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Adaptation of Halophytes to Different Habitats

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Abstract

In recent years, global climate change has been altering environmental (severe drought, soil salinization, irregular precipitation, etc.), around world, decreasing crop yield and upsetting the balance of ecosystems. Nonetheless, a group of plants known as halophytes have the ability to survive and develop in saline soils (wetlands, deserts or temperate zones), may be used in agriculture as a possible alternative to crops (salt-sensitive), as well as for fodder, energy production, medicinal purposes, and desalination of salt-affected areas (phytoremediation). This chapter provides a comprehensive summary of the adaptive strategies used by the annual and perennial halophytes on ecophysiological perspectives, to survive in diverse habitats. The results show a great diverse strategies, such as heteromorphism, seed banks, dormancy, rapid germination, and recovery capacity, from saline shock, favoring the chances of seed survival, although these mechanisms depend on light, moisture, temperature, and the type of salt, in which seeds germinate. In addition, it has been included some molecular, and biochemical aspects, discovered in last years, that might improve our understanding of physiology of these plants. It can conclude that halophytes may be as a possible alternative to ease pressure on cropping systems, restored lands degraded, or confer stress tolerance trough gene transfer.

Keywords: abiotic stress, adaptive strategies, euhalophytes, extremophiles, xerohalophytes

1. Introduction

Soil salinity, a major abiotic stress affecting growth and plant productivity worldwide, constitutes one of the main topics of study in the field of biochemistry, and plant physiology [1, 2]. Salinity exerts various negative effects on germination, as well as on plant growth and development, including water deficit accompanied by reductions in photosynthetic activity, nutritional imbalance, ion toxicity, induction and modulation of plant hormones, and many metabolic changes leading to molecular damage due the production of reactive oxygen species (ROS) [3, 4]. Halophytes are plants that have the availability of survive in saline environment. They account for 1–2% flora of the world, and included both dicots and monocots [5]. Depending of their tolerance and demand for salts, halophytes can be distinguished as obligate and facultative halophytes. Obligate halophytes need salt for growth and development, whereas facultative halophytes can thrive also under strict freshwater conditions and in non-saline habitats, meanwhile that glycophytes (salt-sensitive) include most agricultural crops (**Table 1**) [6]. According to the environmental conditions in which they grow, halophytes are further divided into

Types	Features	Examples
Obligate Halophytes	Growth in saline habitats and stimulating the growth with salt (≥ 200 mM NaCl)	<i>Arthrocnemum</i> sp. <i>Frankenia</i> sp. <i>Kochia</i> sp. <i>Prosopis</i> sp.
Facultative Halophytes	Growth with moderate salt concentration but their optimum lies in a salt-free or at least low-salt conditions (≤ 200 mM NaCl)	<i>Aster tripolium</i> <i>Atriplex</i> sp. <i>Plantago</i> sp. <i>Chenopodium quinoa</i>
Habitat-indifferent	Growth preferently on salt-free soils, but in salt soils has a better growth compared to glycophytes	<i>Salsola</i> sp. <i>Festuca rubra</i> <i>Agrostis stolonifera</i> <i>Juncus bufonius</i>
Glycophytes	Salt-sensitive plants (< 100 mM NaCl)	Most Agricultural crops

Table 1.
Classification of plants according to salinity tolerance.

hydro-halophytes and xerohalophytes. Hydro-halophytes need aquatic conditions, or wet soil (mangroves and salt-marsh species inland or along coastlines). Xerohalophytes survive in dry habitats with saline soils (i.e., arid, semi-arid inland with unpredictable rainfall) and are considered extremophiles when halophytes germinate and reproduce under high-salinity conditions (≥ 500 mM NaCl) [7, 8]. On the other hand, it bears emphasizing the widespread use currently made of halophytes as alternatives to glycophytic crops, forages and animal feeds, oilseeds and protein crops, energy crops (biofuels and fuelwood), phytoremediation, medicinal plants and other commercial products [9].

In the course of evolution, halophytes (ephemeral, shrubs, and trees) have developed different mechanisms for regulating growth, development, to ensure their survival in high-salt environments (inland or coastal areas, salt marshes, dunes, and deserts) [7, 10, 11]. Halophytes need anatomical and morphological adaptations such as salt glands, salt bladders (for selective exclusion or accumulation of ions), or development of succulence (dilution of ion concentration) in the plant tissue. Adaptations at the physiological level include: the control of ion uptake, especially Na^+ , Cl^- , and K^+ by roots and transport to leaves, this maintaining the osmotic balance; the compartmentalization of ions between vacuoles, cytosol, and apoplast through H^+ -pump (vacuolar, and plasma membrane); biosynthesis of compatible solutes, and osmoprotectors, (proline, glycine-betaine, sugar, and polyols); the control of stomatal opening and closing; efficiency of the photosynthetic pathway; the synthesis and activation of antioxidant enzymes; the generation of nitric oxide; and the induction and modulation of plant hormones [3, 5].

The adaptations mentioned above, are completed with effective strategies that allow seed germination in different habitats. Most halophytic species belong to the families Amaranthaceae and Poaceae (Table 2). Strategies such as seed banks, heteromorphism (based on seed size, weight, and time of production), dormancy, rapid germination, and capacity of recovery of germination from exposure to saline shock, provide seeds multiple opportunities to ensure the continuity of a population, and a plasticity that also provides ecological diversity [7]. It is also important to highlights the role of the seed coat, and endogenous hormones in controlling dormancy and germination [12]. Specifically, salt tolerance is also influenced by genetics and the developmental stage. Germination and flowering are sensitive stages that may be altered by an osmotic effect and/or ion toxicity. Finally, the response of the plant also depends on the type of salt, found in the soil, where the seeds germinate (e.g., NaCl, NaHCO_3 , and Na_2SO_4 , etc.) [13, 14]. In several species of Amaranthaceae

Family	Species
Amaranthaceae (formerly Chenopodiaceae)	<i>Allenrolfea occidentalis</i> , <i>Arthrocnemum macrostachyum</i> , <i>Atriplex</i> sp., <i>Suaeda</i> sp., <i>Salsola</i> sp., <i>Salicornia</i> , <i>Haloxylon</i> sp., <i>Kalidium</i> sp., <i>Kochia</i> sp.
Poaceae	<i>Aeluropus</i> sp., <i>Desmostachya</i> sp., <i>Halopyrum</i> sp., <i>Sporobolus</i> sp., <i>Urochondra</i> sp., <i>Hordeum</i> <i>jubatum</i> , <i>Spartina alterniflora</i> ,
Leguminosae (Fabaceae)	<i>Arachis glabrata</i> , <i>Desmodium</i> sp., <i>Lathyrus</i> sp. <i>Stylosanthes</i> sp., <i>Trifolium</i> sp., <i>Prosopis</i> sp.
Asteraceae (Compositae)	<i>Iva annua</i> , <i>Lasthenia glabrata</i> , <i>Cotula cornopifolia</i> ,
Plumbaginaceae	<i>Limonium</i> sp.
Aizoaceae	<i>Mesembryanthemum</i> <i>crystallinum</i>
Tamaricaceae	<i>Tamarix</i> sp.
Malvaceae	<i>Kosteletzkya pentacarpos</i>
Arecaceae	<i>Nypa fruticans</i>
Solanaceae	<i>Solanum chilense</i>
Rhizophoraceae	<i>Rhizophora mangle</i>

Table 2.
Families which present halophytic species.

(formerly Chenopodiaceae), some species show salt-tolerance, while others use a salt-avoidance strategy at germinative level. Typical salt-tolerance is reflected by high germination percentages and/or germination rates under high salinity (e.g., *Haloxylon ammodendron*, *Suaeda physophora*, *Anabasis salsa*, *Suaeda salsa*), while a high percentage of recovery germination after the alleviation of salinity reflects a salt-avoidance strategy (e.g., *Borshchovia aralocaspica*, *Ceratoides latens*, *Bassia dasyphylla*). Other seeds can present both salt-tolerance and salt-avoidance characteristics, or one or the other depending on the type of salt [15].

More information on halophytic species, is available at eHALOPH (<http://www.sussex.ac.uk/affiliates/halophytes/>), a database of halophytes plants offering data on plant type, life form, ecotypes, maximum salinity tolerance, the presence or absence of salt glands, photosynthetic pathway, antioxidant, secondary metabolites, compatible solutes, habitat, and economic use. This database can serve in the selection of halophytes with applications in phytoremediation, ecological restoration, rehabilitation of degraded ecosystems, and biosaline agriculture [16].

Lastly, as it is unfeasible here to survey the large number of articles on dormancy and germination in halophytes published to date, this chapter summarizes only recent key studies on the mechanisms that halophytes use to germinate in the different habitats around of the world. A section on molecular aspects of some halophyte seeds has also been included.

2. Seed heteromorphism

The most detailed studies on heteromorphism, seed banks, and dormancy have been studied in halophytic species from Amaranthaceae family located between Mongolia and China. Most halophytes present dimorphic and heteromorphic species, many annuals and few perennials (Table 3), as an important strategy of

Species	Type of seeds	Habitat
<i>Atriplex</i> spp.	*Brown, Black *Large, small	Desert, Saline soil Inland and coastal marshes
<i>Chenopodium album</i>	*Brown (larger) *Black (smaller)	Light-saline soil
<i>Suaeda</i> spp.	*Brown (larger) *Black (smaller)	Saline soil Salt marshes Salinized desert
<i>Salicornia</i> spp.	*Larger *Small	Inland, saline soil Coastal marshes
<i>Salsola</i> spp.	*Larger with or without winged perianth (WP) *Medium with or without WP *Small with or without WP	Coastal regions Desert Saline soil Cold desert

Table 3.
Heteromorphic seeds species of halophytes under saline conditions.

adapting to habitat variability [17, 18]. One of the most widely studied halophyte species, for its multiple economic and ecological uses (food, forage, bioenergy, medicine, and restoration of salinized or contaminated land) is *Suaeda salsa* L. (Fam. Amaranthaceae). The production of dimorphic seeds helps make the plant more competitive and tolerant to a changeable environment [19, 20]. Some seeds are brown (soft outer seed coat), while other seeds are black (hard and smooth outer seed coat), being able growth in different habitats (i.e., saline inland and intertidal zones) in the Yellow River Delta area (Shandong, China) [19]. Ecophysiological studies have shown that brown seeds absorb water more quickly, and have a higher germination rate than do black seeds, whereas the latter are more sensitive in the absence of light (and remain dormant in light) under high saline concentrations. Black seeds have a lower germination percentage, while brown seeds can germinate under salinity concentrations of up to 600 mM NaCl, regardless of light [20, 21]. In addition, in this last seed was discovered a control of compartmentalization of ions (an accumulation of ions in pericarps cultured with 400 mM NaCl, and a lower amount in embryos), accompanied by rapid germination. This ionic compartmentalization could explain the tolerance of these plants to higher salt concentrations in the intertidal soil and avoid Cl^- and Na^+ toxicity in embryos, during seed development. Also, bracts and the seed coat contribute to ion compartmentalization and prevent excessive accumulation in embryos. On the other hand, brown seeds prove heavier in the intertidal zone (more germination), having a genetic trait that enables tolerance of highly saline environments. Therefore, the production of heteromorphic seeds and different germination characteristics can help mother plants adapt to a fluctuating environment [12].

A more in-depth study has been conducted in the Asian species *Suaeda aralocaspica* (an annual halophyte from the desert) with dimorphic seeds, and C4 photosynthesis pathway [this plant contains two enzymes for the carbon fixation (PEPCK, phosphoenol-pyruvate-carboxylase), and (Rubisco, Ribulose-5-phosphate carboxylase), which provides plants greater efficiency in the carboxylation during the few hours of stomatal opening, due to the high temperatures in the climate zones where this plant lives] [22]. In this species, gene expression has been studied in seeds collected from saline-alkaline sandy soils in the southern margin of Junggar Basin in North China. A series of physiological and biochemical events could take place earlier in the germination of the brown seed as compared to the black seed. A large proportion of genes changed significantly at 3 h in brown seed, as opposed to 8 h in black,

after imbibition; it was observed transcriptional changes greater in brown than black seed. However, the different characteristics shown in germination between dimorphic seeds of *S. aralocaspica* are not transferred to the descendants and soon disappear in later seedlings stages, presenting no significant difference in growth, and physiological response, in the descendants with or without salinity [23, 24].

2.1 Seed size

Physiological studies have shown that larger seed size, compared with small, improves the germination percentage under saline conditions [25], and that stress conditions may provide signals, to mother plants, to produce diverse phenotypic plasticity in different environments [12]. Also, brown seeds reportedly exhibit higher amounts of phytohormones: ABA (abscisic acid), IAA (indole-3-acetic acid), and ZR (zeatin-riboside) than black seeds. ABA prompts the accumulation of numerous storage proteins, which contribute in increasing the embryo size and weight in brown seeds under salt stress [26]. On the other hand, the phosphatidylglycerol (PG), a glycerophospholipid, improves salt tolerance in seeds by boosting the production of unsaturated fatty acids (allowing greater membrane fluidity). The overexpressed of the *SsGPAT* gene in *Arabidopsis* produced high contents of unsaturated fatty acid and significant salinity tolerance [27]. In young seedlings, that germinated from brown seeds of *S. salsa* as well as from the *Thellungiella halophila* (extremophile that can tolerate saline concentrations up to 700 mM NaCl), PG contents were higher and therefore were related to salt tolerance [28, 29].

2.2 Inorganic ions and organic osmolytes

Inorganic ions facilitate seed germination by improving imbibition (by decreasing seeds water potential), prior to radicle emergence. Xu et al. found that the content in Na^+ , K^+ , Cl^- , and Ca^{2+} were higher in brown seed compared to black, as well as a higher activity of relative transporters in brown seeds [e.g., vacuolar Na^+/H^+ antiporter (NHX), potassium transporter (HAK), chloride channel protein (CLC), $\text{Ca}^{2+}/\text{H}^+$ antiporter, and tonoplast (CAX)], which could explain the better germination rate. These mechanisms are involved in maintaining ionic homeostasis and improve water uptake for seeds during germination under salt stress [30].

Halophytes produce or accumulate more organic osmolytes (proline, betaine, soluble sugar, and polyols) and protein in their large seeds as compared with small seeds to ensure optimum germination under salt stress [31]. These osmolytes can help in osmotic adjustment, can serve as membrane protectors, may aid in ROS detoxification or may act as signaling compounds that trigger other stress-alleviation mechanisms [32]. An osmolyte frequently found in halophytes is betaine. An expression analysis of betaine aldehyde dehydrogenase gene (*SsBADH*) in *S. salsa* showed that brown seeds have higher expression of this gene, and exhibit better germination compared with black seeds. Also, larger brown seeds register a greater increase in sugar facilitating a rapid germination [30].

2.3 Seed coat

Dormant seeds have a hard layer that preserves dormancy until a part of the layer breaks and becomes permeable to water, beginning the process of imbibition. The permeability of the layer in the dimorphic seeds is related to the thickness of the seed layer, which is usually lower in non-latent (tolerant) seeds compared to latent (sensitive) ones. In seeds of *Suaeda physophora*, seed coat play an important role in inhibiting Na^+ influx into and K^+ efflux from the embryo to protect the seed from

ion toxicity [33]. In the black seeds of *S. salsa*, a significant accumulation of waxes was detected in the seed coat, in comparison with the brown seeds coat, suggesting that waxes help protect the embryo from ionic toxicity [34]. The waxy substances in the black seeds inhibit water absorption and at the same time maintain the viability of the seeds for longer than in the brown seeds in high-salinity environments [34]. Suberin is one of the major lipids in the seed coat that plays a primitive role in the germination of the seed. Beisson et al. has reported that seed coatings of *Arabidopsis* suberin mutants *jpat5* (Glycerol-3-phosphate acyltransferase 5) sharply increase in the suberin accumulation in response to the tetrazolium salt, compared to the wild-type seed coat, reflecting poor seed germination under salt stress [35].

3. Seed banks

In many plants, seeds banks ensure the persistence of populations and contribute to future genetic variability of the species [36, 37]. The studies by Cao et al. in the halophyte *Suaeda corniculata* subsp. *mongolica*, seek to explain the importance of “dormancy” and “seed bank” for the maintenance and regeneration of populations. This plant, an annual herb with succulent leaves, grows in the cold desert of Inner Mongolia and other parts northern China [38, 39]. Seed-bank dynamics, including dormancy cycling of dimorphic seeds, has been studied in detail. The results indicate that black seeds had an annual dormancy/non-dormancy cycle, while brown seeds, remained non-dormant (**Table 4**). Black seeds also exhibited an annual cycle in the sensitivity of germination to salinity. Seedlings that germinated from black seeds emerged in July and August (mid-summer) and those from brown seeds in May (spring). Seedlings were recruited from 2.6% of the black seeds and from 2.8% of the brown seeds in the soil, and only 0.5 and 0.4% of the total number of black and brown seeds in the soil, respectively, gave rise to seedlings that survived to produce seeds. Salinity (NaCl) and water stress induced by polyethylene glycol (PEG) induced dormancy in black seeds and decreased viability of brown seeds. Brown seeds formed only a transient soil-seed bank while black seeds gave rise to a persistent seed bank. Brown seeds germinated under a wider range of

Station	Black seeds	Brown seeds
Winter: low temperature	Non Dormancy (ND)	ND
Spring: low temperature low precipitation moderate salinity	ND	ND and Germination
Early summer: high temperature high salinity	Conditional dormancy (CD)	Die (85 %)
Mid-summer Late-summer: high temperature high precipitation low salinity	Germination Dormancy	
Autumn: low temperature	CD	
Dormancy cycling	CD →ND →CD→D→CD Persistent soil seed bank	Transient soil seed bank

Table 4.
Changes of dormancy status of black and brown seeds of Suaeda corniculata, soil seed-bank dynamics, and seedling regeneration of the population.

temperatures and salinities than did the black seeds. Early germination gives plants a selective advantage, since they are less prone to predator and pathogen attack than are late-germinating seeds; they have an early advantage to take up resources, grow much larger, and thus tend to produce more seeds. Germination of black seeds is regulated by an annual dormancy cycle, and these seeds have stricter germination requirements than do brown seeds. That is, black seeds do not germinate in naturally saline habits until soil salinity is decreased by precipitation, and emerge in the summer rainy season. Therefore, the presence of a dormancy cycle in black seeds, but not in brown, and differences in germination requirements of the two dimorphic seeds, cause them to differ in their germination dynamics, ensuring seed availability over a wide range of time [39].

4. Seed dormancy

Dormancy constitutes another defense strategy to govern germination pattern and timing in different habitats, enabling adaptation to environmental changes [40]. The production of dormant seeds (small) remains in soil until the salt concentration becomes conducive to germination. In this scenario, large seeds germinate faster and are more tolerant to salt [41]. In addition, the endogenous content of hormones, ABA (abscisic acid) and gibberellins (gibberellic acid) are keys in this process. These phytohormones regulate dormancy, due their antagonistic functions, GA stimulating and ABA inhibiting this state [42]. However, the endogenous nature of these hormones is not plant species specific [12]. Low germination may be related to higher ABA sensitivity rather than the difference in ABA content among dimorphic seeds in *S. salsa* [43]. Other hormones, such as ethylene, may promote seed germination through the antagonism of ABA signaling, and brassinosteroids may also interact with other hormones to influence seed dormancy by reducing ABA sensitivity and thereby increasing germination [30].

Although it is easier to study annual species with a shorter life cycle, woody species have also been investigated. The first report of a seed-dormancy cycle in a cold-desert shrub is in the halophyte *Kalidium gracile*, a small shrub about 20–50 cm high that grows on alkaline plains and saline lakeshores in northwestern China and Mongolia [44]. Cao et al. have hypothesized that *K. gracile* has a seed bank and dormancy cycling that help restrict germination to a time favorable for seedling survival. Seeds of *K. gracile* were found to have a soil seed bank of 7030 seeds m⁻² at the beginning of the growing season. About 72% of the seeds were depleted from the soil seed bank during one growing season, and only 1.4% of the seeds gave rise to seedlings that germinated early enough to reach a growth stage at which they could survive the winter. About 28% of the seeds became part of a persistent soil seed bank. Buried seeds exhibited an annual non-dormancy/conditional dormancy (ND/CD) cycle, and germination varied in sensitivity to salinity during the cycle. Dormancy cycling is coordinated with seasonal environmental conditions in such a way that the seeds germinate in summer, when there is sufficient precipitation for seedling establishment. The strategy of *K. gracile* to ensure it survive in these adverse climate zones includes: a polycarpic perennial life cycle, a persistent seed bank, and dormancy cycling. The annual ND/CD cycle in seeds of *K. gracile* contributes to seedling establishment in the unpredictable desert environment and to the maintenance of a persistent soil seed bank [45].

Salsola ferganica (Amaranthaceae), distributed in cold-desert habitats, grows in a heavy saline-alkaline wasteland at the edge of Junggar Basin, Xinjiang (China). This halophyte represents another case of study of heteromorphic seeds, which differ in dispersal ability, dormancy, and germination characteristics. Light could

significantly promote germination of their heteromorphic seeds, while GA₃ enhances germination, suggesting that *S. ferganica* seeds have a photo-sensitive dormancy type with morphological and non-deep physiological features, light being the dominant factor. In contrast to other desert plant species, *S. ferganica* has comparatively short germinability (only 1–2 years), especially the small seeds, and this is affected by storage time, temperature, salinity, and even the environmental conditions of the maternal plant. It has been reported that both seed polymorphism and seed bank can ensure adequate seedling establishment in unpredictable habitats and consequently promote population propagation. *S. ferganica* has three types of seeds: large sized seeds (LS), middle seeds (MS), and small seed (SS), according to the size of the WP (winged perianth), which has different properties in dispersal ability and germinability. In suitable habitats, the mother plant can produce a large proportion (LP) or middle proportion (MP) of large seeds (LS), or it can produce medium seeds (MS), with a small proportion (SP) of small seeds (SS). They are photo-sensitive species, therefore LP seeds could enter in the potential seed bank, under poor light and unfavorable environments conditions; otherwise, LP seeds would immediately germinate to ensure a large amount of seedling establishment and final population reproduction, under light, and favorable environmental conditions. Therefore, heteromorphic seeds allow *S. ferganica* to gain multiple competitive advantages in unpredictable environments. The seed bank may control the best time for seed germination and seedling establishment, and reduce the risks of spatial and temporal changes of habitats for seed germination, seedling establishment, and population reproduction [46].

5. Germination under saline conditions

Germination is a critical stage in a plant's life cycle, and soil salinity may prevent or inhibit plant development due to osmotic stress and ionic toxicity [7]. As commented above strategies for acclimatization and survival of seeds to various environmental conditions include seed banks, dormancy, and heteromorphism. Nevertheless, germination is the key stage for plant establishment in different habitats [7, 15]. In this section, a number of papers are summarized with regard to the germination of halophytes in different habitats.

The facultative halophyte *Atriplex tatarica* (Amaranthaceae) is a species distributed throughout Central Asia, Asia Minor, south-western Siberia, North Africa and south-eastern Europe (deserts, salt steppes, and disturbed habitats). According to Kochánková and Mandák, seeds germinated as soon as conditions were favorable, thus ensuring short-term survival, but populations risked local extinction when conditions became adverse (i.e., a high-risk strategy). By contrast, germination of the dormant type of seeds was under stronger genetic control and proved to be significantly correlated with basic parameters of population genetics. These seeds ensure long-term reproduction and survival in the field by protracted germination, although in low quantities (i.e., *A. tatarica* also adopts a low-risk strategy), allowing a lasting seed bank over time [47].

Studies on salinity in halophytes are usually carried out with one type of salt; Sosa et al. have investigated *Prosopis strombulifera* (Lam.) Benth (a shrub halophytic), to observe the effect of different types of salt on germination applied alone or mixtures. Seed were collected in southwestern area of the Province of San Luis, Argentina, and the salts used were KCl, NaCl, Na₂SO₄, and K₂SO₄ as well as bisaline iso-osmotic solutions of NaCl + Na₂SO₄ and KCl + K₂SO₄. The germination percentage decreased as salinity increased. In monosaline solutions, SO₄²⁻ with osmotic potentials of –1.2 MPa and lower was more inhibitory than Cl⁻ at iso-osmotic

concentrations. This SO_4^{-2} toxicity was alleviated in salt mixtures and was more noticeable in higher concentrations. Meanwhile, K^+ proved more inhibition than Na^+ , independently accompanying anion. Therefore, this study demonstrates that the germination of *P. strombulifera* is strongly influenced by the nature of the ions in the salt solutions and their interactions [48].

In the case of dimorphic seeds, the obligate halophyte *Salicornia europaea* L. has been studied by Orlovsky et al., who used seeds from Central of Asia and provided evidence of high salt tolerance limits. Germination of large seeds was three-to four-fold higher than of small seeds under control and 0.5–2% of all salts tested (NaCl , $\text{Na}_2\text{SO}_4^{-2}$, $2\text{NaCl} + \text{KCl} + \text{CaCl}_2$, and $2\text{Na}_2\text{SO}_4 + \text{K}_2\text{SO}_4 + \text{MgSO}_4$). The germination and plant growth of *S. europaea* in mixed sulfate-chloride salts was distinctly higher than in pure chloride salts, suggesting a mitigating effect of Ca^{2+} and Mg^{2+} ions on the cell-ion balance, reducing the negative impact of Na^+ and Cl^- ions. Small seeds exhibited deep innate dormancy. However, the application of 0.5–2% of chloride and sulfate salts stimulated germination in these seeds, suggesting that they have a different mechanism of salt tolerance than in comparison with large seeds (different mechanism of salt tolerance). In this species, small seeds develop earlier, are more dormant, and prove less salt-tolerant than large seeds. Possibly, small seeds are evolutionarily older, large seeds in *S. europaea* evolving later, when this species habitat had become more saline as a result of species range expansion or increased salinity of the already occupied environment. In short, dimorphic seeds are more flexible in their response to varying salinity, and more adapted to salt and temperature stresses [49].

Song et al. have studied the strategies of adaptation of *Suaeda physophora* (a euhalophyte), and *Haloxylon ammodendron* (a xerohalophyte) during the seed-germination stage, when they were exposed to a range of iso-osmotic NaCl and PEG solutions. The results showed that the fresh weight of germinating seeds was markedly reduced in -2.24 MPa PEG compared with the same amount of NaCl , while the opposite trend was found in the K^+ concentration during the initial 9 h for both species. *H. ammodendron* and *S. physophora* had higher recovery germination from -3.13 MPa NaCl . These responses may produce a persistent seed bank, in saline desert habitats that will maintain the population over time, this representing an important adaptation to saline conditions in one of the driest regions of the world. Another adaptive strategy is for embryo to accumulate less Na^+ , although more Na^+ is compartmentalized in the seed coats, which might protect embryos from ion toxicity to ensure seed viability during seed development. In *S. physophora* and *H. ammodendron*, seeds have no endosperm and contain only fully spiral embryo coated by a pericarp; therefore the morphological structure may help these plants germinate as rapidly as possible and may be another adaptive strategy for two species to take advantage of transient favorable conditions during the germination stage. These authors conclude that morphological structure and adaptations to salinity during seed germination may determine the geographical distribution of these species in different saline regions [50]. Later, Zhang et al. studied the impact of salinity on seed germination, chlorophyll content, chloroplast structure and photosynthesis of the green embryos in desiccated seeds of the two species mentioned above. Seeds collected in Fukang Desert Ecological Station of the Xinjiang Institute of Ecology and Geography (China) reveal that the chlorophyll in the cotyledons of desiccated seed had a photosynthetic function in the early germination stage, even under high-salinity conditions. In addition, the photosynthesis in the embryonic cotyledons of desiccated seeds, during germination, was similar to that in the leaves of young seedlings for both halophytes. The photosynthetic function in cotyledons of mature seeds may be ecologically important for seedling development in the early stage for plants growing in extremely saline or arid environments [51].

Different germination rates have been found in two halophytes, showing different salinity tolerance, collected from various salt marshes of southern Spain. *Atriplex prostrata* Boucher ex DC (Amaranthaceae) has early and strong adaptive mechanisms that enable the plant to tolerate exposure from 0 to 200 mM NaCl and maintain a high germination capacity (**Figure 1**), whereas the salinity tolerance of *Plantago coronopus* L. (Plantaginaceae), was increased progressively with the exposure time to salt (**Figure 1**), at lower germination levels. A delay in germination and slow growth are essential for the survival of more sensitive plants in saline environments, allowing the synthesis of compounds for defense against stress; this encourages slow uptake of water from the saline solution, and thereby delayed the time of radicle emergence [52].

To evaluate the salt tolerance mechanisms of Egyptian *Pancratium maritimum* plant (a perennial endangered halophytic species native to the sand coasts to the Mediterranean Sea), Mohamed et al. studied seed germination, mobilization reserve enzymes, and antioxidant enzymes, under saline conditions (0–400 mM NaCl). The results obtained seem to indicate tolerance can come from high levels of esterase, amylase, catalase, and peroxidase activities, and the unique black, spongy, thick seed coat which may act as barrier to saline ionic. In this way, they concluded that this species is a good candidate in their conservation, being able to be used in restoration of coastal area of the Mediterranean Sea [53].

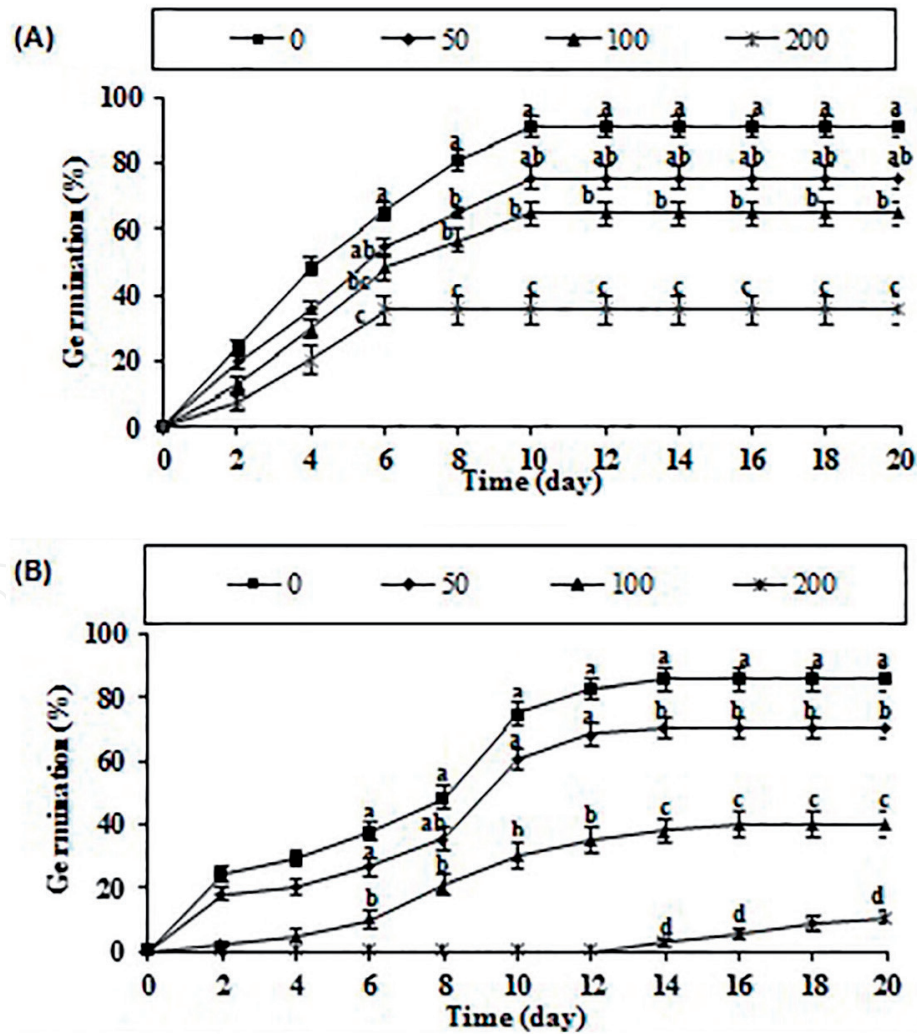


Figure 1. (A) Germination percentage of *Atriplex prostrata* seeds treated for 20 days with 0, 50, 100, and 200 mM NaCl. Values presented are mean \pm SE ($n = 6$). Different letters next to the line indicate significant differences between saline treatments (Tukey's test; $P < 0.01$). (B) Germination percentage of *Plantago coronopus* seeds treated for 20 days with 0, 50, 100, and 200 mM NaCl. Values presented are mean \pm SE ($n = 6$). Different letters next to the line indicate significant differences between saline treatments (Tukey's test; $P < 0.01$).

New technologies in study of seeds have helped reveal mechanisms of salinity tolerance in halophytes. Seeds of many coastal plants can survive exposure to seawater and may be dispersed long distances by the ocean. Guja et al. studied natural plant populations in coastal Holocene sand-dune communities near Perth, Western Australia, and collected mature seeds of *Ficinia nodosa* (Cyperaceae) and *Spyridium globulosum* (Rhamnaceae). To determine the response of seeds to external salinity during imbibition, these authors have quantified salt uptake and have resolved the spatially internal distribution of these ones. Flame photometry was used to quantify salt concentration in imbibing seeds and a new application of full-spectrum X-ray mapping enabled the visualization of the spatial distribution and relative abundance of salts. As external salinity increased in *S. globulosum* seeds (salt-sensitive) accumulated sodium and chloride in the seed embryo, while potassium was increasingly displaced and germination was reduced. Conversely, in *F. nodosa* seeds (salt tolerant) avoided ion uptake and germination was not affected by imbibition in high saline concentration (NaCl). These results provide insight into mechanisms of salt tolerance/avoidance during imbibition and early germination, and suggest that oceanic dispersal can be a viable explanation for the distribution of some plant species [54].

5.1 Ions and osmolytes accumulation in halophytes seeds

Prior to germination, the accumulation of osmolytes in seeds grown under saline conditions lowers the water potential of seeds and facilitates imbibition (uptake water from soil) and rapid germination. These osmolytes include free sugars (mannitol, pinitol), proline, betaine, starch, and ions (Na^+ , Cl^-) [14, 55]. Chlorophyll accumulation in dry and imbibed seeds and oxygen production in the embryos of some halophytes may provide energy for the germination stage. In addition, nitrates provided to seeds by maternal plants, may act as signaling molecules to enhance the germination response [20, 56, 57]. Another vital element is calcium. The beneficial effect of Ca^{2+} treatment are attributed mainly to both reducing the rate of Na^+ uptake by roots resulting from blockage of non-selective cation channels (NSCC) by millimolar Ca^{2+} concentrations, as well as to its ability to prevent NaCl^- induced K^+ leak via outward-rectifying channels [58]. Calcium also operates as a second messenger, in both SOS (salt overly sensitive), and ABA signal pathway. Salt-tolerant genotypes appear to have a larger population of Ca^{2+} -sensitive NSCC channels [8, 59].

5.2 Phytohormones in early germination

Phytohormones play a fundamental role in seed germination under saline conditions, with ABA and GA acting as key molecules in the dormancy/germination cycle. The kinetics of ABA and GA during germination in dimorphic seeds of *S. salsa* have been studied in depth. The differential regulation of ABA and GA homeostasis, by salt stress, might help of *S. salsa* plants survive adverse environmental conditions. Li et al. have concluded through morphological analysis that brown and black seeds are at different development stages. Also, ABA accumulation was found in both germinating seed types, with higher induction effect on black than brown seeds, although this gradually decreased after imbibition in water and salt solution. Black seeds showed lower germination percentages than did brown seeds under both water and salt stress, which might be attributed to their higher ABA sensitivity rather than the difference in ABA content between both seeds. Bioactive GA_4 and its biosynthetic precursor reached higher levels in brown than in black seeds, whereas deactivated GAs registered higher contents in black than

brown seeds in dry or in germinating (water or salt solutions). The effect of salt stress on GA₄ levels in black seeds was stronger than that of brown seeds. Therefore the increased ABA content and sensitivity, as well as the decreased GA₄ content by salinity were more marked in black than brown seeds, contributing to lower germination rates of black seeds exposed to salinity [43].

At the biochemical and molecular level, several genes are strongly induced by NaCl and are involved in the regulation of seed germination through ABA-GA crosstalk during salt stress [60]. A negative regulation of GA and positive biogenesis of ABA is induced by NaCl. Under saline conditions, the ABA level increases several fold due to a stronger expression of genes *ABA-INSENSITIVE 3* (ABI3) and *ABA-INSENSITIVE 5* (ABI5), which in turn activates the ABA signaling pathway, inhibiting seed germination [61]. Meanwhile, *REPRESSOR OF GA-LIKE 2* (RLG2) transcription is also activated by salinity or by the aBI3/ABI5 pathway, leading to inactivation of the GA signaling pathway, which further inhibits germination by blocking or limiting GA signaling. [8, 60]. In addition, in 22 species of halophytes, ethylene has been found to promote seed germination [62]. Therefore, in halophyte seeds, a small amount of ABA is released, more GA accumulates, and more ethylene synthesis occurs during germination [60, 62].

5.3 Light and temperature in halophytic seeds

Light and temperature, as well as water potential, are key environmental signals that can regulate the time of seed germination, which in turn controls seedling emergence and survival [63]. Agricultural crops tend to germinate in darkness, due to the domestication of species for crop production, whereas halophytic seeds growing in the wild are accustomed to germinating in the light. This is especially critical in the dimorphic seeds, where size may also be related to light. In *S. salsa*, brown seeds may germinate in spring, when soil salinity is high, while black seeds germinate in the latter summer when rainfall can bring them on the soil surface [21]. In *S. corniculata*, rainfall in late summer may bring black seeds to the soil surface, and trigger their germination [39].

Temperature also interacts with salinity and affects seed germination. For example, in *Atriplex rosea*, black seeds are more sensitive to temperature changes [64]. Seed germination in black seeds were found to diminish at lower temperatures regardless of salinity concentration, but brown seeds proved more tolerant to temperature and salinity at cooler conditions (5/15°C). It has been suggested that brown seeds may germinate early in the growing season to preempt the habitat for *A. rosea* [64]. In *Salsola ferganica*, a relatively lower daily temperature range (i.e., 5/15, 10/20, or 15/25°C) could enhance germination of heteromorphic seeds [46]. In the central Asian species *Atriplex*, the optimal temperature regime for black seed germination was 15°C, but 25°C for brown seeds. Moreover, low salinity did not influence the seed germination of black seeds under different temperature regimes (25/35°C), indicating that black seeds can germinate in the rainy summer season. These results imply that the response of dimorphic seeds to combined temperature and salinity could be a major strategy for dimorphic halophytes to survive in changeable saline environments [65].

Salsola imbricata, collected on the northeastern coast of the United Arab Emirates (UAE), is adapted to tolerate higher salinity levels during germination. Elnaggar et al. found high percentages of ready-to-germinate seeds that germinate quickly at lower and moderate temperatures with osmotic potentials of up to −0.8 MPa, indicating that seeds of this species can germinate even in years with less rain than average rainfall, if precipitation occurs early in the growing seasons. Seeds of *S. imbricata* also tolerate lower levels of osmotic potential and show fast

germination recovery, especially at lower rather than higher temperatures. These results may indicate the best conditions, especially in dry years, for sowing *S. imbricata* in the restoration of degraded desert sand dunes [66].

6. Recovery of germination

Seed germination recovery ability is a vital adaptive trait for the successful establishment and dispersal of halophytic plants in their native ecosystem. In a Mediterranean climate (warm winters, sunny days year round, and a rainy autumn), seed germination in saline environments usually occurs during spring or a season with high precipitation, when soil-salinity levels are lowered. The capacity of seed dormancy when the soil-water potentials are low, together with the recovery of the germination when the stressful conditions are alleviated, indicate ecological features crucial for the survival of these plants [67]. Pujol et al. studied the recovery of germination in four halophytes of southeastern Spain (the perennials *Halocnemum strobilaceum*, *Arthrocnemum macrostachyum*, *Sarcocornia fruticosa*, and the annual *Salicornia ramosissima*) exposed to is-osmotic stress with different salts (NaCl, MgCl₂, MgSO₄, and Na₂SO₄) and to an osmotic potential between -2.37 and -3.90 MPa. Pretreatment at low osmotic potentials stimulated the germination velocity, indicating that these species have an apparent ecological advantage since seedlings would become established rapidly before osmotic potentials decreased again. The recovery of germination was similar to that in distilled water (controls), irrespective of the salt used in pretreatment. Therefore, the factor involved in enforcing seed dormancy appears to be the decrease in osmotic potential. The germination ability of perennial species and the annual species does not differ under saline conditions. The osmotic potential of the soils that contain the natural communities promote dormancy in the seeds of the four species and, when the stress conditions are alleviated, germination recovers and the germination rate is stimulated. Although they do produce many seeds, these plants maintain a persistent seed bank [68].

A broader study has been conducted by Shen et al. on six forage species (*Bromus inermis*, *Elytrigia elongata*, *Puccinellia tenuiflora*, *Hordeum brevisubulatum*, *Kalidium gracile*, and *Suaeda salsa*). The percentage of germination in all the species, except *E. elongata*, significantly declined with rising salinity (0–445 mmol/liter NaCl). The recovery of germination and the length of radicles and shoots, in Hoagland solution, increased with higher salinity. The germination recovery of the six species indicated that germination under NaCl stress was inhibited by osmotic effects. *E. elongata* germination registered the highest NaCl tolerance among six species tested. However, *S. salsa* had low germination even in the control, but salt pretreatment stimulated it to recover germination, which might be associated with the thermoperiod effect. Shoot growth of *P. tenuiflora* had the highest tolerance to NaCl stress, this being the most widely used plant species for saline-soil rehabilitation in northern China [69].

The annual halophyte *Cakile maritima* (Brassicaceae) grows on littoral sand dunes on the semiarid and arid Mediterranean coast of Tunisia. The study of this plant also had double interest, i.e., environmental (for sand-dune fixation) and economic (as seed-oil species). High salinity inhibits and delays germination of *C. maritima* but stimulates seed vigor under recovery. The low osmotic potential generated by high external NaCl concentrations impairs cell division and prevents turgor pressure sufficient to expand and enter in the last phase germination (radicle emergence). During germination, seed-storage proteins (SSPs) are massively broken down, releasing the 20 amino acids that could be transformed into other amino

acids. S-adenosylmethionine synthetases (SAM), which are involved in the conversion of cysteine into methionine, were induced during germination, with methionine being present in storage proteins [70]. In control, and especially under salt-stress recovery, serine hydroxymethyltransferase is clearly induced, but to a lesser degree during salt stress. This enzyme converts glycine into serine, which could be further converted into cysteine, this being one of the essential building blocks of glutathione biosynthesis [71]. In short, *C. maritima* avoids germination, under high salinity, by producing quiescent seeds, which can quickly germinate and reach the seedling establishment phase under favorable conditions (when the external water potential increases, from rain). This well-developed phenotypic plasticity, during germination, was better highlighted with the help of proteomic data. The protein profile changes during the germination of *C. maritima*, when storage proteins and fatty acids are massively converted into carbohydrates, slowdown in presence of salt, but are rapidly re-induced upon favorable recovery conditions [67].

7. Certain molecular aspects of halophytes germination

Proteomic, metabolomic, and ionomics studies have been made in many halophytes, in order to understand better the mechanisms of salinity tolerance, focusing the investigation specifically in whole-plants (leaves and roots) [5]. On the other hand, the majority of molecular studies have been made on the model plants *Mesembryanthemum crystallinum* L. (Aizoaceae) and *Eutrema/Thellungiella* spp., (Brassicaceae), a halophyte related to *Arabidopsis*, focusing the study on isolation, gene overexpression, or gene introduction into plants (transgenic plants) [72–74]. However, few studies have been made on seed germination, at the molecular level. Below, a brief summary of recent findings provide a better understanding of salt tolerance of halophytes seeds.

Fukuhara et al. have investigated the latency/germination cycle of seeds of *Mesembryanthemum crystallinum* (L.), called common ice plant [C3-CAM (crassulacean acid metabolism)]. This plant is a system model to study tolerance mechanisms in halophytes. The individual seed capsules spread over time, some seeds germinate within 1 d (early, E) and others do not germinate for more than 4 weeks, until after imbibition (late, L). Several processes such as the uptake of water by the seeds, the start of mitotic activity, and the growth of the radicle seem to be controlled by a mechanism that also establishes different expression patterns of *Vp1* (transcript for transcriptional activator VP1), being VP1 (indicator nature for the threshold that leads from latency to germination). L-seeds are characterized by a lack of expression of the *Cdc2*-related protein (transcript for a cell cycle), and an increase in transcripts of *Vp1*, after water uptake, whereas transcripts related to *Cdc2* increase early and decrease *Vp1* at the beginning of E-seeds. Therefore, these authors conclude that the maintenance of the transcription *Vp1* may to be the basis of the prolonged latency in the L-seeds. In addition, the expression of several MIP proteins [proteins for aquaporines (AQP) or water channels (WCH)] was characterized during germination and in organs of adult plants. The use of specific probes for the transcription of *Mip* (transcript for AQP and WCH) revealed differences during germination that were not due exclusively to water absorption. The *Mip* transcripts increase before the L-seeds begin to germinate. MIP presents greater amounts in active growing tissues. These authors concluded that latency mechanisms for a long time period, before seed germination, provide an advantage for these plants, thus maximizing the survival chances of some seeds in their natural habitat, which is characterized by an unpredictable water supply and consequently environmental stress [75]. Subsequent experiments realized by these authors have clearly shown

that the presence and late disappearance of VP1 in L-seeds caused dormancy and after-ripening of L-germinating in these plants [76]. Surówka et al. have realized, an in-depth study, on a transition from C₃ to CAM pathway, suggesting increased temporary of ROS, leading to up-regulation of ROS-responsive genes, catalase (antioxidant enzyme), proline (osmolyte), and polyamines (plant growth regulators). This diurnal rhythm of antioxidant and osmotic compounds could contribute to the maintenance of the water-potential gradient and ROS homeostasis [73].

The extremophile *Eutrema/Thellungiella* spp. is becoming a new model plant because it resembles its relative species (*Arabidopsis thaliana*) in the small genome and the short life cycle. It is highly tolerant to salinity (germination ≤ 700 mM NaCl) and drought resistant. The high content of several metabolites in these plants indicates metabolic pre-adaptation to salinity to regulate osmotic stress [74]. Little is known about the biochemical and gene-expression changes related to salt, in the germination stage of halophytes. To fill this gap, Kazachkova et al. have shown that germination of *E. salsugineum* is inhibited, by salt, in response to the osmotic component. The seeds of *E. salsugineum* remained viable even when the germination is completely inhibited and the germination resumes once the seeds are transferred to non-saline conditions. In addition, the removal of the seed coat treated with salt allows the embryos to germinate in a medium containing salt. The seeds exposed to salt are also characterized by a reduced proportion of GA/ABA (hormones that control germination and dormancy), and a greater expression of germination repressor genes, *RGL2*, *ABI5*, and *DOG1*. In addition, a salt-mediated increase in the expression of a gene encoding “late embryogenesis abundant” proteins (LEA proteins), and the accumulation of metabolites involved in osmo-protection indicates the induction of processes associated with stress tolerance and the accumulation of easily mobilized carbon stocks. These authors suggest that salt inhibits the germination of seeds by inducing a state with molecular characteristics of dormancy, while the layers of the seed coat provide a physical restriction for the emergence of the radicle. This seed status could facilitate survival in saline soils until a rainfall increases the water potential of soil, indicating favorable conditions for seed germination [77]. On the other hand, halophytes adapted to high levels of salinity have useful genes for improving the salinity tolerance of agricultural crops. One of the growth regulators most related to stress, in plants, are polyamines (putrescine, spermidine and spermine). The *EsPDS1* is a gene that participates in spermidine biosynthesis, specifically encoding the synthesis of Spd-synthase. This gene was cloned and characterized from *E. salsugineum*. The *EsPSS1*-overexpression in tobacco transgenic plant, conferred drought tolerance by alleviating oxidative status of the plant, reflecting the great potential of the study of halophytes [72].

In plants, Halliwell-Asada cycle serve to avoid an excess of ROS, which could damage vital cell components (e.g., AND, membrane lipids, and proteins), and recycles antioxidant systems [78]. Key enzymatic systems include ascorbate peroxidase (APX) an enzyme that eliminates H₂O₂. The function, as well as molecular, and regulatory mechanisms of APX in *Eutrema (Thellungiella) salsuginea* have unknown. However, Li et al. have studied an APX gene (*TsApx6*), which was cloned from *T. salsuginea*, and its responses in transgenic plants of *Arabidopsis* were analyzed. In the high-salinity treatment, the expression of *TsApx6* was significantly induced. In the drought treatment, the overexpression of *TsApx6* improved the survival rate and reduced the rate of water loss from the leaves in *Arabidopsis*. Compared with the results for wild-type plants, the high-salinity treatment reduced the concentrations of malondialdehyde (MDA), H₂O₂ (hydrogen peroxide) and proline, but increased the activities of antioxidant enzymes: APX, GPX (glutathione peroxidase), CAT (catalase) and SOD (superoxide-dismutase) in plants overexpressing *TsApx6*. Meanwhile, the germination rate, the greening of the cotyledon and the length of the root improved in the transgenic plants in comparison

Features	Brown seeds	Blacks seeds	Function in seeds
Size and weight	Heavy and big	Light and small	Different dispersion
Ions (Na ⁺ , K ⁺ , Cl ⁻)	↑ upregulated	↓ downregulated	Lower water potential Better absorb water
Vacuolar cation/proton exchanger	↑ CAX3	↓ CAX3	Ion vacuolar compartmentalization
Potassium transport Two-pore potassium channels	↑ upregulated	↓ downregulated	Ion homeostasis
Betaine Aldehyde dehydrogenase (BADH)	↑ upregulated	↓ downregulated	Accumulation of betaine (osmolyte) implied in osmotic adjustment
GA 20-oxidase enzyme catalysis steps related to GA biosynthesis	↑ upregulated	↓ downregulated	Regulation germination/dormancy
ETR receptor regulates ethylene signaling	↑ upregulated	↓ downregulated	Quick and high germination of brown seeds
Genes related to Brassinosteroids	↑ upregulated	↓ downregulated	Stimulation of germination

Table 5.
Transcriptomic profiling of some genes in matured dimorphic seeds of *Suaeda salsa*.

with the wild-type plants, under conditions of salinity and water deficit. These results indicate that, TsApx6 has an important function in plant resistance to certain types of abiotic stress. The bioinformatic analysis indicated that it contains some elements that act in *cis* related to the stress response [79].

In the last years, transcriptomic profiles of some halophytic plants have been carried out by various research groups. The transcriptome dataset permits a better understand of functional genomics in halophytic seeds. Xu et al. realized transcriptomic profiling of genes in matured dimorphic seeds of euhalophyte *Suaeda salsa* (Table 5). Upregulated genes involved in seed development, accumulation of osmolytes, and differentially expressed genes of hormones may relate to seed dormancy/germination, and to bigger size and rapid seed germination in brown seeds, compared to black seeds [30].

At molecular level, of halophyte *Karelinia caspica* (Asteraceae), has been studied by Zhang et al. [80]. In addition, the study of differentially expressed genes in this species, under salt stress, and analysis of the effects of salt stress and regulation of ABA could contribute to the identification and characterization of genes and molecular mechanisms underlying saline stress responses, in these plants [80]. *Haloxylon ammodendron*, a perennial xerohalophyte, is an essential species for investigating the effects of drought on desert trees. The results, via RNA-seq and digital gene expression (DGE), were mainly related to ion transporters, signal transduction, ROS-scavenging, photosynthesis, cell wall organization, membrane stabilization and hormones. Moreover, the physiological changes of inorganic ions and organic solute content, peroxidase (POD) activity and osmotic potential were in accordance with dynamic transcript profiles of the more relevant genes. The data provides valuable genetic resources for future improvement of forage and crop species for better adaptation to abiotic stresses [81].

Finally, another widely studied halophyte is *Sporobolus virginicus* (C4 grass) found from tropical to warm temperate regions of world. To identify the key genes involved in the regulation of salt tolerance in this plant, it was produced 3500 independent transgenic *Arabidopsis* lines expressing random cDNA from *S. virginicus* and screened 10 lines which showed enhanced salt tolerance compared with the wild type in a medium containing 150 mM NaCl. Among the selected lines, two contained cDNA coding glycine-rich RNA-binding proteins (*SvGRP1* and *SvGRP2*). GRPs are involved in diverse biological and biochemical processes including salt tolerance in *Arabidopsis* and some other glycophytes. Metabolomic analysis of the *SvGRP1*-transformant suggested that the increase in 3-aminopropanoic acid, citramalic acid, and isocitric acid content was associated with enhanced salt tolerance [82].

8. Conclusions

This chapter has reviewed the current status of halophytes about the adaptive strategies used to survive in a large heterogeneity of habitats. Phenotypic plasticity, the presence of heteromorphic seeds, persistent and/or transient seed banks, and the cycle of dormancy/germination regulated by ABA and GAs allow ecological diversity, and the most germination appropriate time to achieve success in their survival. The rapid germination and recovery of germination, after drought and saline stress, ensure the propagation of their later generation in areas with varied climatic conditions. These strategies convert halophytes in a viable commercial alternative in countries where the severe climatic conditions do not allow a conventional agriculture, recover degraded lands thanks to phytoremediation action of these plants, and transfer of resistance genes to sensitive agricultural crops, for a better adaptation to abiotic stress. These achievements can help palliate worldwide problems concerning food, ecology, and health, in XXI century.


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