	10	7	10	4	–[a]	–	–	–
Cressa cretica	20–110	1–31	3–30	4–10	42–49	9–14	19–21	4–8	–	–	–	–
Salsola baryosma	44–291	27–78	4–43	6–11	–	–	–	–	37–241	8–49	2–50	1.4–2.9
Sesuvium sesuvioides	16–100	14–36	5–37	3–7	47–98	9–40	11–50	2–4	72–106	9–21	2–20	2–3
Sporobolus helvolus	7–70	4–37	1–89	3–5	22–28	4–12	5–7	1–4	–	–	–	–
Suaeda fruticosa	43–313	10–45	3–55	13–19	45–119	7–63	5–26	7–21	48–315	8–20	1–37	7–15
Trianthema triquetra	29–115	3–33	2–28	3–8	27–112	7–34	3–87	1–11	22–225	9–24	1–30	1.9–2.2
Zygophyllum simplex	42–105	8–15	5–52	11–18	–	–	–	–	–	–	–	–

[a]Plant not seen

concluded that *S. fruticosa*, *T. triquetra*, *S. baryosma*, *C. cretica*, and *Z. simplex* are well suited to these habitats, and thus they are the most salt tolerant species (Mohammed and Sen 1992b, c).

Ion uptake by plants was dependent largely upon their availability in the soil. When ion concentrations fluctuated in the soil by upward or downward movements, their uptake by plants was also affected. Like soil salinity, higher amounts of elements were observed in plants during dry periods in the Indian arid zone.

14.6 Metabolic Behaviour

Salinity is known to affect almost all aspects of plant metabolism. The leaves of plants subjected to water stress often show a decrease in starch, which is usually followed by an increase in sugar content (Levitt 1980; Mohammed 1988; Mohammed and Sen 1992b, c). Plant species from site-II (Didwana), which is less saline as compared to site-I (Pachpadra), showed maximum sugar content during the summer season, when plant-water stress was higher than in winter or in the rainy seasons. Plant species at site-I, which is extremely saline, exhibited higher sugar content during the rainy season, followed by winter, with lowest values in summer (Table 14.5). These observations of varying sugar content may be due to higher salinities at particular sites. Heidari-Sharifabad and Mirzaie-Nodoushan (2006) reported that soluble sugars increased as a result of salinity, which may act as an osmotic adjustment or osmotic conservation factor in *Salsola* species. They further stated that accumulation of soluble sugars acts as an osmotic adjustment factor to maintain turgor, or is related to stabilising cell membranes and proteins and also may be due to further transformation of starch to sugars or a lower consumption of carbohydrates by the tissues.

Metabolism of halophytes is affected by a general increase in salinity as well as by the types of ions present. Salt-tolerant species are able to withstand the

Table 14.5 Seasonal variations in total sugars (mg g^{-1}; dry weight) and crude protein (%; dry weight) contents in some halophytes growing at sites-I and -III (source: Sen and Mohammed 1994). R Rainy, W winter, S summer

Species	Total sugars						Crude protein					
	Site-I			Site-III			Site-I			Site-III		
	R	W	S	R	W	S	R	W	S	R	W	S
Aeluropus lagopoides	34	–[a]	–	–	–	–	12	–	–	–	–	–
Cressa cretica	39	11	17	–	–	–	21	19	17	–	–	–
Salsola baryosma	33	16	18	5	10	18	20	16	15	36	16	22
Sesuvium sesuvioides	22	9	–	16	17	–	20	16	–	19	9	–
Sporobolus helvolus	29	8	14	–	–	–	18	12	8	–	–	–
Suaeda fruticosa	39	35	18	5	14	25	29	25	19	28	25	17
Trianthema triquetra	10	4	–	5	15	19	19	17	–	21	15	12
Zygophyllum simplex	18	25	–	–	–	–	18	17	–	–	–	–

[a]Plant not seen

metabolic disturbances that occur as a result of high salt content. Such changes in ionic content and ionic composition of plant cells induce changes in the activity of certain metabolic systems. The nutritive pattern of plants is very important when fodder values and productivity are taken into consideration. Protein is the most important constituent of cells from both structural and functional points of view. Under conditions of extreme salinity, proteins are precipitated. The protein content of various plant tissues declined under drought or saline conditions because of increased proteolysis and decreased protein synthesis (Waisel 1972). Doddema et al. (1986) observed that soluble protein decreased under saline conditions, being maximal in the rainy season when salinity was less in *Arthrocnemum fruticosum*. The protein content in saline plants at both saline and non-saline sites was maximum during the rainy season, when plant-water status was higher than in winter or summer seasons (Table 14.5).

14.7 Conclusions

It is generally observed that an excess of salts in the soil inhibits plant growth. Halophytes survive under conditions of high salinity, exhibit succulence, and can resort to other physiological adaptations to overcome the adverse saline environment in the soil. The ionic and toxic effects of various salts, especially those of NaCl, play a major role in halophytism. Most halophytes avoid salinity, some evade it, and a few others tolerate it. The accumulation of proline in plants is correlated with the extent of the water stress in the plant. In halophytes, a positive correlation is seen between proline content and the amount of Na^+ and Cl^- in the cell sap. Salt stress induces accumulation of more proline in halophytes, and perhaps plays an essential role in their survival. Ion uptake by plants is dependent largely upon their availability in the soil. Higher levels of minerals in halophytes have been observed during dry periods. Although NaCl is the major salt present in most salt-affected soils, other salts, such as $MgCl_2$, $MgSO_4$, Na_2SO_4, etc., are also present, which play a combined role in the salt tolerance of a species at the time of seed germination. The maximum seed germination in halophytes has been reported during the rainy season due to leaching of salts in deeper soil layers through rainfall. Due to leaching action, there is a decrease in soil salinity. Salinity also affects almost all aspects of plant metabolism. Maximum values of carbohydrate and crude protein in halophytes have been observed during rainy seasons, when plant-water status is higher than in winter or summer seasons.

Most halophytic species investigated so far seem to prefer saline conditions. Salinity plays an important role in the existence and distribution of plants because plant species respond differently to soil salinity. Plant species growing in an area may provide useful information regarding the degree of salinisation and consequent soil deterioration. Such information may be helpful in the more effective planning of practical reclamation of saline wastelands.

Acknowledgements The authors express their gratitude to their esteemed teacher Professor Dr. David N. Sen, a pioneer worker in the Indian desert since 1963, for his help in the preparation and editing of the manuscript. A number of research scholars, namely, Dr. K.S. Rajpurohit, Dr. (Mrs.) R.B. Jhamb, Dr. T.P. Sharma, Dr. (Mrs.) Pramila Rajput, Dr. T.P. Thomas, among others, have worked on the biology of saline plants in our laboratory, and their studies have been profusely included in this chapter. We are also highly thankful to the Professor and Head of the Department of Botany, J.N.V. University, Jodhpur for providing the necessary facilities.

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