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TESIS DOCTORAL

SALINITY AND DROUGHT TOLERANCE IN *SUAEDA VERMICULATA*, A HABITAT INDIFFERENT HALOPHYTE OF THE HYPER-ARID DESERT OF THE UNITED ARAB EMIRATES (UAE)

Doctorando

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Prefacio

Las investigaciones que han conducido a la redacción de la presente Tesis Doctoral se han realizado en el Departamento de Botánica y Fisiología Vegetal de la Universidad de Málaga, en el ámbito de las actividades del Grupo de Investigación RNM 115 "BIODIVERSIDAD, CONSERVACION Y RECURSOS VEGETALES" -del Plan Andaluz de Investigación, Desarrollo e Innovación de la Junta de Andalucía-.

Los trabajos de investigación han sido realizados en el Departamento de Biología Aplicada de la Universidad de Sharjah. Sharjah, Emiratos Arabes Unidos (UAE) y en el Departamento de Biología de la Universidad de los Emiratos Arabes Unidos (UAEU).

Memoria presentada para optar

al Grado de Doctor en Biología

Visado en Málaga

A 10 de octubre del 2021

El Licenciado

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ACREDITA

Que Dña. Naeema Al Shamsi, Licenciada en Biología, ha realizado, en el Departamento de Botánica y Fisiología Vegetal Fisiología Vegetal de la Facultad de Ciencias de la Universidad de Málaga y en el Departamento de Biología Aplicada de la Universidad de Sharjah y de la Universidad de Emiratos Arabes Unidos, las investigaciones que le han conducido a la redacción de la presente Memoria de Tesis Doctoral, titulada: SALINITY AND DROUGHT TOLERANCE IN *SUAEDA VERMICULATA*, A HABITAT INDIFFERENT HALOPHYTE OF THE HYPER-ARID DESERT OF THE UNITED ARAB EMIRATES (UAE).

La presente Memoria, que recoge los resultados obtenidos, las publicaciones científicas de los mismos, así como su interpretación y reúne los requisitos necesarios para ser sometida al juicio de la Comisión correspondiente. Por tanto, como Directora y Tutora de la tesis, autorizo su exposición y defensa para optar al Grado de Doctor en Biología.

Y para que conste en cumplimiento de las disposiciones vigentes, firmo la presente acreditación en,

Málaga, A 10 de octubre del 2021

Prof. Dra. Teresa Navarro

Directora y Tutora de la Tesis

This work is dedicated to:

The soul of my father, who taught me the meaning of life.

My mother, the origin of my success.

My husband & my children, the source of my inspiration.

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ABSTRACT

The Arabian Peninsula, including the United Arab Emirates (UAE), experiences some of the most extreme climatic conditions found on Earth. It is characterized by low, erratic, unpredictable rainfall, high evaporation rates, and very highest temperatures, especially in summer. The UAE climate is classified as hyperarid with spatial and temporal variations in rainfalls. The average annual rainfall is less than 100 mm and mostly occurs from November to March, when average temperatures are lowest. The low rainfall coupled with high temperatures increase the rate of evaporation, which in turn increases soil salinity.

The UAE environment faces one of the harshest climatic conditions found on the Earth, such as low rainfall, high evaporation rates, high temperatures, and high levels of soil and water salinity. Under such harsh environmental conditions in the UAE, plants are suffering from many environmental stresses. Drought and salt stresses are among the most common stresses facing plants in the UAE deserts. They can cause injury, disease and have major impacts on plant development and productivity. Environmental stresses that parental plants experience can induce phenotypic changes that can span multiple generations. Such stresses induce transgenerational plasticity in plants that provides them with phenotypic variation to adapt the environmental stresses. Transgenerational phenotypic plasticity in progeny traits can occur through maternal and/or epigenetic effects. Maternal effects in plants include the maternal genetic effects caused by maternal inheritance of plastids in addition to the non-inheritable effect of endosperm, seed coat, resource provisioning of nutrient resources, hormones, proteins and transcripts. Environmental maternal effects usually diminish in the first generation, but epigenetic effects transmit heritable plastic responses to environmental cues. It is important to assess the differences between populations inhabiting different provenances that differ in the levels of salinity and drought stresses in their response to life-history traits, such as seed dormancy, germination, physiological, and biochemical attributes.

Salt stress is present in soil characterized by high toxic soluble salts, such as sodium and/or chloride ions. Most salts in the soil-affected soils accumulate over time as a result of high evapotranspiration under the hot arid and semiarid areas. The serious impacts of salt stress on plants are two main mechanisms: osmotic effect and specific ion toxicity. Osmotic effect is a rapid response due to the presence of a high amount of salts in the soil that make water harder to be extracted by roots due to the declining soil solute potential. This effect of salt stress is known as the osmotic effect of salt stress, and this is similar to the effect of drought stress. However, the ion-specific effect, which results from the uptake and/or the accumulation of high concentrations of ions such as sodium and chloride, harms ion homeostasis that affects cell growth and associated metabolism. It has been reported that reasonable concentrations of sodium chloride can induce plant growth. Still, the extreme salt levels have very harmful inhibitory effects on several life-history traits, such as vegetative and the most sensitive critical seed germination and seedling establishment stages.

Environmental abiotic stress conditions, especially drought and salinity, are the major factors that reduce crop yields worldwide and affect plant distribution and community structure. The high evapotranspiration coupled with lower rainfall rates exaggerates the soil salinity problem in arid countries, including the UAE. The response traits of plants exposed to salinity and drought stresses have become a crucial environmental research topic in drought-prone regions. The plants respond to drought and salinity stresses at the molecular, biochemical, physiological, and morphological levels. The tolerance to drought and salinity depends on the species and genotype, the length and severity of the stress, and plants age and development stage. Seeds developed differences strategies to cope with the drought and salinity stress. Besides, the response of seeds to drought and salinity stress could be an indicator of the tolerance of plants for the later stages of development. Therefore, defining the habitat type that produces seed with high quality is important for the restoration of salt-affected habitats. Seeds with high quality usually enter a secondary dormancy under unfavorable conditions but germinate under the salinity and drought levels that the seedlings and adult plants tolerate.

Effects of salinity and drought on plants include decreased growth, productivity, and severe conditions leading to plants death. The ion-specific toxicity effects that are result from the accumulation of ions such as sodium and chloride ions within the plant compromises enzyme functions and disrupts metabolic processes. This is mainly due to the production of reactive oxygen species (ROS.) To counteract the toxic effects of ROS, plants usually produce complex defense mechanisms, which include the production of both enzymatic and non-enzymatic antioxidants.

The toxicity of sodium ion caused by salt stress results in acute toxic effects on genes and enzymes, causing plant metabolism disruption. Salt stress enhances the excessive production of ROS, inhibits important enzymes, alters the efficiency of enzymatic reactions in plant cells, changes the metabolite profiles, and destabilizes various cellular proteins, membranes, RNA species, and cytoskeleton structures net result is a state of metabolic imbalance. ROS production occurs naturally in different sites of the plant cell, where plants have various control mechanisms to antagonize and/or balance ROS levels under normal conditions. Salt stress induces ROS production, which is highly reactive and able to cause lipids peroxidation, protein oxidation, enzymatic inactivation, DNA damage, and/or interact with other vital constituents of plant cells. Production of ROS under salt stress is due to water deficit or due to closure of the stomata, which decreases the carbon dioxide abundance inside the leaves and leads to the inhibition of carbon fixation, the net result is the exposure of chloroplasts to higher excitation energy which enhance the production of ROS such as singlet oxygen ($^1O_2$) superoxide ($O_2^{\bullet\,-}$), hydroxyl radical ($OH^{\bullet}$), and hydrogen peroxide (H_2O_2).

ROS production under salt stress conditions is mainly associated with photosynthesis and respiration, where ROS can have a dual role. ROS can be highly toxic and cause cell damage or can serve as signaling molecules. For example, hydrogen peroxide (H_2O_2) can be vital for cell balance and can cause pernicious effects to the cell (dual activity), as it has two roles in the plant cells. Hydrogen peroxide (H_2O_2) is a strong toxic agent that causes cell damage or even cell death during oxidative stress. It is considered a signaling molecule used to activate the defense system to restore the redox homeostasis in plant cells. Moreover, H_2O_2 plays a vital role in mediating the biological plant processes, including ABA-mediated closure of stomata, plant cell death, as well as plant-pathogen interaction, auxin-regulated gravitropism responses, and plant Systematic Acquired Resistance (SAR) to stressful conditions. In addition, H_2O_2 is involved in mechanical wounding response and some other similar processes related to both abiotic and biotic stresses processing. Both glycophyte and halophyte plants are suffering from the osmotic and the toxic ionic effect of salt stress and they develop several salt resistance mechanisms to enable them to grow and produce under salt stress. As halophytes are more tolerant to salt stress, it is necessary to study their salt resistance mechanisms.

The salinity adaptation in a salty habitat could be transferred through seeds, i.e., transgenerational induction, and can occur through maternal and/or epigenetic effects. The maternal effect is adaptive when it enhances offspring fitness in an environment similar to that experienced by the parental generation. Several studies have reported that seed dormancy and germination requirements of the same species differ depending on maternal habitat and time of seed development on the mother plant.

High plants exhibit differences in salinity tolerance and are accordingly classified as halophytes or glycophytes. Based on ecological aspects, halophytes have been classified as obligate, facultative, and habitat-indifferent halophytes. Obligate (true) halophytes grow only in salty habitats. However, facultative halophytes can establish themselves on salty soils but grow better in salt-free or less salt-affected soils. Few plants can grow equally well in both non-saline and saline soils (i.e., habitat indifferent). *Suaeda vermiculata* Forssk. ex J.F.Gmel. (Amaranthaceae) is a C4 evergreen, leaf succulent perennial shrub growing in salty and non-salty habitats (habitat-indifferent halophytes) of the Arab Gulf deserts. It grows nicely in summer, flowers, and fruits in early falls. *S. vermiculata* produces very tiny seeds with no dispersal structures. Habitat-indifferent halophytes offer a good chance for studying the effect of maternal salinity on seed dormancy and germination response to salinity and drought stress. This is especially important as the saline habitats of maternal plants are suffering from both low water osmotic potential (drought effect) as well as specific ion toxicity effect.

Seeds of desert plants use environmental and hormonal signals as sensors for detecting the proper environmental conditions (e.g., temperature and light) that could trigger germination when the environments are suitable for seedling establishment. The environmental factors at the seedbed interact to determine the time of seed germination that helps in successful seedling establishment. Therefore, it is important to assess salt and drought tolerance of seeds of habitat-indifferent halophytes in response to maternal habitat and other environmental signals in seedbeds, such as temperature and light. In addition, assessing the ability of seeds to recover their germination after being exposed to saline solutions could determine conditions for seed survival in salty habitats and successful seedling establishment.

Few studies have assessed the impact of the habitat type (i.e., salty and non-salty) on physiological, and biochemical strategies of habitat-indifferent halophytes.

Therefore, evaluating the tissue-specific strategies of a habitat-indifferent halophyte to deal with maternal salinity could provide insights into salt tolerance mechanisms. Therefore, the objectives of this PhD memory are to (1) Evaluate the effects of maternal salinity, drought, light, and temperature of incubation and their interactions on germination attributes of *S. vermiculata* (2) Assess interactive effects of maternal salinity and incubation conditions on salt tolerance during germination of *S. vermiculata*, and (3) Assess the impacts of maternal salinity on some physiological and biochemical functional traits of *S. vermiculata.*

Effect of maternal habitat and incubation conditions on drought tolerance during germination

The first chapter of the thesis assessed the effects of light, and temperature, and maternal salinity on drought tolerance during seed germination of this habitat-indifferent halophyte species. The effects of light, temperature, salinity and drought on the germination of halophytes have been extensively studied. However, few studies have focused on the germination on habitat-indifferent halophytes. So, in order to assess the impacts maternal salinity, temperature, and light on drought tolerance and their interactions on germination attributes of *S. vermiculata*, seeds from non-saline habitats and saline habitats were tested in different concentrations of polyethylene glycol (PEG 6000) (0, -0.2, -0.4, -0.6, -0.8 and -1.0 MPa) that produced different levels of osmotic stress. Germination experiments had been done at different temperatures (15/25, 20/30 and 25/35 °C) and light conditions and germination recovery and rate index (GRI) were measured.

Generally, the results indicated that seeds of both saline and non-saline habitats showed little dormancy; more than 95% of the seeds germinated within two days of imbibition at higher osmotic potentials (0, -0.2 and -0.4) in all temperatures. This result support that salt desert halophytes generally lack innate dormancy. The ability of *S. vermiculata* to germinate to a very high percentage and speed in higher osmotic pressures at all temperatures is an adaptation to germinate quickly upon the availability of adequate moisture after rainfall precipitation at any time of the growing season. In addition, early germination of freshly harvested seeds of *S. vermiculata* in the presence of enough water confers an ecological advantage to their seedlings, which would reach larger sizes and deeper roots that might have a greater competitive ability, compared

to seedlings appear late in the rainy season. The results showed that seeds of the saline habitats attained significantly lower germination in lower osmotic potentials of PEG (-0.8 and -1.0 MPa), compared to those of the non-saline habitat.

The result showed that the drought tolerance was higher for seeds of the non-saline than those of the saline habitat and this tolerance was more obvious at higher temperatures. In addition, seeds of saline habitats were able to germinate in lower osmotic potentials (-0.8 and -1.0 MPa) at only the lower temperatures, but seeds of non-saline habitats were able to germinate to higher levels at all higher temperatures. This indicates that seeds of non-saline habitats could germinate at the double stresses of drought and temperatures. Seed germination reduction in saline habitat could the result of a maternal salinity effect. Seeds of *S. vermiculata* are usually developed and matured before the onset of the first rainfall (September – November); effective rainfalls are usually received in December – March. This result indicates that *S. vermiculata* relies mainly on atmospheric moisture rather than conventional soil water, especially since it has a shallow root system. This further indicates that seeds matured in non-saline soils are independent of soil water potential. Still, seeds matured in saline habitats experienced the highest possible salinity (i.e., lowest osmotic potential) that is usually reached before the onset of the rainy season. Several reports indicated that lower osmotic potential stress during seed maturation produced seeds with greater dormancy.

The results also indicated that *S. vermiculata* seeds attained a very high germination percentage when germinated in higher osmotic potential solutes and incubated in light and dark. However, decreasing the osmotic potential to -0.8 MPa reduced the final germination, especially for seeds matured in saline soils and incubated at higher temperatures. This result indicates that the germination window is narrower for seeds of the saline soils. The failure of seeds from the saline habitat to germinate in light and darkness at higher temperatures and lower osmotic potentials would be an ecological adaptation for surviving *S. vermiculata* in the saline soils. Little rainfalls would not encourage seed germination at the end of the growing season when high temperatures evaporate water and increase soil salinity. However, the germination window is wider for seeds matured in non-saline soils; they germinated in different temperatures and light regimes in the lower water osmotic potentials.

The results also indicate that germination of seeds matured in the two soil types was greater in darkness than in light in the lowest water osmotic potential (-1.0 MPa)

at lower and moderate temperatures. However, at higher temperatures, germination in darkness was greater than in light in -0.8 MPa for seeds matured in the non-saline soils. Seeds of saline soils failed to germinate at higher temperatures at -0.8 and -1.0 MPa PEG. Such results indicate that some seeds could germinate in the non-saline, but not in the saline soils, when little rainfalls are received by the end of the season, especially if seeds are covered with litter or present in dark cracks. The smaller sizes of *S. vermiculata* seeds indicate that they can hardly emerge from deeper soils; seedlings from small seeds have little metabolic reserves available for seedling emergence from deep soil.

The results of this study showed a limited tolerance to lower osmotic potential during germination of *S. vermiculata* seeds, compared to many other desert plants; few seeds germinated in -0.8 and -1.0 MPa PEG. Such a result indicates that tolerance of *S. vermiculata* to drought is less than other desert plants. The lower ability of *S. vermiculata* seeds to germinate in lower osmotic potentials than other desert plants indicates that they would not germinate below a certain water threshold, above which successful seedlings recruitments would occur. Exposing seeds to water deficiency limits the mobilization of the available reserves.

The results also indicate that seeds matured in saline soils had greater dormancy, especially at moderate and higher temperatures. In addition, seeds of saline soils attained significantly lower germination than those of non-saline soils in the lower water potentials (-0.8 and -1.0 MPa PEG). Around 80% of the seeds that failed to germinate under these PEG concentrations recovered their germination in distilled water, indicating that they were viable. The higher dormancy at the lower water potentials indicates that seeds matured in saline soils postpone germination till the arrival of suitable conditions for seed germination and subsequent seedling survival. Such condition usually happens after effective rainfalls that dilute soil salinity and increase soil water potential. The result indicates that if environmental salinity and drought stresses occur repeatedly, it is advantageous for the produced seeds to be able to remember these stresses and to use this stored knowledge to adapt to new stress challenges. As seeds of *S. vermiculata* do not have any adaptation for dispersal, their multiple existence and exposures to both drought and salinity stresses in the saline soils could enable them to adapt to a new negative water stress by postponing the germination till the arrival of conditions suitable for seedling establishment. In addition, the result indicates that transgenerational phenotypic plasticity may probably be adaptive, in a sense that it could increase stress tolerance among offspring and consequently increase offspring reproductive.

Effect of maternal habitat and incubation conditions on salt tolerance during germination

The second chapter of the thesis assess the interactive effects of maternal habitat and incubation conditions on salt tolerance during germination of the habitat-indifferent halophyte *S. vermiculata.* To achieve this, seeds of both saline and non-saline habitats were germinated at six salinity levels (0, 50, 100, 200, 400 and 500 mM NaCl) in three incubators adjusted to three temperatures (25/15, 30/20 and 35/25°C) and two light regimes. The three temperature regimes consisted of day/night cycles. Studied germination attributes were final germination, germination rate index (GRI) and germination recovery.

Generally, all the main factors (maternal habitat, salinity, temperature and light) and their interactions significantly affected the final germination of *S. vermiculata* seeds. In addition, the two habitats differ in their response to the different levels of salinity. Whereas no significant difference was detected between the seeds from the two habitats at the lower salinities, seeds from the non-saline habitat tolerated more salinity than those of saline habitat at the higher salinities.

At higher salinities (400 and 500 mM NaCl), germination of the saline habitat seeds was almost inhibited, but that of non-saline habitat seeds reached various levels depending on light and temperature. Both higher temperatures and darkness resulted in significant reductions of the final germination at the higher salinities. Recovery was faster for seeds of the saline habitats, especially for those incubated at higher salinities and in the dark. The difference in dormancy and germination attributes of seeds of the two habitat types reflects ecological adaptations for survival in salt marshes of arid deserts.

The inability of *S. vermiculata* seeds of the saline habitat failed to germinate in 400 and 500 mM NaCl indicated that they postpone their germination until salinity is diluted through rainfall. In addition, seeds that failed to germinate in the saline solution recovered their germination within few days when transferred to distilled water. The fast recovery of most of the non-germinated seeds of the saline habitat when

transferred from the saline solutions to distilled water is an ecological adaptation for survival in saline soils. Seeds of *S. vermiculata* recovered almost all the non-germinated seeds within two days after being transferred to distilled water. The ability of the seeds from the saline habitat to delay their germination under salinity stress until the alleviation of such stress is important adaptive features that distinguish seeds of halophyte from those of glycophytes. An important consequence of germination recovery upon the alleviation of salt stress is determining the salinity level at the time of seedling development, which is one of the most sensitive stages in the life cycle of halophytes. Therefore, the amount of precipitation needed to dilute soil salinity would determine the time of seed germination of halophytes.

The results showed no significant difference in the final germination of *S. vermiculata* between the different temperatures for both seeds from the saline and non-saline habitats. In saline solution, however, germination decreased with the increase in both temperature and salinity. Salinity-temperature interaction may have significant ecological implications in terms of the time of germination under field conditions. The higher germination of *S. vermiculata* in the higher salinities (400 and 500 mM NaCl) at lower temperatures (15/25 °C) would indicate a higher chance of seedling survival if germination occurred early in the growing season (e.g., December), when temperatures are low, and the chance of rainfalls is higher. However, the chance of seedling establishment would be much lower if germination occurred at higher temperatures by the end of the growing season, when there are almost no rainfalls to dilute soil salinity. In addition, germination reduction at higher temperatures has been attributed to increased evaporation of moisture, which in turn increases salt concentration by capillary movement. The high temperatures can result in loss of the semi-permeability of the plasma membrane, which leads to an increase in the amount of electrolyte leakage.

The present study results also indicate that the salt tolerance of *S. vermiculata* depended on light and temperature of incubation in seeds of both saline and non-saline habitats. There was no significant difference between germination in dark and light for seeds of both saline and non-saline habitats in the lower salinities (0 and 100 mM NaCl). However, in higher salinities, germination was significantly reduced in dark than in light, especially at higher temperatures.

The presence of multiple generations of *S. vermiculata* that has limited seed dispersed within a single environment would increase the likelihood of population

differentiation between saline and non-saline environments. However, despite seeds of the saline habitat matured under higher salinity stress, they tolerated less salinity during germination stage, as compared with seeds matured in the non-saline habitat. As *S. vermiculata* has limited seed dispersal, ecological significance for the greater germination of non-saline habitat seeds in the high salinity levels is unclear. More research to define the maternal and epigenetic effects of transgenerational changes in germination behaviour is needed. In addition, further studies about the possible roles of seed provisioning, especially phytohormonal signals, would also help understand the physiological bases of high germination of seeds of the non-saline habitats in high salinities.

Effect of maternal salinity on physiological and biochemical features of *S. vermiculata*: a field study

The third chapter investigates the maternal salinity impacts on several physiological and biochemical features of *S. vermiculata*. To do that, samples of different organs and surrounded soil were collected from both a highly saline habitat and a non-salty gravel plain. The changes in growth parameters, elemental composition, and the antioxidation enzymes activities were investigated.

Results showed that plants from the saline habitats had significantly lower values of chlorophyll a, b, carotenoids and leaf biomass compared to those from non-saline one. Roots from saline habitats attained higher levels of antioxidant enzymes (Catalase, CAT; guaiacol peroxidase, GPX; Ascorbate peroxidase, APX) activities and lower values of reactive oxygen species (malondialdehyde (MDA), and hydrogen peroxide (H_2O_2). Indicating that the enzymes are more likely to scavenge the reactive oxygen species (ROS). The enzyme activities and ROS levels were much lower in the shoots of both saline habitats and non-saline than in roots. In addition, the accumulation of sodium was higher in leaves and shoots than roots.

The study results indicated that *S. vermiculata* adjusted several physiological and biochemical attributes to survive in both saline and non-saline habitats. The higher levels of ROS should encourage the formation of significantly greater levels of CAT, APX, and GPX. Yet, ROS should be maintained at an optimum level for proper signaling.

In our study, the response of *S. vermiculata* to salinity through the productions of ROS and enzymatic antioxidants was organ and habitat-specific. For example, roots of non-saline habitat displayed high activities of the three different enzymatic antioxidative enzymes (CAT, GPX and APX), which was associated with significant reductions of reactive oxygen species. Such scavenging activity for the enzymatic antioxidants in the roots of non-saline habitat was especially important as they attained a higher sodium concentration factor (2.05; the ratio of Na^+ in roots to soils) compared with roots of plants from saline habitat (sodium concentration factor was 0.81). In roots from the saline habitat, however, there were higher levels of ROS, but low levels of enzymatic antioxidants. This indicates that plants of the saline habitat have developed biochemical and physiological mechanisms to deal with the high level of Na^+ in the roots that differ from those in plants of the saline habitat. However, the significant increase of ROS in the roots of plants of saline habitat was not associated with a correspondence increase in the enzymatic antioxidants (CAT, APX and GPX), but was associated with an increase in proline concentration which is a part of antioxidative defense systems.

The results of this study indicate that *S. vermiculata* plants from the saline habitat not only tolerated high levels of sodium in the soils (4.85 mg/g), but also tolerated 3.96 mg/g sodium in their roots. Interestingly, sodium accumulated in the leaves of saline habitat was 118.2 mg/g dry weight; the concentration factor was 24.4. Higher accumulation of sodium in plant tissues is reported to induce oxidative damage by accelerating the ROS generation, which can cause damage to important cellular components, including membranes, chlorophyll, proteins, nucleic acids. The leaves of plants from the saline habitat accumulated a high sodium level (24-folds that of the roots); yet the oxidative stress signals (H_2O_2 and MDA) were greater in the roots than in the shoots. This could be attributed to the fact the root is the first part of the plant facing the salinity stress. During its translocation from soils through roots to leaves, sodium is loaded into the xylem by the Na^+/H^+ antiporter located at the plasma membrane of parenchymal cells adjacent to the xylem. During this process, excessive sodium in the cytoplasm could affect essential biochemical processes and injure the plasma membrane. In non-saline habitat, however, it seems that sodium translocation through roots triggered the productions of higher levels of CAT, APX and GPX, which in turn resulted in a significant reduction in ROS. These results indicate that roots of plants from the saline habitat tolerate high levels of ROS, but those from the non-saline

habitat do not. The results also support the hypothesis that plants from the two different habitats developed different tolerance mechanisms for salt accumulation.

The study also indicated that proline level in roots of *S. vermiculata* was significantly greater in the saline habitat (>3-folds) than in the non-saline habitat, indicating a possible role of proline as an osmoregulator to maintain the osmotic potential and to detoxify excess sodium in the roots in the saline habitat. Interestingly, the results showed that the proline level was 4.4-folds greater in shoots of non-saline habitat than those of the saline habitat. This emphasizes different roles for proline, other than osmoregulator in the plants of the non-saline habitat. Proline has been considered a non-enzymatic antioxidant due to its ability to scavenge ROS. In addition, proline can also maintain a low NADPH to $NADP^+$ ratio and stabilize the antioxidant enzymes. It could be concluded that the role of proline in *S. vermiculata* plants differ in the two habitat types.

In this study, K^+ content in leaves of *S. vermiculata* was lower in saline habitat while unaffected in other organs from both habitats. Thus, the accumulation of Na^+ was accompanied by a lower level of K^+ in the leaves of the saline habitat, compared to those of non-saline habitat. It has been documented that a higher level of Na^+ reduces K^+, Ca^{2+} and Mg^{2+} uptake. It could be argued that the decline in K^+ content in plant leaves from saline habitat might be associated with a reduction in its absorption and translocation to leaves from the soil–root plant system. The complex regulatory mechanisms of Na^+ and K^+ uptake play a major role in the distribution of the elements in different cell compartments through ion transport systems. The results showed high levels of both Na^+ and K^+ in the leaves of saline habitat (118.2 and 12.2 mg/g) and non-saline habitat (95.1 and 32.8 mg/g, respectively). The presence of high concentrations of Na^+ and K^+ implies a synergistic impact on cell osmotic adjustment in *S. vermiculata*.

Salinity causes a comparative loss and degradation of photosynthetic pigments in several halophytes, including *S. vermiculata*. the results indicated that chlorophyll a and b, total chlorophyll and carotenoids attained higher values in plants from the non-saline habitat, as compared to those from the saline habitat. The degradation of chlorophyll pigments decreases photosynthesis functions and contributes to stunted growth. The negative effect of high concentrations of salinity on chlorophyll contents was attributed to the negative effect of Na^+ on uptake of essential nutrients, especially

Mg^{2+}. Our results indicated a higher level of Mg^{2+} in *S. vermiculata* leaves from non-saline habitat than those from saline habitat. It has been reported that Mg^{2+} may play a significant role for salinity stress tolerance.

The overall results indicate that the salt-tolerant *S. vermiculata* adapts to different environments through down-regulation of different biochemical and physiological features to avoid oxidative stress and adapt for survival under harsh desert conditions.

It could be concluded that the habitat type (saline and non-saline) influences the seed dormancy, salinity and drought tolerance, light and temperature requirement during the germination stage, and germination speed. These factors determine the time of seed germination in the field, determining future success under different drought and salinity stress scenarios. In addition, these factors determine the germination strategies under the hot hyperarid desert environment in the Arabian Peninsula. Furthermore, the level of salinity in the different habitats (saline and non-saline) determines the morpho-physiological attributes of *S. vermiculata* in the Hyper-arid UAE desert. The high salinity triggered greater production of H_2O_2 in the roots of plants from the saline habitat compared to those of the non-saline habitat. The high proline level in roots of saline habitat and in shoots of non-saline habitat implies that the role of proline differs according to habitat and organ. Higher accumulation of Na^+ in leaves, roots, and shoots indicate that *S. vermiculata* uses this toxic element as an osmoregulator, especially in saline habitats. The results support our hypothesis that the plants of saline habitat rely more on inorganic ions, especially Na^+, as an osmoregulator. Still, those of non-saline habitat rely more on organic osmoregulators such as proline. It could be further concluded that plants from the two different habitats developed different tolerance mechanisms for salt accumulation. The high ability of *S. vermiculata* to accumulate higher Na^+ levels implie that it can serve as a rhizosphere sodium cleaner and as a potential candidate for rehabilitation of the salt-degraded marginal environment.

RESUMEN

La Península Arábiga, incluidos los Emiratos Árabes Unidos (EAU), se ve sometida a algunas de las condiciones climáticas más extremas que se encuentran en la Tierra. Lluvias escasas, erráticas e impredecibles, altas tasas de evaporación y temperaturas muy altas, especialmente en verano. El clima de los Emiratos Árabes Unidos se clasifica como hiperárido con variaciones espaciales y temporales en las precipitaciones. La precipitación media anual es inferior a 100 mm y se produce principalmente de noviembre a marzo, cuando las temperaturas medias son más bajas. La escasez de precipitaciones y las altas temperaturas aumentan la tasa de evapotranspiración, lo que a su vez hace aumentar la salinidad del suelo.

El medio ambiente de los Emiratos Árabes Unidos hace frente a una de las condiciones climáticas más duras que se encuentran en la Tierra, con escasas precipitaciones, altas tasas de evaporación, altas temperaturas y altos niveles de salinidad del suelo y el agua. En condiciones ambientales tan duras en los Emiratos Árabes Unidos, las plantas están sufriendo mucho estrés ambiental. El estrés por sequía y salinidad se encuentra entre los factores de estrés más comunes que afectan a las plantas en los desiertos de los Emiratos Árabes Unidos. Pueden causar lesiones, enfermedades y tener un impacto importante en el desarrollo y la productividad de las plantas. El estrés ambiental puede inducir cambios fenotípicos que pueden abarcar varias generaciones. Tal estrés induce a una plasticidad transgeneracional que ocasiona una variación fenotípica en las plantas para adaptarse al estrés ambiental. La plasticidad fenotípica transgeneracional se puede trasmitir a través de efectos maternos y / o epigenéticos. Los efectos maternos en las plantas incluyen los efectos genéticos maternos causados por la herencia materna de los plástidos, además del efecto no heredable del endospermo, la cubierta de la semilla, el suministro de recursos de nutrientes, hormonas, proteínas y transcripciones. Los efectos ambientales maternos generalmente disminuyen en la primera generación, pero los efectos epigenéticos transmiten respuestas plásticas heredables a las señales ambientales. Es importante evaluar las diferencias entre las poblaciones que habitan en diferentes niveles de salinidad y estrés por sequía en su respuesta a los caracteres del ciclo de vida, como la

latencia (dormancia) de las semillas, la germinación, los caracteres fisiológicos y bioquímicos.

El estrés salino está presente en suelos caracterizados por sales solubles altamente tóxicas, como iones sodio y / o cloruro. La mayoría de las sales en los suelos afectados por la sequía se acumulan con el tiempo como resultado de una alta evapotranspiración en las regiones áridas y semiáridas. Los impactos del estrés salino en las plantas se acentúan en dos mecanismos principales: el efecto osmótico y la toxicidad por iones específicos. El efecto osmótico es una respuesta rápida debido a la presencia de una gran cantidad de sales en el suelo que dificultan la extracción del agua por las raíces debido a la disminución del potencial de solutos del suelo. Este efecto del estrés salino se conoce como efecto osmótico del estrés salino, y es similar al efecto del estrés por sequía. Sin embargo, el efecto iónico específico, que resulta de la captación y/o la acumulación de altas concentraciones de iones como el sodio y el cloruro, daña la homeostasis iónica que afecta el crecimiento celular y el metabolismo asociado. Se ha puesto en evidencia que concentraciones razonables de cloruro de sodio pueden inducir el crecimiento de las plantas. Aun así, los niveles extremos de sal tienen efectos inhibidores muy dañinos en varios caracteres del ciclo de vida de la planta, como el crecimiento vegetativo y las etapas críticas más sensibles de germinación de semillas y establecimiento de plántulas.

Las condiciones ambientales de estrés abiótico, especialmente la sequía y la salinidad, son los principales factores que reducen el rendimiento de los cultivos en todo el mundo y afectan la distribución de las plantas y la estructura de las comunidades vegetales. La alta evapotranspiración junto con las tasas de lluvia más bajas incrementa el problema de la salinidad del suelo en los países áridos, incluidos los Emiratos Árabes Unidos. El estudio de la respuesta de las plantas expuestas a la salinidad y a el estrés por sequía se han convertido en un tema de investigación ambiental crucial en las regiones propensas a la sequía. Las plantas responden al estrés por sequía y salinidad a nivel molecular, bioquímico, fisiológico y morfológico. La tolerancia a la sequía depende de la especie y del genotipo, la duración y la gravedad del estrés, la edad y la etapa de desarrollo de la planta. Además, la respuesta de las semillas al estrés por sequía y salinidad puede ser un indicador de la tolerancia de las plantas en las últimas etapas de su desarrollo. Por lo tanto, definir el tipo de hábitat en el cual las plantas producen un tipo de semillas que pueda resistir el estrés climático y salino es importante para los programas de restauración. Las semillas resistentes al estrés suelen entrar en una dormancia secundaria en condiciones desfavorables, pero germinan bajo los niveles de salinidad y sequía que toleran las plántulas y las plantas adultas.

Los efectos de la salinidad y la sequía en las plantas incluyen una disminución del crecimiento, la productividad y las condiciones severas que conducen a la muerte de las plantas. La acumulación de iones como el sodio (Na^+) y el cloro (Cl^+) dentro de la planta produce efectos de toxicidad osmóticos y/o específicos de los iones. La acumulación de iones compromete las funciones enzimáticas y altera los procesos metabólicos. Esto se debe principalmente a la producción de especies reactivas de oxígeno (ROS). Para contrarrestar los efectos tóxicos de los ROS, las plantas suelen producir mecanismos de defensa complejos, que incluyen la producción de antioxidantes enzimáticos y no enzimáticos.

La toxicidad de los iones de sodio causada por el estrés salino tiene como resultado efectos tóxicos agudos sobre los genes y las enzimas, lo que provoca una interrupción del metabolismo de las plantas. El estrés salino aumenta la producción excesiva de ROS, inhibe enzimas importantes, altera la eficiencia de las reacciones enzimáticas en las células vegetales, cambia los perfiles de metabolitos y desestabiliza diversas proteínas celulares, membranas, especies de ARN y estructuras del citoesqueleto. El resultado neto es un estado de desequilibrio metabólico. La producción de ROS ocurre naturalmente en diferentes sitios de la célula vegetal, donde las plantas tienen varios mecanismos de control para antagonizar y / o equilibrar los niveles de ROS en condiciones normales. El estrés salino induce la producción de ROS, que es altamente reactivo y capaz de causar peroxidación de lípidos, oxidación de proteínas, inactivación enzimática, daño al ADN y / o interactuar con otros componentes vitales de las células vegetales. La producción de ROS bajo estrés salino se debe al déficit de agua o al cierre de las estomas, lo que disminuye la abundancia de dióxido de carbono dentro de las hojas y conduce a la inhibición de la fijación de carbono, el resultado neto es la exposición de los cloroplastos a una mayor energía de excitación que mejorar la producción de ROS, como el superóxido de oxígeno ($^1O_2$) ($O_2^{\bullet -}$), el radical hidroxilo ($OH^{\bullet}$) y el peróxido de hidrógeno (H_2O_2).

La producción de ROS en condiciones de estrés salino se asocia principalmente con la fotosíntesis y la respiración, donde el ROS pueden tener un papel doble. Las producciones de ROS pueden ser muy tóxicas y causar daño celular o pueden servir como moléculas de señalización. Por ejemplo, el peróxido de hidrógeno (H_2O_2) puede ser vital para el equilibrio celular y puede causar efectos perniciosos en la célula (actividad dual), ya que tiene dos funciones en las células vegetales. El peróxido de hidrógeno (H_2O_2) es un agente tóxico fuerte que causa daño celular o incluso la muerte celular durante el estrés oxidativo. Se considera una molécula de señalización que se utiliza para activar el sistema de defensa para restaurar la homeostasis redox en las células vegetales. Además, el H_2O_2 desempeña un papel vital en la mediación de los procesos biológicos de la planta, incluido el cierre de estomas mediado por ABA, la muerte de las células vegetales, así como la interacción planta-patógeno, las respuestas de gravitropismo regulado por auxinas y la resistencia sistemática adquirida (SAR) de la planta a situaciones estresantes. Además, el H_2O_2 participa en la respuesta mecánica de las heridas y en algunos otros procesos similares relacionados con el procesamiento de tensiones abióticas y bióticas. Tanto las plantas glicofitas como las halófitas sufren el efecto osmótico y iónico tóxico del estrés salino y desarrollan varios mecanismos de resistencia a la sal que les permiten crecer y producir bajo estrés salino. Como las halófitas son más tolerantes al estrés salino, es necesario estudiar sus mecanismos de resistencia a la salinidad.

La adaptación a la salinidad en un hábitat salino puede transferirse a través de las semillas, es decir, inducción transgeneracional, y puede ocurrir a través de efectos maternos y/o epigenéticos. El efecto materno es adaptativo cuando mejora la aptitud de la descendencia en un entorno similar al experimentado por la generación parental. Varios estudios han informado que la dormancia de las semillas y los requisitos de germinación de una misma especie difieren según el hábitat materno y el tiempo de desarrollo de la semilla en la planta madre.

En base a los caracteres ecológicos, las halófitas se han clasificado como obligadas, facultativas e indiferentes al hábitat. Los halófitos obligados (verdaderos) crecen solo en hábitats salinos. Sin embargo, las halófitas facultativas pueden establecerse en suelos salinos, pero crecer mejor en suelos sin sal o menos afectados por sal. Pocas plantas pueden crecer igualmente bien tanto en suelos no salinos como salinos (es decir, hábitat indiferente).

Suaeda vermiculata Forssk. ex J.F.Gmel. (Amaranthaceae) es un arbusto perenne suculento de hoja perenne C4 que crece en hábitats salinos y no salinos (halófitas indiferentes al hábitat) de los desiertos del Golfo de Arabia. Crece muy bien en verano y produce flores y frutos a principios de otoño. *S. vermiculata* produce semillas muy pequeñas sin estructuras de dispersión. Las plantas halófitas indiferentes al hábitat, como *S. vermiculata*, ofrecen una buena oportunidad para estudiar el efecto de la salinidad materna en la dormancia de las semillas y la respuesta de la germinación a la salinidad y el estrés por sequía. Esto es especialmente importante ya que las plantas de los hábitats salinos sufren un potencial osmótico bajo (efecto de sequía) y un efecto de toxicidad de iones específicos.

Las semillas de las plantas del desierto utilizan señales ambientales y hormonales como sensores para detectar las condiciones ambientales adecuadas (por ejemplo, temperatura y luz) que podrían desencadenar la germinación cuando las condiciones ambientales son las más adecuadas para el establecimiento de las plántulas. Los factores ambientales en el cultivo experimental interactúan para determinar el momento de la germinación de la semilla que ayuda al establecimiento de la plántula. Es importante evaluar la tolerancia a la salinidad y a la sequía de las semillas de halófitas indiferentes al hábitat en respuesta al hábitat materno y otras señales ambientales como la temperatura y la luz. Además, evaluar la capacidad de las semillas para recuperar su germinación después de haber sido expuestas a soluciones salinas podría determinar las condiciones ecológicas para la supervivencia de las semillas en hábitats salinos y el establecimiento posterior de las plántulas.

Pocos estudios han evaluado el impacto del tipo de hábitat (es decir, salino y no salino) sobre las estrategias fisiológicas y bioquímicas de las halófitas indiferentes al hábitat. Por lo tanto, la evaluación de las estrategias específicas de una halófita indiferente al hábitat para responder al efecto de la salinidad materna podría proporcionar información sobre los mecanismos de tolerancia a la salinidad.

Los objetivos de esta memoria de doctorado son (1) Evaluar los efectos de la salinidad materna, la sequía, la luz y la temperatura de incubación y sus interacciones sobre los caracteres de germinación de *S. vermiculata* (2) Evaluar los efectos interactivos de la salinidad materna y las condiciones de incubación. sobre la tolerancia a la sal durante la germinación de *S. vermiculata*, y (3) Evaluar los impactos de la salinidad materna en algunos caracteres funcionales fisiológicos y bioquímicos de *S. vermiculata*.

Efecto del hábitat materno y las condiciones de incubación sobre la tolerancia a la sequía durante la germinación.

El primer capítulo de la tesis estudia los efectos de la luz, la temperatura y la salinidad materna sobre la tolerancia a la sequía durante la germinación de semillas de esta planta halófita indiferente al hábitat. Los efectos de la luz, la temperatura, la salinidad y la sequía sobre la germinación de las halófitas se han estudiado ampliamente. Sin embargo, pocos estudios se han centrado en la germinación en halófitas indiferentes al hábitat. Con el fin de evaluar los impactos de la salinidad materna, la temperatura y la luz sobre la tolerancia a la sequía y sus interacciones sobre los caracteres de germinación de *S. vermiculata*, se trataron semillas de hábitats no salinos y salinos en diferentes concentraciones de polietilenglicol (PEG 6000) (0, -0,2, -0,4, -0,6, -0,8 y -1,0 MPa) que produjeron diferentes niveles de estrés osmótico. Se han realizado también experimentos de germinación a diferentes temperaturas (15/25, 20/30 y 25/35°C) y condiciones de luz y se midió la tasa de recuperación y la tasa de germinación (GRI).

En general, los resultados indicaron que las semillas de hábitats tanto salinos como no salinos mostraron poca dormancia; más del 95% de las semillas germinaron dentro de los dos días de la imbibición a potenciales osmóticos más altos (0, -0,2 y -0,4) en todas las temperaturas. Este resultado apoya que las halófitas de desiertos salinos generalmente carecen de dormancia innata. La capacidad de *S. vermiculata* para germinar a un porcentaje y una velocidad muy alta bajo presiones osmóticas muy altas y a todas las temperaturas es una adaptación para germinar rápidamente y en cualquier momento cuando el suelo disponga de la humedad adecuada después de la precipitación. Además, la germinación temprana de semillas recién recolectadas de *S. vermiculata* en presencia condiciones de humedad suficientes confiere una ventaja ecológica a sus plántulas, que alcanzarían mayor tamaño y raíces más profundas que podrían tener una mayor capacidad competitiva, en comparación con las plántulas que aparecen al final de la temporada de lluvias que es la que proporciona la humedad necesaria al suelo. Los resultados mostraron que las semillas de los hábitats salinos alcanzaron una germinación significativamente menor en potenciales osmóticos más bajos de PEG (-0,8 y -1,0 MPa), en comparación con las de hábitats no salinos.

Los resultados de esta memoria doctoral muestran que la tolerancia a la sequía es mayor para las semillas de hábitats no salinos que para las de hábitats salinos y que esta tolerancia es más obvia a temperaturas más altas. Además, las semillas de hábitats salinos pueden germinar en potenciales osmóticos más bajos (-0,8 y -1,0 MPa) solo a las temperaturas más bajas, pero las semillas de hábitats no salinos pueden germinar a niveles más altos a todas las temperaturas más altas. Esto indica que las semillas de hábitats no salinos pueden germinar con el doble estrés de sequía y de temperaturas. La reducción de la germinación de semillas en hábitats salinos puede ser el resultado de un efecto de salinidad materna. Las semillas de *S. vermiculata* generalmente se desarrollan y maduran antes del inicio de las primeras lluvias (septiembre-noviembre); las lluvias efectivas son generalmente en diciembre - marzo. Este resultado indica que *S. vermiculata* depende principalmente de la humedad atmosférica en lugar del agua del suelo, especialmente porque tiene un sistema radicular poco profundo. Esto indica además que las semillas maduradas en suelos no salinos son independientes del potencial hídrico del suelo. Aun así, las semillas maduradas en hábitats salinos experimentaron la mayor salinidad posible (es decir, el potencial osmótico más bajo) que generalmente se alcanza antes del inicio de la temporada de lluvias. Varios estudios previos indicaron que un menor potencial osmótico durante la maduración de las semillas producía semillas con mayor latencia.

Los resultados también indicaron que las semillas de *S. vermiculata* alcanzaron un porcentaje de germinación muy alto cuando germinaron en solutos de mayor potencial osmótico y se incubaron en luz y oscuridad. Sin embargo, la disminución del potencial osmótico a -0,8 MPa redujo la germinación final, especialmente para semillas maduradas en suelos salinos e incubadas a temperaturas más altas. Este resultado indica que la ventana de germinación es más estrecha para las semillas de los suelos salinos. El hecho de que las semillas del hábitat salino no germinen en la luz y la oscuridad a temperaturas más altas y potenciales osmóticos más bajos sería una adaptación ecológica para la supervivencia de *S. vermiculata* en los suelos salinos. Las lluvias escasas no estimulan la germinación de las semillas al final de la temporada de crecimiento cuando las temperaturas altas hacen evaporan el agua y aumentan la salinidad del suelo. Sin embargo, la ventana de germinación es más amplia para semillas maduradas en suelos no salinos; que germinan a diferentes temperaturas y regímenes de luz en los potenciales osmóticos del agua bajos.

Los resultados también indican que la germinación de semillas maduradas en los dos tipos de suelo fue mayor en la oscuridad que en la luz en el potencial osmótico más bajo (-1.0 MPa) a temperaturas más bajas y moderadas. Sin embargo, a temperaturas más altas, la germinación en la oscuridad fue mayor que en la luz en -0,8 MPa para las semillas maduradas en suelos no salinos. Las semillas de suelos salinos no germinaron a temperaturas más altas de -0,8 y -1,0 MPa PEG. Dichos resultados indican que algunas semillas podrían germinar en suelos no salinos, pero no en suelos salinos, cuando reciben escasas lluvias al final de la temporada, especialmente si las semillas están cubiertas de basura o presentes en grietas oscuras. Los tamaños más pequeños de las semillas de *S. vermiculata* indican que difícilmente pueden emerger de suelos más profundos; las plántulas de semillas pequeñas tienen pocas reservas metabólicas disponibles para la emergencia de plántulas de suelos profundos.

Los resultados de este estudio mostraron una tolerancia limitada a un potencial osmótico más bajo durante la germinación de las semillas de *S. vermiculata*, en comparación con muchas otras plantas del desierto; pocas semillas germinaron en -0,8 y -1,0 MPa PEG. Tal resultado indica que la tolerancia de *S. vermiculata* a la sequía es menor que otras plantas del desierto. La menor capacidad de las semillas de *S. vermiculata* para germinar en potenciales osmóticos más bajos que otras plantas del desierto indica que no germinarían por debajo de un cierto umbral de agua, por encima del cual se produciría el reclutamiento exitoso de plántulas. La exposición de semillas a la deficiencia de agua limita la movilización de las reservas disponibles.

Los resultados también indican que las semillas maduradas en suelos salinos tuvieron mayor latencia, especialmente a temperaturas moderadas y altas. Además, las semillas de suelos salinos alcanzaron una germinación significativamente menor que las de suelos no salinos en los potenciales hídricos más bajos (-0,8 y -1,0 MPa PEG). Alrededor del 80% de las semillas que no germinaron bajo estas concentraciones de PEG recuperaron su germinación en agua destilada, lo que indica que eran viables. La mayor latencia en los potenciales hídricos más bajos indica que las semillas maduradas en suelos salinos posponen la germinación hasta la llegada de las condiciones adecuadas para la germinación de las semillas y la subsiguiente supervivencia de las plántulas. Esta condición suele ocurrir después de lluvias que diluyen la salinidad del suelo y aumentan el potencial hídrico del suelo. El resultado indica que, si la salinidad ambiental y el estrés por sequía ocurren repetidamente, es ventajoso que las semillas producidas sean capaces de recordar este estrés y utilizar este conocimiento almacenado para adaptarse a los nuevos desafíos de estrés. Como las semillas de *S. vermiculata* no tienen ninguna adaptación para la dispersión, su exposición a estrés tanto por sequía como por salinidad en los suelos salinos podría permitirles adaptarse a un nuevo estrés hídrico negativo posponiendo la germinación hasta la llegada de las condiciones adecuadas. para el establecimiento de plántulas. Además, el resultado indica que la plasticidad fenotípica transgeneracional probablemente puede ser adaptativa, en el sentido de que podría aumentar la tolerancia al estrés entre la descendencia y, en consecuencia, aumentar la reproducción de la descendencia.

Efecto del hábitat materno y las condiciones de incubación sobre la tolerancia a la salinidad durante la germinación.

El segundo capítulo de la tesis evalúa los efectos interactivos del hábitat materno y las condiciones de incubación sobre la tolerancia a la salinidad durante la germinación del halófito indiferente al hábitat *S. vermiculata*. Para evaluar los efectos individuales e interactivos del hábitat materno y las condiciones de incubación de semillas sobre la tolerancia a la sal durante la germinación de *S. vermiculata*, se pusieron a germinar semillas de hábitats tanto salinos como no salinos a seis niveles de salinidad (0, 50, 100, 200, 400 y 500 mM de NaCl) en tres incubadoras ajustadas a tres temperaturas (25/15, 30/20 y 35/25°C) y dos regímenes de luz. Los tres regímenes de temperatura consistieron en ciclos de día/noche. Los caracteres de germinación estudiados fueron la germinación final, el índice de tasa de germinación (GRI) y la recuperación de la germinación.

Generalmente, todos los factores principales (hábitat materno, salinidad, temperatura y luz) y sus interacciones tuvieron efectos significativos en la germinación final de las semillas de *S. vermiculata*. Además, las semillas de los dos hábitats difieren en su respuesta a los diferentes niveles de salinidad. Mientras que no se detectaron diferencias significativas entre las semillas de los dos hábitats en los niveles de salinidades más bajas, las semillas del hábitat no salino toleraron más salinidad, en comparación con las del hábitat salino, en los niveles de salinidad más altos.

En salinidades más altas (400 y 500 mM NaCl), la germinación de las semillas del hábitat salino fue casi inhibida, pero la de las semillas del hábitat no salino alcanzó varios niveles dependiendo de la luz y de la temperatura. Tanto las temperaturas más altas como en la oscuridad dieron como resultado reducciones significativas de la germinación final en las salinidades más altas. La recuperación fue más rápida para las semillas de los hábitats salinos, especialmente para las incubadas a mayor salinidad y en la oscuridad. La diferencia en los caracteres de dormancia y germinación de las semillas de los dos tipos de hábitat refleja adaptaciones ecológicas para la supervivencia en los hábitats salinos de los desiertos áridos.

Las semillas de *S. vermiculata* del hábitat salino no germinaron en NaCl 400 y 500 mM indicando que posponen su germinación hasta que la salinidad se diluya a través de la lluvia. Además, las semillas que no germinaron en la solución salina recuperaron su germinación en pocos días cuando se transfirieron a agua destilada. La rápida recuperación de la mayoría de las semillas no germinadas del hábitat salino cuando se transfieren de las soluciones salinas al agua destilada es una adaptación ecológica a la supervivencia en suelos salinos. Las semillas de *S. vermiculata* germinaron tras los dos días posteriores a su transferencia a agua destilada. La capacidad de las semillas del hábitat salino para retrasar su germinación bajo estrés por salinidad hasta que las condiciones son favorables es una característica adaptativa importante que distingue las semillas de las halófitas de las de glucófitas. Una consecuencia importante de la recuperación de la germinación cuando desaparece el estrés salino es determinar el nivel de salinidad en el momento del desarrollo de la plántula, que es una de las etapas más sensibles en el ciclo de vida de las halófitas. Por lo tanto, la cantidad de precipitación necesaria para diluir la salinidad del suelo determinaría el tiempo de germinación de las semillas de las halófitas.

Los resultados no mostraron diferencias significativas en la germinación final de *S. vermiculata* en diferentes temperaturas para las semillas de los hábitats salinos y no salinos. En solución salina, sin embargo, la germinación disminuyó con el aumento tanto de la temperatura como de la salinidad. La interacción salinidad-temperatura puede tener implicaciones ecológicas importantes en términos del tiempo de germinación en condiciones de campo. La mayor germinación de *S. vermiculata* en las salinidades más altas (400 y 500 mM de NaCl) a temperaturas más bajas (15/25°C) indica una mayor probabilidad de supervivencia de las plántulas si la germinación se produce al principio de la temporada de crecimiento (e.g., diciembre), cuando las temperaturas son bajas y la probabilidad de lluvias es mayor. Sin embargo, la posibilidad de que las plántulas se establezcan sería mucho menor si la germinación se produjera a temperaturas más altas al final de la temporada de crecimiento, cuando casi no hay precipitaciones que diluyan la salinidad del suelo. Además, la reducción de la germinación a temperaturas más altas se ha atribuido a una mayor evaporación de la humedad, que a su vez aumenta la concentración de sal por movimiento capilar. Las altas temperaturas pueden resultar en la pérdida de la semipermeabilidad de la membrana plasmática, lo que conduce a un aumento en la cantidad de fuga de electrolitos.

Los resultados del presente estudio también indican que la tolerancia a la sal de *S. vermiculata* dependió de la luz y la temperatura de incubación en semillas de hábitats tanto salinos como no salinos. No hubo diferencia significativa entre la germinación en la oscuridad y la luz para las semillas de hábitats tanto salinos como no salinos en las salinidades más bajas (NaCl 0 y 100mM). Sin embargo, en salinidades más altas, la germinación se redujo significativamente en la oscuridad en comparación con la luz, especialmente a temperaturas más altas.

La presencia de múltiples generaciones de *S. vermiculata* que dispersan en el mismo ambiente aumentaria la probabilidad de diferenciación poblacional entre ambientes salinos y no salinos. Sin embargo, a pesar de que las semillas del hábitat salino maduraron bajo mayor estrés de salinidad, toleraron menos salinidad durante la etapa de germinación, en comparación con las semillas maduradas en el hábitat no salino. Dado que *S. vermiculata* tiene una dispersión de semillas limitada, la importancia ecológica para una mayor germinación de semillas de hábitats no salinos en los niveles de salinidad altos no está clara. Se necesita más investigación para definir los efectos maternos y epigenéticos de los cambios transgeneracionales en el comportamiento de la germinación. Además, estudios adicionales sobre las posibles funciones del aprovisionamiento de semillas, especialmente las señales fitohormona les, también ayudarían a comprender las bases fisiológicas de la alta germinación de semillas de hábitats no salinos en salinidades elevadas.

Efecto de la salinidad materna sobre las características fisiológicas y bioquímicas de *S. vermiculata*: un estudio de campo.

El tercer capítulo investiga los impactos de la salinidad materna en varias características fisiológicas y bioquímicas de *S. vermiculata*. Para hacer eso, se recolectaron muestras de diferentes órganos y suelo circundante a la planta tanto de un hábitat altamente salino como de una llanura de grava no salina. Se investigaron los cambios en los parámetros de crecimiento, la composición elemental y las actividades de las enzimas antioxidantes.

Los resultados mostraron que las plantas de hábitats salinos tenían valores significativamente más bajos de clorofila a, b, carotenoides y biomasa foliar en comparación con las del no salino. Las raíces de hábitats salinos alcanzaron niveles más altos de actividades de enzimas antioxidantes (catalasa, CAT; guayacol peroxidasa, GPX; ascorbato peroxidasa, APX) y valores más bajos de especies reactivas de oxígeno (malondialdehído (MDA) y peróxido de hidrógeno (H_2O_2). es más probable que eliminen las especies reactivas de oxígeno (ROS). Las actividades enzimáticas y los niveles de ROS fueron mucho más bajos en los brotes de hábitats salinos y no salinos que en las raíces. Además, la acumulación de sodio fue mayor en las hojas y brotes que en las raíces.

Los resultados del estudio indicaron que *S. vermiculata* adquirió caracteres fisiológicos y bioquímicos para sobrevivir tanto en hábitats salinos como no salinos. Los niveles más altos de ROS fomentan la formación de niveles significativamente mayores de CAT, APX y GPX. Sin embargo, ROS debe mantenerse a un nivel óptimo para una señalización adecuada. En nuestro estudio, la respuesta de *S. vermiculata* a la salinidad a través de la producción de ROS y antioxidantes enzimáticos fue específica de órganos y hábitats. Por ejemplo, las raíces de hábitats no salinos mostraron altas actividades de las tres enzimas antioxidantes enzimáticas diferentes (CAT, GPX y APX), lo que se asoció con reducciones significativas de especies reactivas de oxígeno. Dicha actividad depuradora de los antioxidantes enzimáticos en las raíces de hábitats no salinos fue especialmente importante ya que alcanzaron un factor de concentración de sodio más alto (2.05; la proporción de Na^+ en raíces a suelos) en comparación con las raíces de plantas de hábitat salino (factor de concentración de sodio fue 0,81). En las raíces del hábitat salino, sin embargo, hubo niveles más altos de ROS, pero niveles bajos de antioxidantes enzimáticos. Esto indica que las plantas del hábitat salino han desarrollado mecanismos bioquímicos y fisiológicos para lidiar con el alto nivel de Na^+ en las raíces que difieren de los de las plantas del hábitat salino. Sin embargo, el aumento significativo de ROS en las raíces de plantas de hábitat salinos no se asoció con un aumento correspondiente en los antioxidantes enzimáticos (CAT, APX y GPX), sino que se asoció con un aumento en la concentración de prolina que es parte de la defensa antioxidante.

Los resultados de este estudio indican que las plantas de *S. vermiculata* del hábitat salino no solo toleraron altos niveles de sodio en los suelos (4.85 mg/g), sino que también toleraron 3.96 mg / g de sodio en sus raíces. Curiosamente, el sodio acumulado en las hojas del hábitat salino fue de 118,2 mg/g de peso seco; el factor de concentración fue 24,4. Hay estudios que indican que una mayor acumulación de sodio en los tejidos vegetales induce daño oxidativo al acelerar la generación de ROS, lo que puede causar daño a componentes celulares importantes, incluidas membranas, clorofila, proteínas y ácidos nucleicos. Las hojas de las plantas del hábitat salino acumularon un alto nivel de sodio (24 veces el de las raíces); sin embargo, las señales de estrés oxidativo (H_2O_2 y MDA) fueron mayores en las raíces que en los brotes. Esto podría atribuirse al hecho de que la raíz es la primera parte de la planta que se enfrenta al estrés por salinidad. Durante su translocación desde el suelo a través de las raíces a las hojas, el sodio es cargado en la xilema por el anti portador Na^+ / H^+ ubicado en la membrana plasmática de las células parenquimatosas adyacentes al xilema. Durante este proceso, el exceso de sodio en el citoplasma podría afectar los procesos bioquímicos esenciales y dañar la membrana plasmática. Sin embargo, en hábitats no salinos, parece que la translocación de sodio a través de las raíces desencadenó la producción de niveles más altos de CAT, APX y GPX, lo que a su vez resultó en una reducción significativa de ROS. Estos resultados indican que las raíces de las plantas del hábitat salino toleran altos niveles de ROS, pero las del hábitat no salino no. Los resultados también apoyan la hipótesis de que las plantas de los dos hábitats diferentes desarrollaron diferentes mecanismos de tolerancia para la acumulación de sal.

El estudio también indicó que el nivel de prolina en las raíces de *S. vermiculata* fue significativamente mayor en el hábitat salino (> 3 pliegues) que, en el hábitat no salino, lo que indica un posible papel de la prolina como un osmorregulador para mantener el potencial osmótico y para desintoxicar el exceso de sodio en las raíces en el hábitat salino. Curiosamente, los resultados mostraron que el nivel de prolina fue 4,4 veces mayor en los brotes de hábitat no salino que en los del hábitat salino. Esto enfatiza diferentes roles para la prolina, además del osmorregulador en las plantas del hábitat no salino. La prolina se ha considerado un antioxidante no enzimático debido a su capacidad para eliminar ROS. Además, la prolina también puede mantener una proporción baja de NADPH a $NADP^+$ y estabilizar las enzimas antioxidantes. Se podría concluir que el papel de la prolina en las plantas de *S. vermiculata* difiere en los dos tipos de hábitat.

En este estudio, el contenido de K^+ en las hojas de *S. vermiculata* fue menor en el hábitat salino mientras que no se vio afectado en otros órganos de ambos hábitats. Así, la acumulación de Na^+ estuvo acompañada de un menor nivel de K^+ en las hojas del hábitat salino, en comparación con las del hábitat no salino. Se ha documentado que un nivel más alto de Na^+ reduce la captación de K^+, Ca^{2+} y Mg^{2+}. Se podría argumentar que la disminución en el contenido de K^+ en las hojas de las plantas del hábitat salino podría estar asociada con una reducción en su absorción y translocación a las hojas del sistema suelo-raíz de la planta. Los complejos mecanismos reguladores de la absorción de Na^+ y K^+ juegan un papel importante en la distribución de los elementos en diferentes compartimentos celulares a través de los sistemas de transporte de iones. Los resultados mostraron altos niveles de Na^+ y K^+ en las hojas del hábitat salino (118,2 y 12,2 mg/g) y el hábitat no salino (95,1y 32,8 mg/g, respectivamente). La presencia de altas concentraciones de Na^+ y K^+ implica un impacto sinérgico sobre el ajuste osmótico celular en *S. vermiculata*.

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El conjunto de resultados de este estudio indica que *S. vermiculata*, especie tolerante a la salinidad, se adapta a diferentes hábitats mediante la regulación a la baja de diferentes características bioquímicas y fisiológicas para evitar así el estrés oxidativo y adaptarse a sobrevivir bajo las condiciones del desierto.

Se podría concluir que el tipo de hábitat (salino y no salino) influye en la latencia de la semilla, la tolerancia a la salinidad y la sequía, el requerimiento de luz y temperatura durante la etapa de germinación y la velocidad de germinación. Estos factores determinan el momento de la germinación de la semilla en el campo, determinando el éxito futuro en diferentes escenarios de estrés por sequía y salinidad. Estos factores determinan las estrategias de germinación en el desierto de la península arábiga. Además, el nivel de salinidad en los diferentes hábitats (salinos y no salinos) determina los caracteres morfo-fisiológicos de *S. vermiculata* en el desierto de los EAU. La alta salinidad provocó una mayor producción de H_2O_2 en las raíces de las plantas del hábitat salino en comparación con las del hábitat no salino. El alto nivel de prolina en raíces de hábitats salinos y en brotes de hábitats no salinos implica que el papel de la prolina difiere según el hábitat y el órgano. Una mayor acumulación de Na^+ en hojas, raíces y brotes indica que *S. vermiculata* usa este elemento tóxico como osmorregulador, especialmente en hábitats salinos. Los resultados apoyan nuestra hipótesis de que las plantas de hábitat salino dependen más de iones inorgánicos, especialmente Na^+, como osmorregulador. Aun así, los de hábitat no salino dependen más de osmorreguladores orgánicos como la prolina. Además, se podría concluir que las plantas de los dos hábitats diferentes desarrollaron diferentes mecanismos de tolerancia para la acumulación de sal. La alta capacidad de *S. vermiculata* para acumular niveles más altos de Na^+ implica que puede servir como un limpiador de sodio en la rizosfera y como un candidato potencial para la rehabilitación de ambientes degradados por el efecto de la salinidad.

INTRODUCTION

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1. Desert Ecosystems

Desert is one of earth major types of ecosystems, supporting a community of distinctive plants specially adapted to the harsh environment Hot deserts are characterized by intense solar radiation, lashing winds, and little rainfall. The environmental conditions of deserts are among the harshest for living organisms in the biosphere. High temperatures during daytime and persistent winds accelerate water evaporation and transpiration from plants. High evapotranspiration and low rainfall are the chief characteristics of the desert ecosystem, thus producing sparse perennial shrubs vegetation (Singh, 2017). Scarcity of rainfall in deserts ecosystem can be due to high subtropical pressure (e.g., Sahara and Australian deserts), geographical position in the rain shadows (e.g., western North American deserts), and due to high altitude (e.g., Tibetan, Bolivian, or Gobi deserts) (Singh, 2017).

Deserts ecosystems cover about 14 percent of the earth's land and occur mainly near 30º north and south latitude, where global air currents create belts of descending dry air. Some desert ecosystems are also produced in the rain shadows of high mountain ranges, leeward slopes that face away from incoming storms and thereby receive little rainfall. Most deserts ecosystem receives little rainfalls during the year, creating a sparse cover of vegetation (Singh, 2017).

But despite such harsh living conditions, desert ecosystem exhibits a spectacular biological diversity. A large number of plant and animal species thrive in the deserts due to their morphological, anatomical, physiological and behavioral adaptations (Singh, 2017).

In general, the world deserts are divided into four basic types: subtropical, cool coastal, cold winter, and polar deserts (Logan, 1968; El-Ghani et al., 2017; Mares, 2017). Subtropical deserts have the highest temperatures, driest terrain, fast evaporation, and cold winter. The temperature differs significantly from one season to another; it ranges from 38 ºC in the summer to -12 ºC in the winter. Sahara, Arabian, Kalahari, Australian, Mojave, Sonoran, and Thar deserts are examples of subtropical deserts (Laity, 2009).

2. The Arabian Desert Ecosystem

The Arabian Desert is approximately one million square miles in size and has been classified as a subtropical hyper-arid hot desert. It is extended through Saudi Arabia, Qatar, Kuwait, Oman, Yemen, Bahrain and the United Arab Emirates (Huggett, 2007, Bahadur et al., 2015). It has been considered the world second-largest desert after the Sahara Desert in Africa. The Arabian Desert covers most of the Arabian Peninsula and parts of Iraq and Jordan (Figure 1). Both the United Arab Emirates (UAE) and Qatar are located along the southern coast of the Arabian Gulf at the northeastern end of the Arabian desert (Miller and Cope, 1996; Huggett, 2007; Bahadur et al., 2015). This region has one of the world's harshest climatic conditions. It suffers from scarce rainfall, high evaporation, extreme temperatures, extreme saline soil and water, and continuous freshwater depletion (Zahran, 1997; Peacock et al., 2003).

Figure 1. Map of the Arabian Peninsula representing the seven Gulf countries in addition to Iraq and Yemen.

3. The United Arab Emirates (UAE) Desert Ecosystem

The United Arab Emirates (UAE) is located in the southeastern part of the Arabian Peninsula between latitudes 22° 40’ and 26° 00’ N, and longitudes 51° 00’ and 56° 00’ E. It is bounded to the north by the Arabian Gulf and the Sultanate of Oman, to the east and northeast by the Sultanate of Oman and the Gulf of Oman, and to the south and west by the Kingdom of Saudi Arabia (Figure 1). The total area of the UAE is 83,600 km^2. It is stretched for 650 km along the Arabian Gulf coast and 90 km along the Gulf of Oman coast. The UAE has seven Emirates: Abu Dhabi, Dubai, Sharjah, Ras Al Khaimah, Fujairah, Ajman, and Umm Al Quwain (Figure 2) (El-Keblawy et al., 2005; Sherif et al., 2009). The UAE has a flat topography in the coastal and western parts and the Al Hajar Mountain chain in the northeastern part that reaches 1800 m. Sand dunes cover the western part of the UAE and merge into the Empty Quarter of Saudi Arabia. The UAE has a uniform land cover classified as bare land (rural) in the western region and artificial surfaces (urban), particularly in the Emirates of Dubai and Abu Dhabi. There is some dense shrubland to the east of Dubai (Abrams, 2000).

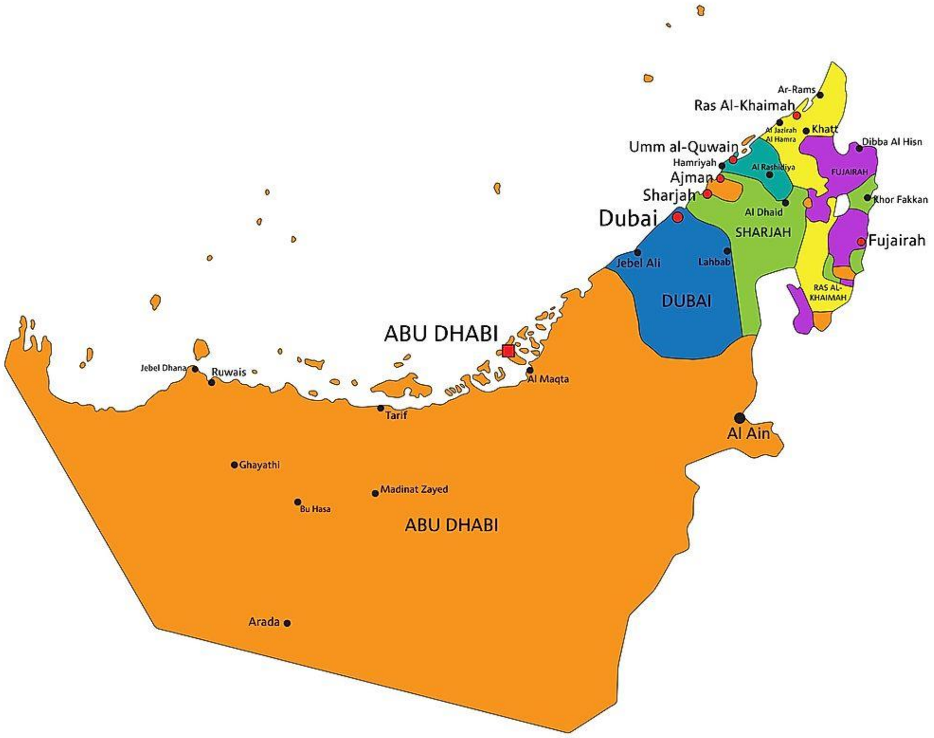

Figure 2. Map of the United Arab Emirates.

The UAE geomorphologic features include mountains, gravel plains, sand sheets, and saline flats (Böer and Chaudhary, 1999; Karim and Fawzi, 2007a, b). Sandy desert covers more than 90% of the country surface area, stretching from the northwest to the east, truncated by the mountains zone (Sherif et al., 2009). The sandy desert region extends from sea level to 300 m (Above Sea Level, asl), rising steadily from the coastal plain to elevations of up to 250 m (asl). The UAE mountainous region consists of the north-south mountain that runs parallel to the east coast and extends to about 150 Km north-south and 50 Km east-west. Several networks of wadis pass through the mountains (El-Keblawy et al., 2005).

The United Arab Emirates has a hyper-arid hot subtropical climate with a long hot summer and a short, mild winter. The rainfall is mainly precipitated in the winter season between November and March, with the highest intensity during February and March. The mean annual rainfall is about 110 mm with extreme temporal and spatial variations; the lowest is in Abu Dhabi (about 45 mm/year), inland desert (28 - 90.7 mm/year), and western coast (97.7 - 105 mm/year). The highest mean annual rainfall is recorded in the northeast mountainous region of the country and ranges between 125.6 and 172 mm/year. The annual average temperature is around 27 °C and humidity 45.0%. The mean temperature is around 20 °C in winter, but ranges between 35 - 40 °C in summer; it reaches above 50 °C on many summer days. In addition, humidity could reach more than 90.0% (UAE Ministry of Energy 2012, UAE Ministry of Environment and Water, 2015).

The combination of the low rainfall, with the high evaporation rates and high temperatures in addition to the high levels of water and soil salinity, are the major components of the drastic arid hot climates. Such climate is one of the most extreme and drastic climates on earth, which proposes the environmental stress as a major challenge faced in the UAE (Miller and Cope, 1996; Böer, 1997; Zahran, 1997; Peacock et al., 2003).

Environmental stresses, which are defined as a combination of biotic and abiotic challenges that cause the crop yields and productivity to decline (Ramegowda and Senthil-Kumar, 2015). The major biotic stresses are the herbivores or the pathogens that may attack various crops, while the abiotic stresses include the salt stress, the drought, the high temperatures and the high concentration of heavy metals. Plants naturally face the biotic stresses all over the world, but the burden of abiotic stresses such as drought and salt stress are added in the desert hyper-arid hot regions (Noy-Meir, 1973; Merquiol et al., 2002; Rewald et al., 2011; Shelef et al., 2016). The environmental stressors abrupt the plant physiology leading to plant injury or diseases. Plant development and productivity are highly impacted by drought and salinity which are the major challenging unfavourable environmental plant stressors occurring in UAE due to the hyper-arid hot desert climate (Flowers, 2004; Godfray et al., 2010; Tester and Langridge, 2010; Agarwal et al., 2013).

4. Major Effects of Drought and Salt Stresses on Plants

Drought and salinity are among the most damaging abiotic stresses affecting agriculture worldwide, limiting crop productivity and playing a major role in determining the distribution of plant species across different types of environments. Drought and salinity affect the plants in different ways. However, plants respond to drought and salinity via different complexes mechanisms and involve adaptive changes and/or deleterious effects. Therefore, most mechanisms were developed by plants to tolerate drought and salinity stress, which are schematically showed in (Figure 3).

4.1. Effects of Drought Stress on Plants

Drought is defined as water scarcity for some time sufficient to deplete soil moisture and negatively impact plants. Drought is regarded as one of the most prevalent stress factors globally, particularly in the arid and semi-arid regions (Galle et al., 2007). It is one of the abiotic stresses that control plant function and ecological stability. With the expected climate global changes, drought is expected to become a limiting factor that affects plant distribution and production (Eziz et al., 2017).

Causes of drought include low rainfall, high temperatures, and salinity. Drought is multidimensional stress and results in significant changes in plants' morphological, physiological, molecular, and biochemical traits (Seleiman et al., 2021). Several plants develop several mechanisms to tolerate drought, but this depends on the plant species. One mechanism that makes some plants tolerant to drought stresses is maintaining cell homeostasis, especially in water-deficit situations (Nalinaet al., 2021). However, many plants cannot develop such mechanisms and experience adverse impacts due to drought (Cosgrove and Rijsberman, 2014). The impacts of drought stress on plants include impaired germination, poor plant establishment, disruption in ion homeostasis, reduction in photosynthesis, inhibition of transpiration, and overall reductions in plant growth and productivity (Seleiman et al., 2021). Some of the major drought and salt stress effects on plants are summarized in (Table 1).

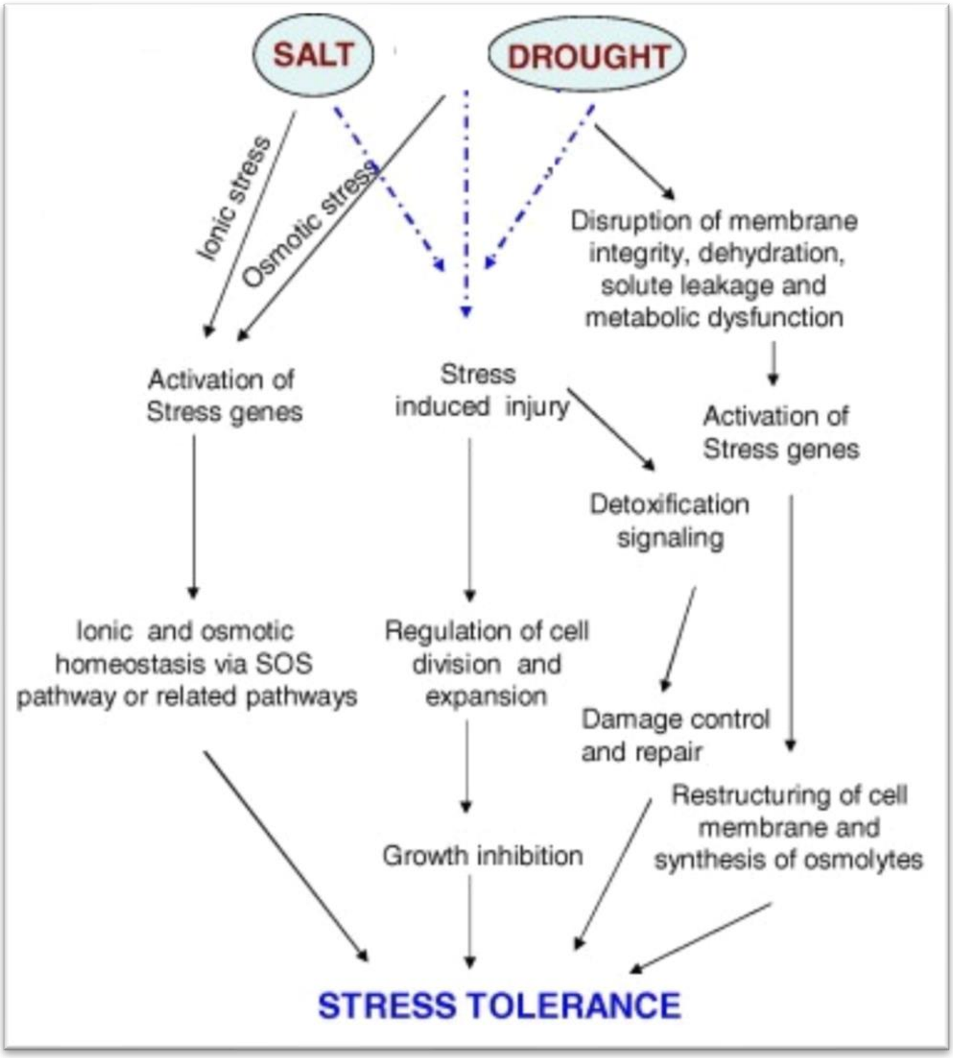

Figure 3. Summary of tolerance mechanisms in plants under drought and salinity stress. Adopted from Verslues et al. (2015).

Table 1. Summary of some of the major drought stress effects on plants.

Drought Stress			
Seed dormancy and germination	➢ Induce seed dormancy. ➢ Decrease the rate of germination. ➢ Reduce germination. ➢ Reduce seed water imbibition. ➢ Affect nutrient, availability, uptake, transport and accumulation. ➢ Affect enzyme activities and plant hormones.	**Plant metabolism**	➢ Disrupt carbohydrate metabolism and sucrose level. ➢ Oxidative damage and impairment. ➢ Reduces photosynthesis and the accumulation of sucrose in the plant leaves. ➢ Effect control signaling networks. ➢ production and accumulation of reactive oxygen species (ROS). ➢ Initiates the accumulation of secondary metabolites.
Plant morphology	➢ Reduce plant size. ➢ Impact the rate of photosynthesis and biomass production. ➢ Reduce leaves size. ➢ Decrease chlorophyll. ➢ Reduce cell enlargement, reduce plant height. ➢ Reduce biomass production. ➢ Effect on root morphology.	**Plant physiology**	➢ Decrease in cell enlargement. ➢ Reduces the photosynthesis process. ➢ Stomatal closure. ➢ Diminishes leaf water potential and turgor. ➢ Damage of the cell membrane and alteration of a plant membrane integrity ➢ Reduces photosynthesis, respiration, nutrients translocation and ion uptake.

4.1.1. Effect of Drought Stress on Seed Dormancy and Germination

Seed germination and early seedling growth are among the most critical stages in plant life sensitive to water stress (Ahmad et al., 2009). Drought significantly impacts seed dormancy and germination by impacting several biochemical and physiological processes concerned with embryo development (Bewley and Black, 1985). Typically, a seed germinates when soil water potential is above certain thresholds, usually after effective rainfalls in desert conditions (El-Keblawy, 2004; Lewandrowski et al., 2017). In the unpredictable arid deserts, however, several years receive little rainfalls. For example, out of 71 years of rainfall records in Sharjah Airport, UAE, 27 years received 50 mm or less; eight years received less than 10 mm (Feulner, 2006). In order to germinate in such dry years, seeds should tolerate drought stress. For example, Li et al. (2013) reported that drought suppresses and delays the germination of *Eremosparton songoricum*, an endemic desert plant. To cope with the drought stress, the plants accumulate osmolytes in the seeds and augments the activity of antioxidative enzymes (Li et al., 2013). Water limitation alters enzyme activity and reduces hydrolysis and utilization of lipids, carbohydrates, and protein (Ahmad, 1992).

The ability of seeds to recover their germination when transferred from an osmotic stress agent, such as polyethylene glycol (PEG), indicates that drought stress is not fatal in some plants. The recovery also indicates that the seeds can retain their germination ability until sufficient moisture is available for optimal germination (Elnaggar et al., 2019). This germination strategy is important for desert plants to adapt to the temporal precipitation unpredictability in the hot arid deserts. In the UAE deserts, where precipitation is greatly variable in time and place, the ability of seeds to maintain their viability in arid and saline conditions ensures their survival and germination when the germination bed receives enough water (Elnaggar et al., 2018).

4.1.2. Effect of Drought Stress on Plant Morphology

Plant morphology is the physical form and external structure of plants. Drought impacts the morphology by reducing the size of the plants, which in turn impacts the rate of photosynthesis and the plant biomass production. Drought also reduces the plant's leaves sizes, decreasing the chlorophyll and affecting plant morphology (Bhatt and Rao, 2005). Moreover, drought can also reduce cell enlargement, which reduces plant height. Drought can also reduce biomass production and affect root morphology and architecture (Malamy, 2005). For example, Bashir et al. (2019) assessed the drought effect on soybean root morphology and reported a significant reduction in root length, root area, and root diameter in drought-sensitive cultivars. Eziz et al. (2017) organized a meta-analysis from 164 studies and indicated that drought significantly increased the biomass allocation to roots than aboveground parts (stem, leaf, and reproductive mass). The response of herbaceous and woody plants to drought varied depending on species. Herbaceous plants allocated more biomass to roots than woody plants under drought stress (Eziz et al., 2017).

4.1.3. Effect of Drought Stress on Plant Metabolism

Drought adversely impacts the life-sustaining chemical transformation in the plants. Metabolism helps sustain the survival of a plant. However, drought disrupts the carbohydrate metabolism and the sucrose level (Møller et al., 2007). In turn, this reduces the export rate of a plant. Also, the condition makes the plant block some enzyme-catalyzed reactions. Oxidative damage and impairment in the plant are also results due to drought. Drought reduces photosynthesis and the accumulation of sucrose in the plant leaves (Miller et al., 2010). As a result, this impacts sucrose export, consequently affecting reproductive development.

Drought triggers control signaling networks by regulating the phytohormones. In addition, drought initiates the accumulation of secondary metabolites (Jogawat et al., 2021). Those authors reported that roots sense drought stress and produce signals that travel to the aboveground tissues to induce systemic phytohormones signaling, triggering the biosynthesis of secondary metabolites and stomatal closure to prevent water loss. Drought enhances the production and accumulation of reactive oxygen species (ROS), negatively affecting plant growth and reproduction. However, the plants produce secondary metabolites, such as enzymatic and nonenzymatic antioxidants, for scavenging ROS to protect them from drought stress (Jogawat et al., 2021).

4.1.4. Effect of Drought Stress on Plant Physiology

Plant physiology is concerned with chemical, physical, and biological functioning. Drought significantly impacts several plant physiological and biochemical processes, such as carbohydrates production, photosynthesis, and respiration (Miller et al., 2010). The main aim of a plant at this point is to bring adjustments. The adjustments ensure that a plant counters any loss of water and ensure maximum preservation of hydric status. For example, photosynthesis decreases as the plant closes the stomata and alters the function of some enzymes. Notably, this ensures that a plant reduces the use of more water during the drought season. The plants also ensure a decrease in cell enlargement of a plant (Farooq et al., 2008; Jaleel et al., 2008). The main drivers of plant responses during drought periods are oxidative stress directly or indirectly generated in plants. In particular, this leads to the damage of the cell membrane and alteration of a plant membrane integrity. Consequently, this results in acute metabolic disorders that make the plant not use water through physiological and biochemical functioning (Kapoor et al., 2020).

4.2. Drought Tolerance Mechanisms

Drought tolerance refers to a cost-intensive phenomenon that enables a plant to develop a mechanism to oppose the drought effects. Drought tolerance involves controlling cellular osmotic water flux and ensuring adjustment through osmoregulation biosynthesis (Wei et al., 2019). Osmotic regulation is essential to plants' survival by helping them grow during drought conditions. Another important mechanism that makes some plants tolerant to drought stresses is maintaining cell homeostasis, especially in water-deficit situations (Flowers and Yeo, 1986; Hasegawa et al., 2000; Apel and Hirt, 2004; Flowers, 2004; Agarwal et al., 2013). Some changes are experienced in the whole plant, molecular, tissue, and physiological level to help a plan tolerate drought periods (Reddy et al., 2004; Zhao et al., 2008). Also, the majority of plants limit the area of leaves to reduce the use of more water.

4.3. Effect of Salt Stress on Plants

Based on adaptive evolution, plants can be classified roughly into two major types: the halophytes that can withstand salinity and the glycophytes that cannot withstand salinity and eventually die (Sairam and Tyagi, 2004). The majority of main crops belong to this second category. Halophytes are the most tolerant plants to high salinity. They can naturally tolerate to grow in salinity higher than seawater and still with a high yield of seeds and biomass (Flowers and Colmer, 2008; Koyro and Lieth, 2008; Ksouri et al., 2008; Shelef et al., 2016). Halophytes can be sub-classified into three categories; facultative, obligatory, and habitat-indifferent halophytes (Von Sengbusch, 2003). Examples of halophytes include the *Iris hexagona* Walter, (Van Zandt and Mopper, 2004) and *Atriplex nummularia* Lindl (Uchiyama, 1987). In addition, habitat-indifferent halophytes can cope with both salty and salt-free soils (Cushman, 2001) and thus, offer an opportunity to study drought and salt tolerances in soils of different salinity. S*alsola drummondii* Ulbr., Z*ygophyllum qatarense* Hadidi., *Suaeda vermiculata* Forssk. ex J. F. Gmel., *Anabasis setifera* Moq. and *Suaeda aegyptiaca* (Hasselq) Zohary are examples of habitat-indifferent plants in the UAE (Jongbloed et al., 2003, El-Keblawy et al., 2016a, b; Elnaggar et al., 2018, 2019; Gairola et al., 2019).

Salt stress is the condition where a high level of soluble salts characterizes the soils. So, salt stress arises in plants due to excess soluble salts. Specifically, sodium and/or chloride salts are accumulated in the plants (Munns, 2005). Salt stress has some adverse effects on plant growth and development. The detrimental effect of salt stress is noticed on the whole plant and different plant parts, resulting in plant death and decreased productivity. The harmful effect of salinity due to excess salts in the plants affects the hormones and enzymes responsible for the effective growth of plants (Munns and Tester, 2008). The salinity in plants can also result in a loss in crop production that threatens global food security. Salt stress occurs in arid and semi-arid areas due to extended drought periods. Generally, salt stress causes the plants to cause physiological and metabolic changes, including nutritional imbalance, seed germination, slow growth rates, and inhabitation of water uptake. The two mechanisms that plants use to respond to soil salinity stress effectively include rapid and slow responses. The rapid response, where high salt concentration complicates water absorption by the roots due to decline in the soil solute potential. This salty soil has direct harmful effects on rooting cell growth and associated metabolism. On the other hand, the slow response happens when the plant uptake of salt. This increases the accumulation of sodium and chloride ions in high concentrations, resulting in ion toxicity (Poljakoff-Mayber et al., 1994; Tobe et al., 2001; Munns and Tester, 2008).

4.3.1. Effect of Salt Stress on Seed Dormancy and Germination

Salt stress inhibits seed germination level and speed. Salinity induces seed dormancy and inhibits germination due to the low osmotic potential of the ambient water and soil. When plants experience salinity conditions, they are likely to face slow germination rates (Khan and Gul, 2006; Soltani et al., 2006; El-Keblawy et al., 2010; Zhang et al., 2010; Laghmouchi et al., 2017). Excess absorption of sodium and chloride ions results in specific ion toxicity stress, disrupting the biochemical processes (Hussain et al., 2019). The biochemical processes include energy production, respiration and protein, and nucleic metabolism (Uçarlı, 2020).

Seed dormancy and germination can also be affected by the soil salinity through epigenetic effects and/or maternal habitat. (El-Keblawy et al., 2017; Siles et al., 2017; El-Keblawy et al., 2018). The environmental factors can cause trans-generational changes in the seeds due to exposure to environmental stress at various generations. Consequently, ecological stress can cause hormonal imbalances of the plants that could be transmitted to seeds. The hormones affected by environmental stress include gibberellins and abscisic acid. In other words, salinity reduces the water availability and the nitric oxide that helps in activating the hormones responsible for growth and dormancy (Tomar et al., 2021). These hormones are mainly responsible for healthy and effective seed germination and dormancy (El-Keblawy et al., 2010). Thus, this means the subjection of salt in harsh weather conditions with high salinity, passing the salt stress information through ineffective seed dormancy and germination. Moreover, high salinity causes oxidative stress since the plant experiences a low intake of oxygen required for food production in the seed. Sodium and chloride ions are the main sources of oxidation stress in the seeds (Kumar et al., 2017).

4.3.2. Effect of Salt Stress on Plant Morphology

Salt stress has several adverse effects on plant morphology. For instance, salt stress inhibits the growth of the plants due to oxidation stress which results from ion toxicity. For example, In *Suaeda salsa*, salt stress impacts its tillers and shoot diameter (Guan et al., 2011). Hence, the plant fails to undertake the metabolic processes that include respiration, photosynthesis, and transpiration. For example, when the plant fails to undertake the transpiration processes, it can wither due to a limited amount of water. The plant can also fail to produce healthy fruits that are prone to diseases and pests. The other effect of salt stress on morphology is the reduced leaf sizes and branches. Reduced leaves are a result of the decreased water leaf potential, which exhibits effective transpiration. Mill *(Foeniculum vulgare*) showed reduced productivity due to salt stress (Dolatabadian et al., 2011). Lower leaf water potential induces physiological and morphological changes, influenced by the increased presence of sodium and chlorine ions.

4.3.3. Effect of Salt Stress on Plant Metabolism

High salt levels increase sodium ions that cause toxic effects on plant metabolism due to disruption of the genes and enzymes. Therefore, the excessive salt produces more reactive oxygen species (ROS), reduces the enzyme efficiency, and prevents the production of important enzymes, causing a metabolic imbalance in the plant. ROS production is associated with respiration and photosynthesis in salt stress conditions because it has a dual role (Miller et al., 2008; Suzuki et al., 2011). When the ROS (reactive oxygen species) has a dual role, then it can result in cell damage because of the increased ionic concentration that is toxic. For example, hydrogen peroxide, responsible for the oxidation of the plant activities, can be highly toxic if assigned more than one role. Notably, salts trigger the production of more oxygen that destroys metabolic activities such as photosynthesis.

4.3.4. Effect of Salt Stress on Plant Physiology

Salt stress causes different flaws in the physiological processes of a plant. The physiological processes include the activities conducted by the plant to enhance more yields. Notably, these processes require ions, hormones, water, and air to run through successfully. In salt stress, plants fail to conduct physiological functions due to disruption caused by the sodium and chloride ions present in saline water and soils (Tavakkoli et al., 2011). The ions occupy the plant cells, making them lacking enough air responsible for the conduction of the physiological processes. There are various physiological processes in the plant that are affected by salt stress. Photosynthesis is among the physiological process affected by salt stress. Salt stress interrupts photosynthesis because the toxic ions prevent the entry of air and transportation of the by-products throughout the plant. In particular, the accumulation of sodium and chloride ions changes the K: Na ratio, which conversely affects the physiological process of photosynthesis (Li et al., 2020).

Salinity also inhibits photosynthesis because the sodium and chloride ions accumulate in the chloroplast cells that contain chlorophyll (Zhang et al., 2002). Therefore, this implies that the content in the chlorophyll reduces the cellular metabolic rates of the plant. The salt stress also affects the stomata conductance responsible for absorbing the CO_2 required for the photosynthesis process (Seemann et al., 1985) The other physiological process affected by plant salt stress is the leaf water potential (Kaymakanova and Stoeva, 2008).

Salinity in a plant reduces the water potential of the roots. Thus, this means that the roots fail to draw water from the soil. The low water potential of the root causes reduction of the water potential in the leaves (Dell'Aversan et al., 2021). When a plant experiences high salt stress, the transpiration rate is likely reduced (Romero-Aranda et al., 2001). Eventually, this can result in a wilting condition. However, the reduction in osmotic pressure when soil receives more water increases leaves water potential, making the plant accumulates enough water required for other metabolic processes.

Among the other physiological process that is affected by salt stress is nutritional imbalance. The condition results from the inability of the plant to absorb enough nutrients required for the plant growth (Tuna et al., 2007). High salt levels increase the sodium ions, which reduce the ability of the plant to absorb other ions like calcium, potassium, magnesium, and nitrogen (Rozeff, 1995). Notably, these ions are responsible for the formation of proteins and starch. In other words, salt stress in plants causes ionic imbalances in the plant. For example, a high salt level reduces nitrogen uptake because of the inverse relationship between the sodium ions and ammonium ions (Qadir and Schubert, 2002). Also, the presence of chloride ions inhibits the absorption of nitrate and phosphate ions.

5. Salt Resistance Mechanisms in Halophytes

Salt resistance mechanisms to salt stress are grouped into two major categories: salt avoidance and salt tolerance (Sabovljevic and Sabovljevic, 2007). Figure 4 summarize these main categories.

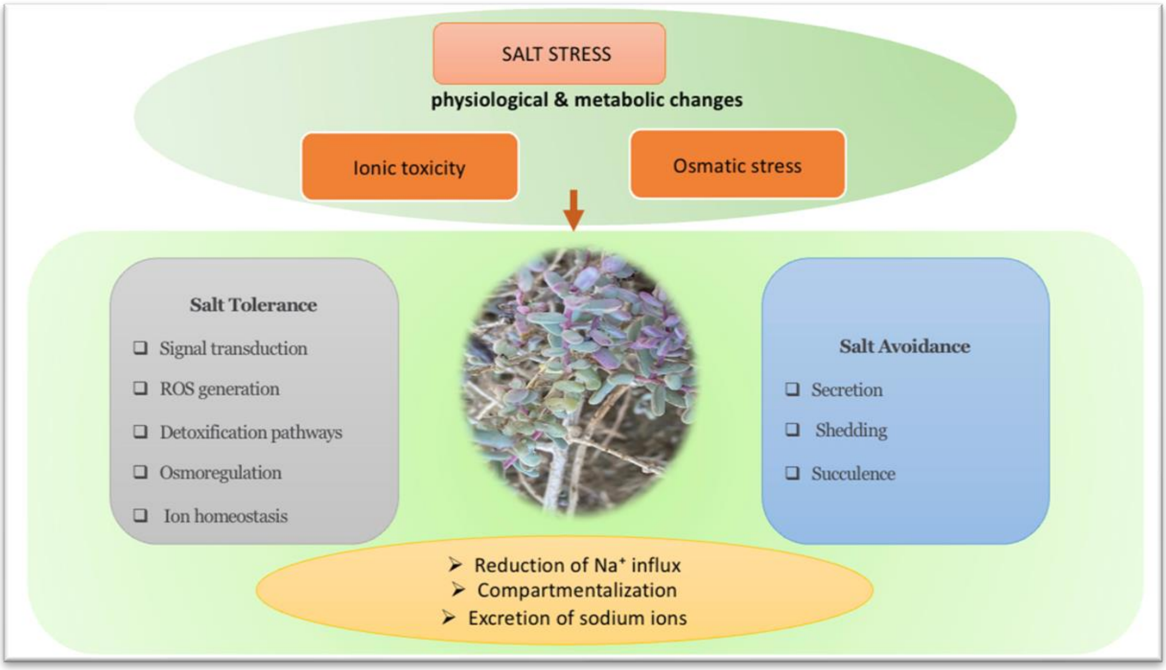

Figure 4. Effects of salt stress on halophytes and main strategies of adaptation.

5.1. Salt Avoidance Mechanisms

Halophytes can resist high salt stress by adopting several special morphological and anatomical adaptations called salt avoidance mechanisms (Flowers et al., 1986). Salt avoidance is a resistance mechanism keeping the salt ions away from the sensitive structures, which could be damaged due to exposure to high salt levels (Allen et al., 1994). Salt avoidance mechanisms help some halophytes to counter the effect of high salt stress. In particular, salt avoidance involves keeping salt ions away from parts that can harm a plant. The plants, especially halophytes, can avoid salinity by growing during the more favorable times and sites. They also limit root growth and root absorption activity to specific soil depth (Breckle, 1990). Three mechanism helps halophytes avoiding salt stress, including salt secretion, salt exclusion, and shedding old leaves. Salt exclusion is essential since it helps plants minimize ion toxicity and accelerates water deficit growth and development (Waisel et al., 1986; Chaudhary, 2019). Besides, it also diminishes CO_2 uptake in plants (Lovelock et al., 2016;

Tomlinson, 2016). For example, 99% of the salts are excluded through the roots in the case of mangrove species (Lovelock et al., 2016; Tomlinson, 2016).

Salt secretion is the ability of some plants to excrete excess salt and enhance plant growth (Weber, 2009). These adaptive features include shedding of leaves, leaf burns and succulence (Figure 5). Moreover, plants can also reduce extra internal salts by shedding off old leaves. Shedding leaves allow plants to diminish and control the accumulation of NaCl concentrations (Albert, 1975; Dawalibi et al., 2015). Plants can also manage salinity through the process of succulence. An example of species with the succulence process is *Suaeda vermiculata*, which belong to the A*maranthaceae* family. This mechanism enables plants to undergo cell size increases and decreases. Consequently, this increases the water content per unit surface area (Grigore and Toma, 2017).

Figure 5. Vegetative branch of *Suaeda vermiculata* Forssk. ex J. F. Gmel. showing succulent leaves.

5.2. Salt Tolerance Mechanisms in Halophytes

Salt tolerance refers to a plant ability to survive, compete, and complete its life cycle under high salinity conditions (Parihar et al., 2015). The tolerance mechanisms involve using physiological, molecular, and metabolic changes in plants to facilitate the adaptation of plants to stressful situations (Ashraf and Harris, 2004; Koyro et al., 2009). The salt tolerance mechanisms include signal transduction, reactive oxygen species (ROS) generation, detoxification pathways, osmoregulation or ion homeostasis through osmoprotectants, and differential expression of salt-responsive genes and transcription factors (Figure 6).

Understanding salt tolerance is essential when developing plants that are resistant to unfavorable conditions. Salt tolerance in crops could be induced through using genetic engineering techniques or traditional breeding processes (Anwar and Kim, 2020). Halophytes can act as good examples to determine the characteristics that plants need to survive in saline environments. The salt tolerance also helps determine the mechanism that can make plants resists salinity.

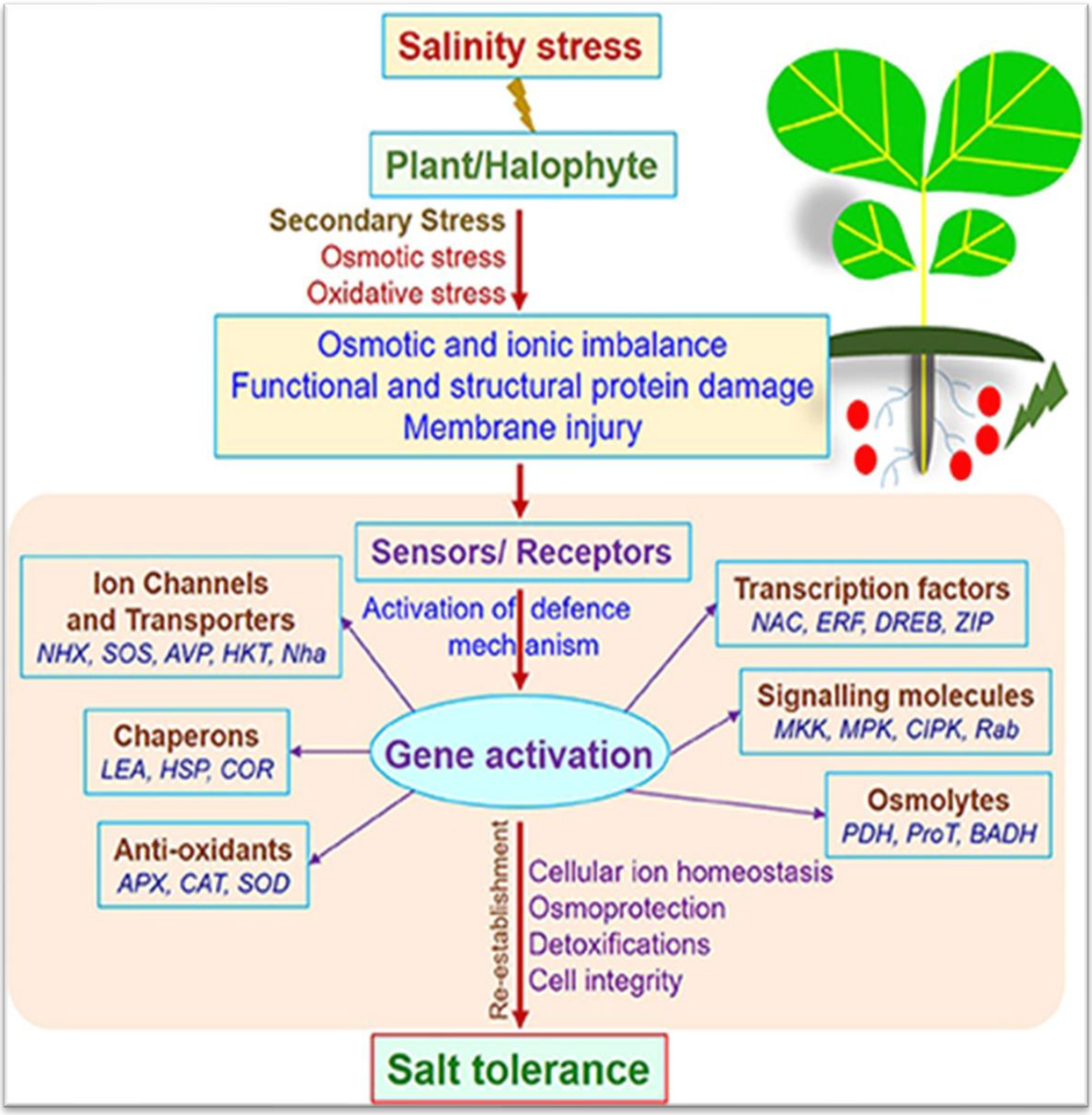

Figure 6. Salinity stress tolerance mechanisms in halophytes. Adopted from Avinash and Bhakti (2017).

5.2.1. Seed Germination Tolerance in Halophytes

Halophytes developed special adaptations at the germination stage of development to tolerate the stressful conditions in their natural habitats. The level of salinity tolerance at the germination stage differs from that at the later growth stages (Ungar, 2017). At higher salinity conditions, halophytes experience delayed germination due to induction of seed dormancy (Ungar, 1996). The ability of seeds to overcome the high level of salinity is essential for seed germination and seedling establishment (Gorai et al., 2014). Therefore, understanding salt tolerance mechanisms during the germination stage in halophytes is important in developing salt-tolerant crops (Aslamsup et al., 2011).

Some halophytes germinate at more than double seawater salinities. For example, *Salsola drummondii* seeds germinated and recovered their germination in up to 1000 mM NaCl (El-Keblawy et al., 2020). Factors determining halophyte seed establishment and plant development are low precipitation, high temperatures, and light intensity (Khan et al., 2000). These factors, together with salinity, determine the level and speed of seed germination and, therefore, the fate of seedling establishment and community structure (El-Keblawy, 2004; Khan and Weber, 2007).

Halophytes can tolerate salinity by developing mechanisms that induce seed dormancy (Wahid et al., 1999; Song et al., 2017). During dormancy, halophytes prevent their seeds from germination (Naidoo and Naicker, 1992;). In particular, this ensures that seeds do not die in high salinity situations. Conversely, in high salinity regions, high precipitation (Shelef et al., 2016) provides the chance for seed germination. Thus, during this period, there is a decrease in soil salinity, and the impact of salt becomes less drastic (Ungar, 1982; Joshi et al., 2015).

5.2.2. Physiological Tolerance Mechanisms in Halophytes

Halophyte plants also develop physiological mechanisms that enable them to cope with periods of salt stress. Physiological mechanisms that make halophyte plants tolerate salinity include compartmentalization, salt accumulation, and ion homeostasis. At the physiological level, halophytes develop a mechanism that helps control the uptake of Na^+ (sodium) and Cl^- (chlorine) (Bose et al., 2014a; Gupta and Huang, 2014). Notably, this ensures that halophytes maintain an osmotic balance. The Plants then preserve the Mg^{2+} (magnesium) and K^+ (potassium) that are necessary to activate essential enzymes. Thus, uptake Mg^{2+} ensures that the seeds can survive during adverse conditions. Another mechanism that plant uses to regulate ionic homeostasis. Ion homeostasis occurs through selective ion accumulation (e.g., Ca^{2+}, K^+) or exclusions of ions (e.g., Na^+ and Cl^-) (Knight and Knight, 2000; Sanders et al., 2002). Sodium absorption competes with that of potassium through the common transport systems. Therefore, activating K^+/Na^+ (sodium chloride) intracellular selective salt accumulation is essential for seed survival (Maathuis and Sanders, 1996). Besides, plants use other stress signaling pathways, such as the salt overly sensitive (SOS) pathway, which can be considered a pivotal regulator of plant ionic homeostasis and salt resistance (Hasegawa et al., 2000; Sanders, 2000). SOS1, SOS2, and SOS3 are the main components of the SOS signaling pathway.

Salt accumulators are a group of plants that tolerate salt stress through accumulating salts in their cells. Among the salt accumulator plants are *Tamarix petandra*, *Distichlis spicata*, and *Spartina alterniflora* (Mishra and Tanna, 2017). Such plants have specialized cells called salt glands present on the surfaces of the leaves and are useful for storing excess sodium chloride (NaCl) (Mishra and Tanna, 2017). Some other halophytes can accumulate excess salts within the cells up to a certain toxic level, behind which the plant cannot survive (Mishra and Tanna, 2017). Some salt accumulators tend to avoid salinity stress by minimizing the leaves cytosolic salt concentrations by transporting sodium and chloride ions into a central vacuole. Meanwhile, the accumulation of salt into the central vacuoles leads to the absorption of more water that causes cell swelling (Mishra and Tanna, 2017).

A typical halophyte salt tolerance mechanisms include the accumulation of salt and water inside the vacuole, pushing the cytosol toward the cell membrane and cell wall, where the cell preserves its turgidity. An example of succulent halophytes is *Salicornia virginica*. The plant's ability to control the salt accumulation and perform compartmentalization of sodium is vital for the development of halophytes (Parks et al., 2002). Sodium (Na^+) and chloride (Cl^-) ions transfer into vacuoles (Compartmentalization) will separate sodium and chloride from the cytosolic activities (Glenn et al., 1999). However, they are considered very active osmolytes that can easily help the plant process the decrease in the extracellular osmotic potential due to salt stress. Ultimately, compartmentalization can sustain the plant water absorption from saline soils (Parks et al., 2002). The main reason for such compartmentalization is to reduce the toxicity resulting from salt stress (Blumwald et al., 2000).

5.2.3. Metabolic and Biochemical Tolerance Mechanisms in Halophytes

Antioxidant production

Several plant species adopt various mechanisms for controlling reactive oxygen species (ROS) levels to optimize their role in signalling and preventing cellular components damage. Detoxification of ROS could be through the production of antioxidants. Antioxidant production enables the plant to optimize its ROS level. Halophytes can tolerate high salinity regions due to their ability to overcome high oxidative stress. Notably, this is made possible by their superior antioxidant capacity allowing them to tolerate conditions of high salt concentration. The threshold of reactive oxygen species (ROS) oxidative damage differs between glycophytes and halophytes. For example, Ozgur et al. (2013) indicated that the significant increase in lipid peroxidation in some halophyte shoots starts only after 150 mM NaCl (sodium chloride) treatment. However, the same concentration is lethal in most glycophytes. Unlike glycophytes, halophytes can tolerate high oxidative stress due to their superior antioxidant capacity, which allows them to tolerate high salt concentrations (Flowers and Colmer, 2008; Kosová et al., 2013; Ozgur et al., 2013).

There are two types of antioxidants: enzymatic and nonenzymatic antioxidants. The key enzymatic antioxidants include superoxide dismutase, catalase, ascorbate peroxidase, guaiacol peroxidase, glutathione s-transferase, and glutathione reductase. In addition, the most important nonenzymatic antioxidants include the ascorbate, carotenoids, glutathione, and proline (Hasanuzzaman et al., 2012)

Enzymatic antioxidants

Superoxide dismutase (SOD)

SOD is an antioxidant enzyme that easily repairs the damage of reactive oxygen species (ROS). The enzyme achieves this by catalyzing superoxide $O_2^{\bullet -}$ to hydrogen peroxide and oxygen (Sharma et al., 2012). Superoxide dismutase (SOD) acts as the first defense line against oxidative damage (Foyer and Shigeoka, 2011). Halophyte plants have an exceptional capability to use SOD to protect themselves from biotic and abiotic stresses (Das et al., 2016).

Catalase (CAT)

CAT is among the most effective antioxidant defending oxidative stress through catalyzing the decomposition of hydrogen peroxide (H_2O_2) into water and oxygen with a very high turnover rate (Verma et al., 2019). CAT activity depends on the species, the plant developmental and metabolic states, and the duration and strength of the stress (Chaparzadeh et al., 2004). Previous results showed inconsistent results for the effect of salinity on CAT in halophytes; it increased in some halophytes but decreased or showed little change in others (Jithesh et al., 2006).

As*corbate peroxidase* (APX)

APX plays a key role against oxidative damage through scavenging hydrogen peroxide in cytosol and chloroplast (Li et al., 2021). Generally, the plant stress tolerance in glycophytes and halophytes is increased with the upregulation of APX expression/activity (Gupta et al., 2018).

Peroxidase (POXs)

Peroxidase is an enzyme that can scavenge the hydrogen peroxide primarily in the apoplast (Fagerstedt et al., 2010). POXs enzymatic family is widely distributed in the higher plants, where they are involved in many biological processes, including lignification, oxidative metabolism, salt, and heavy metal stress tolerance (Passardi et al., 2005; Gao et al., 2008). Halophytes use POXs in the signaling and/or scavenging of reactive oxygen species (ROS) (Jithesh et al., 2006; Bose et al., 2014b).

Non enzymatic antioxidants

The enzymatic antioxidants do not destroy the most toxic reactive oxygen species (ROS) (Ahmad, 2014). Examples of these reactive oxygen species (ROS) include singlet oxygen ($^1O_2$) and hydroxyl radical ($OH^{\bullet}$) (Bose et al., 2014b). When plants experience such toxic ROS, they use the nonenzymatic antioxidant to neutralize the ROS (Racchi, 2013). Examples of nonenzymatic antioxidants include carotenoids, tocopherols, glutathione, flavonoids, and ascorbic acid.

Glutathione (GSH)

GSH, is a very common cysteine-containing tripeptide, plays a critical role in restoring the ascorbic acid through the ascorbate-glutathione cycle (Foyer et al., 1997).

Generally, GSH is found in a reduced form and abundantly present in most cell compartments like chloroplasts, cytosol, mitochondria, vacuole, endoplasmic reticulum, peroxisomes and apoplast (HongBo et al., 2005). GSH is used as a substrate of glutathione S-transferase (GST) enzyme, which results in clearing harmful components and protecting the cell (Gill and Tuteja, 2010). It has been reported that the halophytic *Lycopersicon pennellii* exhibited an increased content of GSH under salt and oxidative stress condition compared to other relatives glycophytes, such as *Solanum lycopersicum* (Shalata et al., 2001).

Carotenoids

Carotenoids are organic lipophilic compounds mainly located in chloroplasts that provide a photo-protection system to the photosynthetic systems. The function of carotenoids is unique as they are considered antenna molecules in absorbing the light beams of the visible spectrum in the region ranging from 450–570 nm and transferring the captured energy to the chlorophylls (Taiz and Zeiger, 2006). It has been reported that carotenoids provide photoprotection to the photosynthetic systems. They are involved in peroxyl and singlet oxygen ($^{1}O_2$) radicals scavenging, generated during extreme chlorophyll excitation (Demmig-Adams and Adams III, 1996). Plant tolerance to oxidative and salt stress increases with the increase of carotenoid concentrations. As carotenoid concentrations had increased significantly in halophytes, but not in glycophytes, during salt stress (Koyro, 2006), this highlights a greater role in quenching reactive oxygen species (ROS) (Youssef, 2009). This is observed in *Suaeda vermiculata* in its salty habitat as shown in the published results of the study of this PhD Memory (Figure 7).

Figure 7. Colored leaves of *Suaeda vermiculata* Forssk. ex J. F. Gmel.in salty UAE habitats.

Osmolytes production

Plants typically produce osmolytes under salt stress. Osmolytes are non-toxic metabolites synthesized and accumulated in the cytosol. The osmotic balance of the osmolytes regulates and maintains water influx and decreases water efflux outside the cell, maintaining the cell volume (Hasegawa et al., 2000). There are several forms of osmolytes, such as amino acids, proline, glycine betaine, polyols, and sugars (Ashraf and Harris, 2004). Osmolytes do not interfere with the plant metabolic activities, as they are accumulated in the cytoplasm to support the plant cell under osmotic and salt stress conditions (Chen and Murata, 2002). Halophytes produce several major osmolytes, such as proline and glycine betaine, to adjust their osmotic potential at saline conditions and provide protection against reactive oxygen species (ROS) (Jithesh et al., 2006). The accumulation of osmolytes in the cytosol enable them to osmotically balance the high salt concentration present outside the cell, thus maintaining the osmotic gradient and reset the effect of the high osmotic pressure of the vacuoles due to high sodium chloride concentrations present therein (Glenn et al., 1999; Zhu, 2001).

Proline analogues

Proline is a non-toxic amino acid with low molecular weight and high solubility in water (Ashraf and Foolad, 2007). Bohnert and Jensen (1996) reported that proline is used for cellular osmotic regulation between cytoplasm and vacuoles, scavenging the reactive oxygen species (ROS) to protect the membrane integrity, maintaining a low NADPH (Nicotinamide adenine dinucleotide phosphate) to $NADP^+$ ratio, and stabilizing the antioxidant enzymes. Several halophyte studies have demonstrated a beneficial effect of proline accumulation (Radyukina et al., 2007; Szabados and Savoure, 2010).

The proline accumulation depends on species and stress levels (Rodriguez et al., 1997; Ghoulam et al., 2002). Free proline accumulation is important for decreasing the reactive oxygen species (ROS) oxidative stress, but its catabolism in the mitochondria can increase ROS production (Miller et al., 2009). Therefore, it has been suggested that the capability of halophytes to control the catabolism of proline may be a key step in understanding salt tolerance (Sanada et al., 1995).

The current research focuses on determining the effects of drought on the germination and seed dormancy in *Suaeda vermiculata,* an important species of Amaranthaceae in UAE.

6. Family Amaranthaceae in the United Arab Emirates (UAE)

Amaranthaceae Juss., is a taxonomic family with a widespread and cosmopolitan distribution, most abundant in tropics, subtropics, and dry, warm-temperate regions (Müller and Borsch, 2005). Amaranthaceae (commonly called the Amarant) and it is one of the more representative families of UAE flora with the Asteraceae, Poaceae, Fabaceae, Boraginaceae, Brassicaceae and Caryophyllaceae.

Amaranthaceae species could be annual or perennial herbs, shrubs, or subshrubs, and rarely liana and trees. There are about 26 halophytes Amaranthaceae species in UAE (Gairola, 2019). Most of the Amaranthaceae species in the UAE are succulent, and many species have stems with thickened nodes. They have simple, alternate, or opposite leaves. They are terete or flat with extremely variable shapes with toothed margins or entire. The flowers are small, solitary, or aggregated in cymes or spikes, hermaphrodite, and rarely unisexual (Jongbloed, 2003). The diaspores are seeds or utricles, and more often, the perianth persists, which is modified in fruit to help in the dispersal. The vertical or horizontal seed often has a thickened or woody seed coat with a white or green embryo, either spirally or without perisperm or annular (rarely straight) (Basu et al., 2014).

Some Amaranthaceae species are used as vegetables, such as *Spinacia oleracea* and *Beta vulgaris*. The seeds of *Chenopodium berlandieri*, *Ch. quinoa and Ch. pallidicauleare* are edible and used as pseudocereals. Many Amaranthaceae species are also used indirectly as a source of soda ash, such as members of the genus *Salicornia*. Some Amaranthaceae species have medicinal properties such as *Dysphania ambrosioides* and *D. anthelmintica*. In addition, several species are used as ornamental plants (Sharma, 2004). In the UAE, *Salicornia bigelovii* Torr., *Suaeda fruticosa* Forssk. ex J.F. Gmel. and *Haloxylon stocksii* (Boiss.) Benth. et Hook. f. are used as feedstocks for biofuels (Abideen et al., 2011; Abideen et al., 2012). Some species are highly palatable for camels feeding (Towhidi and Zhandi, 2007) and *Amaranthus lividus* that was recently discovered (Shahid and Rao, 2015). Most members of the Amaranthaceae family are halophytes (Ocal Ozdamar et al., 2014). Amaranthaceae family shows a greater extent (20%) of salt resistance mechanisms than any other families (Flowers et al., 1986) and play a vital ecological role in the vegetation of the UAE ecosystems (Brown, 2006).

6.1. Genus *Suaeda*

Suaeda Forssk.ex J.F. Gmel., is a genus of the family Amaranthaceae. The species of *Suaeda* are mostly annual or perennial herbs, subshrubs, or trees glabrous or pubescent, glaucous or not. Stems are simple or branched. Leaves alternate or opposite, linear to narrow-elliptic, fleshy (Walsh, 1996). Flowers all bisexual or bisexual with horizontal or vertical seeds (Fisher et al.,1997). This genus includes plants using either C3 or C4 carbon fixation (Schütze et al., 2003).

There are 110 species of *Suaeda* distributed in worldwide (Welsh et al., 2003). Many species have thick, succulent leaves, a characteristic seen in various plant species that could be founds in salty habitats (Bassett et al., 1978). Plants belonging to the genus *Suaeda* are common in arid and semiarid UAE regions. Typically, these plants grow on flat, often dry and/or somewhat saline soils, with some species in salt marshes.

Suaeda species has great economic and medical importance. For example; *S. fruticosa* can be utilized for obtaining high-quality edible oil from seeds (Weber et al., 2007) and domestic soap from burnt leaves (Freitag et al., 2001). *S. asparagoides* has been used as a traditional Korean folk herbal medicine for the treatment of functional gastrointestinal disorders (Park et al., 2007). In Mexico, some species such as *S. pulvinata* are cooked in traditional dishes. In addition, young leaves of *S. maritima* can be consumed raw or cooked and the ashes have been used to create a material used in making soap and glass (Launert, 1981). In United Arab Emirates, *S. aegyptiaca* used for tooth and gum problems and young shoots are eaten (Jongbloed et al., 2003).

6.1.1. Suaeda vermiculata

Suaeda vermiculata Forssk. ex J. F. Gmel., is a habitat-indifferent halophyte that can cope with both salty (Figure 8) and salt-free soils (Figure 9). It is a perennial succulent shrub that can reach up to150 cm in high, with woody and very branched steam (Figure 10). Stems are pale green at first, becoming grey and fissured. Leaves are succulent, alternate, subsessile or sessile; the older leaves are obovate to oblong and elliptical, and flat on upper side. The inflorescences are yellow, minute with 2-5 flowered axillary clustered on terminal spikes interspersed with leaves (Jongbloed, 2003). Flowers are bisexual, bracteated, with scarious bracts. Perianth segments are persistent. Fruits are round, succulent, reddish, without wings. Seeds vertical with spiral embryos, about 1.5 mm in diameter, glossy back, rounded, and slightly flattened (Figure 11).

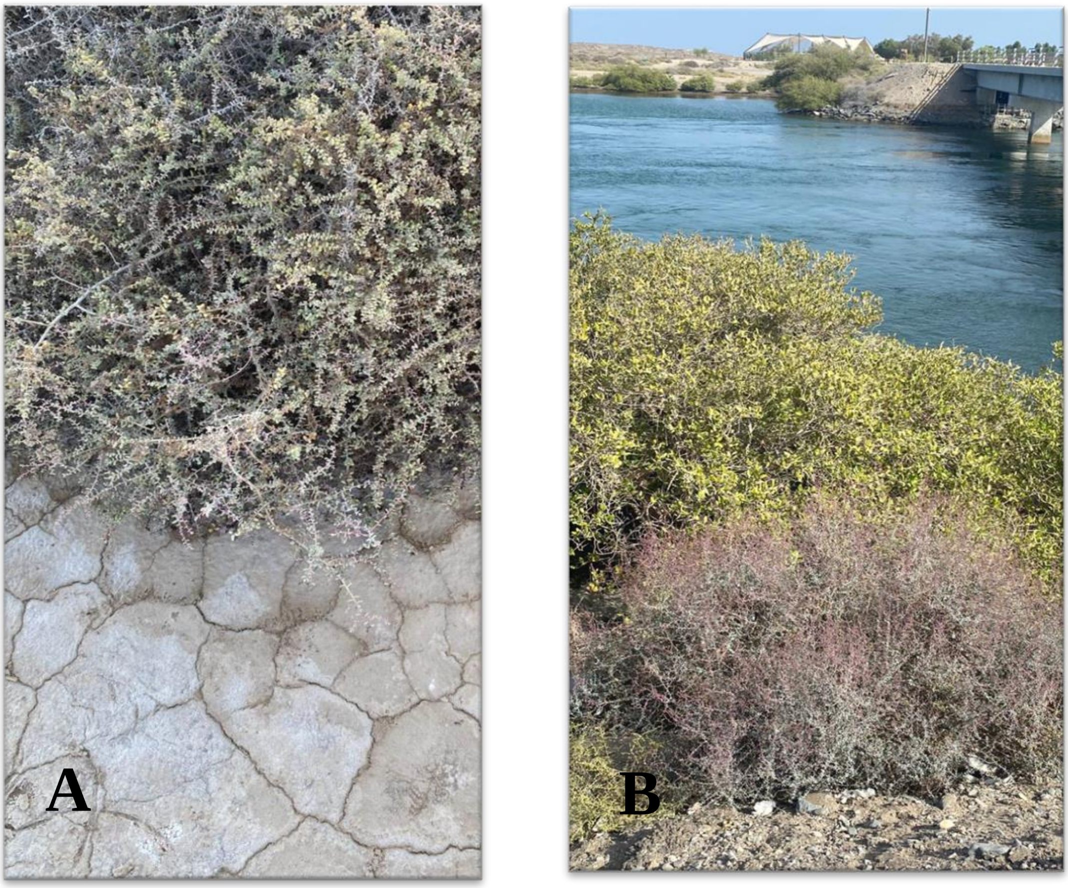

Figure 8. *Suaeda vermiculata* Forssk. ex J. F. Gmel. (A) growing in a hyper-saline salt marsh. (B) in a growing in non-salty coastal zone above an intertidal area with mangrove (*Avicennia marina*) near Khor Kalba (UAE).

Figure 9. *Suaeda vermiculata* Forssk. ex J. F. Gmel. growing in a non-saline soil in the UAE.

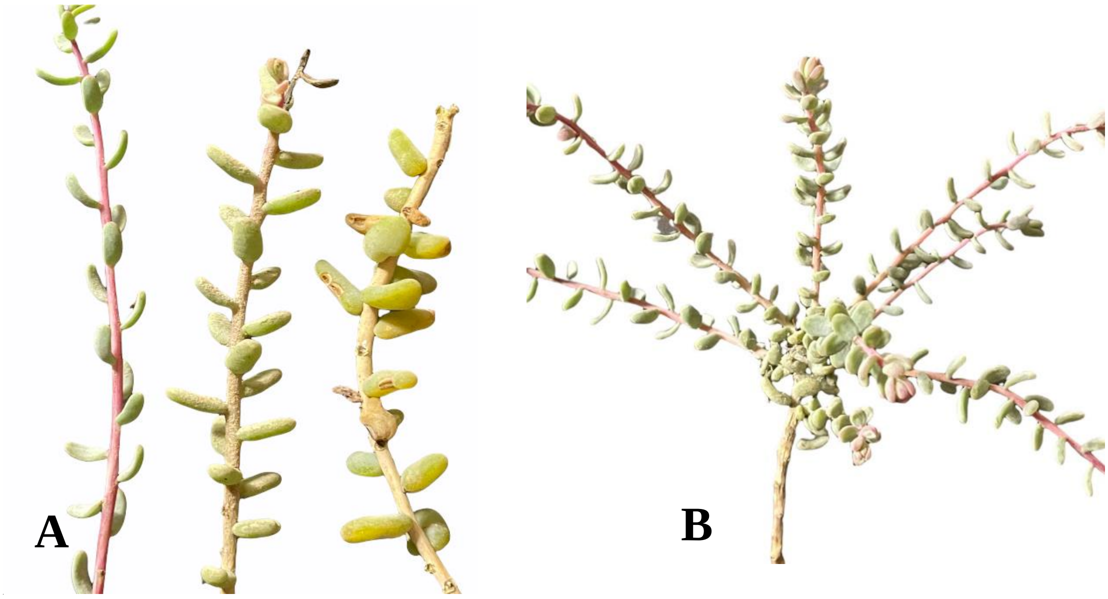

Figure 10. *Suaeda vermiculata* Forssk. ex J. F. Gmel. A: Stems with different ages (youngest is on the left). B: Healthy branched stem.

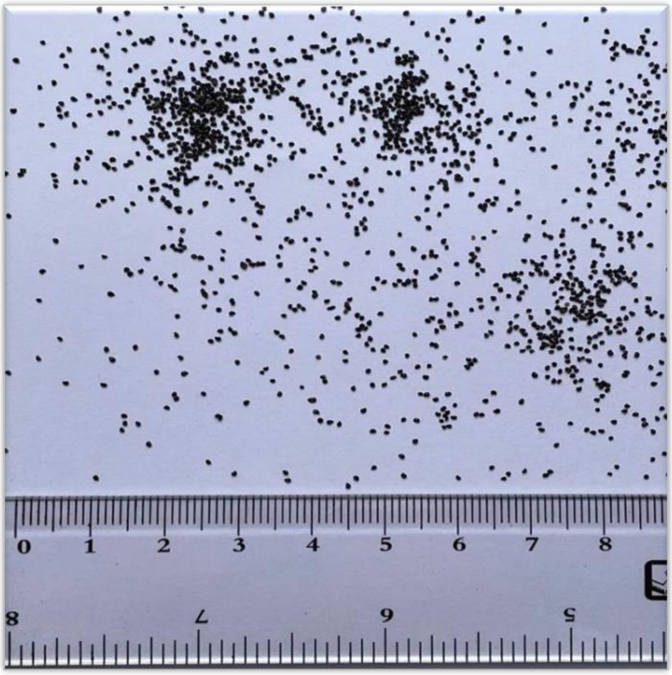

Figure 11. Seeds of *Suaeda vermiculata* Forssk. ex J. F. Gmel.

Suaeda vermiculata is distributed in many world areas, including Arabian Peninsula. It is found in fallow fields, saline sandy soils, and Sabkhas (Jongbloed, 2003). In the United Arab Emirates, it is common in coastal areas along the Arabian Gulf and on offshore islands. Recorded from Khor Kalba and Al Ain (Jongbloed, 2003). *S. vermiculata* is a valuable palatable forage for animals, especially camels, and is also used for fuel (AlFarrajii and Al-Hilli, 1994). In addition, it has many medicnal uses. For example, the smoke of stems is used to relieve asthma and other respiratory disorders (Phondani et al., 2016), hepatitis and viral diseases (Sefidanzadeh et al., 2015). Besides, *S. vermiculata* showed antimicrobial activity (Al-Tohamy et al., 2018). Furthermore, this species is suitable for urban landscape (Jongbloed et at., 2003) and was considered a bioindicator of sewage pollution in urban environments (El Ghazali et al., 2017). The ability of *S. vermiculata* to grow in both salty and salt-free habitats makes it a suitable model for studying salinity and drought stress mechanisms of halophytes.

7. Hypothesis

Desert plants from the United Arab Emirates (UAE) are subjected to environmental stress such as water deficit, salt stress, soil salinity, and heat. Halophytes are a special group of plants that can survive under the harsh conditions of saline habitats that few other plants could survive. Besides, other group of plants can survive and grow equally well in both saline and non-saline habitats (i.e., habitat-indifferent halophytes). These plants offer a good opportunity to study the physiological and biochemical mechanisms regulating salinity and drought stresses. In addition, those habitat-indifferent halophytes are key species to understand the impact of salinity and drought stress on seed dormancy and salt tolerance during seed germination.

To survive the harsh conditions of the salt marshes, we hypothesis that halophytes developed several morphological, biochemical, and physiological mechanisms. In addition, it is hypothesized that plants that survive in salty habitats are equipped with plasticity in all traits that enable them to tolerate the spatial and temporal unpredictability of harsh conditions of salty habitats in arid regions. These hypotheses are linked to the overall objective of the study, which is “assessment of environmental factors (light, temperature, and salinity and drought stresses) on germination, dormancy and biochemical responses of the habitat-indifferent halophyte *Suaeda vermiculata* (Amaranthaceae) in the desert ecosystem of the United Arab Emirates (UAE).

Furthermore, it is hypothesized that habitat-indifferent halophytes growing in salty habitats produce seeds with higher dormancy and greater tolerance to salinity and drought than seeds from plants growing in salt-free soils (El-Keblawy and Al-Shamsi, 2008; El-Keblawy et al., 2007; El-Keblawy et al., 2016b). This hypothesis is linked to the first and second objectives presented in the first and second chapters of this Phd Memory.

We also hypothesize that germination of seeds matured in salty soils differs from those matured in salt-free soils in response to drought and other environmental signals, such as light and temperatures, that could determine successful seeding survival and establishment conditions. This is especially important as seeds developed in non-saline habitats are exposed to water deficit (i.e., drought) in years receive little rainfall, but those of saline habitats are exposed to lower water potential resulting from salinity and water-deficit stresses. This hypothesis is linked to the first objective presented in the first chapter of this PhD Memory.

Accumulation of ions such as sodium (Na) and chloride (Cl) within the plant leads to osmotic and/or ion-specific toxicity effects, which compromises enzyme functions and disrupts metabolic processes (Al-Shamsi et al., 2020). Environmental stress produces reactive oxygen species (ROS) toxic radicals, such as superoxide anion radicals, hydrogen peroxide, and hydroxyl radicals, that have harmful effects (Saed-Moucheshi et al., 2014). Therefore, it is hypothesized that *Saueda vermiculata* plants surviving in salty habitats produce more (ROS) and enzymatic and nonenzymatic antioxidants to counteract the harmful effect. This hypothesis is linked to the third objective, which is “determining the effect of maternal salinity on some plant physiological and biochemical traits on different organs of *Suaeda vermiculata* from salty and non-salty habitats”.

We also hypothesize that the habitat-indifferent *Suaeda vermiculata* differ in morphological physiological and biochemical responses to the different salinities of the salty and non-salty habitats. We assume that the plants of the highly saline marsh habitat rely more on inorganic ions, especially sodium (Na), as osmoregulator, but those of the non-salty gravel plain rely more on organic osmoregulators such as proline. We also expect a differential response to high salinity in the roots and shoots of plants growing in the salty habitats; the roots are in direct contact with high salt levels, but leaves could be adapted through sodium (Na) compartmentalization in vacuoles. This hypothesis is again linked to the third objective presented in chapter number 3 of this PhD Memory.

8. Objetives

Halophytes could be classified ecologically into three categories: obligatory, facultative, and habitat-indifferent halophytes. Obligatory (true) halophytes grow only in saline soils. Still, facultative halophytes can be established in saline habitats, and their optimal growth is in non-saline soil or at least low-salt substrates. However, habitat-indifferent halophytes can cope with salty soils, but they survive equally well in salty and salt-free substrates. Several studies assessed the environmental and biochemical factors that are regulating salinity and drought tolerances in both true halophytes and glycophytes in different parts of the world. However, few studies did that for habitat-indifferent halophytes. The overall aim of the current study was to assess environmental factors (light, temperature, and salinity, and drought stresses) on germination, dormancy, and biochemical responses of the habitat-indifferent halophyte *Suaeda vermiculata* in a desert ecosystem of the United Arab Emirates (UAE).

The specific objectives of the study are:

1. To assess the effects of maternal salinity, temperature and light of seed incubation on seed dormancy and drought tolerance (as stimulated by polyethylene glycol) during the seed germination stage. The question is: “are there differences in germination level, drought tolerance during germination, response to light and temperatures for seeds from different habitats differ in salinity?” Plants growing in salty habitats are also subjected to physiological drought. This objective corresponds to chapter number one of this PhD Memory.
2. To assess the effects of maternal salinity, temperature, and light of seed incubation on seed dormancy and salinity tolerance during the seed germination stage. The question is: “are there differences in germination level, salinity tolerance during germination, response to light and temperatures for seeds developed and matured in salty habitats

and seeds developed and matured in non-saline habitats?" This objective corresponds to chapter number two of this PhD Memory.

3. To determine the maternal salinity on some plant physiological and biochemical traits on different organs of *Suaeda vermiculata* from salty and non-salty habitats. This objective corresponds to chapter number three of this PhD Memory.

9. Importance of This Study for the United Arab Emirates (UAE)

Abiotic stresses, such as drought, salinity, extreme temperatures, chemical toxicity, and oxidative stress, are serious threats to agriculture and result in land production deterioration and loss of biodiversity. It has been reported that the average yields for most major crop plants have reduced by more than 50% due to these stresses (Boyer, 1982; Bray et al., 2000). The UAE has a hyperarid hot climate with an annual average rainfall of less than 100 mm. Such harsh environmental conditions create a vast area of salinized land and decrease the productivity of agricultural lands. Soil salinization is a major limiting factor that causes loss in the productivity of cultivated arid and natural desert lands, including those of the UAE. In addition, the deterioration of the quality of the agricultural land in the UAE is steadily increasing because of global climatic changes and adverse environmental conditions, and the continuously increasing natural calamities and population pressure (Hasanuzzaman et al., 2013a; Hasanuzzaman et al., 2013b). The current study results can help understand salinity and drought tolerances in *S. vermiculata*, a native plant species that could restore both non-saline and saline habitats. *S. vermiculata* is a valuable palatable forage for animals and is considered a useful shrub for restoring degraded rangelands (Osman et al., 2006). In addition, it has been considered a good shrub for landscaping urban cities and combating desertification (Osman and Ghassali, 1997).

The ability of *Suaeda vermiculata* to hyper-accumulate a great amount of sodium makes it a potential candidate for desalination and restoration of saline soils. Besides, the growth of *S. vermiculata* in salt-affected lands can provide cost-effective, sustainable potential lignocellulosic feedstocks for biofuel production and sequester rising carbon dioxide (CO_2). Furthermore, the potential use of this hardy species in landscaping the coastal areas and urban cities will sustain them. This is practically possible as *S. vermiculata*, like most native halophytes, is resistant to most local insects and fungal and bacterial diseases. It grows with these pests for a long history, and consequently, it co-evolved naturally with them under the harsh conditions of the UAE desert. Therefore, *S. vermiculata* is a hardy plant; once established, it needs little or no pesticides or watering. This will save the use of the chemicals (pesticides and fertilizers), saving the groundwater from contamination with these harmful chemicals. All of these practices will sustain the coastal zones of the urban areas.

Using native habitat-indifferent halophytes for various purposes requires using high-quality seeds. For example, seeds that can germinate in salty habitats should resist high salinity in addition to extreme temperatures and extended drought that might be found in the salt marshes of the UAE. Furthermore, several studies have shown that habitat-indifferent halophytes growing in salty habitats produce seeds with higher dormancy and greater tolerance to salinity and drought than seeds from plants that grow in salt-free soils (El-Keblawy and Al-Shamsi, 2008; El-Keblawy et al., 2007; El-Keblawy et al., 2016b). Therefore, species with plasticity in seed germination are considered excellent candidates for restoring degraded habitats with spatial and temporal unpredictability of climatic conditions, similar to those of the UAE.

Halophytes are characterized by their ability to tolerate high salinity levels due to the effective coordination between various physiological and metabolic processes and pathways (Kumari et al., 2015). In recent years, it is suggested that halophytes can be used to desalinate and restore saline soils in a process known as phyto-desalination (Rabhi et al., 2009; Riadh et al., 2010). The restored saline lands could be used as agricultural lands to produce healthy crops (Kiridi and Zalmon, 2020). Utilizing habitat-indifferent halophytes to restore salt-affected lands in the UAE could be a sustainable solution for recovering biodiversity and ecosystem services and a real contribution of the country in achieving the United Nations Sustainable Development Goals.

There are around 830 plant species in the flora of the UAE; about 400 species of them in the Abu Dhabi Emirate (Gairola et al., 2016; Brown, G., & Sakkir, S., 2004). Most of these plants have evolved naturally under harsh environmental conditions, such as drought, salinity, and high temperatures that can reach up to 50 °C during summer. Many UAE plants are naturally inhabiting saline environments (i.e., halophytes), and others can survive in both saline and non-saline habitats (i.e., habitat-indifferent halophytes). Boer and Gliddon (1998) recorded 22 halophytes (nine of them are tolerant to inundation by seawater) in a survey conducted in only the coastal zone of Abu Dhabi Emirate, UAE. The present study assesses salinity tolerance mechanisms at both seed and adult plant stages of *Suaeda vermiculata,* one of the most common habitat-indifferent halophytes. The present study results would help learn more about the factors limiting the geographical and habitat distributions and the adaptation of habitat-indifferent halophytes to survive in different habitats. Therefore, the study results could help propose proper strategies for conservation of the endangered and propagate the economically important habitat-indifferent halophytes. Defining the tolerance mechanisms under salt stress would also help understand the causes of the presence of habitat-indifferent halophytes under the hyper-saline conditions of the hyperarid hot environments such as the UAE desert. Besides, the results would help understand some of the mechanisms that regulate stress tolerances and, consequently, help in their adoption for greening the desert of UAE and as phyto-desalination.

10. Structure of Phd Memory

This PhD Memory is structured in three Chapters which correspond to three articles published in scientific journals included in the ISI web of Knowledge. Below are the names of the co-authors, the title of the publication, the reference of the journal, the DOI and a brief summary in english and spanish.

Chapter 1: Al-Shamsi, N., El-Keblawy, A., Mosa, K. A., & Navarro, T. (2018). Drought tolerance and germination response to light and temperature for seeds of saline and non-saline habitats of the habitat-indifferent desert halophyte *Suaeda vermiculata. Acta Physiologiae Plantarum, 40* (200): 1-13. http://dx.doi.org/10.1007/s11738-018-2771-z.

Few plants are habitat-indifferent halophytes (i.e., grow well in both saline and non-saline soils). These plants offer a good opportunity to study drought and salinity tolerances during germination for seeds developed and matured in soils differ in salinity. Here, we assessed drought tolerance during germination, as simulated with PEG (Polyethylene glycol), and response of germination to light and temperature for *Suaeda vermiculata*, a habitat-indifferent shrub. Seeds matured in saline and non-saline soils were germinated in six PEG concentrations (0 to − 1.0 MPa) and put in three incubators adjusted at different temperatures in both light and dark regimes. Drought tolerance was greater for seeds of the non-saline than those of saline soils, especially at higher temperatures. Seeds of the saline soils germinated in the lowest osmotic potentials (− 0.8 and − 1.0 MPa) only at lower temperatures, but seeds of the non-saline soils germinated to higher levels at all temperatures. Tolerances to drought and high temperatures were greater in light for seeds of saline soils, but in darkness for seeds of non-saline soils. Germination rate index did not differ significantly between seeds of the two soil types in higher osmotic potentials, but was significantly greater in seeds of non-saline at lower osmotic potentials. Most seeds that failed to germinate in the PEG (Polyethylene glycol) concentrations recovered their germination when transferred to distilled water. Germination recovery levels and speeds increased with the decrease in osmotic potentials. Seeds of the saline soil postpone their germination until arrival of suitable temperatures and effective rainfalls that ensure seedling survival in salty habitats of the arid unpredictable deserts.

Existen pocas especies de plantas halófitas indiferentes al hábitat (es decir, que crecen bien en suelos salinos y no salinos). Estas plantas ofrecen una buena oportunidad para estudiar las tolerancias a la sequía y la salinidad durante la germinación de semillas desarrolladas y maduradas en suelos que difieren en salinidad. Aquí, evaluamos la tolerancia a la sequía durante la germinación, simulada con PEG (polietilenglicol), y la respuesta de la germinación a la luz y la temperatura para Suaeda vermiculata, un arbusto halófito indiferente al hábitat. Las semillas maduradas en suelos salinos y no salinos se pusieron a germinar en seis concentraciones de PEG (polietilenglicol) (0 a -1,0 MPa) y se colocaron en tres incubadoras ajustadas a diferentes temperaturas en regímenes de luz y oscuridad. La tolerancia a la sequía fue mayor para las semillas de los suelos no salinos que para las de los suelos salinos, especialmente a temperaturas más altas. Las semillas de los suelos salinos germinaron en los potenciales osmóticos más bajos (- 0,8 y - 1,0 MPa) solo a temperaturas más bajas, pero las semillas de los suelos no salinos germinaron a niveles más altos a todas las temperaturas. Las tolerancias a la sequía y las altas temperaturas fueron mayores en luz para semillas de suelos salinos, pero en oscuridad para semillas de suelos no salinos. El índice de tasa de germinación no difirió significativamente entre las semillas de los dos tipos de suelo en potenciales osmóticos más altos, pero fue significativamente mayor en semillas no salinas con potenciales osmóticos más bajos. La mayoría de las semillas que no germinaron en las concentraciones de PEG (polietilenglicol) recuperaron su germinación cuando se *transfirieron a agua destilada. Los niveles y velocidades de recuperación de la germinación aumentaron con la disminución de los potenciales osmóticos. Las semillas del suelo salino posponen su germinación hasta la llegada de temperaturas adecuadas y de lluvias efectivas que aseguren la supervivencia de las plántulas en los hábitats salados de los desiertos.*

Chapter 2: El-Keblawy, A., Al-Shamsi, N., & Mosa, K. (2018). Effect of maternal habitat, temperature and light on germination and salt tolerance of *Suaeda vermiculata*, a habitat-indifferent halophyte of arid Arabian deserts. *Seed Science Research,* 28(2), 140-147. http://dx.doi.org/10.1017/S0960258518000144.

Habitat-indifferent species that can grow well in both saline and non-saline soils offer a good opportunity for studying seed dormancy and salt tolerance during germination. Here, we assess interactive effects of maternal habitat and incubation conditions on salt tolerance during germination of the habitat-indifferent halophyte *Suaeda vermiculata,* a common perennial shrub of the arid Arabian deserts. Seeds collected from saline and non-saline habitats were germinated at six salinity levels (0–500 mM NaCl, sodium chloride) and incubated at three temperatures and under two light regimes. Studied germination attributes were final germination, germination rate index (GRI) and germination recovery of non-germinated seeds when transferred to distilled water. The results showed insignificant difference in salt tolerance between seeds of the two habitat types at the lower salinities. At higher salinities (400 and 500 mM NaCl), germination of the saline habitat seeds was almost inhibited, but that of non-saline habitat seeds reached various levels depending on light and temperature. Both higher temperatures and darkness resulted in significant reductions of the final germination at the higher salinities. Seeds of the two habitats that did not germinate in the different treatments recovered their germination when transferred to distilled water, indicating that these seeds maintained their viability in saline solution and were able germinate upon the arrival of suitable conditions. Seeds of the two habitats germinated within two days at the lower salinities and GRI decreased with the increase in salinity level. Such reduction was obvious for seeds of the saline habitat. Recovery was faster for seeds of the saline habitats, especially for those incubated at higher salinities and in the dark. The difference in dormancy and germination attributes of seeds of the two habitat types reflects ecological adaptations for survival in salt marshes of arid deserts.

Las especies indiferentes al hábitat que pueden crecer tanto en suelos salinos como no salinos ofrecen una buena oportunidad para estudiar la dormancia de las semillas y la tolerancia a la sal de las misamas durante la germinación. Se evaluan los efectos interactivos del hábitat materno y las condiciones de incubación sobre la tolerancia a la sal durante la germinación de la planta halófita e indiferente al hábitat, Suaeda vermiculata, un arbusto perenne común de los desiertos árabes. Las semillas recolectadas de hábitats salinos y no salinos se hicieron germinar a seis niveles de salinidad (0-500 mM NaCl, de cloruro sódico) y se incubaron a tres temperaturas y bajo dos regímenes de luz. Los caracteres de germinación estudiados fueron germinación final, índice de tasa de germinación (GRI) y recuperación de la germinación de semillas no germinadas cuando se transfieren a agua destilada. Los resultados mostraron una diferencia insignificante en la tolerancia a la sal entre las semillas de los dos tipos de hábitats en las salinidades más bajas. En salinidades más altas (400 y 500 mM NaCl), la germinación de las semillas del hábitat salino fue casi inhibida, pero la de las semillas del hábitat no salino alcanzó varios niveles dependiendo de la luz y la temperatura. Tanto las temperaturas más altas como la oscuridad dieron como resultado reducciones significativas de la germinación final en las salinidades más altas. Las semillas de los dos hábitats que no germinaron en los diferentes tratamientos recuperaron su germinación al ser transferidas a agua destilada, lo que indica que estas semillas mantuvieron su viabilidad en solución salina y pudieron germinar al llegar las condiciones adecuadas. Las semillas de los dos hábitats germinaron en dos días en las salinidades más bajas y el GRI disminuyó con el aumento del nivel de salinidad. Tal reducción fue obvia para las semillas del hábitat salino. La recuperación fue más rápida para las semillas de los hábitats salinos, especialmente para las incubadas a mayor salinidad y en la oscuridad. La diferencia en los caracteres de dormancia y germinación de las semillas de los dos tipos de hábitat refleja adaptaciones ecológicas para la supervivencia en las marismas de los desiertos áridos.

Chapter 3: Al-Shamsi, N., Hussain, M. I., & El-Keblawy, A. (2020). Physiological responses of the xerohalophyte *Suaeda vermiculata* to salinity in its hyper-arid environment. *Flora*, *273*, 151705. http://dx.doi.org/10.1016/j.flora.2020.151705.

Few plants can survive and grow equally well in salty and salt-free substrates (i.e., habitat-indifferent halophytes). Such plants provide a good opportunity to understand physiological and biochemical mechanisms underlying salinity tolerance. In this study, we investigated the environmental salinity impacts on several physiological and biochemical features of *Suaeda vermiculata*, a habitat-indifferent halophyte. Samples of different organs were collected from *S. vermiculata* from both a highly Saline Marsh Habitat (HSMH) and Non-Salty Gravel Plain (NSGP) for the determination of the following physiological and bio-chemical features: chlorophyll and carotenoids, proline, malondialdehyde (MDA), and hydrogen peroxide (H_2O_2), antioxidant enzymes (Catalase, CAT; guaiacol peroxidase, GPX; Ascorbate peroxidase, APX) activities. Elemental compositions in soil and plant samples from both habitats were also assessed. Results showed that plants from HSMH had significantly lower values of chlorophyll *a*, *b*, carotenoids and leaf biomass, compared to those from NSGP. Roots from HSMH attained higher levels of antioxidant enzymes (CAT, GPX, APX) and lower values of reactive oxygen species (MDA and H_2O_2), indicating that the enzymes are more likely scavenging the Reactive Oxygen Species (ROS). The enzyme activities and ROS levels were much lower in the shoots of both HSMH and NSGP than in roots. Accumulation of sodium was higher in leaves and shoots than roots of *S. vermiculata*. This study indicates that *Suaeda vermiculata* is a salt tolerant plant with adaptations to different environments through down-regulation of different biochemical and physiological features to avoid oxidative stress.

Hay pocas especies de plantas que pueden sobrevivir y crecer igualmente bien en sustratos salados y sin sal (es decir, halófitas indiferentes al hábitat). Estas plantas constituyen una buena oportunidad para comprender los mecanismos fisiológicos y bioquímicos que subyacen a la tolerancia a la salinidad. En este estudio, investigamos los impactos de la salinidad ambiental en varias características fisiológicas y bioquímicas de Suaeda vermiculata, una especie halófita indiferente al hábitat. Se recolectaron muestras de diferentes órganos de S. vermiculata tanto de un hábitat pantanoso altamente salino (HSMH) como de una llanura de grava no salada (NSGP) *para la determinación de las siguientes características fisiológicas y bioquímicas: clorofila y carotenoides, prolina, malondialdehído (MDA) y peróxido de hidrógeno (*H_2O_2*), actividades de enzimas antioxidantes (catalasa, CAT; guayacol peroxidasa, GPX; ascorbato peroxidasa, APX). También se evaluaron las composiciones elementales en muestras de suelo y plantas de ambos hábitats. Los resultados mostraron que las plantas de HSMH tenían valores significativamente más bajos de clorofila a, b, carotenoides y biomasa de hojas, en comparación con las de NSGP. Las raíces de HSMH alcanzaron niveles más altos de enzimas antioxidantes (CAT, GPX, APX) y valores más bajos de especies reactivas de oxígeno (MDA y H2O2), lo que indica que es más probable que las enzimas eliminen las especies reactivas de oxígeno (ROS). Las actividades enzimáticas y los niveles de ROS fueron mucho más bajos en los brotes de HSMH y NSGP que en las raíces. La acumulación de sodio fue mayor en hojas y brotes que en raíces de S. vermiculata. Este estudio indica que Suaeda vermiculata es una planta tolerante a la sal con adaptaciones a diferentes ambientes a través de la regulación a la baja de diferentes características bioquímicas y fisiológicas para evitar el estrés oxidativo.*

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CONCLUSION

CONCLUSION

1. Seeds of *Suaeda vermiculata* had little dormancy; non-saline treated seeds from the two habitats (saline and non-saline) germinated up to 100% in both light and dark at all temperatures.

   Las semillas de Suaeda vermiculata tuvieron poca dormancia; las semillas no tratadas con solución salina de los dos hábitats (salino y no salino) germinaron hasta un 100% tanto en la luz como en la oscuridad a todas las temperaturas.

2. The seeds of *Suaeda vermiculata* germinated very fast; the germination rate of non-saline treated seeds of both saline and non-saline habitats was about 48, indicating that the seeds germinated within two days after imbibition.

   Las semillas de Suaeda vermiculata germinaron muy rápido; la tasa de germinación de las semillas no tratadas con solución salina de hábitats tanto salinos como no salinos fue de aproximadamente 48, lo que indica que las semillas germinaron dentro de los dos días posteriores a la imbibición.

3. Seeds of *Suaeda vermiculata* developed in saline soils had relatively higher dormancy than seeds developed in non-saline habitats, especially at moderate and higher temperatures (20/30 and 25/35 ℃). Seeds from the non-saline habitats germinated to higher percentages in both light and dark conditions and light at all temperatures. This indicates that seeds of saline habitats restrict their germination to the time that triggers the seedling establishment.

   Las semillas de Suaeda vermiculata desarrolladas en suelos salinos tuvieron una dormancia relativamente más alta que las semillas desarrolladas en hábitats no salinos, especialmente a temperaturas moderadas y altas (20/30 y 25/35 ℃). Las semillas de los hábitats no salinos germinaron en porcentajes más altos tanto en condiciones de luz como de oscuridad y con luz a todas las temperaturas. Esto indica que las semillas de hábitats salinos restringen su germinación al momento en que se lleva a cabo el establecimiento de las plántulas.

4. The inhibitory effect of saline solution (sodium chloride; NaCl) was greater than the iso-osmotic PEG (polyethylene glycol) on seed germination of *S. vermiculata*, indicating that osmotic, rather than specific-ion toxicity effect, is responsible for germination inhibition. The ability of non-germinated seeds to recover their germination when transferred from both saline and iso-osmotic PEG solutions indicates that the osmotic effect is responsible for seed germination inhibition.

El efecto inhibidor de la solución salina (cloruro de sodio; NaCl) fue mayor que el PEG (polietilenglicol) iso-osmótico sobre la germinación de semillas de S. vermiculata, lo que indica que el efecto de toxicidad osmótica, más que de iones específicos, es responsable de la inhibición de la germinación. La capacidad de las semillas no-germinadas para recuperar su germinación cuando se transfieren de soluciones de PEG tanto salinas como iso-osmóticas indica que el efecto osmótico es responsable de la inhibición de la germinación de las semillas.

5. *Suaeda vermiculata* seeds germinated to very high percentage and speed in higher osmotic pressures (up to 100%) at all temperatures (15-35 ℃), indicating the ability of immediate seed germination after rainfalls.

   Las semillas de Suaeda vermiculata germinaron en muy alto porcentaje y velocidad en presiones osmóticas altas (hasta 100%) y a todas las temperaturas (15-35 ℃), lo que indica la capacidad de germinación inmediata de la semilla después de las lluvias.

6. Drought tolerance, as simulated by PEG (polyethylene glycol), was higher for seeds of the non-saline than those of saline, and this tolerance was more obvious at higher temperatures; no seeds from saline habitats germinated in -0.8 and -1.0 MPa, but around 23% and 4% of seeds from non-saline habitats germinated at these water potentials.

   La tolerancia a la sequía, simulada por PEG (polietilenglicol), fue mayor para las semillas del hábitat no salino que para las del salino, y esta tolerancia fue más obvia a temperaturas más altas; ninguna semilla de hábitats salinos germinó en -0,8 y -1,0 MPa, pero alrededor del 23% y 4% de las semillas de hábitats no salinos germinaron en estos valores de potenciales hídricos.

7. *Suaeda vermiculata* seeds attained lower germination in lower osmotic potentials indicating that they would not germinate below a certain water threshold, above which successful seedlings recruitments would occur. Seeds of *S. vermiculata* can germinate the non-saline, but not in the saline soils, when little rainfalls are received (April-May), especially if seeds are covered with litter or present in cracks.

   Las semillas de Suaeda vermiculata alcanzaron una germinación más baja en potenciales osmóticos bajos, lo que indica que no germinarían por debajo de un cierto umbral de agua, para asegurar el desarrollo de las plántulas. Las semillas de S. vermiculata pueden germinar en suelos no salinos, pero no en suelos salinos, cuando reciben escasas lluvias (abril-mayo), especialmente si las semillas están cubiertas por restos de vegetales o se encuentran en grietas.

8. *Suaeda vermiculata* seeds of the saline habitat failed to germinate in 400 and 500 mM sodium chloride solution (NaCl), especially at higher temperatures, indicating that they postpone their germination until salinity is diluted through rainfall to ensure seedling survival in the salty habitats. Germination was higher in the higher salinities (400 and 500 mM NaCl) at lower temperatures (15/25 °C), indicating a higher chance of seedling survival if germination occurred early in the growing season when temperatures are low.

   Las semillas de Suaeda vermiculata de hábitats salinos no germinaron en solución de cloruro de sodio (NaCl) 400 y 500 mM, a temperaturas más altas, lo que indica que posponen su germinación hasta que la salinidad se diluye mediante la lluvia para asegurar la supervivencia de las plántulas en los hábitats salinos. La germinación fue mayor en salinidades más altas (NaCl 400 y 500 mM) y a temperaturas más bajas (15/25 ° C), lo que indica una mayor probabilidad de supervivencia de las plántulas si la germinación se produce al principio de la temporada de crecimiento cuando las temperaturas son bajas.

9. The saline and non-saline habitats impacted the morpho-physiological characters of *Suaeda vermiculata*. Roots from the saline habitat attained higher levels of antioxidant enzymes and lower values of reactive oxygen species, indicating the enzymes are more likely to scavenge the reactive oxygen species. Plants from two different habitats developed different tolerance mechanisms for salt accumulation; plants from saline habitats used sodium (Na^+) as osmoregulators, but those in non-saline habitats used proline. The accumulation of higher Na^+ levels implies that the plant can serve as rhizosphere sodium cleaner and for sodium phytoremediation in the salt-degraded habitats.

   Los hábitats salinos y no salinos afectaron los caracteres morfofisiológicos de Suaeda vermiculata. Las raíces de plantas de hábitats salinos alcanzaron elevados valores de enzimas antioxidantes y valores bajos de oxígeno reactivo. Las plantas de los dos hábitats desarrollaron diferentes mecanismos de tolerancia para la acumulación de sal; las de hábitats salinos utilizaron sodio (Na^+) como osmorregulador, pero las de los no salinos utilizaron prolina. La acumulación de niveles más altos de Na^+ implica que la planta puede servir como "limpiador" de sodio de la rizosfera y para la fitorremediación de sodio en habitats degradadso por sal.

10. The results of this study indicate that *Suaeda vermiculata* is a salt-tolerant plant with adaptations to different environments through down-regulation of different biochemical and physiological features to avoid oxidative stress.

    Los resultados de este estudio indican que Suaeda vermiculata es una planta tolerante a la sal con adaptaciones a diferentes ambientes a través de la regulación a la baja de diferentes características bioquímicas y fisiológicas para evitar el estrés oxidativo.