TESIS DOCTORAL

REGULACION DE LA TOLERANCIA A LA SALINIDAD Y A LA SEQUIA EN SPECIES DEL *SALSOLA* L., DE LOS DESIERTOS ÁRIDOS DE LOS EMIRATOS ÁRABES UNIDOS

REGULATIONS OF SALT AND DROUGHT TOLERANCE IN *SALSOLA* L., SPECIES OF ARID DESERTS OF THE UNITED ARAB EMIRATES

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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-.

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Memoria presentada para optar
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ACREDITA

Que Dña. Attiat Attia Mohi Elnaggar, Licenciada en Biología, ha realizado, en el Departamento de Botánica y Fisiología Vegetal de la Facultad de Ciencias de la Universidad de Málaga y en el Departamento de Biología Aplicada de la Universidad de Sharjah (Emiratos Árabes Unidos), las investigaciones que le han conducido a la redacción de la presente Memoria de Tesis Doctoral, titulada REGULATIONS OF SALT AND DROUGHT TOLERANCE IN *SALSOLA* L. SPECIES OF ARID DESERTS OF THE UNITED ARAB EMIRATES.

La presente Memoria, que recoge los resultados obtenidos, así como su interpretación, 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, ocho de febrero del 2020

Prof. Dra. Teresa Navarro

Directora de la Tesis

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ABSTRACT

ABSTRACT

The Arabian Peninsula comprises seven countries of the Arab Gulf Cooperation Council (AGCC); The United Arab Emirates (UAE) is one of the AGCC. The UAE lies in the north-eastern part of the Arabian Peninsula. It covers a total surface of 83,600 Km^2 and consists of seven Emirates: Abu Dhabi, Dubai, Sharjah, Ras Al Khaimah, Fujairah, Ajman and Umm Al Quwain. Most of the UAE land is desert with predominance of Aeolian landform system. UAE geomorphologic features include mountains, gravel plains, sand sheets and saline flats. The rainfalls of the Arabian Peninsula are erratic and temporarily and spatially unpredictable; in some years, certain areas may not receive rainfall, but could receive more than 200 mm in other years. This hyper-arid hot desert (subtropical hot desert) ecosystem has only two main seasons: a long hot summer (April to October) and a short mild winter (November to March). The rain falls mainly in winter season with maximum intensity during February and March. The mean annual rainfall is about 110 mm, with Abu Dhabi (southern Emirates with sandy habitat) receives the lowest (about 45 mm/year) and north-east emirates of the country, which are mountainous, receive the highest (125.6 - 172 mm/year). The annual average temperature is approximately 27 °C and humidity 45.0%. For the winter, the mean temperature is around 20 °C, while mean temperature of summer ranges between 35 - 40 °C. In addition, humidity could reach more than 90.0% in the coast region.

Plants in the hyper-arid hot desert of the UAE suffer from many environmental stresses. The UAE environment is facing 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. 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 are experienced by parental plants 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 are usually diminished 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 differ in the levels of salinity and drought stresses in their response to life history traits, such as seed dormancy, germination, physiological, biochemical and genetic attributes.

Drought stress is the severe scarcity of water resources and occurs when the available water in the soil is reduced due to many factors such as low rainfalls and continuous loss of water by transpiration or evaporation due to the high temperatures. Drought can damage membrane integrity, decrease pigment content, cause imbalance in osmotic adjustment, reduce photosynthetic activity and reduce or even damage the growth and production. Drought stress also has harmful effects on seed germination and dormancy, morphology, physiology and metabolism of plants.

Salt stress is a soil condition characterized by high levels of soluble salts such as sodium, Na^+ and/or chloride, Cl^- ions. Most of salt affected soils resulted from accumulations of salts over time in arid and semiarid areas due to high temperatures that increase evaporation rate. Two main mechanisms are behind the serious impacts of salt stress on plants: osmotic effect and specific ion toxicity. Osmotic effect is a rapid response due to the presence of high amount of salts in the soil that make water harder for roots to be extracted due to the declining soil solute potential. This effect of salt stress is known as 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, has a harmful effect on ion homeostasis that affects cell growth and associated metabolism. It has been reported that reasonable concentrations of sodium chloride can induce plant growth, but 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.

Plants of the arid and semiarid soils have developed several mechanisms that enable them surviving the low water osmotic potential of salty soil. Based on their tolerance to salt stress, plants could be categorized to salt tolerant (i.e. halophytes) and salt sensitive (i.e. glycophytes). The first group can grow on seawater and produce high yields of seed and biomass. In addition, halophytes could be classified ecologically into three categories: obligatory (true), facultative, and habitat-indifferent halophytes. Obligatory halophytes grow only in salty habitats but facultative halophytes are able to establish themselves on salty soils and attain their optimal growth in non-saline substrates. Habitat-indifferent halophytes can grow and tolerate salty soils, but they survive equally well in salty as well and salt-free soils. Many habitat-indifferent halophytes are surviving in both hyper-saline and non-saline

habitats of the arid Arabian desert. *Salsola drummondii* Ulbr., is among the most common habitat-indifferent halophytes in the Arabian desert.

It is difficult for the initial growth stages, such as germination and seedling recruitment, to cope with drought and salt stress, even for halophytes. So the plants have evolved several physiological and biochemical salt tolerance mechanisms that protect major photosynthetic activities and respiration. Among these mechanisms are ion homeostasis and selective accumulation or exclusion of ions, control of ion uptake by roots and transport into leaves, compartmentalization of ions at the cellular and whole-plant levels, modification in photosynthesis process, membrane integrity, production of osmolytes, enhancing the production of enzymatic and non-enzymatic antioxidants and plant hormones. The physiological and biochemical responses to salinity stress are based on alterations in gene expression. Most of the salinity genes are involved in signal transduction, transcriptional regulation and encode for sodium/ hydrogen, Na^+/H^+ antiporters, ion channels potassium transporters, vacuolar pyrophosphatase and antioxidants. Identifying the mechanisms of plant salt tolerance will help in breeding or genetic engineering to produce salt-tolerant crops. Therefore, studying the mechanisms by which halophytes respond or adapt to salt stress is important for their sustainable use.

Studying habitat-indifferent halophytes that are evolutionary developed and surviving contrasting salinity conditions could provide a good chance to understand mechanisms of salt tolerance at different life history stages including seed dormancy, germination attributes, such as final germination and germination rates, seedling growth and other plant traits under growth chamber and field conditions.

The habitat-indifferent halophytes are characterized by wider physiological and biochemical attributes that enables them to cope with both salty and non-salty substrates. Assessing different metabolites responsible for salt tolerance in habitat-indifferent halophytes would also help in understanding salinity tolerance mechanisms. By studying how plants respond to severe stresses, we can learn more about the limits of their geographical and habitat distributions, their flexibility, and their response to global environmental changes. In addition, defining the tolerance mechanisms under salt stress might help in the conservation of habitat-indifferent halophytes in the hot dry desert.

The molecular and biochemical mechanisms regulating the survival of habitat-indifferent halophytes should differ from those of both true halophytes and glycophytes. In order to grow equally well in both saline and non-saline habitats, habitat-indifferent halophytes should have a salinity tolerance gene(s) that could be turned on/off, depending on the soil salinity. Turning on of a salt tolerance gene(s) might enable these plants to survive the salinity stress. Identifying genes responsible for biosynthesis and catabolism of common osmolytes and antioxidant metabolites in a habitat-indifferent halophyte under saline and non-saline conditions would again help in understanding more mechanisms about salt tolerance in plants. Furthermore, such studies might provide a novel approach to increase plant tolerance to salt stress and developing salt-tolerant crops.

The ability of halophytes to tolerate high salt levels is determined by the effective coordination between various physiological processes, metabolic pathways and protein or gene networks responsible for delivering salinity tolerance. Few studies assessed the difference in seed dormancy and germination between seeds of habitat-indifferent halophytes collected from salinity different habitats. There are also few studies attempted to evaluate the difference between plants of saline and non-saline habitats at biochemical, physiological and molecular point of view. Therefore, the main objective of the present study was to assess the germination traits, dormancy level, biochemical, physiological, and genetic attributes in plants of the habitat-indifferent halophyte *Salsola drummondii* Ulbr., under salt stress. The study also aimed to compare the effect of drought on germination, and dormancy traits in two congeneric species *S. drummondii* Ulbr., (growing in saline and non-saline habitat) and *S. imbricata* Forssk., (growing in non-saline habitat). We recorded *S. imbricata* Forssk., from non-saline sandy soils, despite we surveyed most of the habitat types in the UAE.

The specific objectives of this study are to:

1. Evaluate the effects of temperatures (thermoperiod) and light (photoperiod) and their interaction on drought tolerance, seed dormancy and germination traits in two congeneric species of the genus *Salsola* L.: *S. drummondii* Ulbr., and *S. imbricata* Forssk.
2. Assess the effects of temperatures (thermoperiod) and light (photoperiod) and their interaction on salinity tolerance, seed dormancy and germination traits in *S. drummondii* Ulbr.
3. Assess the effect of salt stress on some functional traits (e.g. physiological and biochemical) of *S. drummondii* Ulbr., at different stages of the life cycle.
4. Identify transcripts encoding proteins involved in salt stress regulation in *S. drummondii* Ulbr.

We studied the effects of light and temperature on drought tolerance during seed germination of *Salsola imbricata* Forssk., which correspond to the objective number 1 of this doctoral thesis.

Plant recruitment in desert ecosystems is rare and highly unpredictable due to unfavorable conditions inhibiting germination events. Few studies addressed the impacts of water deficiency, temperature and light on germination of desert shrubs. Here, we assessed the impact of drought (osmotic stress) as simulated by polyethylene glycol (PEG), light and temperature of incubation on seed germination of *S. imbricata* Forssk., a leaf succulent perennial shrub of the Arabian deserts. PEG (polyethylene glycol) is the most preferred osmotic substance that can be dissolved in aqueous solution at different concentrations to create solutions with various negative water potentials. Such study provides us with a good chance to compare two congeneric species of the genus *Salsola* L.

S. imbricata produces and disperses a large number of ready-to germinate fruits during December and January. Fresh seeds were germinated in different osmotic potentials (0, -0.2, -0.4, -0.6, -0.8, -1.0, -1.4, -1.8 and -2.4 MPa) at three temperatures (15/25, 20/30 and 25/35 °C) and in two light regimes (12 hrs light/12 hrs darkness and complete darkness). The interaction between temperature and PEG level significantly affected seed germination ($P < 0.001$), indicating that the response to osmotic stress depended on temperature. In distilled water, germination was significantly greater at higher than at lower temperatures when seeds germinated in light, but the reverse was true in darkness. Both final germination and germination rate index (GRI) decreased gradually with the increase in osmotic stress, but the reduction was more pronounced at higher, compared to lower temperatures. Final germination and GRI decreased from around 70% and 49%, respectively, in distilled water at both low and high temperatures to 44% and 39% in -1.4 MPa at low temperatures, but to 5% and 26%, respectively, at higher temperatures.

Our study showed that the highest germination of *S. imbricata* occurred in both light and darkness at lower and moderate temperatures (15/25 and 20/30 °C), a trend reported in other succulent halophytes of subtropical regions. Our study also showed that the germination rate index was close to 50 in distilled water and higher PEG osmotic potentials (down to -0.8 MPa), especially at lower and moderate temperatures, a trend similar to that in *S. drummondii*. This indicates that seeds can germinate within 24 hrs following imbibition. The faster germination at higher osmotic potential has been considered as a strategy for seedling establishment when little rainfalls are received early in the growing season. At higher

temperatures, germination was significantly reduced in darkness, compared to under light conditions, for most tested osmotic potentials. At higher temperatures (25/35 °C), however, both final germination and GRI were significantly lower at lower osmotic potentials (≤ -1.4 MPa), indicating a lower chance for germination and seedling establishment when little rain precipitates late in the growing seasons.

Our results showed little germination of *S. imbricata* seeds in lower osmotic potential at lower temperatures (4% and 14% germinated at -2.2 and -1.8 MPa, respectively) and moderate temperatures (12% germinated at -1.8 MPa). The ability of seeds to germinate under such lower osmotic potential further support the hypothesis that some of them might germinate in dry years and could contribute to the future generation even in the very dry years. Most non-germinated seeds of *S. imbricata* at lowest osmotic potentials (-1.8 and -2.2 MPa PEG) recovered their germination immediately once they were transferred to distilled water. In fact, there was no significant difference in total germination (i.e. in PEG and after seeds transferred to distilled water) between higher and lower osmotic potentials (-2.2 MPa) at the lower temperatures. This result indicates that osmopriming with PEG could be used to enhance germination level and speed of *S. imbricata* seeds upon the arrival of effective rainfalls, which usually come after long periods of drought in arid deserts. Our results showed that seed germination was significantly greater at lower, as compared to higher temperatures. Our results indicate that germination of *S. imbricata* seeds was significantly lower in darkness than in light, at lower osmotic potentials (≤ -0.6 MPa PEG) at moderate temperatures (20/30 °C) and most of PEG levels at the higher temperatures (25/35 °C). Seeds germinated in up to -1.8 MPa PEG at lower temperatures, but few seeds germinated at -1.4 MPa at higher temperatures. *S. imbricata* seed germination could be negatively affected by climate change and this would affect local abundance of *S. imbricata*, especially in the hyper arid desert of the UAE.

We studied the effects of light, temperature and maternal salinity on drought tolerance during germination of *Salsola drummondii* Ulbr., which correspond to the objective number one of this doctoral thesis.

The effects of temperature, light, salinity, and drought on germination of halophytes have been extensively studied. However, few studies have focused on the germination of plants that grow well in both saline and non-saline habitats (i.e., habitat-indifferent halophytes). Here, we assess the impacts of population origin, temperature, and light on

drought tolerance, as simulated by polyethylene glycol (PEG), during germination of *S. drummondii*, a habitat-indifferent halophyte from the arid Arabian deserts of the UAE. Seeds were collected from both saline and non-saline habitats and germinated at six PEG levels (0, -0.4, -0.7, -1.0, -1.2 and -1.5 MPa) at three temperatures (15/25, 20/30 and 25/35 °C) and two light regimes (12 hrs light/12 hrs darkness and complete darkness). The results of our study showed significantly greater germination of seeds from the non-saline habitat as compared with those from saline habitat in all PEG concentrations up to -1.2 MPa. At -1.5 MPa; however, there were non-significant differences in the final germination of the two seed lots. The results also showed insignificant differences in the viability of non-saline and saline habitat seeds. This indicates that seeds from the saline habitat are more dormant, as compared to those from the non-saline habitats when germinated in lower osmotic potential solutions of PEG. The greater dormancy of the saline habitat seeds of *S. drummondii* helps them postpone their germination until the onset of favorable conditions for seedling establishment.

Our results showed non-significant differences between the germination of seeds at the three temperatures, when *S. drummondii* seeds were incubated at low levels of drought (0 and -0.4 MPa). At higher drought levels, however, germination was significantly reduced at high temperatures (25/35 °C) as compared to lower temperatures (15/25 °C). In the present study, however, seeds of *S. drummondii* germinated only to less than 20% in -1.5 MPa PEG solutions but the same seeds were able to germinate in 1200 mM NaCl (around -5.0 MPa). The greater tolerance to lower osmotic potential resulted from NaCl than that from PEG has been reported in several other species. The greater tolerance of *S. drummondii* to NaCl, compared to drought simulated by PEG indicates that osmotic, rather than toxicity effect would be responsible for the failure of germination of this species in saline solutions. The result also indicates that PEG might cause irreversible damage to the cells. The broad windows of germination under different temperature and light regimes and the ability of seeds to germinate under relatively lower osmotic potentials indicate that *S. drummondii* is less threatened by the projected climate change in the Middle East. Our results indicated that *S. drummondii* and *S. imbricata* germinated significantly better at the lower thermoperiods (15/25 °C) than at the higher thermoperiods (25/35 °C). Also our results indicated that *S. imbricata* tolerates higher drought stress more than *S. drummondii* where *S. imbricata* can tolerate up to -2.2 MPa while *S. drummondii* can tolerate up to -1.5 MPa only.

We studied the effects of light, temperature and maternal salinity on salinity tolerance during germination of *Salsola drummondii* Ulbr., which correspond to the objective number two of this doctoral thesis.

Few species can survive well in both salty and non-salty soils (i.e., the habitat-indifferent halophytes). Little is known about the effect of soils differ in salt levels on salt tolerance of seed progeny. This study assesses the effects of seed maternal habitat of *S. drummondii*, a habitat-indifferent halophyte, on the individual effects and interactions between salt tolerance, light and temperatures on final germination, germination rate index and recovery of germination from salt solution. Seeds collected from plants grown in salty and non-salty soils were germinated in six salt solutions (0, 200, 400, 600, 800 and 1000 mM NaCl) and incubated in three thermoperiod (15/25, 20/30 and 25/35 °C) and two photoperiod regimes (12 hrs light/12 hrs darkness and complete darkness). Seeds were able to germinate and recover their germination in up to 1000 mM NaCl. Seeds from plants of non-saline soils germinated significantly better in up to 800 mM than for those of saline soils, but the reverse was true at 1000 mM.

Seeds of *S. drummondii* from the saline soils showed relatively greater dormancy than those from the non-saline soils; maximum germination for seeds of non-saline and saline soils was about 85% and 70%, respectively in distilled water and low temperatures. The greater dormancy of seeds from saline soils is further confirmed by the greater dormancy of seeds failed to recover their germination after their transfer from NaCl solutions to distilled water; seeds of saline habitats that did not recover their germination, after being transferred to distilled water, were more viable (20%) than those of non-saline seeds (5%). The higher dormancy of the saline habitat seeds could be ecologically important in a temporally and spatially arid unpredictable environment. Our study showed the ability of *S. drummondii* seeds to germinate and recover their germination in up to 1000 mM NaCl. This indicates that this species is among the most salt tolerant halophytes; up to 25 and 31.5% of seeds from the non-saline and saline soils germinated in 1000 mM NaCl, respectively.

In the present study, germination recovery was around 40% for seeds from the non-saline soils, but was about 10% for seeds from saline soils. Interestingly, the recovery from higher salinities (>800 mM NaCl) was greater at lower, than at higher thermoperiods for seeds from the two habitat types, but the response to the photoperiod did not differ between the two habitats. In the present study, around 25% and 32% of seeds from the non-saline and saline soils, respectively, germinated in 1000 mM NaCl. However, seeds of the same habitats were able to germinate only to less than 20% in -1.5 MPa PEG solutions. The ability of *S. drummondii* seeds to germinate in 1000 mM NaCl (around -5.0 MPa), but only in less than -1.5 MPa PEG indicates that the failure of germination in saline solutions could be osmotic, rather than ion-specific toxicity effect. This is further confirmed by the greater ability of *S. drummondii* seeds to recover from 1000 mM NaCl, but not from -1.5 MPa PEG; less than 25% of PEG treated seeds recovered their germination from -1.5 MPa PEG. Our results indicated that *S. drummondii* germinated significantly greater at the lower thermoperiods (15/25 °C) than at the higher thermoperiods (25/35 °C). The results of germination speed in *S. drummondii* showed that seeds from plants of the saline soils germinated faster than those from non-saline soils. The increase in salinity did not significantly affect GRI. Germination recovery was greater for seeds of plants from non-saline than those from saline soils and for seeds germinated at lower than at higher temperatures. GRI of germination recovery increased with the increase in salinity level and was significantly faster for seeds of non-saline than those of saline soils. Despite seeds of the two habitats are able to disperse to each other's habitat, they differed in dormancy, GRI, and response to light and temperature. Such difference could be considered as environmental cues to determine the proper space and time of germination that help in successful seedling establishment.

We studied the ecophysiological adaptations of *Salsola drummondii* Ulbr., at adult stage under natural saline and non-saline habitats, which correspond to the objective number three of this doctoral thesis.

Assessment of physiological, biochemical and morphological adaptations of habitat-indifferent halophytes that can grow well in both saline and non-saline habitats are important in understanding salt tolerance. Here, we studied some morphological, physiological and biochemical traits for *S. drummondii*, a habitat-indifferent halophyte that grow well in both saline and non-saline soils in the Arabian deserts. Samples from different organs as well as from soils were collected from plants of the two habitat types to assess average leaf fresh and dry weights (FW and DW), leaf succulence (SWC), chlorophyll pigments (Chl *a*, *b*, carotenoids), lipid peroxidation (MDA; malondialdehyde), H_2O_2 content, antioxidant enzymes activity, catalase (CAT), ascorbate peroxidase (APX), guaiacol peroxidase (GPX), stable carbon isotope composition ($\delta^{13}C$), carbon isotope discrimination ($\Delta^{13}C$), and accumulation of ions such as Na^+, K^+, Ca^{2+}, Mg^{2+} and Fe^{2+}. Results revealed that plants from saline habitat showed no significant reduction in the leaf growth (FW, DW) and leaf succulence, as compared to non-saline habitat. Our results showed that greater accumulation of Na^+ in saline habitat was not accompanied by any changes in K^+ contents. The Ca^{2+}, Mg^{2+} and Fe^{2+} content was statistically unaffected in leaves, stems and roots of *S. drummondii* collected from both saline and non-saline natural habitat and this indicate that *S. drummondii* is a habitat-indifferent halophyte that can maintain ion homeostasis even under high salinity in saline habitat.

We found increased antioxidant enzymes (CAT, APX) in *S. drummondii* that enhanced the performance of plants from saline habitat. MDA levels remained unchanged in plants from saline when compared with those from non-saline habitats. Hydrogen peroxide; H_2O_2 increased in roots but remained unaffected in shoots of plants from saline when compared with those from non-saline habitats. The $\Delta^{13}C$ was lowered in saline habitat as compared to non-saline habitat that indicates uninterrupted stomatal conductance in non-saline habitat but it did not contribute much to the improvement of plant biomass that did not statistically differed in plants from both habitats. The lower carbon isotope discrimination in *Salsola drummondii* leaves from saline when compared with those from non-saline habitats might suggest that plants from saline habitats decreased their stomatal conductance to decrease water loss and to increase water use efficiency. We concluded after this study that *S. drummondii* has the ability to accumulate high sodium levels without disturbing much its normal plant growth. Therefore, *S. drummondii* may be useful for restoring degraded sodium-contaminated sites.

We studied the effect of salt stress on physiological and biochemical traits in *Salsola drummondii* Ulbr., at seedling stage under experimental conditions, which corresponds to the objective number three of this doctoral thesis.

Habitat-indifferent halophytes that can grow well in both saline and non-saline soils offer a good opportunity to understand the physiological and biochemical responses of salt tolerance. The changes in growth parameters, sodium accumulation and elemental composition, and the antioxidant enzymes activities of habitat-indifferent *S. drummondii* under different concentrations of salinity stress (0, 200, 500 and 800 mM NaCl) during the vegetative stage were investigated. Results of our study showed that *S. drummondii* grew very well in up to 500 mM NaCl.

Interestingly, there was no significant difference in the biomass of shoots, roots and leaves between control and plants treated with 500 mM NaCl (equivalent to seawater

salinity). Such results confirm the hypothesis that *S. drummondii* are habitat-indifferent halophytes There were no significant changes in water contents at 200 and 500 mM NaCl, while at the high salt concentration (800 mM NaCl), *S. drummondii* exhibited decreased values of succulence (water content) in both shoot and root. The decrease in tissue water content was related to decreasing plant growth at high salinity. Furthermore, chlorophyll and carotenoids contents were reduced at 500 and 800 mM NaCl, which might result in photo inhibition at higher salinity level. The decrease in the chlorophyll content at higher salinity was associated with a significant increase in hydrogen peroxide and lipid peroxidation (MDA; Malondialdehyde) that are responsible for chlorophyll degradation. The negative effect of high salinity on chlorophyll content has been ascribed to negative effect of Na^+ on uptake of some important elements, especially Mg^{2+}.

Our results indicated a significant reduction in Mg^{2+} in *S. drummondii* leaves treated with higher levels of NaCl. The Na^+ contents in both shoots and roots were increased with increases in sodium chloride concentrations. In contrast, *S. drummondii* plants treated with NaCl exhibited significant reduction in levels of essential ions in different plant organs. The Na translocation ability of *S. drummondii* from roots to shoots as a possible adaptive mechanism. As *S. drummondii* could be accumulator for Na^+, our results suggest the use of this species in salt affected habitats for their removal of Na^+ and therefore for their reclamation. Additionally, proline concentrations were significantly increased with increasing salinity treatment. The level of proline in the shoot system was higher than the root. In our study, the concentration of H_2O_2 and MDA (malondialdehyde) increased significantly only in shoots at the highest salinity levels while remained unchanged in the root.

Antioxidant enzyme GPX was induced under salinity stress in both roots and shoots and showed higher activity in roots than shoots. While CAT (catalase) was induced in roots of *S. drummondii* at 800 mM NaCl. The level of H_2O_2 in roots was unchanged due to the high level of GPX (guaiacol peroxidase) in this region, while GPX activity in shoots was not high enough to scavenge the produced H_2O_2. Additionally, APX (ascorbate peroxidase) was increased in shoot at 500 and 800 mM NaCl. In contrast, APX (ascorbate peroxidase) levels were decreased significantly in the roots of *S. drummondii*. Induction of antioxidant enzymes activities and proline accumulation in *S. drummondii* plants were correlated with enhanced salt tolerance. Our data also demonstrated that CAT (catalase) and GPX (guaiacol peroxidase) enzymes had the greatest H_2O_2 scavenger activity in roots. Collectively, our findings provide novel insight into the salt tolerance ability of this habitat-indifferent halophyte *Salsola drummondii*.

We studied the transcriptomic analysis of *Salsola drummondii* Ulbr., under salt stress which correspond to the objective number four of this doctoral thesis.

Salt tolerance is occurred by the interaction of multiple genes, which involves many physiological, biochemical, and molecular processes. Salt tolerance is a characteristic feature of habitat-indifferent halophytes that can grow well in both saline and non-saline soils which offer a good opportunity to understand the molecular mechanisms of salt tolerance. Hence, the present study was conducted to understand the molecular basis of salt tolerance through the transcriptome profiling of the habitat-indifferent halophyte *S. drummondii*, which is succulent perennial habitat-indifferent halophyte that can survive and tolerate high salinity levels. Illumina Hiseq 2000 platform was used to sequence 12 cDNA libraries prepared from control (0 mM NaCl) and treated (1200 mM NaCl) for both shoot and root samples with three replicates for each treatment. Compared transcriptomes between salt treated and control samples resulted 17361 differentially expressed genes (DEGs) (including 11998 upregulated transcripts and 5363 downregulated transcripts), and 272643 unigenes were functionally annotated. The majority of DEGs represented functional groups of transcription factors, signal transduction, defense metabolism, transporters, cell wall metabolism, regulatory processes, respiration, chaperons and ubiquitination involved in salt tolerance. This study has identified potential genes involved in salt tolerance in *S. drummondii* and showed that tolerance of *S. drummondii* to high salinity concentrations might depend on the induction of some genes in shoot tissues which are involved in ABA pathway (carrot ABA-induced in somatic embryos 3, probable protein phosphatase 2C 24), ion transporter (Magnesium transporter 2 isoform 2), sucrose transport (Bidirectional sugar transporter SWEET14-like protein), carbohydrate metabolism (Glucose and ribitol dehydrogenase homolog 1) and transcription factors such as homeobox 40 (ATHB 40) and protein FAR1-RELATED SEQUENCE 5-like. Also the salt tolerance in *S. drummondii* might depend on the induction of some genes in root tissues which play a role in nitrogen assimilation (Glutamine synthetase), redox homeostasis (superoxide dismutase (SOD)), chaperons (18.1 kDa Class 1 heat shock protein-like), respiratory pathway and sucrose metabolism (cytochrome c oxidase subunit 1 and cytochrome c oxidase subunit 2) and polysaccharide metabolism and transport (Barwin-like endoglucanase).

RESUMEN

La Península de Arabia comprende siete países que constituyen el “Arab Gulf Cooperation Council (AGCC)”, siendo los Emiratos Árabes Unidos (UAE) uno de ellos. Los UAE se sitúan en el noreste de la Península de Arabia, cubren una superficie total de 83,600 Km^2 y constan de siete Emiratos: Abu Dhabi, Dubai, Sharjah, Ras Al Khaimah, Fujairah, Ajman y Umm Al Quwain. La mayor parte de los EAU es un desierto. Las características geomorfológicas de los EAU incluyen montañas, llanuras de grava, arenas y salinas. El desierto de arena cubre más del 90.0% de la superficie del país. La mayor parte del desierto de arena se caracteriza por la presencia de dunas que se elevan gradualmente desde las llanuras costeras alcanzando hasta 250 m sobre el nivel del mar (ASL). Las regiones montañosas de los Emiratos Arabes Unidos (EAU) se sitúan de norte-sur paralelas a la costa este. En algunos años, ciertas de estas áreas podrán no recibir lluvia. El ecosistema de los Emiratos Árabes Unidos puede definirse como un desierto caliente híper-árido (desierto caliente subtropical) con dos estaciones: un verano largo y caluroso (de abril a octubre) y un invierno templado y corto (de noviembre a marzo). Las precipitaciones tienen lugar principalmente en invierno con máxima intensidad durante febrero y marzo. La precipitación media anual es de unos 110 mm con una variabilidad extrema en el espacio y el en tiempo. En Abu Dhabi (Emiratos del sur), se ha registrado la precipitación anual más baja (aproximadamente 45 mm / año). La precipitación anual más alta corresponde a la región montañosa del noreste del país y oscila entre 125.6 y 172 mm / año. La temperatura media anual es de aproximadamente 27 °C y la humedad es de 45.0%. En el invierno, la temperatura media es de alrededor de 20 °C, mientras que la temperatura media del verano oscila entre 35 y 40 °C. Además, la humedad puede alcanzar más del 90.0%.

Los Emiratos Árabes Unidos es un desierto cálido e híper-árido que sufre mucho estrés ambiental debido a unas condiciones climáticas duras, tales como la escasa lluvia, altas tasas de evaporación, temperaturas altas y altos niveles de salinidad del suelo y del agua. En general, el estrés ambiental es una combinación de estrés biótico y abiótico. El estrés abiótico como sequía, estrés salino, metales pesados y altas temperaturas y el estrés biótico como la herbívora o los agentes patógenos. El estrés ambiental que experimentan las especies de plantas puede inducir a cambios fenotípicos que abarcan varias generaciones. La plasticidad transgeneracional proporciona una variación fenotípica que contribuye a la adaptación al estrés ambiental. La plasticidad fenotípica transgeneracional en los caracteres de la progenie

puede llevarse a cabo a través del efecto maternal y / o epigenético. El efecto maternal en las plantas incluye los efectos genéticos maternos causados por la herencia (plastidios), además del efecto no hereditario del endospermo, la cubierta de semillas, las hormonas, proteínas y transcripciones genéticas. Mientras que los efectos maternos ambientales generalmente disminuyen en la primera generación, los efectos epigenéticos transmiten respuestas plásticas heredables a los efectos ambientales. En nuestro estudio, no está claro si las diferencias en la latencia (dormancia) de las semillas, las respuestas de germinación a la sequía y a la tolerancia a la salinidad entre semillas procedentes de especies que viven en hábitats no salinos se deben al efecto maternal y / o epigenético. Por lo tanto, se necesitan estudios que ayuden a dilucidar el efecto epigenético del efecto de salinidad en el hábitat donde la planta crece (efecto maternal) en halófitos indiferentes al hábitat, como por ejemplo *Salsola drummondii* Ulbr., Las plantas en áreas desérticas cálidas híper-áridas están expuestas a tensiones abióticas como la sequía y la sal. La sequía y el estrés salino causan lesiones, enfermedades, crecimiento anormal y tienen un gran impacto en el desarrollo y la productividad de la planta.

El estrés por sequía es debido a la escasez de recursos hídricos y ocurre cuando el agua disponible en el suelo se reduce debido a muchos factores, como precipitación muy escasa o nula y la pérdida continua de agua por transpiración o evaporación debido a las condiciones atmosféricas. La sequía es la amenaza más crítica para la seguridad alimentaria mundial y fue el catalizador de las grandes hambrunas del pasado. La sequía conduce a una reducción en el contenido de agua del suelo y, en consecuencia, es uno de los factores de estrés ambiental más perniciosos al que se enfrentan las plantas. La sequía inhibe el crecimiento, daña la integridad de la membrana, disminuye el contenido de pigmento, desequilibra las relaciones hídricas de ajuste osmótico, reduce la actividad fotosintética y reduce o incluso daña la producción de rendimiento de las plantas. El estrés por sequía tiene efectos nocivos de la germinación, la morfología, la fisiología y el metabolismo de las semillas de las plantas. En esta memoria de doctorado, verificamos el efecto del estrés por sequía en dos especies del genero *Salsola* L. (Amaranthaceae*)* que viven en los Emiratos Árabes Unidos (EAU) durante la etapa de latencia (dormancia) y germinación de sus semillas.

El estrés salino es una condición del suelo caracterizada por altos niveles de sales solubles. La mayoría de los suelos afectados por la sal provienen de la acumulación de sales durante largos períodos de tiempo en áreas áridas y semiáridas debido a causas naturales. El estrés salino del suelo ocurre debido a dos razones; en primer lugar (respuesta rápida), la alta cantidad de sales en el suelo dificulta que las raíces extraigan agua debido a la disminución del potencial de soluto del suelo y el efecto de las sales fuera de las raíces tiene un efecto nocivo inmediato sobre la célula en crecimiento y el metabolismo asociado y este efecto del estrés salino se conoce como efecto osmótico del estrés salino y es similar al efecto de las plantas de estrés por sequía. En segundo lugar (respuesta más lenta), la absorción y / o la acumulación de altas concentraciones de iones como sodio y cloruro dentro de la planta que pueden ser tóxicas y esto se conoce como efecto de toxicidad específica de iones debido al estrés salino, siendo diferente del efecto de la sequía. Los altos niveles internos de iones de sodio y cloruro pueden ser tóxicos para las plantas, ya que comprometen la función enzimática e interrumpen los procesos metabólicos causando la aceleración de la senescencia de las hojas. El estrés salino es el efecto adverso del exceso de minerales como el sodio, Na^+ y / o el cloro, Cl^- en la planta. El estrés salino sigue siendo uno de los factores limitantes más críticos para el crecimiento de las plantas, la producción de cultivos y la seguridad alimentaria. El efecto perjudicial se observa a nivel de toda la planta, como por ejemplo la muerte de la plantas o disminución de la productividad de las mismas. El estrés salino es un fenómeno común en suelos áridos y semiáridos, por lo que las plantas han desarrollado mecanismos para tolerar el bajo potencial hídrico del suelo causado por la salinidad, así como por la sequía, por lo que la tolerancia al estrés osmótico es una característica de la mayoría de los halófitos.

En función de su tolerancia al estrés salino, las plantas podrían clasificarse en halófitos tolerantes a la sal y glucófitos, sensible a la sal. Los halófitos son el grupo de plantas más tolerantes que puede tolerar la alta salinidad; por ejemplo, los halófitos cultivados en agua de mar pueden producir altos rendimientos de semillas y biomasa. Además, los halófitos se pueden clasificar ecológicamente en tres categorías: halófitos obligatorios, facultativos e indiferentes al hábitat. Los halófitos obligatorios (verdaderos) crecen solo en hábitats salinos, pero los halófitos facultativos son capaces de establecerse en suelos salinos, pero su crecimiento es óptimo en sustratos sin sal o al menos con bajo contenido de sal.

Los halófitos indiferentes al hábitat pueden hacer frente a suelos salinos, pero sobreviven igualmente bien en suelo salino y sin sal. Los halófitos que son tolerantes a la salinidad también son tolerantes al estrés por sequía. Los halófitos indiferentes al hábitat pueden prosperar y tener un rendimiento igualmente bueno tanto en hábitats salinos como no salinos. Algunos halófitos facultativos pueden tolerar altos niveles de salinidad (algunas veces el doble de salinidad del agua de mar) sin una reducción significativa en el crecimiento.

Muchos halófitos indiferentes al hábitat, como *Zygophyllum qatarense* Hadidi y *Salsola drummondii* Ulbr., sobreviven tanto en hábitats híper salinos como no salinos del desierto híper árido de la Península de Arabia. Hacer frente a la sequía y la salinidad en las etapas iniciales de crecimiento de la planta es difícil, incluso para los halófitos. En esta memoria de doctorado analizamos el efecto del estrés salino en una especie (*S. drummondii* Ulbr.) de la familia Amaranthaceae en los EAU. El estrés salino afecta a todos los principales procesos biológicos de las plantas, como la germinación, el crecimiento, la fotosíntesis, la relación hídrica, el desequilibrio de nutrientes. Según varios estudios, la concentración óptima de cloruro de sodio induce el crecimiento de la planta, pero los niveles extremos de sal tienen efectos inhibitorios muy dañinos en varios rasgos de la historia de la vida, como la etapa vegetativa y la etapa crítica de latencia de semillas, germinación y plántulas más sensibles. Esto es especialmente importante en suelos híper salinos que podrían causar daños severos al crecimiento y desarrollo de las plantas.

Los mecanismos para la resistencia a la sal en los halófitos generalmente se dividen en dos categorías principales: tolerancia a la sal y evitación de la sal. Algunos halófitos tienen la capacidad de resistir el alto estrés salino debido a adaptaciones anatómicas y morfológicas especiales o mecanismos de evitación. Evitar la sal es un mecanismo de resistencia en el que la planta trata de mantener los iones de sal lejos de las partes de las plantas que podrían dañarse debido a su exposición a un alto estrés salino. Hay diferentes maneras de permitir que los halófitos eviten el estrés salino, como la exclusión de sal, la secreción de sal, el desprendimiento de hojas viejas, la suculencia y la respuesta estomática. La exclusión de sal es el método más popular para sobrevivir en altas concentraciones de sal en halófitos. La secreción de sal se realiza gracias a glándulas salinas especializadas que son responsables de la secreción del exceso de sal de la planta. La caída de hojas viejas permite a algunos halófitos liberar el exceso de sal. La suculencia es un carácter adaptativo característico para la supervivencia bajo estrés en muchos de los halófitos. Respecto a la respuesta estomática, hay dos respuestas estomáticas de la planta a la salinidad; las células protectoras que pueden utilizar potasio para lograr su regulación normal de turgencia en lugar de sodio o las células protectoras que pueden usar potasio para limitar su ingesta de sodio, este tipo de mecanismo es más importante en esos halófitos que carecen de glándulas.

La tolerancia a la sal es la capacidad de las plantas para crecer y completar su ciclo de vida en un sustrato que contiene altas concentraciones de sales solubles. La viabilidad de las plantas en hábitats salinos depende de su capacidad para hacer frente a varias limitaciones importantes, ya que hay déficit de agua, restricción de la absorción de CO_2, toxicidad iónica y desequilibrio de nutrientes. Los mecanismos de tolerancia a la sal implican cambios en muchas vías fisiológicas y bioquímicas y cambios que protegen procesos importantes como la fotosíntesis y la respiración. Las estrategias fisiológicas y bioquímicas incluyen homeostasis de iones, acumulación selectiva o exclusión de iones, control de la absorción de iones por las raíces y transporte a las hojas, compartimentación de iones a nivel celular y de toda la planta, síntesis de solutos compatibles, cambio en la ruta fotosintética, alteración en la estructura de la membrana, inducción de enzimas antioxidantes e inducción de hormonas vegetales. La respuesta fisiológica y bioquímica al estrés salino se basa en cambios en la expresión génica. La mayoría de estos genes están involucrados en la transducción de señales, la regulación transcripcional y codifican para antipuertos de sodio/hidrogeno, Na^+/H^+ (membrana vacuolar o plasmática), pirofosfatasa vacuolar, transportadores de potasio, canales iónicos, antioxidantes, captadores de ROS (Reactive Oxygen Species) y proteínas que participan en la función protectora y la transducción de señales. Comprender los mecanismos de tolerancia a la sal de las plantas ayuda a los cultivos de plantas resistentes a la sal. Por lo tanto, los estudios sobre los mecanismos por los cuales los halófitos responden o se adaptan al estrés salino son cruciales para una agricultura sostenible. Las ventajas de estudiar las plantas halófitas indiferentes, (especies que pueden crecer en hábitats salinos y no salinos) es que se desarrollan y evolucionan en dos hábitats diferentes, esto nos da una buena oportunidad para estudiar los diferentes caracteres asociados a su ciclo de vida, incluida la latencia (dormancia) de las semillas, atributos como la germinación final y las tasas de germinación, el crecimiento de las plántulas, la tolerancia a la sal en condiciones de campo y la tolerancia a la sal en condiciones de laboratorio. La importancia de estudiar halófitos indiferentes al hábitat es comprender los mecanismos de la tolerancia a la salinidad en la germinación, en el crecimiento de las plántulas y en etapas adultas, como por ejemplo en *S. drummondii* Ulbr., que podrían ser importantes para comprender diferentes estrategias de supervivencia de especies halófitos en diferentes hábitats. Los halófitos indiferentes del hábitat se caracterizan por una diversidad fisiológica más amplia que les permite hacer frente a las condiciones salinas y no salinas. Evaluar los diferentes compuestos responsables de la tolerancia a la sal en el hábitat de los halófitos indiferentes que, crecen en condiciones salinas y no salinas, ayudaría a comprender los mecanismos involucrados en la tolerancia de tal estrés. Al estudiar cómo las plantas responden al estrés severo, aprendemos más sobre los límites de sus distribuciones geográficas, de su hábitat y de su diversidad. Además, definir los mecanismos de adaptación bajo estrés salino ayudaría a comprender las causas de la presencia de hábitat en diferentes halófitos bajo las condiciones híper-salinas de los ambientes cálidos y secos, como el desierto de los EAU, y esto podría ayudar en la conservación de hábitats de los halófitos indiferentes en el desierto. Los mecanismos moleculares y bioquímicos que regulan la supervivencia del hábitat en halófitos deben diferir entre los halófitos y los glucófitos estrictos.

Para crecer en hábitats tanto salinos como no salinos, los halófitos deben tener uno o más genes asociados a la tolerancia a la salinidad que puedan activarse/desactivarse, dependiendo de la salinidad del suelo. La activación de los genes de tolerancia a la sal debería permitir que los diferentes tipos de halófitos sobrevivan al estrés salino. Identificar los genes responsables de la biosíntesis y el catabolismo de los osmolitos comunes y los metabolitos antioxidantes en plantas halófitas indiferentes ayudaría a comprender los mecanismos que intervienen en la tolerancia a la salinidad en las plantas. Además, puede proporcionar una nueva estrategia para aumentar la tolerancia de las plantas al estrés salino y el desarrollo de plantas tolerantes a la sal. La capacidad de los halófitos para tolerar altos niveles de sal está determinada por la coordinación efectiva entre varios procesos fisiológicos, vías metabólicas y redes de proteínas o genes responsables de administrar la tolerancia a la salinidad. Hay pocos estudios que evalúen la diferencias de dormancia y de germinación de las semillas recolectadas en dos hábitats diferentes, salinos y no salinos. La memoria de doctorado evalúa la diferencia dentro de una misma especie que crece en hábitats salinos y no salinos desde el punto de vista bioquímico, fisiológico y molecular.

Se estudia el efecto de la luz y temperatura en la tolerancia a la sequía durante la germinación de *Salsola imbricata* Forssk., lo cual corresponde al objetivo número uno de esta tesis doctoral.

El crecimiento de plántulas en ecosistemas desérticos es a veces raro y altamente impredecible debido a condiciones desfavorables que inhiben la germinación. Pocos estudios abordan los impactos de la deficiencia de agua, la temperatura y la luz en la germinación de las especies arbustivas del desierto. En esta memoria de doctorado, evaluamos el impacto de la sequía simulada (estrés osmótico) utilizando polietilenglicol (PEG), la luz y la temperatura de incubación en la germinación de semillas de *S. imbricata*, un arbusto perenne de hoja suculenta típico de los desiertos árabes áridos. PEG (polietilenglicol) es la sustancia osmótica que se disuelve en solución acuosa a diferentes concentraciones para producir soluciones con diferentes potenciales negativos. Este estudio se compara dos especies del genero *Salsola* L. *S. imbricata* produce y dispersa una gran cantidad de semillas que germinan durante los meses de diciembre y enero. Las semillas frescas germinan bajo diferentes potenciales osmóticos (0, -0.2, -0.4, -0.6, -0.8, -1.0, -1.4, -1.8 y-2.4 MPa) a tres temperaturas (15/25, 20/30 and 25/35 °C) y en dos regímenes de luz diferentes (12 hrs luz/12 hrs completa oscuridad). En agua destilada, la germinación fue significativamente mayor a la luz a temperaturas más altas que a temperaturas y lo contrario en la oscuridad. Tanto la germinación final como el índice de tasa de germinación (GRI) disminuyeron gradualmente con el aumento del estrés osmótico, pero la reducción en la tasa de germinación fue más pronunciada a temperaturas más altas en comparación con las más bajas. La germinación final y el GRI disminuyeron alrededor del 70% y 49%, respectivamente, en agua destilada a bajas y altas temperaturas a 44% y 39% en -1.4 MPa a bajas temperaturas, y a 5% y 26%, respectivamente, a temperaturas más altas.

Nuestro estudio de memoria de tesis doctoral mostró que la mayor germinación de esta especie se produjo tanto en luz como en oscuridad a temperaturas más bajas y moderadas (15/25 y 20/30 °C). Siendo una tendencia también observada en otros halófitos suculentos de regiones subtropicales desérticas. También mostró que el índice de tasa de germinación era próximo al 50% en agua destilada y mayores potenciales osmóticos de PEG (hasta -0.8 MPa), especialmente a temperaturas más bajas y moderadas. Esto indica que las semillas pueden germinar dentro de las 24 horas posteriores a la imbibición.

La germinación más rápida y con mayor potencial osmótico se ha considerado como una estrategia para el establecimiento de plántulas, cuando las precipitaciones son escasas, al comienzo de la temporada de crecimiento. A temperaturas más altas, la germinación se redujo significativamente en la oscuridad, en comparación con las condiciones de luz, para la mayoría de los potenciales osmóticos probados. Sin embargo, a temperaturas más altas (25/35 °C), tanto la germinación final como el GRI fueron significativamente menores a potenciales osmóticos más bajos (≤ -1.4 MPa), lo que indica una menor probabilidad de germinación y establecimiento de plántulas cuando la lluvia es escasa durante en las estaciones de crecimiento de la planta. Nuestros resultados mostraron poca germinación de semillas de *S. imbricata* en potencial osmótico bajo a temperaturas bajas (4% y 14% germinaron a -2.2 y -1.8 MPa, respectivamente) y temperaturas moderadas (12% germinaron a -1.8 MPa).

La capacidad de las semillas para germinar bajo un potencial osmótico tan bajo respalda aún más la hipótesis de que algunas de ellas podrían germinar en años secos e incluso muy secos. La mayoría de las semillas no germinadas de *S. imbricata* con los potenciales osmóticos más bajos (-1.8 y -2.2 MPa PEG) recuperaron su germinación inmediatamente una vez que fueron transferidas al agua destilada. De hecho, no hubo una diferencia significativa en la germinación total (es decir, en PEG y después de que las semillas se transfirieron al agua destilada) entre los potenciales osmóticos más altos y más bajos (-2.2 MPa) a las temperaturas más bajas. Este resultado indica que la osmopriming con PEG podría usarse para mejorar el nivel de germinación y la velocidad de las semillas de *S. imbricata* al llegar las lluvias, que generalmente ocurren después de largos períodos de sequía en desiertos áridos.

Nuestros resultados mostraron que la germinación de las semillas fue significativamente mayor a temperaturas más bajas en comparación con las altas. Nuestros resultados indican que la germinación de las semillas de *S. imbricata* fue significativamente menor en la oscuridad que en la luz, a potenciales osmóticos más bajos (≤ -0.6 MPa PEG) a temperaturas moderadas (20/30 °C) y la mayoría de los niveles de PEG a temperaturas más altas (25/35 °C). Las semillas germinaron en hasta -1.8 MPa PEG a temperaturas más bajas, pero pocas semillas germinaron a -1.4 MPa a temperaturas más altas. La germinación de las semillas de *S. imbricata* podría verse afectada negativamente por el cambio climático y esto afectaría la abundancia local de *S. imbricata*, especialmente en el desierto hipar árido de los EAU.

Se estudia el efecto de la luz, la temperatura y el efecto maternal de la salinidad en la tolerancia a la sequía durante la germinación de *Salsola drummondii* Ulbr., lo cual corresponde al objetivo número uno de la memoria de tesis doctoral.

Los efectos de la temperatura, la luz, la salinidad y la sequía en la germinación de halófitos han sido ampliamente estudiados. Sin embargo, pocos estudios se han centrado en la germinación de plantas que crecen bien en hábitats tanto salinos como no salinos (es decir, halófitos indiferentes al hábitat). En esta memoria de doctorado, evaluamos los impactos del origen de las semillas (hábitat), la temperatura y la luz sobre la tolerancia a la sequía, como lo simula el polietilenglicol (PEG), durante la germinación de *S. drummondii*, un halófito indiferente al hábitat de los desiertos árabes.

Las semillas se recolectaron en hábitats tanto salinos como no salinos y germinaron a seis niveles de PEG a tres temperaturas y dos regímenes de luz diferentes (15/25, 20/30 y 25/35 °C). Los resultados de nuestro estudio mostraron una germinación significativamente mayor de semillas del hábitat no salino en comparación con las del hábitat salino en todas las concentraciones de PEG hasta -1.2 MPa. A -1.5 MPa; sin embargo, hubo diferencias no significativas en la germinación final de los dos lotes de semillas. Los resultados también mostraron diferencias no significativas en la viabilidad de las semillas procedentes del hábitat no salino y salino. Esto indica que las semillas del hábitat salino están más inactivas, en comparación con las de los hábitats no salinos cuando germinan en soluciones de PEG con potencial osmótico inferior. La mayor latencia (dormancia) de las semillas del hábitat salino de *S. drummondii* les ayuda a posponer su germinación hasta el inicio de condiciones favorables para el establecimiento de las plántulas. Nuestros resultados mostraron diferencias no significativas entre la germinación de semillas bajo los tres regimenes diferentes de temperaturas, cuando las semillas de *S. drummondii* se incubaron a bajos niveles de sequía (0 y -0.4 MPa). Sin embargo, a niveles de sequía más altos, la germinación se redujo significativamente a altas temperaturas (25/35 °C) en comparación con temperaturas más bajas (15/25 °C).

Sin embargo, en el presente estudio, las semillas de *S. drummondii* germinaron solo a menos del 20% en soluciones de PEG de -1.5 MPa, pero las mismas semillas pudieron germinar en NaCl 1200 mM (alrededor de -5.0 MPa). La mayor tolerancia al menor potencial osmótico resultante del NaCl que la del PEG se ha informado en varias otras especies. La mayor tolerancia de *S. drummondii* al NaCl, en comparación con la sequía simulada por PEG, indica que el efecto osmótico, en lugar de toxicidad, sería responsable de la falta de la germinación de esta especie en soluciones salinas. La elevada tasa de germinación bajo diferentes temperaturas y regímenes de luz y la capacidad de las semillas para germinar bajo potenciales osmóticos relativamente más bajos indican que la especie, *S. drummondii*, está menos amenazada por el efecto del cambio climático proyectado en los desiertos de los Emiratos Árabes Unidos. Los resultados de esta tesis doctoral muestran que *S. drummondii* y *S. imbricata* germinan significativamente más a termo periodos bajos (15/25 °C) que altos (25/35 °C). Nuestros resultados indican también que *S. imbricata* tolera un alto estrés a la sequía en comparación con *S. drummondii* puesto que *S. imbricata* puede tolerar valores hasta -2.2 MPa mientras que *S. drummondii* tolera solo por encima de los -1.5 MPa.

Se estudia el efecto de la luz, la temperatura y el efecto materno de la salinidad en la tolerancia a la salinidad durante la germinación de *Salsola drummondii* Ulbr., lo cual corresponde al objetivo número dos de esta memoria de doctorado.

Pocas especies pueden sobrevivir bien en salinos y no salinos (es decir, los halófitos indiferentes al hábitat). Poco se sabe sobre el efecto de los suelos con diferentes niveles de sal en la germinación de semillas. Esta memoria de doctorado evalúa los efectos del hábitat materno de semillas de *S. drummondii*, un halófito indiferente al hábitat, sobre los efectos individuales y las interacciones entre la tolerancia a la sal, la luz y las temperaturas en la germinación final de las semillas, así como el índice de tasa de germinación. Las semillas recolectadas de plantas que crecen en suelos salinos y no salinos se pusieron a germinar en seis soluciones salinas diferentes y se incubaron en tres regímenes de termo período y dos fotos períodos. Las semillas germinaron en cloruro de sodio, NaCl hasta 1000 mM. Las semillas procedentes de plantas de suelos no salinos germinaron significativamente hasta 800 mM más que las de suelos salinos y lo contrario a 1000 mM. Las semillas de *S. drummondii* de los suelos salinos mostraron una latencia (dormancia) relativamente mayor que las de los suelos no salinos. La germinación máxima para semillas de suelos no salinos y salinos fue de aproximadamente 85% y 70%, respectivamente, en agua destilada y a bajas temperaturas.

La mayor latencia (dormancia) en las semillas de los suelos salinos se confirma, aún más, por la mayor latencia de las semillas que no pudieron germinar después de su transferencia de las soluciones de NaCl a soluciones de agua destilada. Las semillas de hábitats salinos que no recuperaron su germinación, después de ser transferidas al agua destilada, fueron más viables (20%) que las semillas no salinas (5%). La mayor latencia de las semillas del hábitat salino podría ser ecológicamente importante en un árido entorno impredecible.

Nuestro estudio mostró la capacidad de las semillas de *S. drummondii* para germinar y recuperar su germinación en NaCl hasta de 1000 mM. Esto indica que esta especie se encuentra entre los halófitos más tolerantes a la sal; hasta 25 y 31.5% de semillas de suelos no salinos y salinos germinaron en NaCl 1000 mM, respectivamente. En el presente estudio, la recuperación de la germinación fue de alrededor del 40% para las semillas de suelos no salinos, y de aproximadamente el 10% para las semillas de suelos salinos. Curiosamente, la recuperación a salinidades más altas (> 800 mM NaCl) fue mayor en los termo períodos más bajos para las semillas de los dos tipos de hábitat, pero la respuesta al fotoperíodo no difirió entre los dos hábitats. En el presente estudio, alrededor del 25% y el 32% de las semillas de los suelos no salinos y salinos, respectivamente, germinaron en NaCl 1000 mM. Sin embargo, las semillas de los mismos hábitats solo pudieron germinar a menos del 20% en soluciones de -1.5 MPa PEG. La capacidad de las semillas de *S. drummondii* para germinar en NaCl 1000 mM (alrededor de -5.0 MPa), pero solo en menos de -1.5 MPa PEG indica que la no germinación en soluciones salinas podría ser osmótica, en lugar de debida al efecto de toxicidad específica de iones. Esto se confirma aún más por la mayor capacidad de las semillas de *S. drummondii* para recuperarse de 1000 NaCl mM, pero no de -1.5 MPa PEG;

menos del 25% de las semillas tratadas con PEG recuperaron su germinación de -1.5 MPa PEG. Nuestros resultados indican que *S. drummondii* germinó significativamente mayor en los termo períodos más bajos (15/25 °C) que en los termo períodos más altos (25/35 °C).

Los resultados de la velocidad de germinación en *S. drummondii* mostraron que las semillas de plantas de suelos salinos germinaron más rápido que las de suelos no salinos. El aumento de la salinidad no afectó significativamente el GRI. La recuperación de la germinación fue mayor para las semillas de plantas no salinas que las de suelos salinos y para las semillas germinadas a temperaturas más bajas que a altas. El GRI de la recuperación de la germinación aumentó con el aumento en el nivel de salinidad y fue significativamente más rápido para las semillas no salinas que las de los suelos salinos. A pesar de que las semillas de los dos hábitats pueden dispersarse entre sí, diferían en latencia, GRI y respuesta a la luz y la temperatura. Dicha diferencia podría considerarse como señales ambientales para determinar el espacio y el tiempo de germinación adecuada que ayudan al establecimiento exitoso de las plántulas de esta especie.

Se estudian las adaptaciones ecofisiologicas de *Salsola drummondii* Ulbr., en hábitats naturales salinos y no salinos lo cual corresponde con el objetivo número tres de esta memoria de doctorado.

La evaluación de las adaptaciones fisiológicas, bioquímicas y morfológicas de los halófitos indiferentes al hábitat que pueden crecer bien tanto en hábitats salinos como no salinos es importante para comprender la tolerancia a la sal. En esta memoria de doctorado, estudiamos algunos rasgos morfológicos, fisiológicos y bioquímicos para *S. drummondii,* un halófito indiferente al hábitat que crece bien en suelos salinos y no salinos en los desiertos árabes. Se recolectaron muestras de diferentes órganos de la planta y de suelos de los dos tipos de hábitat. Se evaluó el peso medio de hojas frescas y secas (FW y DW), la suculencia foliar (SWC), pigmentos clorofílicos (Chl *a*, *b,* carotenoides), lípidos, peroxidasa (MDA), contenido de H_2O_2, actividad de enzimas antioxidantes, catalasa (CAT), ascorbato peroxidasa (APX), peroxidasa de guayacol (GPX), composición estable de isótopos de carbono ($\delta^{13}C$), discriminación de isótopos de carbono ($\Delta^{13}C$) y acumulación de macro elementos, Na^+, K^+, Ca^{2+}, Mg^{2+} y Fe^{2+}. Los resultados revelaron que la planta de hábitats salinos no mostró una reducción significativa en el crecimiento (FW, DW) y la suculencia de la hoja, en comparación con la de hábitats no salinos. Nuestros resultados muestran que una mayor acumulación de Na^+ en habitats salinos no estuvo acompañada por cambios en los contenidos de K^+. El contenido de Ca^{2+}, Mg^{2+} y Fe^{2+} no se afecto en hojas, tallos y raices de *S. drummondii* recolectada en habitats naturales salinos y no salinos, esto indica que *S. drummondii* es un halófito indiferente al hábitat que puede mantener una homeostasis ionica incuso bajo alta salinidad en hábitat salinos.

Encontramos un aumento de las enzimas antioxidantes (CAT, APX) en *S. drummondii* que mejoraron el rendimiento de salinos. Peroxidación lipídica; MDA levels remained unchanged in plants from saline when compared with those from non-saline habitats. Hydrogen peroxide; H_2O_2 increased in roots but remained unaffected in shoots of plants from saline when compared with those from non-saline habitats (Peróxido de hidrógeno; H_2O_2 y aumentaron en las raíces, pero no se ve afectado en los tallos). El $\Delta^{13}C$ se redujo en salinos en comparación con no salinos, lo que indica una conductancia estomática ininterrumpida en no salinos, pero no contribuyó mucho a la mejora de la biomasa vegetal que no difirió estadísticamente en las plantas de ambos hábitats. La baja discriminación del isotopo de carbón en las hojas de *S. drummondii* de habitats salinos comparadas con aquellas de habitats no salinos sugiere que plantas proceentes de habitats salinos decrecen su conductancia estomatica para disminuir la perdida de agua e incrementar el uso eficiente de la misma. Concluimos tras este studio que *S. drummondii* tiene la capacidad de acumular elevadas cantidades de sodio lo cual no perturbó mucho su crecimiento normal. Por lo tanto, *S. drummondii* puede ser útil para restaurar sitios degradados y contaminados con sodio.

Se estudia el efecto del estrés salino sobre caracteres fisiológicos y bioquímicos en plántulas de *Salsola drummondii* Ulbr., bajo condiciones experimentales, lo cual corresponde al objetivo número tres de la tesis de doctorado.

Los halófitos indiferentes al hábitat que pueden crecer bien en suelos tanto salinos como no salinos ofrecen una buena oportunidad para comprender las respuestas fisiológicas y bioquímicas de la tolerancia a la salinidad. Se investigaron los cambios en los parámetros de crecimiento, la acumulación de sodio y la composición elemental y las actividades de las enzimas antioxidantes de *S. drummondii* bajo diferentes concentraciones de estrés de salinidad (NaCl 0, 200, 500 y 800 mM) durante las etapas de crecimiento vegetativo.

Los resultados de nuestro estudio mostraron que *S. drummondii* creció muy bien en NaCl hasta 500 mM. Curiosamente, no hubo diferencias significativas en la biomasa de tallos, raíces y hojas entre las plántulas control y las tratadas con NaCl 500 mM (equivalente a la salinidad del agua de mar). No hubo cambios significativos en el contenido de agua a 200

y 500 mM NaCl, mientras que a la alta concentración de sal (NaCl 800 mM). *S. drummondii* exhibió valores disminuidos de suculencia (contenido de agua) tanto en el tallo como en la raíz. Además, los contenidos de clorofila y carotenoides se redujeron a NaCl 500 y 800 mM. La disminución en el contenido de clorofila a una mayor salinidad se asoció con un aumento significativo en el peróxido de hidrógeno y MDA que son responsables de la degradación de la clorofila. El efecto negativo de la salinidad elevada en el contenido de clorofila se debe al efecto negativo del Na^+ en la absorción de algunos elementos importantes, especialmente Mg^{2+}.

Los resultados indican una reducción significativa en Mg^{2+} en las hojas de *S. drummondii* tratadas con elevados niveles de cloruro sódico NaCl. Los contenidos de Na^+ tanto en los tallos como en las raíces aumentaron con el incremento de la salinidad. Por el contrario, las plantas de *S. drummondii* tratadas con NaCl exhibieron una reducción significativa en los niveles de iones esenciales en diferentes órganos de la planta. La capacidad de translocación del Na^+ en *S. drummondii* desde las raíces hasta los tallos es un posible mecanismo de adaptación. *S. drummondii* podría ser acumulador de Na^+, y nuestros resultados sugieren el uso de esta especie en hábitats afectados por la sal para la eliminación de Na^+ y, por lo tanto, para su recuperación. Además, las concentraciones de prolina aumentaron significativamente con el aumento del tratamiento de salinidad. El nivel de prolina en el tallo fue más alto que en la raíz. En nuestro estudio, la concentración de H_2O_2 y MDA (malondialdehído) aumentó significativamente en los tallos a niveles más altos de salinidad, mientras que permaneció sin cambios en la raíz.

La enzima antioxidante GPX se indujo bajo estrés de salinidad tanto en las raíces como en los tallos y mostró una mayor actividad en las raíces. CAT (catalasa) se indujo en raíces de *S. drummondii* a NaCl 800 mM. El nivel de H_2O_2 en las raíces no cambió debido al alto nivel de GPX (peroxidasa de guayacol) en este órgano de la planta, mientras que la actividad de GPX en los tallos no fue lo suficientemente alta como para eliminar el H_2O_2 producido. Además, APX (ascorbato peroxidasa) se incrementó en el tallo a 500 y 800 mM de NaCl. Por el contrario, los niveles de APX (ascorbato peroxidasa) disminuyeron significativamente en las raíces de *S. drummondii*. La inducción de actividades de enzimas antioxidantes y la acumulación de prolina en plantas de *S. drummondii* se correlacionaron con una mayor tolerancia a la sal. Nuestro estudio también demuestra que las enzimas CAT (catalasa) y GPX (peroxidasa de guaiacol) tenían la mayor actividad captadora de H_2O_2 en las raíces. Nuestros resultados proporcionan una nueva visión de la capacidad de tolerancia a la sal de este halófito indiferente al hábitat.

Se realiza un análisis transcriptomico de *Salsola drummondii* Ulbr., bajo estrés salino el cual corresponde al objetivo número cuatro de la memoria de doctorado.

La tolerancia a la salinidad se produce por la interacción de múltiples genes, que implica muchos procesos fisiológicos, bioquímicos y moleculares. La tolerancia a la sal es un rasgo característico de los halófitos, los halófitos indiferentes al hábitat que pueden crecer bien en suelos tanto salinos como no salinos ofrecen una buena oportunidad para comprender los mecanismos moleculares de la tolerancia a la salinidad. Por lo tanto, el presente estudio se realizó para comprender la base molecular de la tolerancia a la sal a través del perfil transcriptómico del halófito indiferente *S. drummondii,* que es una especie suculenta perenne y un halófito indiferente que puede sobrevivir y tolerar altos niveles de salinidad. La plataforma Illumina Hiseq 2000 se usó para secuenciar 12 bibliotecas de ADNc preparadas a partir del control (NaCl 0 mM) y tratadas (NaCl 1200 mM) para muestras de tallos y de raíces con tres repeticiones en cada tratamiento. Los análisis transcriptomicos comparados entre las muestras tratadas con sal y las de control dieron como resultado 17361 genes expresados diferencialmente (DEG) (incluyendo 11998 transcripciones con regulación positiva y 5363 transcripciones con regulación baja), y 272643 unigenes fueron anotados funcionalmente. La mayoría de los DEG representaban grupos funcionales de factores de transcripción, transducción de señales, metabolismo de defensa, transportadores, pared celular y crecimiento, procesos regulatorios, respiración y ubicación involucrados en la tolerancia a la sal.

Este estudio ha identificado genes potenciales involucrados en la tolerancia a la sal en *S. drummondii* y mostró que la tolerancia de *S. drummondii* a altas concentraciones de salinidad podría depender de la inducción de algunos genes en los tejidos del tallo que están involucrados en la vía ABA (inducida por ABA de zanahoria en somática embriones 3, probable transportador de iones proteína fosfatasa 2C 24) (transportador de magnesio 2 isoforma 2), transporte de sacarosa (transportador de azúcar bidireccional proteína similar a SWEET14), metabolismo de carbohidratos (homólogo de glucosa y ribitol deshidrogenasa 1) y factores de transcripción como homeobox 40 (ATHB 40) y la proteína SECUENCIA RELACIONADA CON FAR1 tipo 5. Además, la tolerancia a la sal en *S. drummondii* depende de la inducción de algunos genes en los tejidos de la raíz que juegan un papel en la asimilación de nitrógeno (glutamina sintetasa), homeostasis redox (superóxido dismutasa (SOD)), chaperones (18.1 kDa Clase 1 de proteína de choque térmico), vía respiratoria y metabolismo de sacarosa (subunidad 1 de citocromo c oxidasa, subunidad 2 de citocromo c oxidasa) y metabolismo y transporte de polisacáridos (endoglucanasa tipo Barwin).

1. INTRODUCTION

1. INTRODUCTION

DESERT ECOSYSTEMS

Desert ecosystems are described as arid areas abundant with hills, rocks or salt where the annual rainfall is less than 300 mm and the annual amount of precipitation is less than the evaporation rates (Marshak and Repcheck, 2009). The sustainability of the plant and animal life in the desert depends on several factors including the precipitation, temperature, humidity, rate of evaporation, evapotranspiration, and the ground moisture content, etc. Significantly, It is observed that plant growth is enhanced by rain falling in the cold season (Laity, 2009). In fact, deserts are considered “water-controlled ecosystems” (Noy-Meir, 1973). As such, water availability is the results of the balance between water contribution and water loss. In deserts, water is obtained from water flow, precipitation, groundwater and atmospheric moisture (Flanagan and Ehleringer, 1991). However, studies show that in most arid environments, groundwater has a high degree of salinity (Akram and Chandio, 1998).

In general, deserts could be classified into four types: subtropical, cool coastal, cold winter and polar deserts (Logan, 1968; El-Ghani et al., 2017; Mares, 2017). Subtropical deserts have the highest temperature, driest terrain, fast evaporation, and cold winter. The temperature differs significantly from season to another; the temperature 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).

According to World Atlas of Desertification (UNEP, 1997; Parsons and Abrahams, 2009), there are four types of desert, which differ based on Aridity Index: hyper-arid, arid, semiarid and dry sub-humid. The aridity index is estimated based on temperature and precipitation monthly data (Parsons and Abrahams, 2009). Annual rainfall in hyper-arid deserts is less than 25 mm whereas there is no annual seasonal cycle of precipitation. Finally, annual rainfall is between 25 and 200 mm in arid deserts and between 200 and 500 mm in semiarid deserts (John, 2005; Laity, 2009).

The Arabian desert ecosystem

Arabian deserts are considered to be a hyper-arid hot desert that stretches across one million square miles in different counties such as Saudi Arabia, Kuwait, Qatar, UAE, Oman, and Yemen (Huggett, 2007; Bahadur et al., 2015). While Sahara in northern Africa is considered the largest hyper-arid hot desert on earth, the Arabian desert comes second.

The Arabian Desert extends over most of the Arabian Peninsula (including a part of the Iraqi and Jordanian deserts) (Fig. 1). At the north-eastern limit of the desert, both the United Arab Emirates and Qatar are located along the southern coast of the Arabian Gulf (Miller and Cope, 1996; Huggett, 2007; Bahadur et al., 2015). This area is characterized by the most severe climatic conditions in the world in terms of rarity of freshwater, scarce rainfall, strong evaporation, sever temperatures and extreme saline soil and water (Miller and Cope, 1996; Böer, 1997; Zahran, 1997; Peacock et al., 2003).

Figure 1. Map of the Arabian Desert location. The map includes the countries of Arabian Peninsula in brown color.

The United Arab Emirates (UAE) desert ecosystem

Geographically, the desert of United Arab Emirates occupies the south-eastern region of the Arabian Peninsula between latitudes 22 º 40´ and 26 º 00´ North and longitudes 51 º 00´ and 56 º 00´ East. The UAE exists along the south-eastern coast of the Arabian Gulf. On the east, it is boarded by Oman and the Gulf of Oman. On the south and west, it is boarded by Saudi Arabia (Fig. 2). The UAE is composed of seven emirates: Abu Dhabi, Dubai, Sharjah, Ajman, Umm Al Quwain, Ras Al Khaimah, and Fujairah (El-Keblawy et al., 2005; Sherif et al., 2009). The UAE has severe climatic conditions of dry land with different geographic features such as sand dunes, plains, mountains and saline flats (Boer and Chaudhary 1999). El-Keblawy et al. (2005) and Sherif et al. (2009) reported that desert lands in the UAE constitute about 83,600 km^2, representing 90% of its total area. Overall, the land of the UAE could be differentiated into two zones: the larger low-lying zone and the mountains zone. The sandy desert constitutes more than 90% of the country, covering the north-west to the eastern side of the country. However, the mountain zone exists inside that sandy desert. The sandy desert zone is characterized by several altitudes, which ranges from sea level up to 300 m, and includes sand dunes that gradually rise from the coastal plain to reach as high as 250 m above sea level (asl.). The low-lying land exists along the coast of the Arabian Gulf and is limited by beaches and separated hills that can be as high as 40 m a.s.l. in specific regions (El-Keblawy et al., 2005; Sherif et al., 2009). The mountainous zone is comprised of the north-south mountain stretches in parallel with the east coast, which is located about 150 km north-south and about 50 km east-west. The summit of the mountains is as high as 2000 m asl. However, the mountains are truncated by many networks of valleys (El-Keblawy et al., 2005). Regarding the UAE coastal, they contain many small shoals, islands, protected lagoons, channels and deltas, an inner zone of intertidal flats and broad areas of humid and salty regions termed ‘sabkha’ (Brown, 2006; Kitto and Reginald, 2011). The UAE desert has a severe climate as it includes long, dry summers and moderate winters.

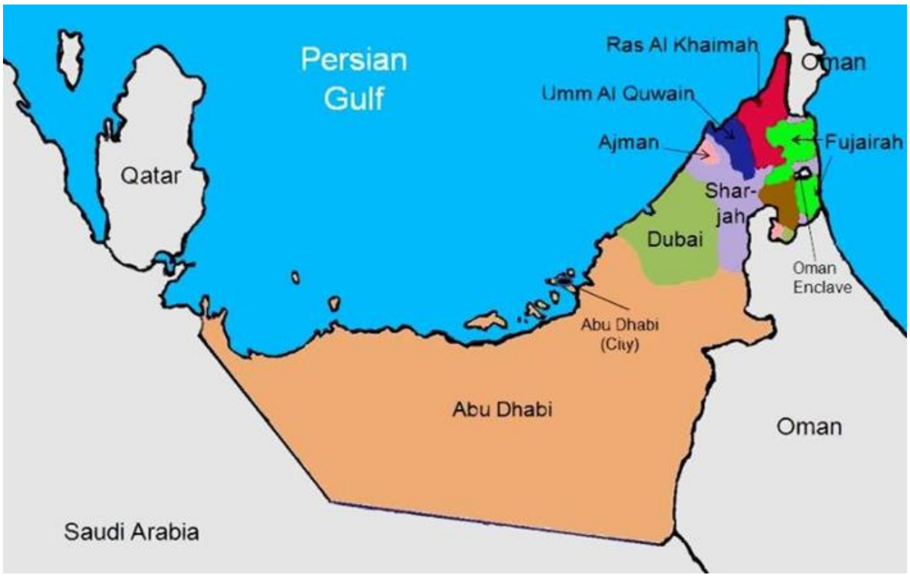


Figure 2. Map of the seven United Arab Emirates (UAE) in different colors, the surrounding countries appears in grey color.

The climate of the United Arab Emirates ecosystems is similar in all Arabian Peninsula and it is characterized as arid and/or hyper-arid climate, namely the desert climate. The region is characterized by two main seasons; the first of which is the very hot extreme summer where the temperature usually exceeds 45 °C to 50 °C. On the contrary, the winter is usually warm or mild, with very little sporadic rainfall (Alsharhan and Kendall, 2002; Abdelfattah and Pain, 2012). Most of the rain experienced during the winter occur in December and January of every year, where the average rainfall is less than 10 mm^3 super index per year (Feulner, 2006). All over the Arabian Peninsula, the time and quantity of rain greatly vary every year. Some winters are completely dry, where no rain is received at all. Thus, the rainfall of the peninsula is mostly considered erratic and unpredictable (Miller and Cope, 1996; Böer, 1997; Almazroui et al., 2012). For example, although the average annual long-term rainfall in Sharjah emirate (1934-2004) was reported to be 102.8 mm^3, only 27 years out of 71 years of rainfall records have received 50 mm^3 or less. Where another 8 years have recorded rainfall of less than 10 mm^3 (Feulner, 2006).

In UAE, January is the coolest month of the year during the winter, where the average temperature recorded is 12 °C. Meanwhile, the mean air temperature from November to March (during the winter season) can reach 20 °C. On the other hand, the maximum air temperature from April to October (During the summer) is up to 48 °C or more (Miller and Cope, 1996; Böer, 1997; Zahran, 1997; El-Keblawy et al., 2005). UAE climate has a very high relative humidity (RH) all over the country. The Relative Humidity usually increases toward the coastal regions and decreases in other regions. The Maximum Relative Humidity recorded in inland areas (regions other than the coastal areas) is 84%, while the extremely humid areas at the costs may reach 97% during the summer season. The Average Relative Humidity is up to 56.4% and the Average Minimum Annual Humidity is 28% (Karim and Dakheel, 2006; Sherif et al., 2009).

The sunlight usually lasts from 8 to 12 hours daily, causing a very high annual evaporation rate especially in the inland areas, where the mean annual evaporation rate of UAE is 3350 mm^3. For example, the Annual Evaporation rate of Al Ain area is about 30 times the amount of annual rainfall, where the amount evaporating reaches approximately 4000 mm^3. The wind speed varies between windy and normal days; in normal days, for example, it ranges from 6 to 9 knots, while it may be up to 32 knots for windy days (Karim and Dakheel, 2006).

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).

The environmental stresses are especially important in arid and deserts regions and can be defined as the combination of the biotic and the abiotic challenges that causes 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).

MAJOR EFFECTS OF DROUGHT AND SALT STRESSES ON PLANTS

Effects of drought stress on plants

Drought stress is the severe scarcity of water resources. It is a critical challenge in the UAE ecosystems and threats the World Food Security. Drought is usually faced when the available water in the soil is reduced, which is usually happen when evapotranspiration exceed rainfall. This is usually take place naturally due to the drastic weather conditions in the hot arid and hyper-arid climates (Wery et al., 1994), similar to the desert conditions occurring in UAE. Drought is considered as one of the most drastic stressors impacting plants (Somerville and Briscoe, 2001). It has many major consequences impacting plants (Cosgrove and Rijsberman, 2014). These include, for example:

- Inhibition of plant growth,
- Damage plant cells membrane integrity.
- Decrease the plant pigment content, thus disrupting the photosynthesis.
- Misbalance the plant osmosis, disrupting the water relations.
- Reduce photosynthetic activity

The overall consequence of all the above impacts is the reduction and disruption of crops yield and productivity (Benjamin and Nielsen, 2006; Praba et al., 2009). The impacts of drought is not limited to the plant yield, as it also extends to the earlier stage of the life cycle, such as seed dormancy and germination , morphology, as well as physiology and metabolism (as explained in Table 1) (Nam et al., 2001; Chaves et al., 2002; Martínez et al., 2007; Jaleel et al., 2008b; Razmjoo et al., 2008; Mosa et al., 2017). In the current doctoral thesis, we are being investigated the drought effects in seed dormancy and germination on two *Salsola* species (Amaranthaceae) in the UAE. We are going to describe the more important effects of drought in plants while as the plant drought tolerance mechanisms.

Effect of drought on seed dormancy and germination

For the next plant generation to start, the seed, (which is the structure containing the plant embryo) must be well developed; where the period between seed maturation and seedling establishment can be described as the period that enables the embryo to survive (Koornneef et al., 2002).

The most sensitive stage of the plant life cycle is the germination stage. Seed germination is a very complex series of plant physiological and biochemical changes, that are sequenced in a process necessary for embryo activation (Bewley and Black, 1985). The drought occurring due to the scarcity of the rainfall leads to increasing the soil salinity, impacting both glycophytes (salt-sensitive plants) and halophytes (salt-tolerant plants) of the Arabian hyper-arid hot deserts and leading both to face serious challenges. Halophytes’ seeds tend to postpone their germination in such conditions, waiting for the seed to settle into a more suitable less stressful environment, which is usually stimulated effective rainfall that increases the soil reserves of water and optimizes many other environmental conditions; namely, the temperature and light, which become suitable as well (Khan et al., 2000; El-Keblawy, 2004; Khan and Weber, 2007; El-Keblawy, 2014).

Meanwhile, seeds that have experienced drought show several physiological imbalances such as the reduction in water imbibition, which ultimately results in germination reduction or inhibition (Almansouri et al., 2001). Decreased water imbibition and subsequently water limitation during germination would severely impact the plant by several metabolic disorders, including altering the enzymatic activity, as well as the general reduction in hydrolysis and utilization of the seeds’ natural food reserves, such as proteins, carbohydrates, and lipids (Ahmad, 1992).

Effect of drought on plant morphology

Drought greatly inhibits cell expansion and cell growth leading to a severe reduction in the low turgor pressure. Drought stress also induces leaf senescence and reduce plant cell enlargement, plant height (Bhatt and Rao, 2005), and leaf growth (total number of leaves, total leaves area and total leaves biomass) (Sacks et al., 1997; Zhang et al., 2004; Wullschleger et al., 2005; Manivannan et al., 2007; Jaleel et al., 2009).

Effect of drought on plant physiology

Drought affected various physiological and biochemical processes in plants, such as photosynthesis, respiration and carbohydrates production, in addition to nutrient metabolism and growth regulators, leading to closure of stomata and decrease in cell enlargement (Farooq et al., 2008; Jaleel et al., 2008a). Additionally, leaf water potential and turgor loss were greatly diminished due to drought. Drastic drought conditions shall result in severe drastic impacts such as increased photorespiration and disturbing photosynthesis (Miller et al., 2010). Nutrients and ions uptake, as well as the apoplastic (or acropetal) translocation (i.e. the translocation upward in the plant’s xylem) of some nutrients, are also impaired due to drought stress, leading to severe impact on plant growth (Hu and Schmidhalter, 2005).

Effect of drought on plant metabolism

Drought causes disruption of cell metabolism and structures, where some of the enzymes catalysed reactions may be blocked, ultimately leading to plant death (Smirnoff, 1993; Jaleel et al., 2007; Jaleel et al., 2008c). Drought caused an increase of Reactive Oxygen Species (ROS) production (Miller et al., 2010). Drought also has several impacts over photosynthesis, either directly or indirectly. The direct drought effect on photosynthesis include stomata and the mesophyll diffusion limitations, in addition to the alterations in photosynthetic metabolism. The direct or the secondary impacts of drought on photosynthesis include oxidative stress increase, arising due to the accumulation of several stressors (Moran et al., 1994; Sharma and Dubey, 2005; Miller et al., 2010). Farooq et al. (2009) has reported that the oxidative impairment and damage are induced due to drought stress, through the production of ROS. Membrane lipids are attacked by ROSs (including: singlet oxygen ($1O_2$) superoxide ($O_2^{\bullet-}$), hydroxyl radical ($OH^{\bullet}$), and hydrogen peroxide (H_2O_2)), resulting in peroxidation of lipids, where the content of malondialdehyde (MDA) increases (Mittler, 2002). The MDA content is considered as an indicator of the damage resulting from the oxidative stress (Møller et al., 2007).

Plant drought tolerance mechanisms

Plants challenged by drought conditions, develop a plant drought tolerance mechanism, which is a complex regulatory processes that include control of water flux, cellular osmotic adjustment through the biosynthesis of osmoregulators, in addition to balancing the ratio of different osmolytes such as proline and glycine betaine, as well as the production of antioxidants in order to mitigate the oxidative stress (Flowers and Yeo, 1986; Hasegawa et al., 2000; Apel and Hirt, 2004; Flowers, 2004; Agarwal et al., 2013). Osmotic regulation can maintain cell turgor, helping the plant to survive, or even to assist plant growth under severe drought conditions (Shao et al., 2008). Plants respond to oxidative stress through producing antioxidant both through the production of enzymatic antioxidants such as ROS scavenging enzymes (for example, enzymes such as, catalase (CAT), and superoxide dismutase (SOD), as well as ascorbate peroxidase (APX), and peroxidase (POD), and/or other antioxidants that are non-enzymatic in nature, such as low-molecular mass antioxidants (including ascorbate (Vitamin C), and glutathione (GSH), as well as carotenoids) (Apel and Hirt, 2004). The comprehensive understanding of the process and mechanisms of plant drought tolerance can be considered the cornerstone and the fundamental component in the process of developing stress tolerant crops (Reddy et al., 2004; Zhao et al., 2008).

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

	Drought stress	**Salt stress**
Seed dormancy and germination	• Induce seed dormancy. • Reduce seeds' water imbibition. • Reduce nutrients hydrolysis and food reserves use by the seed. • Decrease the rate of germination and reduce the percentage of seeds germinated. • Changes enzyme activities within the sedes. • Inhibits germination-regulating substances such as plant hormones and imbalances them.	• Induces seed dormancy. • Reduces seeds' water imbibition • Reduces food reserves use by the seed. • Decreases the speed of germination and the number of germinated sedes. • Changes enzyme activities within the sedes. • Inhibits germination-regulating substances such as plant hormones and imbalances them. • Causes ion toxicity in the seed.
Plant morphology	• Reduce plant elongation and expansion growth. • Induces leaf senescence. • Reduce cell enlargement. • Reduce plant height reduction. • Reduces leaf growth (decreases leaves number, leaves area and total leaves biomass). • Inhibits growth and plant	• Severe damage to plant establishment and growth development. • Reduction of plant height. • Reduction of tiller numbers. • Reduction in the shoot diameter. • Decrease the shoot weight, roots weight and leaves

	productivity.	numbers and área. • Yellowish of the plant leaves and fast leaf senescence.
Plant physiology	• Diminishes leaf water potential and turgor • Stomatal closure • Damages membrane integrity, decreases the plant chlorophyll's content, imbalances osmotic regulation and water relations, and Reduces the photosynthesis process. • Reduces turgor pressure. • Reduces photosynthesis, respiration, nutrients translocation and ion uptake.	• Induces specific ion toxicities. • Decreases uptake of essential minerals (ion imbalance). • Decreases the photosynthesis. • Causes water deficit and stomatal closure. • Reduction of leaf water potential. • Chlorophyll and pigment content reduction.
Plant metabolism	• Impairment of cell metabolism and structure. • Blockage of enzyme catalyzed reactions. • Causes oxidative impairment due to ROS production. • DNA damage and carbon fixation inhibition.	• Causes deterioration of plant enzymes, metabolic processes and cell membrane damage. • Oxidative damage by production of ROS that cause peroxidation of lipids, oxidation of protein, inactivation of enzymes and DNA damage. • Inhibits carbon fixation.

Effect of salt stress on plants

The term salt stress is the condition where the soil is characterized by high levels of soluble salts. When the electrical conductivity of (ECe) of the soil reaches 4 dS/m or more, it can be considered a saline soil (Brown, 2008). The ECe of 4 dS/m is almost equal to 40 mM NaCl and produce an osmotic pressure almost 0.2 MPa. Salt stress is an adverse effect of the excess minerals such as Na^+ and/or Cl^- accumulation in the plant, and it is still a critical and crucial limitation of plant development and growth, crop production and food security (Munns, 2005).

The detrimental effect of salt stress is noticed on the whole plant as well as plant parts; where the whole plant effect includes plants death and/or decreased productivity of various plants. Salt stress is common phenomena in arid and semiarid desert soils, so plants have largely developed several mechanisms that allows them to tolerate the decrease in water potential resulting from soil salinity and drought conditions; that is why osmotic stress tolerance is recorded as an important feature of most halophytes and some glycophytes (Munns and Tester, 2008). Increase in the osmotic pressure will reduce most of the glycophytes yield (Munns and Tester, 2008). Most of the saline soils of arid or semi-arid regions have experienced salt accumulation over extended periods of time due to natural causes (Rengasamy, 2002). Plants respond to soil salt stress by two major mechanisms:

- The rapid response: where high salt concentrations complicate the process of water absorption by the roots due to the soil solute potential decline, in addition, the salt in the soil has direct immediate harmful effect to the roots cell growth and associated metabolism. The rapid response to salt stress is known as the osmotic effect of salt stress (almost like the drought stress mechanism).
- The slower response: where the plant uptake of salt increases resulting in the accumulation of high concentrations of ions such as sodium and chloride within the plant, leading to ion-specific toxicity effect of salt stress. The ion toxicity effect is very different from the drought or osmotic effect (Poljakoff-Mayber et al., 1994; Tobe et al., 2001; Munns and Tester, 2008). The accumulation of high ions concentration within the plant compromises the enzymes' functions and disrupts metabolic processes causing acceleration of leaf senescence (Baldwin et al., 1996; Munns and Tester, 2008).

Plants can be classified into salt-tolerant halophytes and salt-sensitive glycophytes, based on their tolerance to salt stress (Sairam and Tyagi, 2004). Halophytes are the group that is most tolerant to high salinity, they are naturally grown on seawater and can produce high yields of seeds and biomass (Flowers and Colmer, 2008; Koyro and Lieth, 2008; Ksouri et al., 2008; Shelef et al., 2016). Halophytes, in turn, may be ecologically sub-classified into three categories, (Von Sengbusch, 2003), which are:

- Obligatory halophytes
- Facultative halophytes
- Habitat-indifferent halophytes

Obligatory halophytes are commonly named as true halophytes (or euhalophytes). They are plants that grow only in salty habitats and can also tolerate drought stress as well as high salinity conditions (Ashraf and Harris, 2004). Examples of true halophytes include, *Atriplex nummularia* Lindl. (Uchiyama, 1987) and *Iris hexagona* Walter. (Van Zandt and Mopper, 2004), as well as the annual desert *halophyte Suaeda aralocaspica* (Bunge) Freitag and Schütze (Wang et al., 2012). Meanwhile, facultative halophytes which can grow and develop on salty soils, but their optimal growth takes place in soils that are free of salt or at least contain low-salt substrates, where they are able to tolerate high salinity levels (sometimes double seawater salinity) without significant reduction in growth (Rozema, 1996). On the other hand, habitat-indifferent halophytes are still able to cope with salty soils, but they survive equally well in both salty soils as well and salt-free substrates (Cushman, 2001). Many habitat-indifferent halophytes, such as *Zygophyllum qatarense* Hadidi., *Salsola drummondii* Ulbr., *Suaeda aegyptiaca* (Hasselq.) Zohary, and *Suaeda vermiculata* Forssk. ex. J.F.Gmel., are surviving in both hyper-saline and non-saline soils of the arid Arabian deserts (Jongbloed et al., 2003). Other examples of habitat-indifferent halophyte include *Festuca rubra* L. (Bülow-Olsen, 1983).

Effect of salt stress on seed dormancy and germination

Salt stress is considered one of the most crucial factors that limit seed germination and seedling establishment of halophytes and glycophytes, especially in hot arid and hyper-arid desert climates, where evapotranspiration exceeds precipitation (Tlig et al., 2008). Salt stress causes impairment of seed germination, either through complete inhibition of seed germination at higher levels or through induction of secondary (induced) dormancy at a lower levels (De Villiers et al., 1994; Khan and Ungar, 1997). Salt stress-induced dormancy is usually alleviated upon availability of enough rainfalls and the existence of other favourable conditions for seedling recruitment (Zhang et al., 2010; Gorai et al., 2014). The increase in the NaCl concentration is one of the prominent causes of seed germination impairment. The effect of NaCl on germination could be either through altering plant seeds' water imbibition that results from lower osmotic potential of germination media (Khan and Gul, 2006; Soltani et al., 2006; El-Keblawy et al., 2010; Zhang et al., 2010; Laghmouchi et al., 2017), or through ion-specific toxicity effects (Soltani et al., 2006). Ion specific toxicity is induced via several mechanisms such as changes of nucleic acid acting enzymes (Soltani et al., 2006; Gomes-Filho et al., 2008; Santo et al., 2014), alteration of protein metabolism (Hare and Cress, 1997; Dantas et al., 2007), disruption of plant growth regulators balance (Gaffney et al., 1993; Khan and Rizvi, 1994; Clarke et al., 2000), and reduction of seed reserves utilization (Othman et al., 2006). Salt stress decreases the germination rates and percentage of germinated seeds (Läuchli and Grattan, 2007; Bybordi, 2010; Kaveh et al., 2011; Khodarahmpour et al., 2012). Salt stress causes an adverse inhibition germination of many species, which could be explained by internal factors of the seeds such as: the presence of inherited inhibitors and imbalance of some germination-regulating substrates (Carpýcý et al., 2009; El-Keblawy et al., 2010; Akbarimoghaddam et al., 2011; Xu et al., 2011; Khodarahmpour et al., 2012; El-Keblawy, 2013; Fernández-Torquemada and Sánchez-Lizaso, 2013).

It has been reported that seed germination and dormancy requirements could be affected by the soil salinity of the maternal habitat and environmental conditions prevailing during the time of seed development (El-Keblawy et al., 2017a; Siles et al., 2017; El-Keblawy et al., 2018). Environmental signals of the parental generations can cue transgenerational changes in offspring phenotype. Such changes are expressed independently as alterations in the offspring genotype (Holeski et al., 2012). Transgenerational changes in plants may be induced due to exposure to environmental stresses over several generations (Reza Rahavi et al., 2011). Maternal effects often provide the plant with several mechanisms for adaptive transgenerational phenotypic plasticity, in which the environment experienced by the mothers is translated into phenotypic variation in the offspring (El-Keblawy et al., 1996; Mousseau and Fox, 1998; Gutterman, 2000). The environmental stresses can also cause changes in both plant physiology and the offspring's genome when parents are repeatedly exposed to the same type of stresses (Migicovsky et al., 2014). Hence, when plants are subjected to harsh environmental stresses, they usually pass some information about a specific stress to the following successive generations, which lead to coping and developing stress tolerance characteristics among the offspring (Boyko and Kovalchuk, 2011).

Effect of salt stress on plant morphology

Under salt stress conditions, the salt enters in the plant's transpiration stream, ultimately leading changes in several morphological attributes. Salt stress greatly impairs the growth parameters and reduces the growth rate of all plant organs as an initial disruption caused by the osmotic effect of salt stress or through injuries of plant cells (Munns, 1993, 2005; Parihar et al., 2015).

Plant height and branch numbers, as well as leaves surface area, are reduced in plants growing in saline soils, which are usually attributed to ion toxicity effect (Hasanuzzaman et al., 2009). In *Suaeda salsa* (L.) Pall., for example, salt stress significantly affected plant height, the number of tillers, length of tillers, and diameter of the shoot. Such effects were attributed to the increase of Na^+ and Cl^- ions concentrations (Guan et al., 2011). Similarly, salt stress significantly decreased the shoot and root weight, as well as total plant biomass, plant height and leave numbers in *Glycine max* (L.) Merr. (Dolatabadian et al., 2011). *Foeniculum vulgare* Mill., showed significant reduction of productivity and other plant growth parameters including fresh weight as well as plant height upon irrigation with saline water (Semiz et al., 2012). The osmotic stress and ion toxic effect of NaCl inhibit the growth of most of the plants, even of halophytes when the levels approaching seawater salinity (Koyro, 2006).

Effect of salt stress on plant physiology

Plant physiology is significantly impaired due to excessive salt accumulation, namely Na^+ and Cl^- ions. Major ions that play key roles in various physiological processes would have detrimental impacts on plants, when their concentration increased above certain level. Importantly, Na^+ accumulation would disrupt the concentrations of other ions. For example, Na^+ is the primary ion controlling the intake of potassium (K^+) ion, which disturb stomata regulation resulting into water loss (drought resembling activity). On the other hand, Cl^- ion disturbs the chlorophyll pigment production which usually result in subjecting the plant to chlorotic toxicity. This chloride ion accumulation is considered more serious than Na^+ accumulation (Tavakkoli et al., 2011). Furthermore, Cl^- is necessary for the regulation of turgor pressure, enzymatic activities and cytoplasmic pH in the plant cell cytoplasm (Dang et al., 2006; Dang et al., 2008). Despite the great importance of chloride ions in the physiological processes, the high concentrations that exceed the critical level are toxic to the plant (Xu et al., 1999; White and Broadley, 2001).

Photosynthesis is an important phytochemical process through which plants make their own food to grow *via* converting sunlight energy into chemical energy. Photosynthesis is significantly impacted by salt stress due to various reasons as shown in (Fig. 3). The plant photosynthetic rates are mainly reduced under salt stress conditions as a result of the reduction of water potential and the excessive accumulation of Sodium and/or chloride ions in the chloroplasts (Zhang et al., 2002). Chlorophyll is the cornerstone structure for the photosynthesis; thus the decrease in chlorophyll content due to salt stress can be used as a sensitive indicator of the plant cellular metabolic state (Amirjani, 2011; Chutipaijit et al., 2011). Plant contents of chlorophyll *a*, chlorophyll *b*, xanthophylls and carotenoids were found to decline under salt stress (Mane et al., 2010; Saha et al., 2010; Chutipaijit et al., 2011). One of the reasons related to the reduction of chlorophyll content under stress is related to cellular membrane impairment (Mane et al., 2010).

Carbon isotope ratio ($^{13}C/^{12}C$) is a useful eco-physiological trait that measures the leaf CO_2 assimilation and changes in photosynthesis due to environmental constraints (Farquhar et al., 1989; Hussain and Reigosa, 2014; Bai and Purcell, 2018; Chaudhary et al., 2018). It is an integrative indicator of CO_2 assimilation (photo-respiration during day respiration) and discrimination that could occur during the night-time respiration (Farquhar et al., 1989; Hussain and Reigosa, 2014; Hussain et al., 2018a; Ubierna et al., 2018). The potential changes of isotopic signatures in plant organic matter are of relevance for the use of ^{13}C in ecosystem studies (Liu et al., 2018). There are only few reports in the literature on the carbon isotope composition of CO_2 respired by halophytic plants following exposure to environmental stress (Chaudhary et al., 2018; Liu et al., 2018; Pérez-Romero et al., 2018). Changes in leaf water status due to abiotic stress will significantly alter changes in normal stomatal functions and therefore, leaf carbon isotope discrimination ($\Delta^{13}C$). Therefore, carbon isotope discrimination measurements in the leaf dry matter of halophytic plant *Salsola drummondii* can provide help in an integrative assessment of environmental abiotic stresses such as salinity.

Water potential is also a crucial and critical physiological parameter for the identification of the water status of the plants in both normal and salt stress conditions (Parida and Das, 2005). The excessive salt concentration in the root medium can cause a reduction in the water potential of the leaves and this would affect various physiological plant processes (Romero-Aranda et al., 2001). Water potentials of the soils decrease inversely with the increase in soil salinity. This can hinder the plant ability to uptake water from the soil and maintain their turgor. However, at low or moderate salt levels, the water potential of the soil would increase, and the plants can accumulate solutes for osmoregulation and can be able to preserve a potential gradient for the water influx (Khan et al., 2013; Parihar et al., 2015).

Salt stress status can induce **nutritional disturbance** because it reduces the uptake and accumulation of the nutrients into the plants (Rogers et al., 2003; Hu and Schmidhalter, 2005). Salt stress is a common cause for micronutrient deficiencies that occur due to increased soil solutions acidity (Zhu et al., 2004; Parihar et al., 2015). For example, when sodium content increases in plant tissues the concentration of Nitrogen, K^+, $Mg^{+2,}$ and Ca^{2+} decrease resulting in ionic imbalances (Hasegawa et al., 2000; Hu and Schmidhalter, 2005; Tuna et al., 2007; Keutgen and Pawelzik, 2009; Hussin et al., 2013). Salt stress also reduces nitrogen uptake or accumulation in plants , due to the inverse relationship between Na^+ and NH_4^+ accumulation and/or between Cl^- and NO_3^- that should lead to the reduction of the growth and productivity of the plants (Rozeff, 1995). The reason for the reduction in NO_3^- uptake is due to Cl^- antagonism (Bar et al., 1997) or because of the decrease in water uptake under the impact of salt stress (Lea-Cox and Syvertsen, 1993). In addition, the reduction in phosphorus availability in saline soil leads to a reduction in PO_4^{3-} activity due to the ionic strength effect, as well as the low solubility of calcium phosphate solutes and reduction of water absorption from the saline soil solution (Qadir and Schubert, 2002).

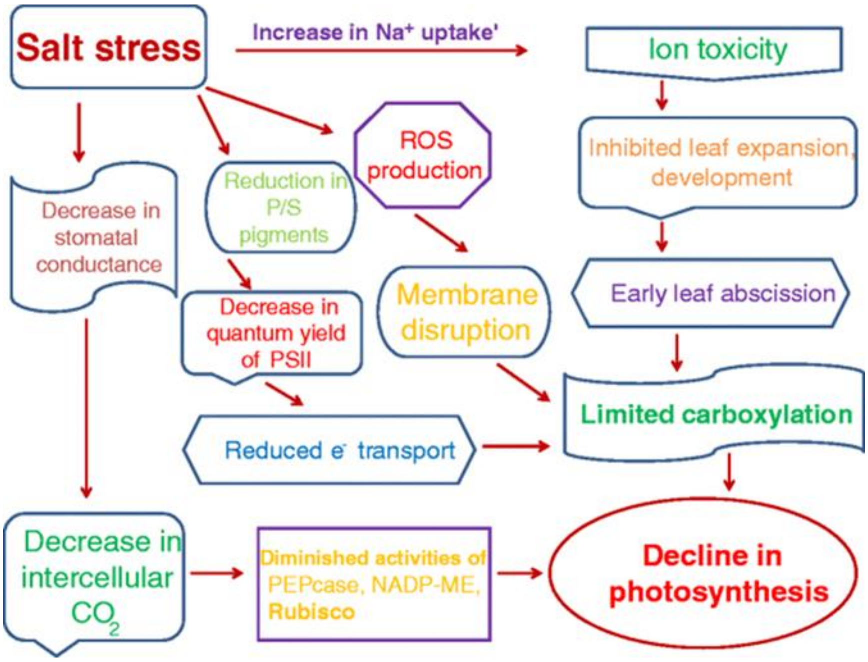


Figure 3. Effect of salt stress on plants and reasons for photosynthesis inhibition. Adopted from Farooq et al. (2015).

Effect of salt stress on plant metabolism

Ion sodium, Na^+ toxicity is caused by salt stress that results in acute toxic effects to genes and enzymes, causing plant metabolism disruption (Conde et al., 2011; Hasegawa et al., 2011). Salt stress enhances the excessive production of ROS (Miller et al., 2008; Suzuki et al., 2011), inhibits important enzymes, alters the efficiency of enzymatic reactions in plant cells (Laluk et al., 2011), changes the metabolite profiles (Shulaev et al., 2008), and destabilizes various cellular proteins, membranes, RNA species and cytoskeleton structures (Lugan et al., 2010; Peleg et al., 2011), where the net result is a state of metabolic imbalance (Rivero et al., 2014).

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 (Bose et al., 2015) as shown in (Fig. 4). Salt stress induces the production of ROS, which is highly reactive and able to cause lipids peroxidation, as well as protein oxidation, several enzymatic inactivation, DNA damage, and/or interact with other vital constituents of plant cells (Apel and Hirt, 2004; Ahmad et al., 2010; Hasanuzzaman and Fujita, 2011). Production of ROS under salt stress is due to water deficit (Halliwell and Gutteridge, 1985; Elstner, 1987) or due to closure of the stomata, which decreases the carbon dioxide abundance inside the leaves and leads to 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) (Parida and Das, 2005; Ahmad and Sharma, 2008; Ahmad et al., 2010).

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. Whereas hydrogen peroxide (H_2O_2) is a strong toxic agent that causes cell damage or even cell death during oxidative stress, it is considered as a signaling molecule that is used for the activation of the defence 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 (Pei et al., 2000), plant cell death (Desikan et al., 1998), as well as plant-pathogen interaction (Mittler et al., 1999), auxin-regulated gravitropism responses (Joo et al., 2001), and plant Systematic Acquired Resistance (SAR) to stressful conditions (Inzé and Van Montagu, 1995). In addition, H_2O_2 is involved in mechanical wounding response (Orozco-Cardenas and Ryan, 1999) and some other similar processes related to both abiotic and biotic stresses processing (Desikan et al., 2003). The major sites of ROS production during abiotic stresses, (including salt stress), are the apoplast, peroxisome, chloroplast and mitochondria (Dietz et al., 2016; Gilroy et al., 2016; Huang et al., 2016; Rodríguez-Serrano et al., 2016; Takagi et al., 2016). ROS producing locations in plant cells and methods of controlling the concentration thereof were shown in (Fig. 4). Both glycophyte and halophyte plants are suffering from the osmotic and the ionic toxic 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.

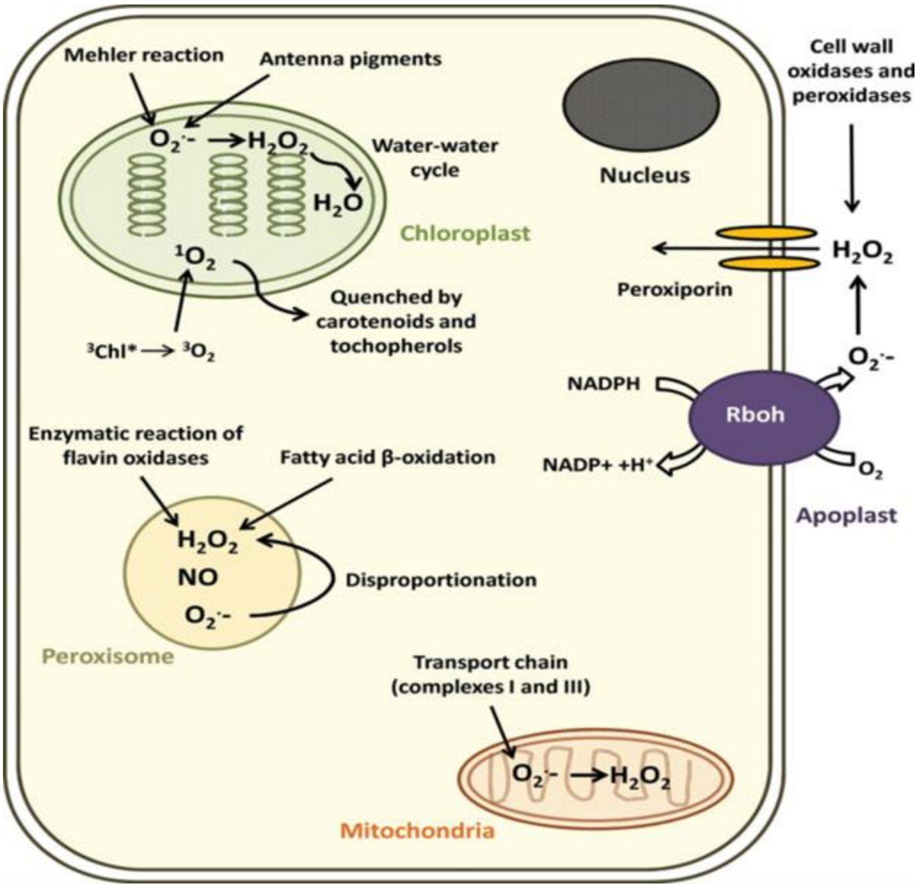


Figure 4. Major ROS (reactive oxygen species) producing sites in plant cells and ways for controlling their concentrations. Adopted from Bose et al. (2014b).

SALT RESISTANCE MECHANISMS IN HALOPHYTES

Salt resistance is defined as a response of the plant toward the salt stress (Yeo, 1983; Breckle, 1990; Aslamsup et al., 2011). Salt resistance mechanisms in halophytes are generally classified into two main categories. These are salt avoidance and salt tolerance mechanisms (Sabovljevic and Sabovljevic, 2007).

Salt avoidance mechanisms in halophytes

Some halophytes have the capacity to resist high salt stress due to very special morphological and anatomical adaptations called salt avoidance mechanisms (Flowers et al., 1986). Salt avoidance is a resistance mechanism in which a plant tries to keep the salt ions away from its sensitive structures that might be damaged due to exposure to high salt levels (Allen et al., 1994). Plants, especially halophytes, can avoid salinity by growing only during favourable seasons and favourable sites, and limitation of root growth and root absorption activity to distinct soil types (Breckle, 1990). There are different mechanisms that enable halophytes to avoid salt stress such as salt exclusion, salt secretion, shedding of old leaves (including the salt content thereon), stomatal response and succulence (Aslamsup et al., 2011).

Salt exclusion is the most common mechanism to surviving halophytes in high salt concentration environments (Waisel et al., 1986; Chaudhary, 2019),. This process is usually performed by the roots, where the casparian strips is suggested to be a major component of the salt exclusion process from inner plant tissues (Flowers et al., 1986; Reginato et al., 2014). 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 process used by certain halophytes that have specialized salt glands responsible for excretion of excess salt outside the plant (Weber, 2009). Another method that can be used to decrease internal salt concentration is **shedding old leaves**. This is a mechanism developed by plants growing under high salt concentrations as a strategy to avoid the toxic effects of excessive sodium salts accumulation in leaves (Albert, 1975; Dawalibi et al., 2015). Some other halophytes get rid of excess salt through the accumulation into particular organs and discarding salt-saturated organs (Naseer et al., 2014).

Meanwhile, as for the **stomatal response**, usually plants provide two different responses regarding salinity conditions. The first is to direct the potassium ions to guard cells in order to be used for acquiring a normal turgor instead of sodium ions. Therefore, the potassium is used in the guard cells to decrease sodium intake of the plants (Robinson et al., 1997). Such an important mechanism is used as a stomatal response practiced by halophytes that lack glands. On the other hand, glycophytes lack such stomatal response, where the sodium ions impair the stomatal function leading to disruption of the plant and eventually plant death due to lack of survival mechanisms.

Succulence is another mechanism used by plants to adapt to high salinity environments. In this process, a plant undergoes a cell size increase, and a decrease in extension of growth and surface area per tissue volume, leading to water content increase per unit surface area (Flowers and Yeo, 1986; Weber, 2009; Grigore and Toma, 2017). When halophytes, especially those of arid desert climates, are exposed to salinity conditions, they undergo succulence, where it is used as an adaptive feature that is helpful for stress survival (Grigore and Toma, 2017). Succulent plants usually have very thick leaves, where the plant increases the size of the mesophyll cells, giving less intracellular spaces when compared to other non-succulent plants (Grigore and Toma, 2017). Succulent leaves are well adapted to their function, presenting a higher number of mitochondria, which are usually relatively larger showing that some extra energy is required in these plants for the salt compartmentalization and excretion (Siew and Klein, 1969). In this doctoral thesis study, *Amaranthaceae* species belonging to *Salsola* genus have been chosen as an example of a family presenting succulent leaves to resist high soil salinity.

Salt tolerance mechanisms in halophytes

Plant salt tolerance can be defined as the ability to survive, grow, and complete their life cycle on highly saline substrates and environments (Parihar et al., 2015). Salt tolerance is a complex process involving several inter-related and inter-acting processes.

The importance of investigating various well-established salt tolerance mechanisms in plants is greatly based on the importance of developing salt resistant crops, either through traditional breeding processes or through recombinant genetic engineering techniques. Investigating mechanisms used by halophytic plants to resist saline saturated soils provides us with sustainable resources that are crucial for the development of stress resistant crops. Plants that are able to manage drastic salt concentration and survive their impacts are able to reproduce and overcome the challenges imposed on them in saline habitats, where the challenges include water deficit (drought status), the CO_2 intake limitations, in addition to nutrients intake impairment and ionic toxicity. Additionally, the mechanisms used to resist salinity are usually multi-genic in nature, where various genes are evolved to develop the required character. The mechanisms of salt tolerance include the induction of various morphological, physiological, metabolic and molecular changes in plants in order to facilitate adaption to the stressful conditions (Ashraf and Harris, 2004; Koyro et al., 2009), as will be discussed in more details below.

Seed germination tolerance in halophytes

Both halophytes and glycophytes suffer a delay in the germination as well as an induction of seed dormancy at higher salinity levels (Ungar, 1996). The ability of seeds to overcome high salinity levels is important for germination and seedling establishment (Gorai et al., 2014). Understanding salt tolerance mechanisms in halophytes during germination stage is important in developing salt-tolerant crops (Aslamsup et al., 2011). Some halophytes use a salt-tolerance strategy at germination, whereas some use a salt-avoidance strategy (Wahid et al., 1999; Joshi et al., 2015). Many factors besides high salinity such as high temperature, low precipitation, and light interact at the soil interface to determine the time of germination and consequently determine the fate of seedling establishment and plant fitness (Tlig et al., 2008; El-Keblawy, 2017). Halophytes escape from the adverse impact of salinity by entering a dormancy stage (Wahid et al., 1999; Song et al., 2017). During dormancy, halophytes seeds can easily remain viable during long periods of salt stress (Naidoo and Naicker, 1992; Shelef et al., 2016).

High precipitation seasons such as spring are more suitable for seed germination in saline environments. At that time, soil salinity usually drops and the salt stress becomes less drastic (Ungar, 1982; Joshi et al., 2015). High final germination percentages, germination rates and germination recovery percentage are good indicators of salt tolerance during seed germination (Wahid et al., 1999). Halophytes’ seeds usually have a very little salt content, even under saline condition (Zhang et al., 2015). Salt tolerance of halophytic species during seed germination was correlated with seed mass at high salinities (Wahid et al., 1999; Joshi et al., 2015). Seeds with big sizes have greater germination chances, vigorous seedling growth and this help halophytes to escape from salinity and enable the seeds to absorb low content of toxic ions per unit weight because it has higher content of food reserves (Easton and Kleindorfer, 2008; Zhang et al., 2015). Under salt stress, a thicker seed coat diminishes the ions content entering the embryo (Wahid et al., 1999; Song et al., 2017).

Physiological tolerance mechanisms in halophytes

Plants, especially halophytes, have evolved and developed several physiological mechanisms to cope with the detrimental effects of salt stress. Such mechanisms include ion homeostasis, salt accumulation, and compartmentalization (trans-location of salt to specialized organs). The key to salt tolerance is the capability of halophytes to organize Na^+ and Cl^- uptake while preserving cytoplasmic K^+ and Mg^{2+} levels required for activation of essential enzyme (Bose et al., 2014a; Gupta and Huang, 2014). Ion homeostasis occurs through selective accumulation or exclusions of ions; for example, plants tend to increase the calcium concentration inside the plant cell, which is known to play vital role in the maintenance of cellular homeostasis under different abiotic stresses (Knight and Knight, 2000; Sanders et al., 2002). Na^+ competes with K^+ uptake through common transport systems, where sodium concentration in saline environments is considerably greater than that of potassium and calcium. Thus, potassium uptake is usually achieved effectively to allow for plant survival. Consequently, promoting K^+/Na^+ intra-cellular selective salt accumulation is essential for survival (Maathuis and Sanders, 1996). Several molecular structures are mediating Na^+ and K^+ homeostasis, including the action of Ca^{2+} that function in the regulation of ion transport systems. Meanwhile, plants use other stress signaling pathway such as salt overly sensitive (SOS) pathway, which can be considered as 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 SOS signaling pathway (Fig. 5).

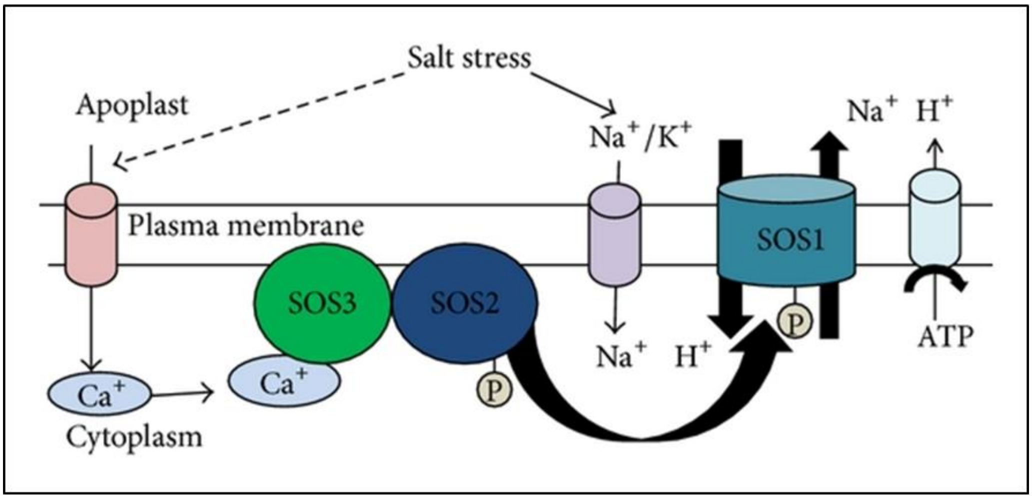


Figure 5. Model of salt overly sensitive (SOS) pathways in a plant cell subjected to a salt stress. Adopted from Gupta and Huang (2014).

Plants that tolerate salt stress through accumulating salts in their cells have been known as salt accumulators. The most famous examples of salt accumulators are tamarisk (*Tamarix petandra*), saltbush (*Atriplex*), saltgrass (*Distichlis spicata*), and smooth cordgrass (*Spartina alterniflora*). Such plants have salt glands that are specialized cells located on the surfaces of the leaves and useful for storing excess NaCl (Mishra and Tanna, 2017). Some other halophytes have the ability to accumulate excessive salts inside the cells up to certain toxic concentration, behind which the plant would fail to survive (Mishra and Tanna, 2017). Some salt accumulators tend to avoid the salinity stress through minimizing the leaves cytosolic salt concentrations, through transporting sodium and chloride ions into a central vacuole. Meanwhile, accumulation of salt into the central vacuoles leads to absorption of more water that causes cell swelling (Mishra and Tanna, 2017).

A typical halophyte' salt tolerance mechanisms include 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 ability to control the salt accumulation and perform compartmentalization of sodium is vital for the development of halophytes (Parks et al., 2002). Sodium and chloride ions transfer into vacuoles (Compartmentalization) will separate sodium and chloride from the cytosolic activities (Glenn et al., 1999), although they are considered very active osmolytes that can easily help the plant to process the decrease in the extracellular osmotic potential achieved 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).

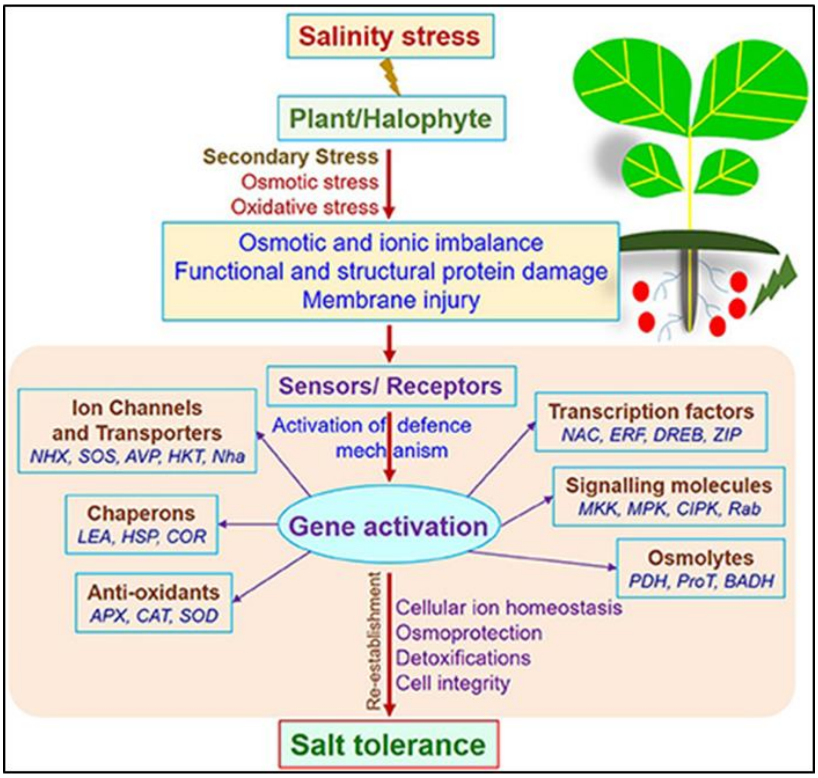


Figure 6. A schematic representation of salt tolerance mechanisms in halophyte plants. Adopted from Mishra and Tanna (2017).

Metabolic and biochemical tolerance mechanisms in halophytes

Antioxidant production

Plants have several mechanisms for optimizing the level of ROSs in a way to optimum their role in signalling and preventing the damage for cellular components (Fig. 6). One of the major detoxification mechanisms is the production of antioxidants. Glycophytes and halophytes differ in the ROS threshold that can impose oxidative damage. For example, the first significant increase in lipid peroxidation in some halophytes, appeared in shoots only after 150 mM NaCl in soil solution (Ozgur et al., 2013), while the same concentration is lethal for most of glycophytes. Unlike glycophytic plants, halophytes are characterized by their powerful ability to 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).

Generally, antioxidants are classified into two different groups, i.e., enzymatic and non-enzymatic antioxidants. Enzymatic antioxidants such as superoxide dismutase, catalase, ascorbate peroxidas, peroxidase, guaiacol peroxidase**,** glutathione s-transferase and glutathione reductase are responsible for the reduction of ROS levels in plants to protect the cell from the oxidative stress damage (Ali and Alqurainy, 2006; Gao et al., 2008) and nonenzymatic antioxidants such as carotenoids, tocopherols, glutathione and ascorbic acid (Ozgur et al., 2013) coordinate altogether to detoxify other ROSs.

Enzymatic antioxidants

Superoxide dismutase

Superoxide dismutase (SOD) is an important antioxidant enzyme that can easily repair the damage caused by ROSs through catalysing the dismutation of the super oxide $O_2^{\bullet -}$ into molecular oxygen and hydrogen peroxide. SOD acts as the first line of defence against oxidative damage in plants (Foyer and Shigeoka, 2011). Halophyte plants have an exceptional capability to use SOD to protect themselves from biotic and abiotic stress (Jithesh et al., 2006; Ozgur et al., 2013).

Catalase

Catalase (CAT) is among the most active antioxidant enzyme as a defence system against oxidative stress through catalysing the decomposition of hydrogen peroxide (H_2O_2) into water and oxygen with very high turnover rate (Mittler, 2002; Ali and Alqurainy, 2006). CAT activity depends on the species, the developmental and metabolic states of the plant, in addition to the duration and strength of the stress (Chaparzadeh et al., 2004). Previous results showed inconsistent results for the effect of salinity on CAR in halophytes. Whereas some studies showed an , increase, other showed a decrease and yet some other showe no changes in the levels of CAT in halophytes exposed to salinity stress(Jithesh et al., 2006).

Ascorbate peroxidase

Ascorbate peroxidase (APX) also plays a key role against oxidative damage through scavenging hydrogen peroxide in cytosol and chloroplast (Asada, 1992). Generally, the plant stress tolerance in glycophytes and halophytes is increased with the upregulation of APX expression/activity (Shigeoka et al., 2002; Jithesh et al., 2006).

Peroxidase

POXs are enzymes that are able to scavenge the hydrogen peroxide primarily in the apoplast (Fagerstedt et al., 2010). POXs enzymatic family is widely distributed in the higher plants, where they 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 signalling and/or scavenging of ROSs (Jithesh et al., 2006; Bose et al., 2014b).

Non-enzymatic antioxidants

Some highly toxic ROSs such as ·OH (hydroxyl radical) and $^1O_2$ (singlet oxygen) cannot be scavenged by enzymatic antioxidant (Bose et al., 2014b). For such highly toxic ROSs, the plants use the non-enzymatic antioxidant to scavenge those ROS. Examples of such non-enzymatic antioxidants include glutathione, carotenoids ascorbic acid, tocopherols and flavonoids (Shu et al., 2011).

Glutathione

Glutathione (GSH) is a very common cysteine-containing tripeptide. Generally it is found in a reduced form and abundantly localized in almost all cell compartments like mitochondria, chloroplasts, cytosol, vacuole, peroxisomes, endoplasmic reticulum and apoplast (Millar et al., 2003; HongBo et al., 2005). GSH plays a vital role in restoring another potential water-soluble antioxidant, namely ascorbic acid, via the ascorbate-glutathione cycle that is considered a major stress tolerance mechanism (Foyer et al., 1997). GSH is used as a substrate of glutathione S-transferase (GST) enzyme, results in clearing harmful components and protecting the cell (Marrs, 1996; Sanchez-Fernandez et al., 1997; Gill and Tuteja, 2010). It has been reported that the halophyte plant *Lycopersicon pennellii* (Correll) D'Arcy exhibited an increased content of GSH under salt and oxidative stress condition compared to other relatives glycophytes, such as *Solanum lycopersicum* L. (Shalata et al., 2001). Other researcher has also reported an increase in glutathione in *Suaeda maritima* (L.) Dumort., under the combined salinity and waterlogging stresses (Alhdad et al., 2013).

Carotenoids

Carotenoids have a different role in plant metabolism, in addition to the role it plays in oxidative stress tolerance. Carotenoids are organic lipophilic compounds that are mainly located in chloroplasts. The function of carotenoids is unique as they are considered as antenna molecules in absorbing the light beams of the visible spectrum in the region ranging from 450–570 nm and transfer the captured energy on to the chlorophylls (Taiz and Zeiger, 2006). Carotenoids are considered as a safety network that provides photo-protection to the photosynthetic systems. They are involved in peroxyl and singlet oxygen ($^1O_2$) radicals scavenging, which are generated during extreme chlorophyll excitation (Demmig-Adams and Adams III, 1996). Plant tolerance to oxidative and salt stress increases with the increase of carotenoids concentrations, and this is the main reason that causes halophytes to be more salt stress-tolerant, as they produce more carotenoids than glycophytes (Stepien and Johnson, 2009; Yang et al., 2009). As carotenoids concentrations had increased significantly in halophytes, but not in glycophytes, during salt stress (Koyro, 2006), this highlight it is greater role in quenching ROS in (Aghaleh et al., 2009; Youssef, 2009).

Osmolytes production

Osmotic balance regulates and maintains water influx and decrease water efflux outside the cell that maintain the cell volume (Hasegawa et al., 2000). Therefore, plants tend to produce osmolytes under salt stress. Osmolytes are non-toxic molecules that are synthesized and accumulated in the cytosol. Examples of osmolytes include amino acids (proline), glycinebetaine, polyols and sugars (Kumar et al., 2003; Ashraf and Harris, 2004). Osmolytes do not interfere with metabolic activities of the plant, as they just accumulate 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, in order to adjust their osmotic potential at saline conditions and also provide protection against ROS (Jithesh et al., 2006). The major location of osmolytes accumulation is in the cytosol, where they 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 low molecular weight, non-toxic amino acid with high solubility in water (Ashraf and Foolad, 2007). As reported by (Bohnert and Jensen, 1996), proline is used for cellular osmotic regulation between cytoplasm and vacuoles, scavenging the ROSs to protect the membrane integrity, maintaining a low NADPH to $NADP^+$ ratio and stabilizing the antioxidant enzymes. The study of several halophyte species has demonstrated the beneficial effect of proline accumulation (Radyukina et al., 2007; Szabados and Savoure, 2010).

Accumulation of proline varies according to the species (Rodriguez et al., 1997; Ghoulam et al., 2002). Free proline accumulation is important to decrease ROS oxidative stress but its catabolism in the mitochondria can increase the production of ROS (Miller et al., 2009). It has been suggested that the capability of halophytes to control the catabolism of proline may be a key step in understanding the salt tolerance (Sanada et al., 1995).

Plant hormones

Plant hormones are chemical messengers that regulate plant growth, development and responses to changing environmental conditions through signal transduction pathway. Phytohormones such as gibberellic acid (GA), abscisic acid (ABA), jasmonates (JA), cytokinins (CK), salicylic acid (SA), indole acetic acid (IAA), brassinosteroids (BR), and triazoles (TR) play important roles in salt tolerance (Cao et al., 2007; Tuteja, 2007; Javid et al., 2011). Typically, salt stress induced a decline in auxin, cytokinin, gibberellins and SA levels in the plant tissues and an increase in the levels of abscisic acid (ABA), and jasmonates (JA) (Parida and Das, 2005; Kant et al., 2006; Koyro et al., 2009).

Abscisic acid (ABA)

Abscisic acid (ABA) is a key component of plant drought and high salinity tolerance stresses (Mahajan and Tuteja, 2005). ABA is called drought tolerance hormone as it plays a key role in signal transduction pathway and used for controlling the stomatal movements (Davies et al., 2002; Cabot et al., 2009). Stomatal closure due to increased ABA concentration protects the plant from intercellular water loss (Hariadi et al., 2010; Keskin et al., 2010; Javid et al., 2011). Upon an increase in salt stress, ABA proportionally increases, especially where the salt stress is related to leaves water potential. It is suggested that ABA concentration is related to the water deficit resulting from salt accumulation rather than being a result of a salt ionic toxic effect (Davies et al., 2002; Ghanem et al., 2008). Halophytes usually promote the production of ABA in response to water deficit stress resulted from the effect of high salinity. ABA mediates the transcription of several stress-responsive genes and pathways in leaves and roots, In addition to its role in controlling the stomatal closure (Wilkinson and Davies, 2002; Yuan et al., 2018). ABA delays seeds germination and causes the seed dormancy as it actually helps seeds to avoid germination during stress conditions and prepares them to germinate only when the conditions are favourable for germination and growth (Piskurewicz et al., 2008; Li et al., 2016).

Gibberellic acid (GA3)

Gibberellic acid (GA_3) counteracts salt stress through membrane permeability improvement and increasing the nutrient amount in the leaves, which leads to a better seedling growth. GA_3 also enhanced the activity of several antioxidant enzymes such as superoxide dismutase and peroxidase (Tuna et al., 2008). Plant growth is restricted upon exposure to several stressors such as salt stress, osmotic stress and cold stress due to the reduction of GA_3 levels (Colebrook et al., 2014). Yuan et al. (2018) reported that the seeds of halophytes collected from plants grown under salty conditions showed greater salt tolerance than those harvested under non-salty condition due to increased osmolyte content, high gibberellic acid and low abscisic acid content. In the halophyte *Mesembryanthemum crystallinum* L., gibberellin regulated gene family was upregulated in response to salt stress which indicates the importance of gibberellic acid in salinity tolerance (Oh et al., 2015).

Molecular tolerance mechanisms in halophytes

Salt tolerance is mediated by interaction between various genes, such interplay of genes involves several physiological, biochemical, and molecular processes (Flowers, 2004). A particular gene would be expressed differently, in the case of salt stress, to give the desired physiological response. These genes encode proteins of known biological importance. Transcription factors and plant kinases are part of a vast group of affected genes with functions involved in salt stress tolerance mechanisms (Kreps et al., 2002; Kant et al., 2006). Researchers strongly suggests that most plants (if not all) present similar stress tolerance regulatory mechanisms. However, the quantitative differences thereof distinguish between halophytes and glycophytes (Anjum et al., 2012; Rai et al., 2012; Bartels and Dinakar, 2013; Sreeshan et al., 2014; Joshi et al., 2015; Volkov, 2015; Muchate et al., 2016). Such quantitative differences may be referred to higher expression of the genes responsible for salt stress tolerance mechanism (namely known as halophytic proteins), which tend to be naturally more active than the corresponding glycophytic proteins (Anjum et al., 2012; Das and Strasser, 2013; Himabindu et al., 2016; Muchate et al., 2016). Majority of these genes are concerned with regulatory processes of both transcription and transduction of signals and encode for antioxidants, ROS scavengers, Na^+/H^+ antiporters, potassium transporters, vacuolar pyrophosphatase, ion channels, and proteins that function as protective proteins as well as signal-transducing proteins.

Recently, several novel salt stress tolerances (salt responsive) genes of halophtyes were cloned and characterized in some plants, including such plants include *Salicornia brachiate* (Chinnusamy et al., 2006; Singh et al., 2016; Udawat et al., 2016; Udawat et al., 2017). Identification of these genes was the foundation of significant improvement of plant salt stress tolerance through genetic engineering, and halophytic genes were incorporated into a group of crops to enhance their salt tolerance (Udawat et al., 2014; Singh et al., 2016; Udawat et al., 2017). These affected genes include three major categories. The first category is involved in signalling cascades as well as in transcriptional control, such as phospholipases, SOS pathway, MAP (Mitogen-activated protein) and MyC (Myelocytomatosis oncogene cellular homolog) kinases, and transcriptional factors such as ABF/ABAE and HSF (Heat-shock factor) family. The second category is functioning directly for the protection of membranes and proteins, such as LEA (Late embryogenesis abundant) proteins, heat shock proteins and chaperones, free radical scavengers and osmo-protectants. Meanwhile, the third category is involved in water and ion uptake and transport such as ion transporters and aquaporins (Wang et al., 2003). Various omics tools are used, i.e., proteomics, genomics, metabolomics, transcriptomics etc. to identify and understand salt tolerance components and mechanisms of halophytes at the molecular level, followed by identification and validation of the functions thereof through transgenic approaches (Rajalakshmi and Parida, 2012). In this doctoral thesis, transcriptomic analysis is used to identify the candidate genes responsible for salt stress tolerance in the habitat-indifferent halophyte *Salsola drummondii* Ulbr., of the UAE desert ecosystems.

Plant transcriptomic analysis using next-generation sequencing technologies

Regulation of gene expression in salt stress includes a wide array of mechanisms that are used by plants to upregulate or downregulate the production of specific gene products (i.e., RNA or proteins). Through transcriptomic analysis, comprehensive deep knowledge of gene expression at mRNA level can be provided, where such knowledge can be used for screening candidate genes that could be involved in stress tolerance responses. RNA sequencing (RNA-Seq) technology is considered a major quantitative platform for transcriptome analysis, which is efficiently and economically enables investigation of transcriptomes in various gene expression studies, even for species that lack a reference genome (Schuster, 2007; Wang et al., 2009). Whereas, RNA transcript profiling is also an important strategy for studying the expression of a large number of genes in a given tissue at a given time point (Wilhelm et al., 2008). The sequencing methods have been widely applied to transcript profiling in numerous non-model species, and related candidate genes, single-nucleotide polymorphisms SNPs, and simple-sequence repeat SSRs have been identified (Guo et al., 2010; Zhang et al., 2013). Transcriptome analysis of the salt tolerance mechanisms in response to an increase in sodium chloride concentrations are also able to provide several insights on halophytes growth. Several genes are also well considered in the processes of the cell wall and carbohydrate metabolism, ion relation, redox responses, transcription factors and G protein, phosphoinositide and hormone signalling (Gharat et al., 2016).

The salt-responsive transcriptome of *Suaeda glauca* (Bunge) Bunge., was analysed to identify genes involved in salt tolerance and study halophilic mechanisms therein (Jin et al., 2016). There are several transcriptomic reports that have been completed on halophytes under salt stress conditions including, succulent xerophyte *Zygophyllum xanthoxylum* (Bunge) Engl., (Ma et al., 2016), *Suaeda maritima* (L.) Dumort., (Gharat et al., 2016), *Millettia pinnata* (L.) Panigrahi, a semi-mangrove (semi-mangrove plants form a group of transitional species, that are considered as intermediates between glycophytes and halophytes) (Huang et al., 2012), *Bruguiera gymnorhiza* (L.) Lam,, (Yamanaka et al., 2009), *Reaumuria trigyna* Maxim., (Dang et al., 2013), *Suaeda fruticose* (L.) Forssk., (Diray-Arce et al., 2015) and *Halogeton glomeratus* (M. Bieb.) C.A.Mey., (Dang et al., 2013; Wang et al., 2015). Transcriptomic and other genomic approaches have significantly contributed to identifying, cloning, and characterization of important genes, leading to revealing a huge number of salinity responsive transcription factors and genes, that are either upregulated or downregulated in response to salt stress (Krishnamurthy et al., 2017). Transcription factors are highly controlling the expression of a broad range of target genes through binding to specific cis-acting components in the promoters of such genes, and among these factors are C2H2 (Cys2/His2), AP2 (Apetala 2), NAC (NAM-ATAF1,2-CUC2), bZIP (Basic Leucine Zipper), WRKY zinc finger gene, and DREB (Dehydration-Responsive Element-Binding) families, which represented various stress-responsive members (Hong et al., 2016; Liu and Howell, 2016; Phukan et al., 2016; Zhu, 2016; Tang et al., 2018).

FAMILY AMARANTHACEAE JUSS., IN THE UNITED ARAB EMIRATES (UAE)

Amaranthaceae Juss., family have been chosen for the current doctoral thesis study because it can provide us with notable information about salt resistance mechanisms of halophytes. Most of the members of Amaranthaceae family are halophytes (Ocal Ozdamar et al., 2014). Amaranthaceae family shows 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).

Amaranthaceae are annual or perennial herbs or subshrubs; whereas a small group of its members are shrubs, a very few species that are vines or trees and some are succulent species. Leaves are simple and mostly alternate, as well as the occurrence of opposite leaves, and never possess stipules. Flowers are solitary or aggregated in cymes, spikes, or panicles, hermaphrodites and actinomorphic and few species appears to be unisexual. The diaspores are utricles, and more often the perianth persists, which is modified in fruit for means of dispersal. Amaranthaceae is a widespread family predominantly tropical climate, but also tend to grow in a dry hot climate and warm regions (Müller and Borsch, 2005). Some species are used as vegetables, pseudo-cereals, medicinal herbs, and ornamental plants. Several Amaranthaceae species are also used indirectly as a source of soda ash, such as *Salicornia* L. species. One of the effective uses in the UAE is as feedstocks for biofuels, including *Salicornia bigelovii* Torr., *Suaeda fruticosa* Forssk. ex J.F. Gmel. and *Haloxylon stocksii* (Boiss.) Benth. et Hook. f. (Abideen et al., 2011; Abideen et al., 2012) and animal foods including highly palatable for camels (Towhidi and Zhandi, 2007). Amaranthaceae can also be used as sea water irrigated crop (Cybulska et al., 2014).

GENUS *SALSOLA* L.

Salsola L., is a genus of the family Amaranthaceae Juss. The species of *Salsola* are mostly perennial subshrubs, shrubs, small trees, but rarely annuals. The leaves are mostly evergreen, alternate, simple, entire leaves and sometimes succulent. The flowers are bisexual, showing five petals and five stamens, whereas the pistil ends into two stigmata. The fruit is spherical in shape, presenting a spiral embryo and no perisperm (Mosyakin, S. L, 2004). This genus is distributed in central and south-western Asia, North Africa, and the Mediterranean regions (Akhani et al., 2007). Saltwort is a common name of various members of this genus and other related genera, the name is used in reference to their salt tolerance. Plants belonging to the genus *Salsola* are common in arid and semiarid UAE regions (Karim and Dakheel, 2006). Typically, these plants grow on flat, often dry and/or somewhat saline soils, with some species in salt marshes. In *Salsola* species, succulent leaves are the main morpho-physiological character of the tolerance mechanism used by the plant for coping with salinity stress (Sen and Rajpurohit, 2012). *Salsola sp.* has great medical and economic importance (Hamed et al., 2011; Abdou et al., 2013).

Salsola drummondii **Ulbr.**

Salsola drummondii Ulbr., is a perennial, leaf succulent, habitat-indifferent halophyte. In the United Arab Emirates (UAE), this evergreen species grows equally well in both non-saline (Fig. 7) and saline soils (Fig. 8). Our personal intensive surveys in the hyper-arid hot desert of the UAE indicated the plants that are associated with *S. drummondii* in the saline soils include *Halocnemum strobilaceum* (Pall.) Bieb., *Halopeplis perfoliata* (Forssk.) Bunge, and *Aeluropus lagopoides* (L.) Thwaites. However, plants that associated with *S. drummondii* in the non-saline habitats are classified as glycophytes (salt-sensitive plants), such as *Indigofera oblongifolia* Forssk., *Pennisetum divisum* (Gmel.) Henr., *Cornulaca monacantha* Delile, and *Launaea capitata* (Spreng.) Dandy. Other habitat-indifferent halophytes, such as, *Zygophyllum qatarense* Hadidi. and *Suaeda vermiculata* Forssk. ex. J.F. Gmel., were also reported to grow with *S. drummondii* in both habitat types (saline and non-saline) (Jongbloed et al., 2003). This species is economically useful in several ways; for example, leaves can be burnt to produce soda ash. In addition, different parts of this plant have medicinal uses (Gilani et al., 2010), and the plant leaves can also be used for animals feed (Qureshi et al., 1993). Additionally, *S. drummondii* is an important ecological plant for the restoration of salt-affected or degraded habitats (Dagar and Minhas, 2016).

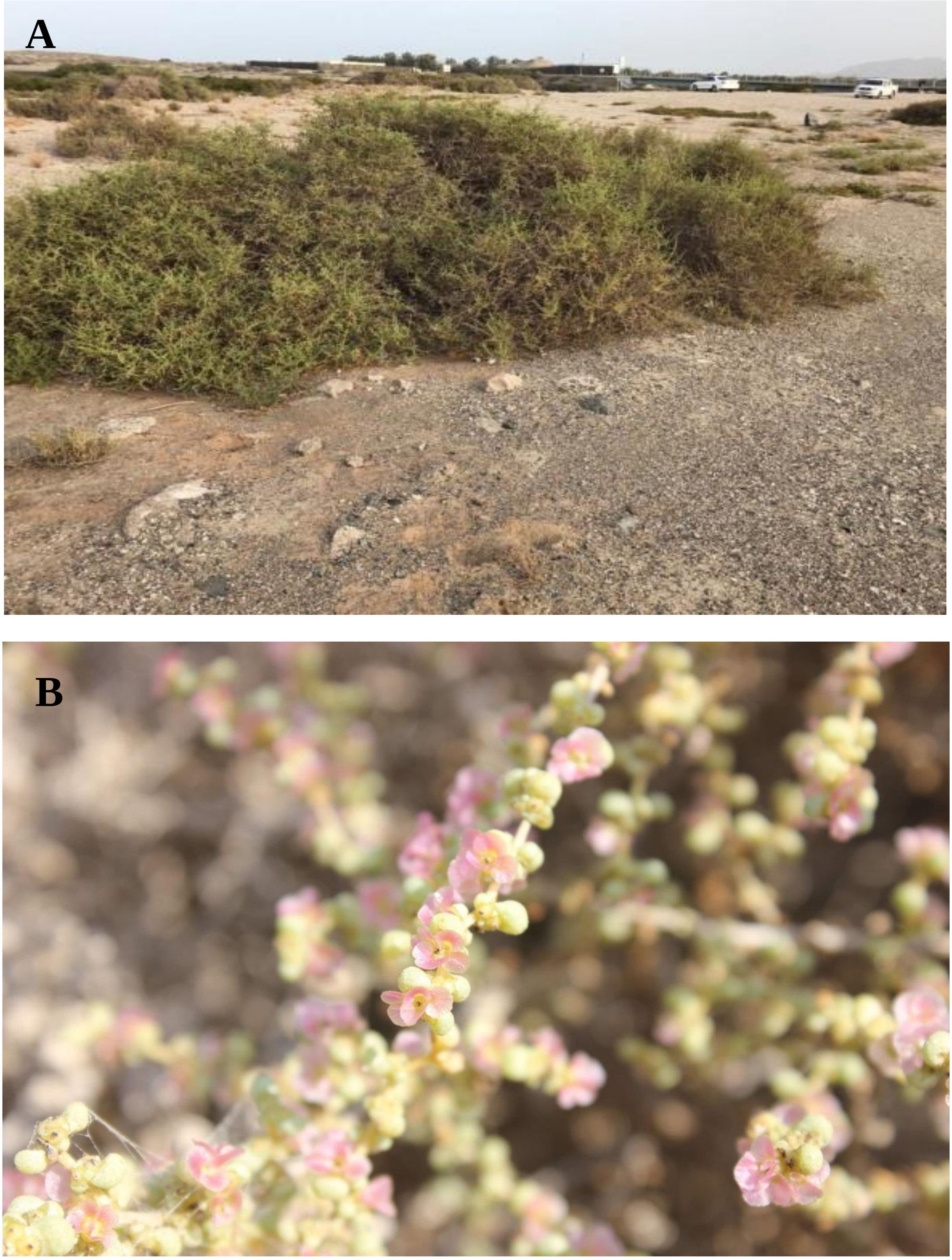


Figure 7. *Salsola drummondii* Ulbr., growing on non-saline sandy dunes in the UAE. (A) General habit. (B) Stems, leaves and fruits.

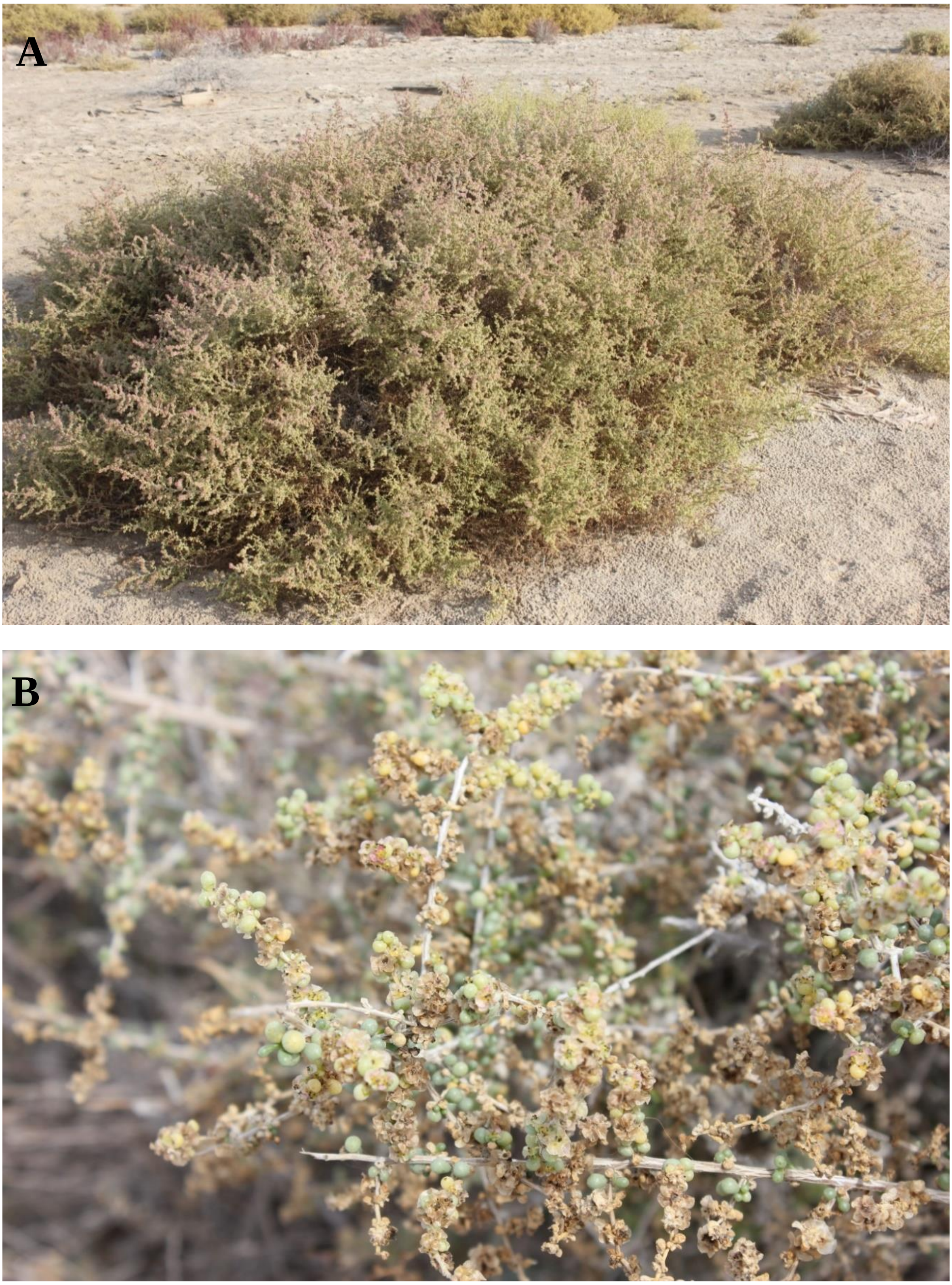


Figure 8. *Salsola drummondii* Ulbr., growing on hyper-saline salt marshes in the UAE. (A) General habit, (B) Stems, leaves and fruits.

Salsola imbricata Forssk.

Salsola imbricata Forssk., is a leaf succulent perennial halophyte shrub widely distributed in both coastal and inland salty habitats of subtropical regions of Pakistan (Khan and Weber, 2007). In the subtropical hot hyper-arid desert of the UAE, our personal intensive surveys indicated that *S. imbricata* is mainly distributed in non-saline sandy habitats. *S. imbricata* has an important ecological role as phytoremedy in habitat restoration (Khan et al., 2006; Ghazanfar and Osborne, 2010). In addition, it has the ability to stabilize sand dunes and to restore degraded, oil-polluted soils (Hegazy, 1997; Radwan et al., 1998). Furthermore, it has been indicated that *S. imbricata* has economic potential as a source for producing alkali (Khan and Weber, 2007). Furthermore, Mehrun-Nisa et al. (2007) indicated that *S. imbricata* has an economic potential as a source for producing alkali that is widely used by locals. Similarly, Shehab et al. (2015) reported a protective effect of this species against liver damage and attributed this to the ability of the plants to produce high quercitrin and rosmarinic acid contents. In addition, (El-Keblawy et al., 2007) compared seed germination of *S. imbricata* in the Pakistan and Arabia and concluded that seeds of the former tolerated more salinity during germination than the latter. Seeds from Pakistan desert tolerated up to 800 mM NaCl, but those from the UAE tolerated only up to 400 mM NaCl and seeds of the Kuwaiti deserts tolerated only up to 200 mM NaCl (Zaman et al., 2010). In the UAE, *S. imbricata* produce flowers and fruits before the rainfall season (November-December) (Fig. 9) indicating that it can tolerate the drought after germination, even during summer in spite, *S. imbricata* has shallow root system.

Little information is available about germination tolerance of this species under different temperature and light conditions, whereas the seeds of this species have short life span (i.e. can survive few months) under natural habitats. If seeds do not germinate within a few months after dispersal, they would lose their viability without contribution to the future plant generation (El-Keblawy, 2014). For this reason, the study of the germination of seed of this species under drought stress is of great interest.

Figure 9. *Salsola imbricata* Forssk., in vegetative growth in non-saline soil in the UAE. (A) General habit. (B) Stems and leaves.

STATEMENT OF THE PROBLEM

Soil salinization is a major limiting factor that causes loss in the productivity of cultivated arid and desert lands. The total area of salt-affected soils in the world is over 800 million hectares, including one third of the cultivated land (FAO, 2008; Naz et al., 2010; Kosová et al., 2013). More than 45 million hectares of irrigated land is affected by salt stress conditions, accounting for 20% of total land and 1.5 million ha of land suffering decreased or lack of production each year owing to high salinity levels (FAO, 2008; Munns and Tester, 2008). The agricultural land is steadily decreasing because of global climatic changes, as well as adverse environmental conditions, in addition to the continuously increasing natural calamities, and population pressure (Hasanuzzaman et al., 2013a; Hasanuzzaman et al., 2013b).

Salt-affected soils are found mainly in the arid and semi-arid regions (FAO, 2015). About 10% of the total arable land as being affected by salinity and sodicity and expected to increase up due to global change and human activities (Ruiz-Lozano et al., 2012; FAO, 2015; Shahid et al., 2018; Becerra et al., 2019). In recent years, it is suggested that halophytes can be used for desalination and restoration of saline soils in a process known as phyto-desalination (Rabhi et al., 2009; Riadh et al., 2010). Halophytes are characterized by their ability to tolerate high salinity levels due to the effective coordination between various physiological and metabolic processes and pathways, in addition to the distinctive network of genes and proteins that helps them develop salinity tolerance (Kumari et al., 2015). Identification of the molecular and biochemical mechanisms regulating the survival of halophytes is crucial for the development of the salt phyto-desalinators. Unlike halophytes, glycophytes show other less variant tolerance mechanisms. The identification of such mechanisms may provide a novel strategy that would potentially result in increasing plant salinity stress tolerance and provide a method to produce salt-tolerant crops. UAE is one of the countries that is challenged by the extreme environmental conditions, such as hyper-arid hot climate, the high temperatures and high salinity that characterize the Arabian Gulf. The plants developed in this region potentially have specific mechanisms and unique compounds that are different from other species and help them to increase their tolerance toward such extreme conditions (Cybulska et al., 2014). We decided to study the response and tolerance mechanisms at the physiological, biochemical and molecular levels in *Salsola drummondii* Ulbr., (Amaranthaceae) which is a habitat-indifferent halophyte grows abundantly in the UAE. As *S. drummondii* is a hábitat-indifferent halophyte, we hypothesize that the plants could develop biochemical, physiological, molecular adaptation mechanisms that enable them to perform well under higher levels of salinity.

In addition, defining the tolerance mechanisms under salt stress would help in understanding the causes of presence of habitat-indifferent halophytes under the hyper-saline conditions of the hyper-arid hot environments such as the UAE desert and this might help in the conservation of habitat-indifferent halophytes in this habitat type. The molecular and biochemical mechanisms regulating the survival of habitat-indifferent halophytes should differ from both strict halophytes and glycophytes. In order to grow in both saline and non-saline habitats, habitat-indifferent halophytes might have a salinity tolerance gene(s) that could be turned on/off, depending on the soil salinity. Turning on of the salt tolerance gene(s) should enable the hábitat-indifferent halophytes to survive the salinity stress. Identifying the genes responsible for the biosynthesis and catabolism of common osmolytes and antioxidant metabolites in plants of the same habitat-indifferent halophytes species growing under saline and non-saline conditions would help in understanding the mechanisms that are involved in salinity tolerance in plants. Furthermore, it may provide a novel strategy to increase plants tolerance to salinity stress and developing salt-tolerant plants.

OBJECTIVES

The overall aim of this doctoral thesis study was to assess the impact of environmental factors (light, temperature, salinity and drought stresses) on germination and dormancy of *Salsola imbricata* Forssk., and *S. drummondii* Ulbr. (Amaranthaceae), and the impact of salt stress on the biochemical and molecular responses of *S. drummondii* Ulbr., in the desert ecosystems of the United Arab Emirates (UAE).

The specific objectives are as follows:

1- Evaluate the effects of temperatures (thermoperiod) and light (photoperiod) and their interaction on drought tolerance, seed dormancy and germination traits in two congeneric species of the genus *Salsola* L.: *Salsola drummondii* Ulbr., and *S. imbricata* Forssk.

The results of this first objective are two published articles:

- Elnaggar, A., El-Keblawy, A., Mosa, K.A., Navarro, T., 2018. Adaptive drought tolerance during germination of *Salsola drummondii* seeds from saline and non-saline habitats of the arid Arabian deserts. Botany, 97, 123-133
- Elnaggar, A., El-Keblawy, A., Mosa, K.A., Soliman, S., 2018. Drought tolerance during germination depends on light and temperature of incubation in *Salsola imbricata*, a desert shrub of Arabian deserts. Flora, 249, 156-163.

2- Assess the effects of temperatures (thermoperiod) and light (photoperiod) and their interaction on salinity tolerance, seed dormancy and germination traits in *Salsola drummondii* Ulbr.

3- Assess the effect of salt stress on some functional traits (e.g. physiological and biochemical) of *Salsola drummondii* Ulbr., at different stages of the life cycle.

4- Identify transcripts encoding proteins involved in salt stress regulation in *S. drummondii* Ulbr.

Part of the study in this doctoral thesis has been carried out under an international research project developed between Malaga University (UMA) and University of Sharjah (United Arab Emirates) with the title: Transcriptomics and Metabolics analysis to Reveal Salt and Heat Stress Related Genes, Phytohormones and Osmolytes in Facultative Halophytes plant of the UAE (2017- 2019). UMA Reference Number 1602145041-P. Other part of the doctoral study was carried out in the Department of Applied Biology of University of Sharjah (UAE). Part of the results have been published in scientific journals included in the ISI web of Knowledge.

2. MATERIAL AND METHODS

2. MATERIAL AND METHODS

2.1. Study site description

The study site of this doctoral thesis was done in two habitats in Kalba city, the eastern coast of the UAE (Fig. 10). The first site with saline compacted soils (24°99′68.68″N and 56° 34′91.90″E) and the second site with a non-saline soils (25° 02′94.17″N and 56° 36′17.56″E). The saline and non-saline soil types could be classified according to the USDA soil taxonomy as Haplosalids and Typic Torripsamments, respectively (Shahid et al. 2014). The saline soils correspond to sands and the non-saline to the gravel plain. The associated plants in saline habitats are halophytes, such as *Suaeda vermiculata* Forssk. ex. J.F.Gmel., *Aeluropus lagopoides* (L.) Thwaites, *Halopeplis perfoliata* (Forssk.) Bunge, *Halocnemum strobilaceum* (Pall.) Bieb., and *Zygophyllum qatarense Hadidi*. However, the associated species in the non-saline substrate are glycophytes, such as *Launaea capitata* (Spreng.) Dandy, *Cornulaca monacantha* Delile, *Pennisetum divisum* (Gmel.) Henr. and *Indigofera oblongifolia* Forssk.

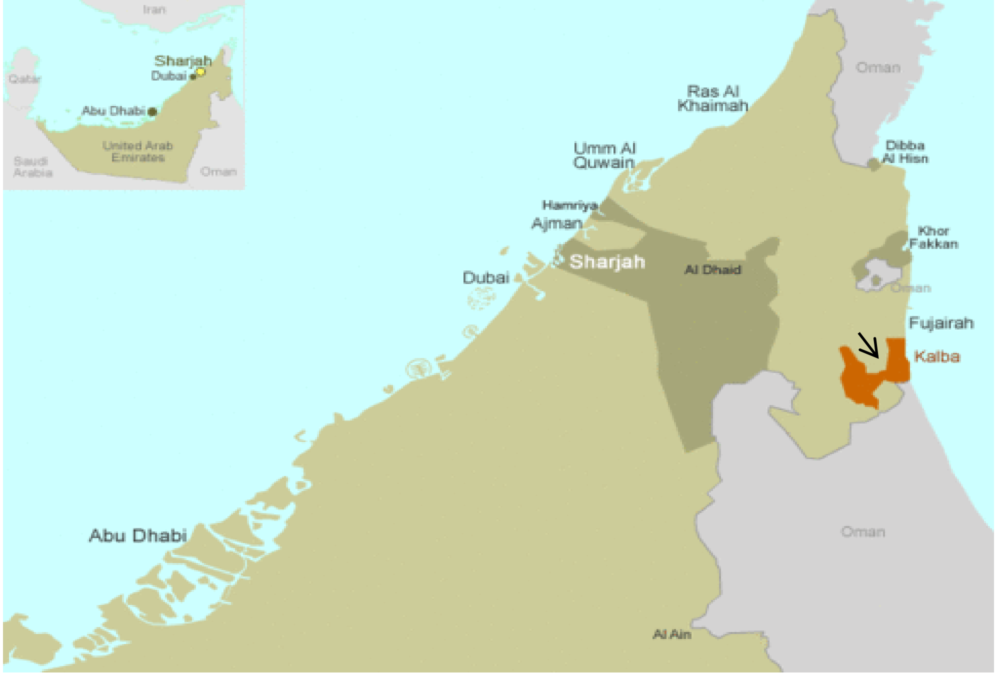


Figure 10. Location map showing the study site at Kalba city, the East Coast of the United Arab Emirates. The orange color pointed with black arrow refers to Kalba city.

2.2. Sample collection

In this part we will focus on soils and plants samples collected from the field. The plant material samples correspond to the *Salsola drummondrii* Ulbr. and *S. imbricata* Forssk.

2.2.1. Soil

Five soil samples were collected around *S. drummondii* roots in 15cm depth and stored in bags at each habitat (saline and non-saline). Soil samples were air dried and sieved to get fine soil to be ready for elemental analysis, E elemental carbon (EC), pH and salinity.

2.2.2. Fruits and seeds

Mature fruits of *S. imbricata* were collected during December 2016 from the second non-saline sandy site in Kalba city. Fruits were randomly collected from 30 shrubs to represent the genetic diversity of the population. Immediately after collection, seeds were air dried and threshed to separate debris by using a hand-made rubber thresher (Fig. 11A). Threshed seeds (without wing structure) were stored in brown paper bags at room temperatures (22 ± 2 °C) until their use in the germination experiment in January 2017. At that time of the year, effective rainfalls usually occur and therefore germination takes place.

S. drummondii were collected from the two sites, salt marsh and a non-saline gravel plain in Kalba city during December 2015. Fruits of each habitat were randomly collected from 50-60 plants (Fig. 11B). Collected fruits were cleaned and seed stored in brown paper bags at -18 °C until the seed germination experiment was initiated in the first week of January 2016. The average mass of an individual seed was calculated by weighing three batches of seeds, each with 100 seeds, from both saline and non-saline habitats.

S. drummondii losses its viability fast therefore, seeds collected in 2015 lost their viability in 2016 therefore we collected the seed again in December 2016. These seeds were used to grow plants for testing effect of salt stress in potted soil under controlled conditions.

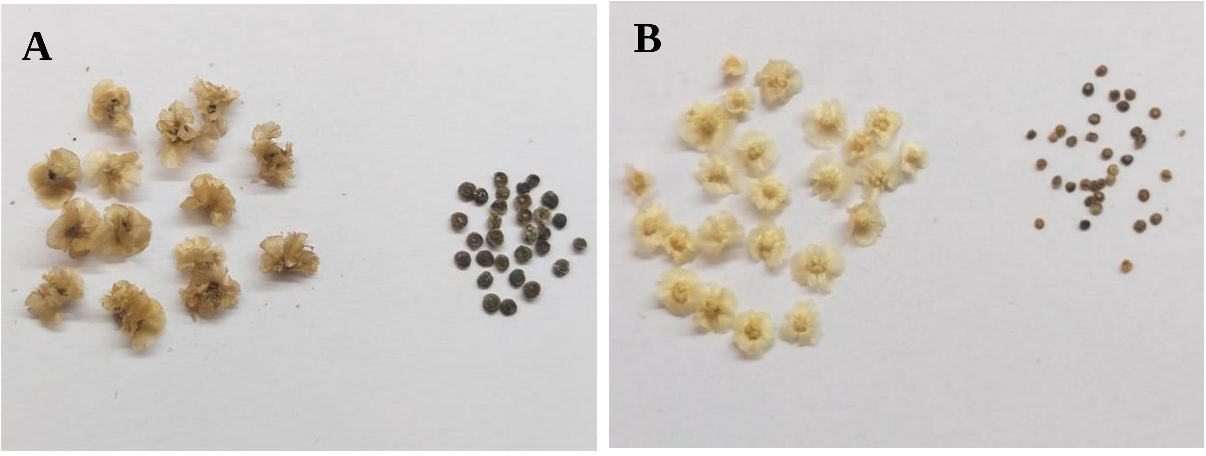


Figure 11. Fruits and seeds of (A) *Salsola drummondrii* Ulbr., and (B) *Salsola imbricata* Forssk.

2.2.3. Plant leaves, stems and roots

S. drummondii plants were collected from two habitats around Kalba city, on the northeast coast of the UAE, during April 2018. The first site was a salt marsh and the second site was a non-saline gravel plain. The plant samples were collected and washed by tap water and distilled water and separated directly into three parts: leaves, stems and roots. Some fresh samples were kept in falcon tubes and stored in liquid nitrogen during the field trip then once we arrived to the lab we stored them in -80 ^oC for using in the biochemical analysis such as chlorophyll, Malondialdehyde (MDA), H_2O_2, catalase, ascorbate peroxidase, guaiacol peroxidase and proline. The other samples we dried in oven at 60 ^{o} C for three days, to use the dried leaves in carbon isotope analysis and the dried parts roots, stems, leaves were used them in elemental analysis by inductive couple plasma mass spectroscopy **(**ICP-MS). In addition to the collected plant material.

2.3. Experimental designing and samples analysis

2.3.1. Soil analysis

Soil salinity, electrical conductivity (EC), and pH were measured from a 1:5 soil: water suspension (Dahnke and Whitney, 1988). After 24 hrs of shaking, the suspension was left undisturbed for 1h, then pH and electrical conductivity (EC) were measured by Thermo

Scientific Orion Star A211 pH Benchtop Meter. Salinity was measured using a HQ40d salinity meter (HACH, Loveland, Colorado, USA).

2.3.2. Seed germination

2.3.2.1. Effects of light and temperature on drought tolerance during seed germination of *Salsola imbricata* Forssk., and *S. drummondii* Ulbr.

Maternal salinity means salinity of plant maternal habitat, we adopted the terms “maternal habitat” when we test the effect of soil salinity prevailing in natural habitat during seed maturation on drought and salinity tolerance of the habitat-indifferent halophyte *S. drummondii* during seed germination where we compare the drought and salinity tolerance between seeds of *S. drummondii* collected from saline and non-saline habitats. Seed viability of both saline and non-saline habitat was assessed for three batches, each consisting of 100 seeds, using 1% (w/v) 2, 3, 5- triphenyl-tetrazolium chloride solution (Bradbeer, 1998). When seed attained red color, this was indication for seed viability.

Polyethylene glycol (PEG) is an inert polymer. It is nonionic, has high molecular weight, and can be dissolved in water. It is the most preferred osmotic substance that can create solutions with various negative water potentials. We used PEG to assess the drought tolerance during germination, which would determine the minimum water potential threshold for germination (Bradford, 2002). Solutions with higher levels of PEG have higher negative water potentials (Money, 1989; Munns, 2002). Several studies have used PEG to simulate drought during germination in several species (Okçu et al., 2005; Sidari et al., 2008; Muscolo et al., 2014; Cochrane et al., 2015; Kołodziejek and Patykowski, 2015; Cavallaro et al., 2016). As PEG is a non-penetrating polymer, it affects seed germination through its osmotic effect (Munns, 2002).

The interactive effects of drought stress as simulated with PEG, light and temperature of incubation on germination response of *S. imbricata* collected from non-saline habitat and *S. drummondii* collected from saline and non-saline habitat were assessed by germinating the seeds of *S. imbricata* in nine PEG 6000 (Sigma-Aldrich) levels that created nine osmotic potentials (0, -0.2, -0.4, -0.6, -0.8, -1.0, -1.4, -1.8 and -2.4 MPa; Michel and Kaufmann, 1973) and seeds of *S. drummondii* from the two habitat types were germinated in six PEG 6000 levels (0, -0.4, -0.7, -1.0, -1.2 and -1.5 MPa). The different osmotic potentials were verified with Wescor Vapro 5520 (Wescor Inc., UT, USA).

Seeds of *Salsola imbricata* and *S. drummondii* treated with different PEG concentrations were incubated in three CONVIRON plant growth chamber (model E-15) adjusted at three temperatures and two light regimes. The three temperature regimes were the daily night/light of 15/25, 20/30 and 25/35 °C, where high temperatures coincided with 12 hrs white light (1400 µmol m^{-2} s^{-1} of photosynthetic photon flux density PPFD). The lighting in the chamber was provided by five (400 W) metal halide and five (400 W) high pressure sodium lamps. The light regimes were 12 hrs light/12 hrs darkness and complete darkness (hereafter referred as light regimes as light and dark, respectively). Polyethylene glycol PEG levels were selected based on the result of a preliminary experiment assessing drought tolerance during germination of *S. imbricata* and *S. drummondii*. Germination was carried out in tight fitting 9-cm Petri dishes on a layer of Whatman No.1 filter paper moistened with 10 ml of a test solution.

Dark treatment was achieved by wrapping the dishes with aluminum foil to prevent any exposure to light. Four replicates of 25 seeds each were used for each treatment. PEG-treated dishes were sealed with parafilm as an added precaution against water evaporation. Seeds were considered to be germinated once a radicle had emerged. Germinated seedlings were counted and removed every alternative day for 20 days following seed sowing. The data of the last three counts was excluded since there were no new seedlings appearing after day 14. In the dark treatment, seeds were counted after 20 days.

Germination recovery of seeds of *Salsola imbricata* Forssk., and *S. drummondii* Ulbr., treated with polyethylene glycol (PEG)

At the end of germination experiment (i.e., after 20 days), non-germinated seeds in the different polyethylene glycol solutions at different light and temperature regimes, were washed and placed in distilled water to determine if they would germinate. This recovery experiment was conducted at the same temperature regimes mentioned above and under the same light conditions. Germinated seeds were counted every other day for 10 days.

2.3.2.2. Effect of light, temperature and maternal habitat on salinity tolerance during seed germination of *Salsola drummondii* Ulbr.

To assess seed germination tolerance to salinity stress and the dependence of that stress on light and temperature, seeds from both saline and non-saltine habitats were germinated in six salinity levels (0, 200, 400, 600, 800 and 1000 mM NaCl) and incubated in three CONVIRON plant growth chambers (model E-15) adjusted at three temperatures and two light regimes as mentioned above. The selection of the used salinity levels was based on a preliminary experiment assessed salinity tolerance during germination of *S. drummondii*. Germination was carried out in tight fitting 9-cm Petri dishes on two-layers of Whatman No.1 filter paper moistened with 10 ml of the test solution. Dishes that were treated in dark were wrapped with two-layers of aluminum foil to ensure that seeds are not exposed to any light. Four replicates were used for each treatment; each replicate has 25 seeds. Seeds were considered to have germinated when the emerging radicle was at least 2 mm long.

The germinated seeds were recorded and removed every other day for 20 days. After 16 days, no further seeds germinated in the different treatments, so we decided to stop the germination counting after 20 days. Seeds germinated in the dark condition were counted only after 20 days.

Germination recovery of *Salsola drummondii* Ulbr., seeds treated with sodium chloride (NaCl)

After 20 days, any seeds in the NaCl treatment that had not germinated were transferred to distilled water to test the recovery germination. The seeds were incubated again at the same thermoperiod regimes mentioned above and in light regimes (12 light/12 dark). Germination was counted daily for 10 days. Viability of seeds from both saline and non-saline habitats that failed to recover germination were tested using 1% (w/v) 2,3,5-triphenyle-tetrazolium chloride solution (Bradbeer, 1988). Three seed batches from each habitat type, each with 100 seeds, were used in the viability test.

2.3.3. Seedlings growth of *Salsola drummondii* Ulbr., under different salinity levels

Fruits of *S. drummondii* were collected from naturally grown plants in a salt marsh located at Kalba city during December 2016. Seeds were separated from mature perianth (fruit) manually, surface sterilized by using 5% commercial bleach for five minutes, rinsed with distilled water, air dried and used directly for planting on autoclaved sandy soil. The pots were placed under 12 hours light (30 ^{o}C) and 12 hours dark (25 ^{o}C) cycle conditions with light intensity of approximately 300 µmol m^{-2} S^{-1}. *S. drummondii* plants were irrigated with 10 % Hoagland no-2 salt mixture (Sigma-Aldrich, UK) twice a week.

Four month seedlings of *S. drummondii* grown on sandy soil pots were treated with four levels of salinity: (0, 200, 500, and 800 mM NaCl) in 10 % Hoagland no-2 salt mixture (Sigma-Aldrich, UK) (Fig. 12). Treated seedlings were grown in a growth chamber adjusted at 25°C for 12h dark/30 °C for 12h light. To keep the same salinity levels unchanged, all pots receiving the different salinities were weighted daily, and any loss in weight (as a result of evaporation) was restored by water addition. In addition, pots treated with a specific sodium chloride (NaCl) concentration were leached every four days with same concentration. Plants were then harvested after 20 days of sodium chloride (NaCl) treatment. Shoots and roots were separated and kept at -80 °C for further biochemical and physiological analysis such as elemental analysis by XRF (X-ray florescence) machine and atomic absorption spectroscopy (AAS), biomass and succulence, pigments content, estimation of damage signals, estimation of antioxidant enzymes and proline content.

Figure 12. Cultivated specimens of *Salsola drummondii* Ulbr., under four different sodium chloride (NaCl) concentrations: 0, 200, 500 and 800 mM, after 20 days of treatment. The specimens are ordered in the figure from left to right following salt concentrations.

2.3.4. Elemental analysis of the soils and *Salsola drummondii* Ulbr., plant material using inductively coupled plasma mass spectrometry

The soil and the whole plant samples of *S. drummondii* which were collected from Kalba city, UAE from both saline and non-saline habitat during April 2018. The plant samples were washed by using distilled water, air dried and separated into leaves, stems and roots. The samples were further dried in an oven at 60 ^{o}C for three days and ground. A dry biomass (0.25 g) of plant samples from each organ were weighed and shifted into the digestion vessels.

The soil and the whole plant samples of *S. drummondii* were processed for acid digestion using *aqua regia* (wet method) in a mixture of high-purity concentrated HNO_3 and

HCl (5:1) then the samples were processed for microwave reaction system (multipro (Anton paar) for digestion.

The elements were determined from both plant and soil samples through inductive couple plasma mass spectroscopy (ICP-MS) (Varian 715-ES). Multi standards (STD) were used at different concentrations (0.1 ppm, 1 ppm, 10 ppm, 50 ppm) to detect the elements in the samples (Na^+, K^+, Ca^{2+}, Mg^{2+} and Fe^{2+}).

2.3.5. X-ray fluorescence analysis of plant material: leaves, stems and roots

X-ray fluorescence (XRF) microscopy, a comparative chemical analysis technique, was used for elemental analysis of S. drummondii fresh roots, stems and leaves of plants treated with 0, 500 and 800 mM NaCl. The XRF analysis was performed using a Horiba XGT 7200 X- ray analytical microscope (Kyoto, Japan) to determine the percentage of Na^+, K^+, Cl^-, Mg^{+2} and Ca^{+2}. The microscope is equipped with a 50-W Rhodium X-ray source and a silicon drift detector. Two beam sizes of diameter 50 µm and 1.2 mm are available for spot analysis (Attaelmanan and Kawam, 2012). Fresh separated plant organs (roots, stems and leaves) were placed in triplicate on plastic sample holders. X-ray beams were focused onto the sample and the XRF spectra were obtained from 10 points on each sample using analysis time 1000 second per point and 300-lA tube current. Elements levels were calculated from the collected spectra using fundamental parameter (FP) software that considers the standard operating conditions. The concentration of each element was represented as a relative percentage from the concentrations of all elements in the plant sample (Attaelmanan and Kawam, 2012).

2.3.6. Determination of sodium content by atomic absorption spectroscopy

To estimate sodium content, 10 ml of 0.5 M HNO_3 were added to 100 mg of fine powder dried material of plants treated with different NaCl levels (0, 200, 500, 800 mM NaCl) in a polystyrene tube. All samples were shaken well to suspend all plant materials in the dilute acid, and placed on a shaker for 2 days at room temperature. The samples were filtered and diluted to100 ml with high-purity water and then sodium concentrations were measured using atomic absorption spectroscopy (model: AA 7000, SHIMADZU) equipped with a transversely heated graphite furnace. Different sodium standard solutions have been prepared to make the standard curve to calculate the concentration of sodium in different samples.

2.3.7. Determination of sodium influx by atomic absorption spectroscopy

Three-month old plants were transferred from potted sandy soil into a hydroponic system has 10% Hoagland solution and allowed to grow for a month. These four-month old plants were used for sodium influx evaluation. For analyzing short-term sodium influx, the well-established plants treated with 1200 mM NaCl in the hydroponic system were harvested at different time points (0, 0.5, 1, 2, 4 and 8 hrs). Shoots and roots were separated, washed carefully, and dried in an oven till complete dryness. The tissues were ground in mortar and sodium concentrations were analyzed using atomic absorption spectroscopy (AAS) as described above.

2.3.8. Carbon isotope discrimination measurements

The plant leaf samples collected from the field from saline and non-saline habitats were oven dried at 70 ºC and ground to a fine powder using a Ball Mill (Retsch MM 2000, Haan, Germany). The powder was transferred to tin capsules (5 x 3.5 mm, Elemental Microanalysis Limited, U. K.). A sample (1900-2100 µg) was combusted (1000 ºC) in an Isotope Ratio Mass Spectrometer (Delta-V Plus of Thermo Scientific, Swerte; Germany) at stable isotope facility, Servicios Centrales de Apoyo a la Investigación (SCAI), at Universidad de Málaga, Spain. Carbon isotope composition ($\delta^{13}C$) was expressed relative to the international standard PDB (Pee Dee belemnite). The carbon isotope composition ($\delta^{13}C$) and discrimination ($\Delta^{13}C$) were calculated through standard procedure as reported by (Farquhar and Richards, 1984; Farquhar et al., 1989) and documented by (Hussain and Reigosa, 2011; Hussain and Al-Dakheel, 2018; Hussain et al., 2018b).

2.3.9. Plant biomass and leaves succulence measurements

The plant biomass was measured from fresh plant leaves collected from the field. The fresh leaves weight (FW) of 100 leaf samples was recorded through an analytical balance. The leaf samples were oven dried at 60 ºC for 48 hrs and dry weights (DW) (100 leaves) was measured. For the plants grown under controlled laboratory condition and treated with different concentrations of sodium chloride, fresh weights (FW) and dry weights (DW) of shoot, root, and leaf tissues were measured after 20 days of NaCl treatment. Succulence of shoot, root and leaf tissues was determined by using the following formula: Succulence = (FW-DW)/ DW.

2.3.10. Estimation of leaves chlorophyll and carotenoids pigment content

To assess chlorophyll contents, 200 mg of fresh leaves collected from the field were sliced into small pieces and then were ground to fine powder with liquid nitrogen. Powder tissues were mixed with 5 ml 80% acetone in 15 ml falcon tubes in dark for 15-30 min, and then centrifuged at 4 °C for 15 min (3,000 rpm). Supernatants were transferred to a new centrifuge tube, and kept in dark. The extraction step was repeated, tubes were mixed thoroughly, and the absorbance (A) of chlorophyll content was measured using spectrophotometer (6300-JENWAY) at 645, 663, and 470 nm, respectively. The chlorophyll and carotenoids concentrations were calculated according to (Lichtenthaler and Wellburn, 1983; Şükran et al., 1998) as shown in (Table 2).

Table 2. Equations for chlorophyll and carotenoids calculations.

Chl *a* (mg/g) = (12.7 x A663 – 2.69 x A645) ×V/(1000×W)
Chl *b* (mg/g) = (22.9 x A645 – 4.86 x A663) × V/(1000×W)
Chl *a*+*b* (mg/g) = (8.02 × A663 + 20.20 x A645) ×V/(1000×W)
CX+C (mg/g) = (l000A470- 3.27Chla- 104Chlb)/229)) ×(V/(1000×W)

V = Volume of the extract (ml), W = Weight of fresh leaves (g),
Chl = Chlorophyll and CX+C = Carotenoids, A = Absorbance

2.3.11. Determination of damage signals (oxidative damage)

2.3.11.1. Estimation of lipid peroxidation

Lipid peroxidation was measured as the amount of malondialdehyde (MDA) produced by the 2-thiobarbituric acid (TBA) reaction, as described by (Zhou and Leul, 1998). Fresh samples of roots and shoots (0.1 g) of plants collected from the field from saline and non-saline habitats and of plants treated with the different concentrations of NaCl (0, 200, 500, 800 mM) were homogenized in 2 ml of 0.1 % (w/v) trichloroacetic acid (TCA). The homogenate was centrifuged at 10,000 g for 15 min. 2ml of 20 % TCA containing 0.5 % (w/v) TBA were added to 0.8ml of the aliquot of the supernatant. The mixture was heated at 95 °C for 30 min and then quickly cooled in ice. The contents were centrifuged at 13,500 rpm for 15 min at 4 °C and the absorbance was measured at 532 nm. The supernatants were transferred into cuvettes and absorbance was measured at 532 and 600 nm respectively after blanking. The level of MDA was represented as nmolg^{-1} FW using an extinction coefficient of 155 mM^{-1} cm^{-1}.

2.3.11.2. Estimation of the hydrogen peroxide (H_2O_2) content

Hydrogen peroxide content was determined according to (Velikova et al., 2000). 0.1 g of fresh *S. drummondii* roots and shoot tissues collected from the field from saline and non-saline habitats and from plants treated with the different concentrations of NaCl (0, 200, 500, 800 mM) were homogenized in an ice bath with 5 ml of 0.1 % (w/v) trichloro acetic acid. The homogenate was centrifuged for 15 min at 12,000 g and 0.5 ml of the supernatant was mixed with 0.5ml of 10mM potassium phosphate buffer (pH 7.0) and 1 ml of 1 M potassium iodide (KI). The absorbance of the supernatant was measured at 390 nm in a spectrophotometer (6300-JENWAY). Standard curve was prepared by using different concentrations of H_2O_2, and the H_2O_2 content was calculated.

2.3.12. Extraction and estimation of antioxidant enzymes

2.3.12.1. Preparation of enzyme extract and assay of enzyme activity

We weighed 0.1 g of *S. drummondii* fresh shoots and roots which were collected from the field from saline and non-saline habitat and from plants treated with the different concentrations of NaCl (0, 200, 500, 800 mM) were ground to a fine powder in liquid nitrogen and mixed with 50 mM potassium phosphate buffer (pH 7.0), 1 mM EDTA, 1 mM D-isoascorbic acid, 2 % (w/v) polyvinyl pyrrolidone (PVP) and 0.05% (w/v) Triton X-100 using a chilled pestle and mortar following the method of (Gossett et al., 1994). The homogenate was centrifuged for 10 min at 4 °C at 10,000 g and the supernatants were collected and utilized for catalase, ascorbate peroxidase and guaiacol peroxidase assays.

2.3.12.2. Estimation of catalase, ascorbate peroxidase and guaiacol peroxidase activity

Catalase (CAT) activity was determined spectrophotometrically by measuring the rate of H_2O_2 disappearance at 240 nm, taking extinction coefficient ($\Delta\varepsilon$) 2.8 $mM^{-1}cm^{-1}$ at 240 nm as 43.6 $mM^{-1}cm^{-1}$ (Patterson et al.,1984). Catalase (CAT) activity was determined using enzyme extract containing 20 μg of protein and a reaction mixture containing 50 mM potassium phosphate (pH 7.0), 10.5 mM H_2O_2 at 25 °C for 2 min (Miyagawa et al., 2000) and the initial linear rate of decrease in absorbance at 240 nm was used to calculate the activity.

Ascorbate peroxidase (APX) was assayed as described by (Nakano and Asada, 1981) using enzyme extract containing 50 μg of protein and a reaction mixture containing 50 mM potassium phosphate (pH 7.0), 0.2 mM EDTA, 0.5 mM ascorbic acid and 0.25 mM H_2O_2 at 25 °C. The decrease in absorbance at 290 nm for 1 min was recorded and the amount of ascorbate oxidized was calculated from the extinction coefficient ($\Delta\varepsilon$) 2.8 $mM^{-1}cm^{-1}$.

Guaiacol peroxidase (GPX) activity was assayed as described by (Zaharieva et al., 1999) using enzyme extract equivalent to 5 μg protein. The reaction mixture (2 ml) contained 50 mM potassium phosphate (pH 7.0), 2 mM H_2O_2, and 2.7 mM guaiacol. The increase in the absorbance for 3 min was measured at 470 nm due to the formation of tetraguaiacol ($\Delta\varepsilon$ = 26.6 $mM^{-1}cm^{-1}$).

2.3.13. Proline analysis

Samples of *S. drummondii* shoots and roots from the two habitats (saline and non-saline) and from plants treated with the different concentrations of NaCl (0, 200, 500, 800 mM) were used for analysis of proline using the methodology described by (Bates et al., 1973). The plant tissues were immediately frozen in liquid nitrogen after harvesting and then kept in -80 ºC. 0.5 g fresh weight of the frozen material was ground to a fine powder in a pre-cooled mortar with liquid nitrogen. The powder was homogenized with 5 ml of 3% aqueous sulfosalicylic acid and then the homogenate was centrifuged at 14,000 g for 2 minute. 2ml of the homogenate was mixed with 2 ml of glacial acetic acid and 2 ml of acid-ninhydrin. The mixture was then incubated at 100 ºC for 1 h, 4 ml of toluene was added to the mixture and vortexed for 15-20 second. The absorbance at 520 nm of the organic toluene phase was used to quantify the amount of proline using toluene as a reference. The proline concentration was determined using a standard concentration curve and calculated on fresh weight basis (Ábrahám et al., 2010).

2.3.14. Estimation of total glutathione content

S. drummondii fresh shoots and roots from plants treated with the different concentrations of NaCl (0, 500, 800 mM NaCl) were used to determine the reduced and oxidized forms of glutathione using the total Glutathione (GSSG/ GSH) assay kit (Oxiselect STA-312 (CELL BIOLABS, San Diego, CA, USA). After addition of glutathione reductase enzyme, the glutathione oxidized form was reduced and the level of total glutathione was measured (Kao et al., 2016).

2.3.15. Transcriptomic analysis of *Salsola drummondii* Ulbr.

Fruits of *S. drummondii* were collected from naturally grown plants in a salt marsh located at Kalba city then the wings were removed. Seeds were sterilized and planted in plastic pots contained autoclaved sand. Pots were placed under 12 hours light (30 ^{o}C) and 12 hours dark (25 ^{o}C) cycle conditions with light intensity of approximately 300 μmol m^{-2} S^{-1}. The plants were irrigated with 10 % Hoagland no-2 salt mixture (Sigma-Aldrich, UK) twice a week. Two months old seedlings were used for the salinity treatment (0 and 1200 mM of NaCl). Samples were harvested after 0, 6, 12 and 24 hrs of NaCl treatment then separated into roots and shoots (Fig. 13) and stored at -80 ^{o}C until further analysis.

Figure 13. Separation into shoots and roots of the control and salt treated *Salsola drummondii* Ulbr., plants.

2.3.15.1. RNA isolation and cDNA library preparation

Total RNA of the control and sodium chloride (NaCl) treated shoot and root samples (0 and 24 hours) was isolated using RNeasy Plant Mini kit (Qiagen, Germany) according to the manufacturer's instructions. To remove the genomic DNA contamination, on-column DNase treatment was performed using RNase-Free DNase set, (Qiagen, Germany) according to the manufacturer's instructions. The quality of the RNA samples was determined using a Bioanalyzer (Agilent Technologies). True seq standard library prep kit was used for library preparation. Later, sequencing was performed on Hi-seq 2500 platform with paired-end (2*100 bps) orientation at AgriGenome Labs Pvt, Ltd, India.

2.3.15.2. RNA-seq data processing and *de novo* transcriptome assembly

Using Cutadapt (v1.8.1) algorithm, the adaptor sequences were removed from all the reads (Martin, 2011). The reads with average quality score less than 20 in any of the paired end and reads are filtered out using the program, Sickle (v1.33) (Joshi and Fass, 2011). The high quality reads were aligned to Silva (high quality ribosomal RNA databases) (Quast et al., 2013) with the program bowtie2 (v2.2.9) (Langmead et al., 2009). The high quality reads were used for final *de novo* assembly using Trinity assembler (version: v2.4.0) (Garber et al., 2011). Unigenes were generated using "cd-hit-est" (version: 4.6) which removes redundant transcripts. Using bowtie2 and various other in-house pipeline tools, expression levels of unigenes were estimated.

2.3.15.3. Functional annotation

The *de novo* assembly of the transcriptome were made using the high quality sequence reads. The unigenes (FPKM (fragments per kilobase per million mapped reads) ≥ 1) were annotated and sequence based homology search was performed using NCBI, Swiss-prot and various other major databases (Altschul et al., 1997) with Blast2GO tool (Götz et al., 2008). Plant Metabolic Network Analysis was carried, based on blast with PMN database search and annotations (Schläpfer et al., 2017).

2.3.15.4. Identification of differentially expressed genes

DESeq (version 1.16.0) was used to calculate differentially expressed sequences from the *de novo* assembly (Anders and Huber, 2010). The log2 fold changes were calculated based on cutoff value of 0.05. FPKM (fragments per kilobase per million mapped reads) are calculated from the number of reads that mapped to each particular gene sequence taking into account gene length. The candidates of DEGs were individually searched on the plant genomic databases and relevant literatures for more insights about their functions and their association with salinity stress.

2.3.15.5. Quantitative real time - polymerase chain reaction (qRT-PCR) analysis

For qRT-PCR experiments, total RNA was isolated from 100 mg of control and salt treated root and shoot tissues of various time points (0 hrs, 6 hrs, 12 hrs, 24 hrs), and was used to synthesize cDNA using SuperscriptTM III First-Strand Synthesis kit (InvitrogenTM) for qRT-PCR following manufacturer's instructions. The qRT-PCR reaction was performed using SensiFAST™ SYBR® No-ROX Kit (Bioline), with 200 ng of cDNA and 10 pmol of each forwards and reverse primers in a 20 µl final reaction volume on BIORAD CFX96TM multiplex PCR machine, under the following settings: 95 °C for 2 min and 40 cycles of denaturation at 95 °C for 5 seconds, annealing at 56 °C for 10 seconds and extension at 72 °C for 20 seconds. The melting curve analysis was done immediately after RT-PCR reaction from 65-95 °C in 0.5 °C increment to prove the absence of DNA contaminants, primer dimers and secondary products. Three biological replicates of each time point were tested in triplicate for some of candidate's transcripts (Table 3). The salt responsive transcripts were identified based on our differentially expressed transcripts comparing with available literature and their sequences were retrieved from our raw files. Using Primer 3 tool (NCBI), the real time PCR primers were designed (Table 3).

Table 3. List of primers used for Quantitative real time - polymerase chain reaction (qRT-PCR) verification.

Gene description	**Transcript ID**	**Forward**	**Reverse**	**Amplicon size**
Elongation factor 1 (EF1) alpha (Housekeeping gene)	TRINITY_DN229493_c12_g4_i1	AACACTGGGGCGTAACCATT	TTGAGATGCACCACGAGTCC	208
Downregulated in root				
Cyclophilin 1	TRINITY_DN569649_c7_g8_i1	GGCCATGGACAAGAGGTAAG	GGAAACGGAACTGGTGGAA	96
Malonyl-CoA-acyl carrier protein Transacylase, mitochondrial	TRINITY_DN587067_c1_g1_i1	CCTCTGTCATTGAGGCAGTAAG	CTATCCGCGAAGTTATGGAAGG	105
Upregulated in root				
Glutamine synthetase	TRINITY_DN556783_c2_g1_i2	CAGACGACGACGAAGTAGAAAG	GGTCCGACTGAGTTATGATTGG	124
Glycine-rich RNA-binding protein 4, mitochondrial	TRINITY_DN354150_c0_g1_i1	AGCGAGTGACATCCTCTCTA	GGAGCGTGACAGCCTTATTA	110
Downregulated in shoot				
Gibberellin-regulated protein 6	TRINITY_DN602037_c1_g1_i4	AACAGGGAAACGGCAAAGA	GGGTAATTAGTTCACTGCTCCA	111
Peroxidase P7-like	TRINITY_DN599776_c0_g2_i3	CAGGGAGATTAAGGTGCTTAGG	GGCAAGTACCATTGGGAAGA	104

Upregulated in shoot				
Carrot ABA-induced in somatic embryos 3	TRINITY_DN558998_c1_g2_i2	CTGTTATCCCTGGTGGTACTG	CTAGTTGATCCCTCCTTGTCTG	99
Magnesium transporter 2 isoform 2	TRINITY_DN574004_c0_g5_i1	TTGTCGCTGCTCTGTGAAG	CCGTTCCAAGTTGCGTAGT	110
Homeobox-leucine zipper protein ATHB-40	TRINITY_DN610243_c0_g1_i11	CCAACAAATGCCTCCACAAC	CCCTCACTCTTGCTCTTTCTC	87

2.4. Statistical analysis

For the seed germination data of *S. imbricata* and *S. drummondii*, the rate of germination was estimated by using a modified Timson index of germination velocity: $\Sigma G/t$, where G is the percentage of seed germination at 2-day intervals, and t is the total germination period (Khan et al., 2000; Ranal and Santana, 2006). The maximum possible value in our data, using this germination rate index, was 50. This value means that all germination occurred in the first count (i.e., after two days).

The germination recovery percentage of *S. imbricata* and *S. drummondii* was calculated using the following formula (Khan et al., 2000): Recovery percentage = (a-b)/(c-b) *100, where **"a"** is the total number of seeds germinated after being transferred to distilled water, **"b"** is the total number of seeds germinated in PEG solution, and c is the total number of seeds.

For *S. imbricata*, three-way ANOVAs were used to assess the significance of the main factors (PEG, temperature and light) and their interactions on final germination, germination recovery and total germination (germination in PEG solution + recovery germination). Two-way ANOVA was used to assess the impact of PEG and temperature and their interaction on the germination rate index (GRI).

For *S. drummondii*, four-way ANOVAs were used to evaluate the significance of the four factors (i.e., maternal habitat, drought, temperature, and light) and their effects on final germination, germination recovery, and total germination (germination in saline solution plus recovery germination). Three-way ANOVA was used to assess the impacts of maternal habitat, drought, and temperature and their interactions on germination rate index (GRI). Pearson correlation coefficients were calculated to assess the relationship between PEG concentrations and total germination. One way ANOVAs were performed to assess the significant differences between the saline and non-saline habitats in EC, salinity and pH. In both *S. imbricata* and *S. drummondii* germination data, Tukey's tests were performed to test pair-wise differences between means. The GRI was log-transformed and germination percentages were arcsine-transformed to meet the assumptions of ANOVA. This transformation improved the normality of the distribution of the data. One-way ANOVA were performed to assess the effect of habitat (saline and non-saline) on elemental composition in soils, some growth and physiological traits, some antioxidants and damaged signals in different organs of *S. drummondii*. All statistical analyses were performed using SYSTAT, version 13.0.

3. RESULTS

3. RESULTS

3.1. Effects of light and temperature on drought tolerance during seed germination of *Salsola imbricata* Forssk.

3.1.1. Effects of polyethylene glycol (PEG) solutions on final germination

The fresh collected seeds had 95% viability and were able to germinate within few days after collection. The main factors temperatures, polyethylene glycol (PEG) level and light conditions had significant effects on final germination of *S. imbricata* ($P < 0.001$, Table 4). Overall germination decreased with the increase in PEG levels and temperatures. The overall germination was 70% in distilled water, but reduced to 5.2% at -1.8 MPa and almost inhibited at -2.2 MPa PEG (Fig. 14).

The interaction between temperature and PEG level affected significantly seed germination ($P < 0.001$, Table 4), indicating that the response to osmotic stress depended on temperature. There was no significant difference in the final germination between the three tested temperatures when seeds were germinated in distilled water. In all PEG levels, however, germination was significantly greater at the lower (15/25 °C) and moderate (20/30 °C) than at higher (25/35 °C) temperatures. This trend was more obvious with the increase in PEG level. In higher levels of PEG (-1.0 and -1.4 MPa), germination was significantly greater at 15/25 °C than at both 20/30 and 25/35 °C (Fig. 14).

The response of *S. imbricata* to simulated drought was light dependent; the interaction between PEG level and light was significant ($P < 0.05$, Table 4). There was not significant difference between germination in light and dark at higher osmotic potentials (0 and -0.2 MPa). At lower osmotic potentials (≤ -0.4 MPa), however, germination in dark was lower than in light (Fig. 14). The response to simulated drought stress did not depend significantly on both temperature and light; the effect of the interaction between the three factors (PEG, light and temperature) was not significant ($P > 0.05$).

Table 4. Results of three-way ANOVA showing the effects of polyethylene glycol (PEG), temperature and light and their interactions on final germination in PEG solutions, germination recovery and total germination (i.e., germination in PEG solutions plus germination recovery) of *Salsola imbricata* Forssk., seeds. *: P ≤ 0.05, **: P ≤ 0.01 and ***: P ≤ 0.001.

Source of variation	**df**	**Final germination**		**Germination recovery**		**Total germination**	
		Mean squares	**F-Ratio**	**Mean squares**	**F-Ratio**	**Mean squares**	**F-Ratio**
PEG concentration	8	2.399	201.7***	1.130	47.6***	0.249	13.4***
Temperature (T)	2	2.266	190.5***	0.061	2.56	1.208	64.916***
Light (L)	1	0.763	64.2***	1.947	82.1***	0.004	0.206
PEG × T	16	0.163	13.7***	0.110	4.64***	0.061	3.288***
PEG × L	8	0.034	2.82**	0.089	3.74***	0.016	0.860
T × L	2	0.008	0.72	0.045	1.90*	0.009	0.497
PEG × T × L	16	0.028	2.34**	0.046	1.95*	0.012	0.664
Error	162	0.012		0.024		0.019	

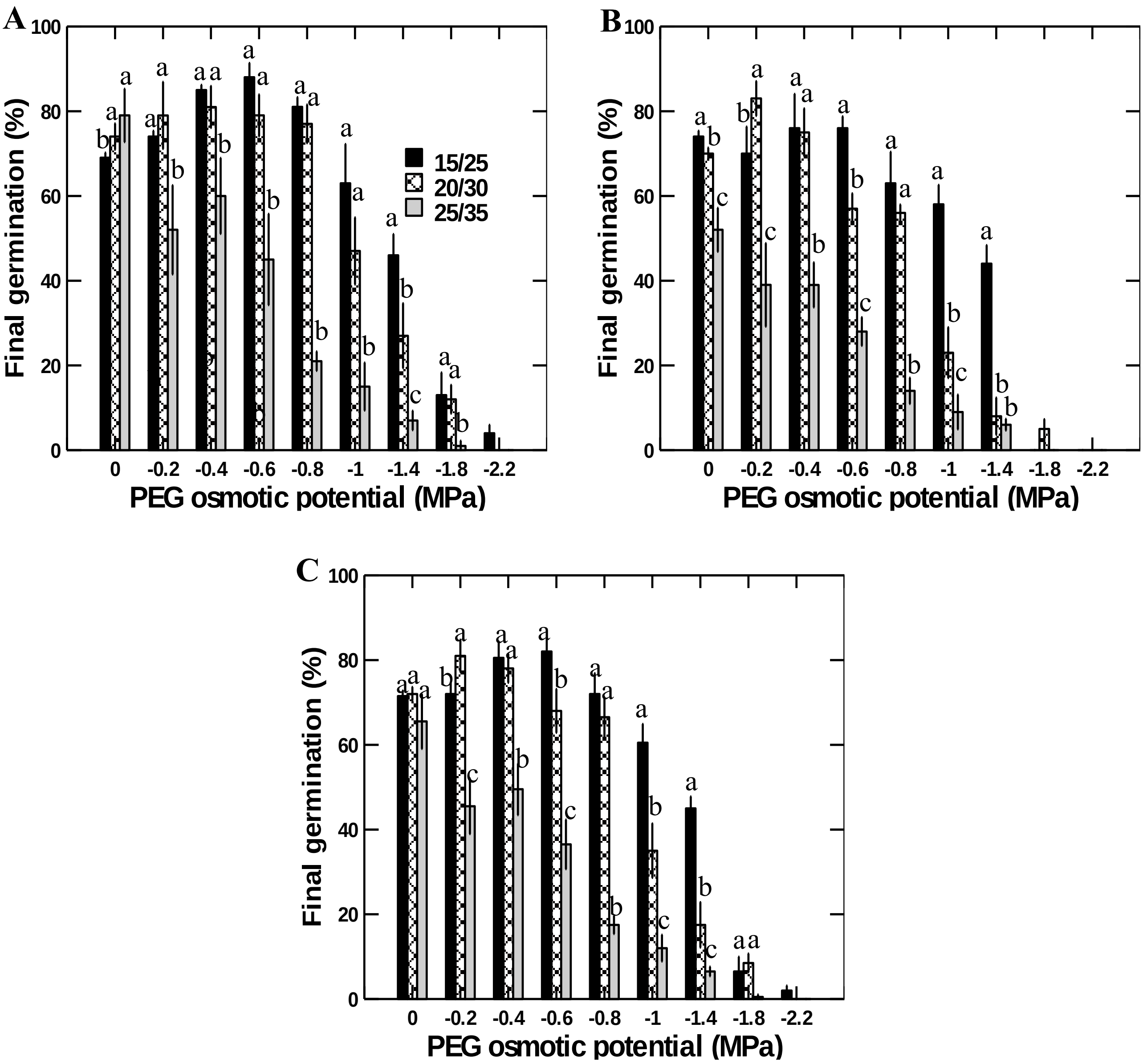


Figure 14. Effects of polyethylene glycol (PEG), and light and temperature of incubation (15/25, 20/30, 25/35 °C at dark / light) on final germination percentage (mean ± SE, n = 4) of *Salsola imbricata* Forssk., seeds. (A) Light germination, (B) Dark germination and (C) Overall light and dark germination.

3.1.2. Effects of polyethylene glycol (PEG) solutions on germination rate index (GRI)

The interactions of both temperatures and PEG level had significant effects on the GRI (germination rate index) of *S. imbricata* ($P < 0.001$, Table 5). Germination speed decreased with the decrease in PEG osmotic potential (Fig. 15). The overall GRI decreased from around 48 at higher osmotic potentials (≤ -0.4 MPa) to 28.5 and 9.6 at -1.8 and -2.2 MPa, respectively. At the higher osmotic potentials (0 and -0.2 MPa), almost all seeds germinated in the first count (i.e. within 2 days) at all temperatures; GRI was close to 50. The germination speed significantly decreased at lower osmotic potential ≤ -1.0 MPa at all tested temperatures. Such reduction was significantly greater at higher, compared to lower temperatures (Fig. 15).

Table 5. Results of two-way ANOVA showing the effects of polyethylene glycol (PEG) and temperature and their interactions on germination rate index of *Salsola imbricata* Forssk., seeds.

Source of variation	df	Mean squares	F-Ratio	P-value
PEG concentration	8	11.621	36.431	<0.001
Temperature (T)	2	5.251	16.463	<0.001
PEG × T	16	1.937	6.072	<0.001
Error	81	0.319		

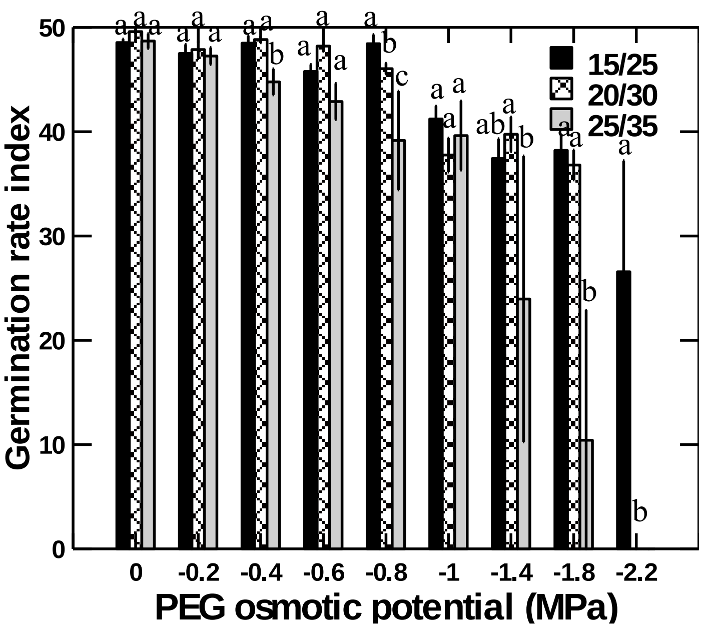


Figure 15. Effects of polyethylene glycol (PEG) and temperature of incubation (15/25, 20/30, 25/35 °C at dark/light) on germination rate index (GRI) (mean ± SE, n = 4) of *Salsola imbricata* Forssk., seeds.

3.1.3. Germination recovery of *Salsola imbricata* Forssk., seeds

The interactions between temperatures, PEG and light of incubation had significant effects on germination recovery ($P \leq 0.05$, Table 4). The overall germination recovery increased with the increase in both PEG levels and temperatures (Fig. 16). It was also higher in seeds incubated in darkness, compared to those incubated in light. Germination recovery at most higher osmotic potential (0.0 to - 0.8 MPa) was significantly greater at 25/35 °C, compared to 15/25 °C. However, at lower osmotic potentials (-1.8 and -2.2 MPa), the reverse was true; recovery was greater at lower than at higher temperatures. The trend in germination recovery was opposite to that in the PEG solutions. This indicates that most of the non-germinated seeds in PEG recovered their germination when transferred to distilled water.

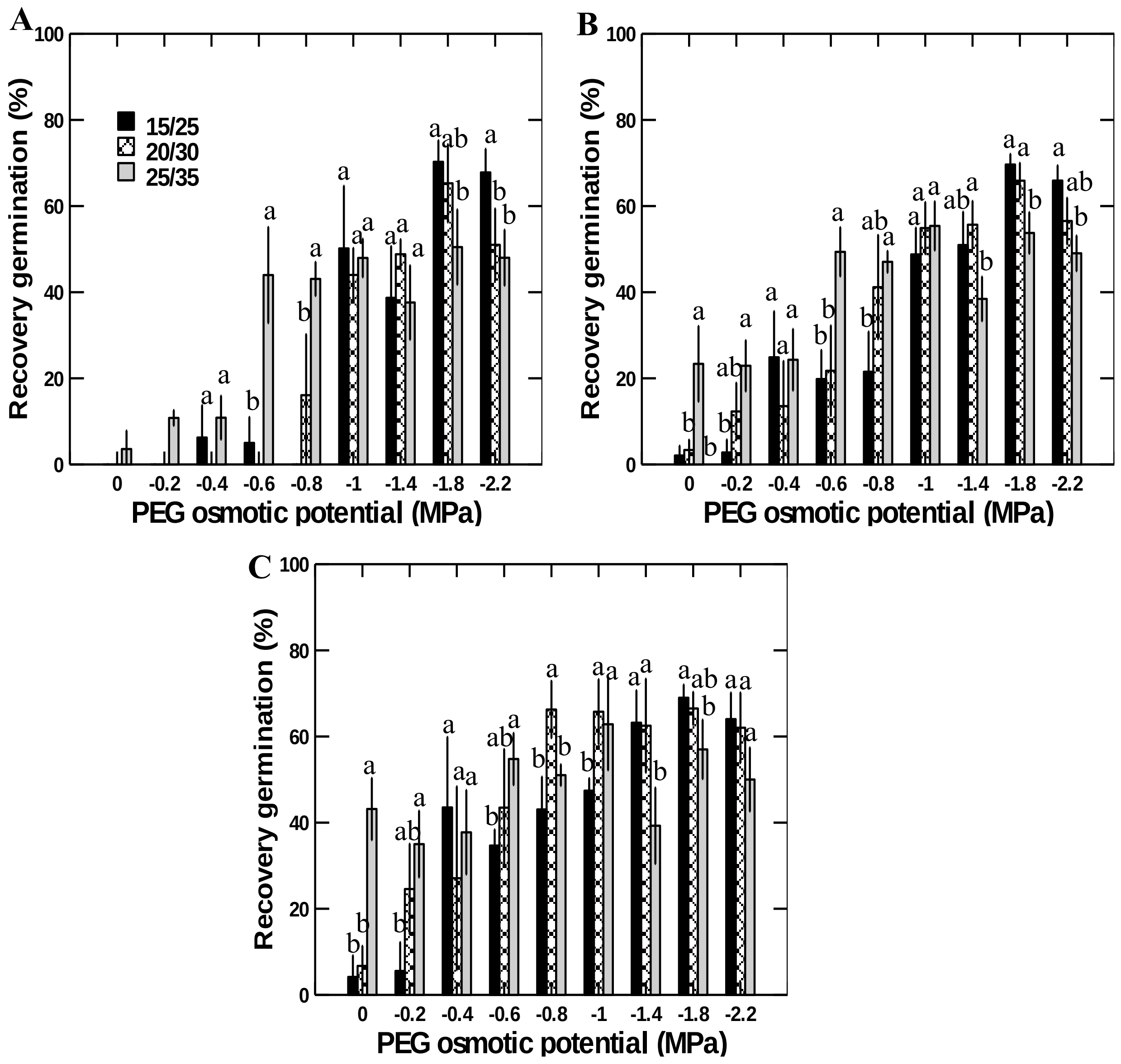


Figure 16. Effects of polyethylene glycol (PEG), and light and temperature of incubation (15/25, 20/30, 25/35 °C at dark/light) on germination recovery (mean ± SE, n = 4) of *Salsola imbricata* Forssk., seeds. (A) Recovery germination of seeds incubated in light, (B) Recovery germination of seeds incubated in dark and (C) Overall recovery germination from light and dark.

The effect of interactions between light and PEG on germination recovery was highly significant ($P \leq 0.001$, Table 4). At the higher osmotic potentials (up to -0.8 MPa), germination recovery from dark was significantly greater than from light. At the lower osmotic potentials, however, there was no significant difference in recovery of seeds germinated in light and darkness (Fig. 16). In PEG levels up to -0.8 MPa, the germination recovery was higher in both light and dark at 25/35 °C, compared to it at both 15/25 and 20/30 °C. At the lowest PEG osmotic potential (-1.8 and -2.2 MPa), however, there was no significant difference between the three temperatures either in light or in dark (Fig. 16). Recovery occurred within 24 hours after seed transfer from the different PEG treatments to distilled water.

3.1.4. Total seed germination

The total germination (germination in PEG solutions plus germination recovery) was significantly ($P \leq 0.001$) affected by both PEG and temperature, but not by light ($P > 0.05$, Table 4). There was no significant difference in total germination between the different PEG levels up to -1.0 MPa. All of these lower PEG levels showed significantly higher germination than the higher ones (-1.4, -1.8 and -2.2 MPa). In addition, total germination was significantly higher at both 15/25 and 20/30 °C than at 25/35 °C. The only significant interaction was between PEG and temperature ($P \leq 0.001$, Table 4). There was no significant difference between total germination at the three temperatures in distilled water. At all PEG levels, however, germination at the lower and moderate temperatures was significantly greater than that at the higher temperatures (Fig. 17)

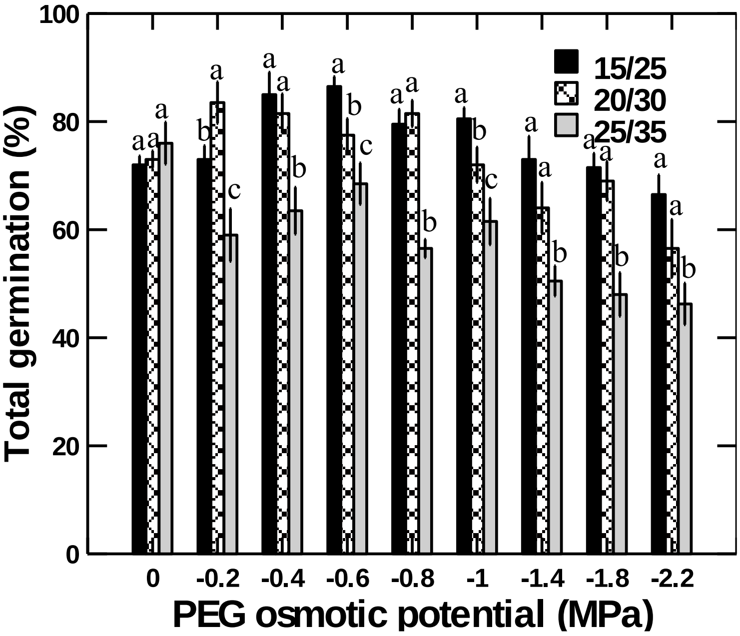


Figure 17. Effects of polyethylene glycol (PEG), and temperature of incubation (15/25, 20/30, 25/35 °C at dark/light) on total germination (mean ± SE, n = 4) of *Salsola imbricata* Forssk., seeds.

3.2. Effects of light, temperature and maternal salinity on drought tolerance during germination of *Salsola drummondii* Ulbr.

3.2.1. Properties of soils and seeds collected in saline and non-saline habitats

Soils of the saline habitat attained significantly greater electric conductivity (EC) (21.3 mS/cm), in comparison to the non-saline habitat (1.4 mS/cm, F = 270, $P \leq 0.001$). In addition, the pH was significantly greater in soils of the saline habitat (pH = 9.0), compared to those of the non-saline habitat (pH = 8.0, F = 83.0, $P \leq 0.001$). Furthermore, salinity attained significantly greater values in the saline (5.5 g/l) than in the non-saline habitats (0.38 g/l, F = 12.2, $P \leq 0.001$). There was no significant difference between the average seed mass of the saline (0.680 mg) and non-saline (0.745 mg) habitats (F = 2.2, $P > 0.05$). In addition, seed viability did not differ significantly between the seed lots of the two habitats (88.7% and 92.6%, for saline and non-saline habitats, respectively, F = 3.2, $P > 0.05$).

3.2.2. Final germination in polyethylene glycol (PEG) solutions

There were significant effects for the main factors and many of their interactions on the final germination of *S. drummondii* ($P \leq 0.05$, Table 6). The significant interaction between maternal salinity and PEG concentration indicates that tolerance to drought as simulated by PEG depended on seed source. No germination occurred at -1.8 MPa PEG for seeds from the two habitat types. Seeds of the non-saline habitat attained significantly greater germination levels, as compared to those of the saline habitat, in PEG concentrations up to -1.0 MPa (Fig. 18). The difference diminished in -1.2 MPa PEG and completely disappeared in -1.5 MPa. This result implies that seeds of the non-saline habitat had greater germination in higher osmotic potential, compared to those of the saline habitat. At lower osmotic potentials (-1.5 MPa), however, there was no significant difference in final germination between seeds of the two maternal habitats (Fig. 18A).

The interactions between PEG treatment and both temperature and light were significant ($P \leq 0.01$, Table 6), indicating that the tolerance to PEG osmotic potential depended on these conditions during seed sowing. For example, whereas no significant difference was observed in final germination at lower (15/25 °C) and higher temperatures (25/35 °C) in distilled water and -0.4 MPa PEG, germination was significantly greater at lower than at higher temperatures at PEG levels ≥ -0.7 MPa (Fig. 18B). However, the effect of light on drought tolerance was not clear; whereas germination was significantly greater in light than in dark in -0.7 and -1.2 MPa, there was no significant difference between germination in light and dark at the other PEG concentrations (Fig. 18C).

Table 6. Results of four-way ANOVA showing the effects of maternal salinity and environmental factors during incubation (drought, as stimulated by polyethylene glycol (PEG), temperature and light) and their interactions on final germination in PEG solution, germination recovery after seeds transferred from PEG to distilled water and total germination (i.e., germination in PEG solutions plus germination recovery) of *Salsola drummondii* Ulbr., seeds.

Source of variation		**Final germination**		**Recovery germination**		**Total germination**	
	df	Mean squares	F-Ratio	Mean squares	F-Ratio	Mean squares	F-Ratio
Maternal salinity (MS)	1	3.016	411.6***	0.030	58.60***	3.757	434.40***
PEG	5	1.801	245.8***	0.046	90.27***	1.276	147.56***
Temperature (T)	2	0.250	34.2***	0.009	18.19***	0.376	43.44***
Light (L)	1	0.140	19.2***	0.001	1.850	0.113	13.06***
MS * PEG	5	0.158	21.5***	0.016	31.98***	0.067	7.71***
MS * T	2	0.003	0.458	0.001	1.874	0.004	0.486
MS * L	1	0.003	0.403	0.000	0.031	0.004	0.427
PEG * T	10	0.024	3.22**	0.006	12.17***	0.035	4.00***
PEG * L	5	0.027	3.68**	0.000	0.948	0.024	2.72*
T * L	2	0.068	9.29***	0.001	0.996	0.077	8.90***
MS * PEG * T	10	0.009	1.246	0.001	1.595	0.010	1.178
MS * PEG * L	5	0.021	2.92*	0.001	1.597	0.020	2.136
MS * T * L	2	0.002	0.322	0.002	3.37*	0.001	0.068
PEG * T * L	10	0.021	2.9**	0.000	0.677	0.017	2.007
MS * PEG * T * L	10	0.008	1.088	0.001	1.65	0.010	1.196
Error		216	0.007	0.001		0.009	

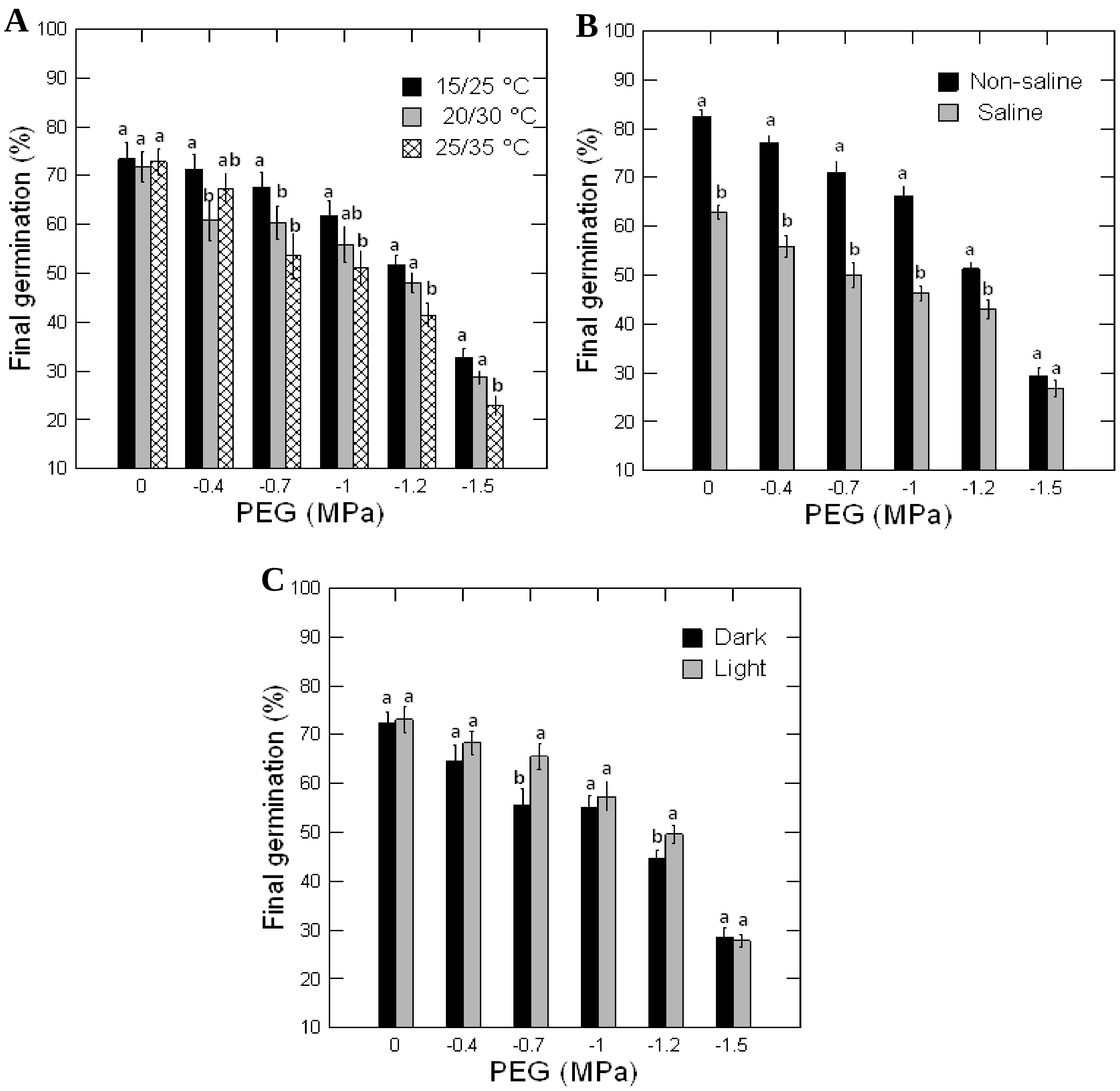


Figure 18. Interactive effects of drought, simulated using polyethylene glycol (PEG), with (A) maternal salinity, (B) temperature of incubation and (C) light of incubation on final germination percentage (mean ± S.E.) of *Salsola drummondii* Ulbr., seeds.

3.2.3. Germination rate index in the polyethylene glycol (PEG) solutions

The effects of maternal salinity, PEG, and temperature on GRI were significant (P ≤ 0.001, Table 7). GRI decreased with increasing PEG concentrations; GRI was 49.6 in the control but reduced to 32.1 at -1.5 MPa. There were significant effects of the interaction between PEG and both maternal salinity and temperature of incubation on the GRI (P ≤ 0.001, Table 7). No significant difference in GRI was observed between seeds of the two habitats at lower concentrations of PEG (0, -0.4 and -0.7 MPa). However, seeds of the saline habitat attained significantly higher GRI (i.e., germinated faster) in the higher concentrations of PEG (Fig. 19A). In addition, GRI did not differ between the different temperatures at higher osmotic potentials (PEG levels ≤ -1.0 MPa). However, at lower osmotic potential (PEG levels = -1.2 and -1.5 MPa), germination was significantly faster at higher than at lower temperatures (Fig. 19B).

Table 7. Results of three-way ANOVA showing the effects of maternal salinity, and polyethylene glycol (PEG) concentration and temperature and their interactions on germination rate index of *Salsola drummondii* Ulbr., seeds.

Source of variation	df	Mean squares	F-Ratio	P-value
Maternal salinity (MS)	1	0.247	46.971	< 0.001
PEG	5	0.471	89.674	< 0.001
Temperature (T)	2	0.051	9.723	< 0.001
MS * PEG	5	0.055	10.404	< 0.001
MS * T	2	0.004	0.793	ns
PEG * T	10	0.010	1.848	ns
MS * PEG * T	10	0.005	0.920	ns
Error	108	0.005		

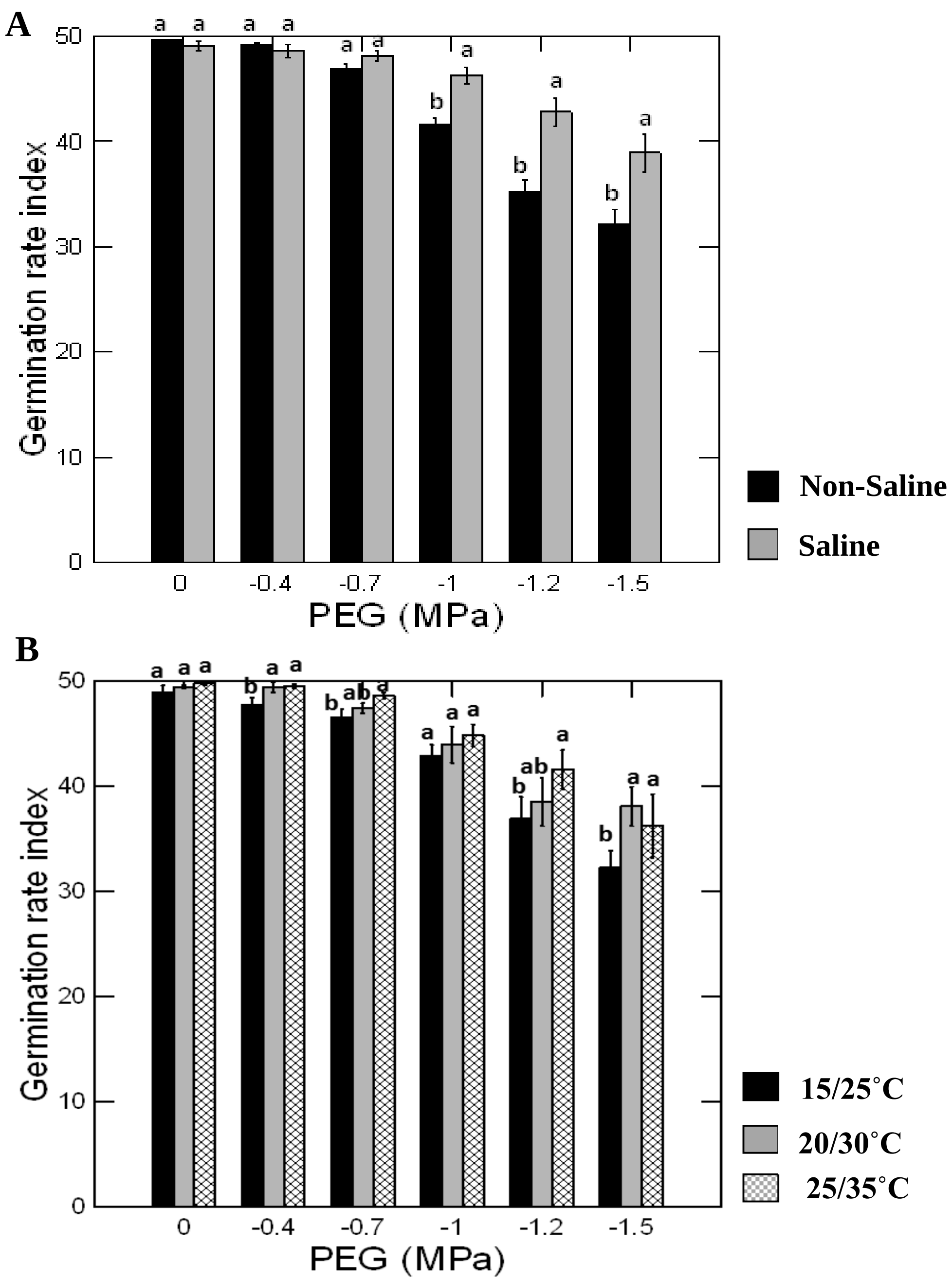


Figure 19. Interactive effects of drought, as simulated using polyethylene glycol (PEG), with (A) maternal salinity and (B) temperature of incubation on germination rate index (GRI) (mean ± S.E.) of *Salsola drummondii* Ulbr., seeds.

3.2.4. Germination recovery of *Salsola drummondii* Ulbr., seeds

There were significant effects of maternal salinity, drought, and temperature, but not light, on germination recovery ($P \leq 0.001$, Table 6). The significant effect of the interaction between maternal salinity and PEG indicates that recovery of seeds from different PEG concentrations depended on the seed source (i.e., maternal habitat). Germination recovery occurred mainly in seeds that failed to germinate in -1.2 and -1.5 MPa and was significantly greater for seeds of plants in non-saline habitats than for those of plants in saline habitats (Fig. 20A). In addition, the response of germination recovery at different concentrations of PEG depended on temperature of incubation; the interaction between PEG concentration and temperature was significant ($P \leq 0.01$, Table 6). There was no significant effect for temperature on germination recovery in all osmotic potential, expect in the lowest osmotic potential (-1.5 MPa), in which germination recovery was significantly greater at lower than at higher temperatures (Fig. 20B). The interaction between PEG and light was not significant. However, recovery was greater for seeds incubated in light, as compared to those in dark, in osmotic potential -1.2 and -1.5 MPa (Fig. 20C).

3.2.5. Total germination relationships

All the four main factors showed significant effects on the total germination (i.e., germination in PEG solution plus germination recovery) ($P \leq 0.05$). However, only three interactions between the main factors were significant, compared to six significant interactions for germination in PEG (Table 6). In addition, Pearson correlation coefficients assessing the relationship between total germination and PEG concentrations indicated significant negative relationships at all temperatures for seeds of the non-saline habitat ($r = -0.77$, $P \leq 0.001$ at 15/25 °C; $r = -0.59$, $P \leq 0.001$ at 20/30 °C; $r = -0.65$, $P \leq 0.001$ at 25/35 °C). For seeds of the saline habitat, however, the negative relationship was significant at 15/25 °C ($r = -0.50$, $P \leq 0.001$) and 20/30 °C ($r = -0.49$, $P \leq 0.001$), but not at 25/35 °C ($r = -0.04$, $P > 0.05$). This result indicates that the germination of *S. drummondii* seeds of the saline habitats was less affected by the increase in PEG concentration at higher temperatures, but seeds of the non-saline habitats were negatively affected by the increase in the PEG concentrations at all temperatures.

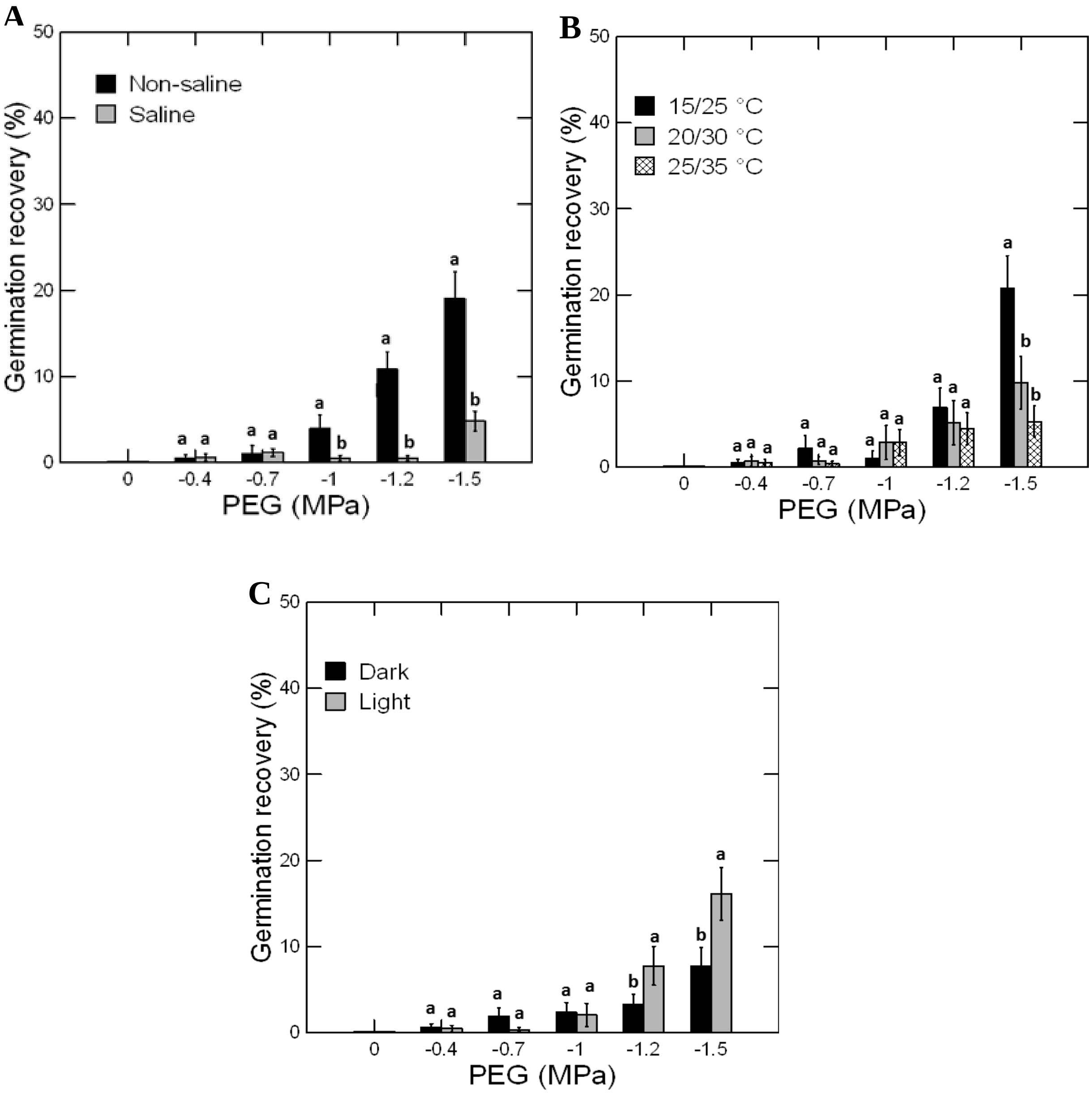


Figure 20. Interactive effects of drought, as simulated using polyethylene glycol (PEG), with (A) maternal salinity, (B) temperature of incubation and (C) light of incubation on germination recovery percentage (mean ± S.E.) of *Salsola drummondii* Ulbr., seeds.

3.3. Effects of light, temperature and maternal salinity on salinity tolerance during germination of *Salsola drummondii* Ulbr.

3.3.1. Variation in seed mass, and plant community and soil properties from saline and non-saline habitats

The average mass of seeds collected from plants of the non-saline soils (0.745 mg) did not differ significantly from those collected from saline soils (0.686 mg, $P > 0.05$). Similarly, there was no significant difference in the seed viability between the seeds of the saline (88.7%) and those of non-saline habitats (92.6%, $P > 0.05$). Electric conductivity (EC) was significantly greater for the saline soils (20.28 mS/cm^2), as compared with that of the non-saline soils (1.3 mS/cm^2, $P < 0.01$). In addition, saline soils were significantly more alkaline (pH = 9.0) than the non-saline soils (pH = 8.0, $P \leq 0.001$, Table 8).

Table 8. Variation in seed mass and viability, soil properties and plant community in saline and non-saline habitats.

Parameter	Non-saline site	Saline site	F-value	P-value
Seed mass (mg)	0.745 ± 0.034	0.686 ± 0.019	2.24	0.208
Seed viability (%)	92.6 ± 1.7	88.7 ± 1.3	3.273	0.145
pH	8.0	9.0	85.7	<0.001
EC (mS/cm)	20.28	1.3	864.0	<0.001
Associate species growing with *Salsola drummondii* in the same community	*Salsola imbricata*, *Cornulaca monacantha*, *Aerva javanica*, *Indigofera oblongifolia*, *Launea capitata*, *Lawsonia inermis*	*Suaeda vermiculata*, *Aeluropus lagopoides*, *Halopeplis perfoliata*, *Halocnemum strobilaceum*, *Zygophyllum qatarense*		

3.3.2. Effects of maternal habitat on salinity tolerance

Four-way ANOVA showed significant effects for all factors (maternal salinity, and sodium chloride (NaCl) concentration, thermoperiod and photoperiod of seed incubation) and most of their interactions on final germination of *S. drummondii* ($P \leq 0.001$, Table 9). The overall germination of seeds collected from non-saline soils was significantly greater than that of seeds from saline soils. Germination decreased with the increase in thermoperiod and was greater in darkness than in light. Furthermore, germination decreased with the increase in NaCl concentration; yet around 25 and 31.5% of seeds from the non-saline and saline soils germinated in 1000 mM NaCl. There was a negative relationship between NaCl concentration and final germination at the different temperatures as well as for the overall germination ($P < 0.001$, Table 10).

The response of *S. drummondii* to salt stress during germination depended on the maternal salinity. Whereas germination of seeds from non-saline soils was significantly greater than that of seeds from saline soils in NaCl concentrations ranged between zero and 800 mM NaCl, the reverse was true in the highest NaCl concentration (1000 mM NaCl). The germination of seeds from non-saline soils was greater than those from saline soils by 34.8%, 42%, 54.6%, 51.6% and 24.1% in 0, 200, 400, 600 and 800 mM NaCl, respectively, but seeds from saline soils germinated 21% more than those from the non-saline soils in 1000 mM NaCl. The higher germination of seeds from saline soils in 1000 mM NaCl, compared to those of non-saline soils, was only significant in light at higher temperatures. In 1000 mM NaCl, the germination of seeds from the saline soils was greater than those from the non-saline soils by 81.3% at 25/35 °C, but with only 10% and 23% at 20/30 °C and 15/25 °C in light, respectively, and by 19%, 13% and 21%, respectively, in dark (Fig. 21).

Table 9. Results of four-way ANOVA showing the effects of maternal salinity, factors during incubation (salinity, temperature and light) and their interactions on final germination (i.e., germination in saline solutions), germination recovery, total germination (i.e., germination in saline solutions plus germination recovery) and germination rate index (GRI) during recovery of *Salsola drummondii* Ulbr., seeds. *: P ≤ 0.05, **: P ≤ 0.01 and ***: P ≤ 0.001.

Source of variation		**Final germination**		**Recovery germination**		**Total germination**		**GRI for germination recovery**	
	df	**Mean Squares**	**F-Ratio**	**Mean Squares**	**F-Ratio**	**Mean Squares**	**F-Ratio**	**Mean Squares**	**F-Ratio**
Maternal salinity (MS)	1	2.899	297.9***	0.000	161.5***	5.591	514.3***	66.157	14.18***
Salinity (S)	5	2.498	256.7***	0.000	152.7***	1.054	96.96***	258.716	55.46***
Temp. (T)	2	0.161	16.56***	0.000	16.18***	0.397	36.5***	0.465	0.100
Light (L)	1	0.564	58.0***	0.000	8.02**	0.428	39.4***	0.681	0.146
MS * S	5	0.324	33.3***	0.000	53.8***	0.042	3.84**	9.599	2.058
MS * T	2	0.050	5.13**	0.007	5.77**	0.076	6.95**	0.188	0.040
MS * L	1	0.003	0.353	0.553	39.9***	0.128	11.78**	9.145	1.960
S * T	10	0.034	3.5***	0.000	5.78***	0.046	4.27***	5.447	1.168
S * L	5	0.032	3.3**	0.007	3.52**	0.020	1.816	3.888	0.833
T * L	2	0.196	20.1***	0.000	1.335	0.166	15.3***	22.986	2.57
MS * S * T	10	0.023	2.3*	0.012	1.757	0.030	2.72***	3.095	0.663
MS * S * L	5	0.030	3.1*	0.010	10.94***	0.050	4.58**	8.098	1.736
MS * T * L	2	0.004	0.415	0.661	4.36*	0.011	1.054	2.374	0.509
S * T * L	10	0.045	4.64***	0.000	2.45**	0.031	2.83**	7.608	1.631
MS * S * T * L	10	0.021	2.16*	0.021	3.3**	0.025	2.31*	5.042	1.081
Error	216	0.010				0.011		4.665	

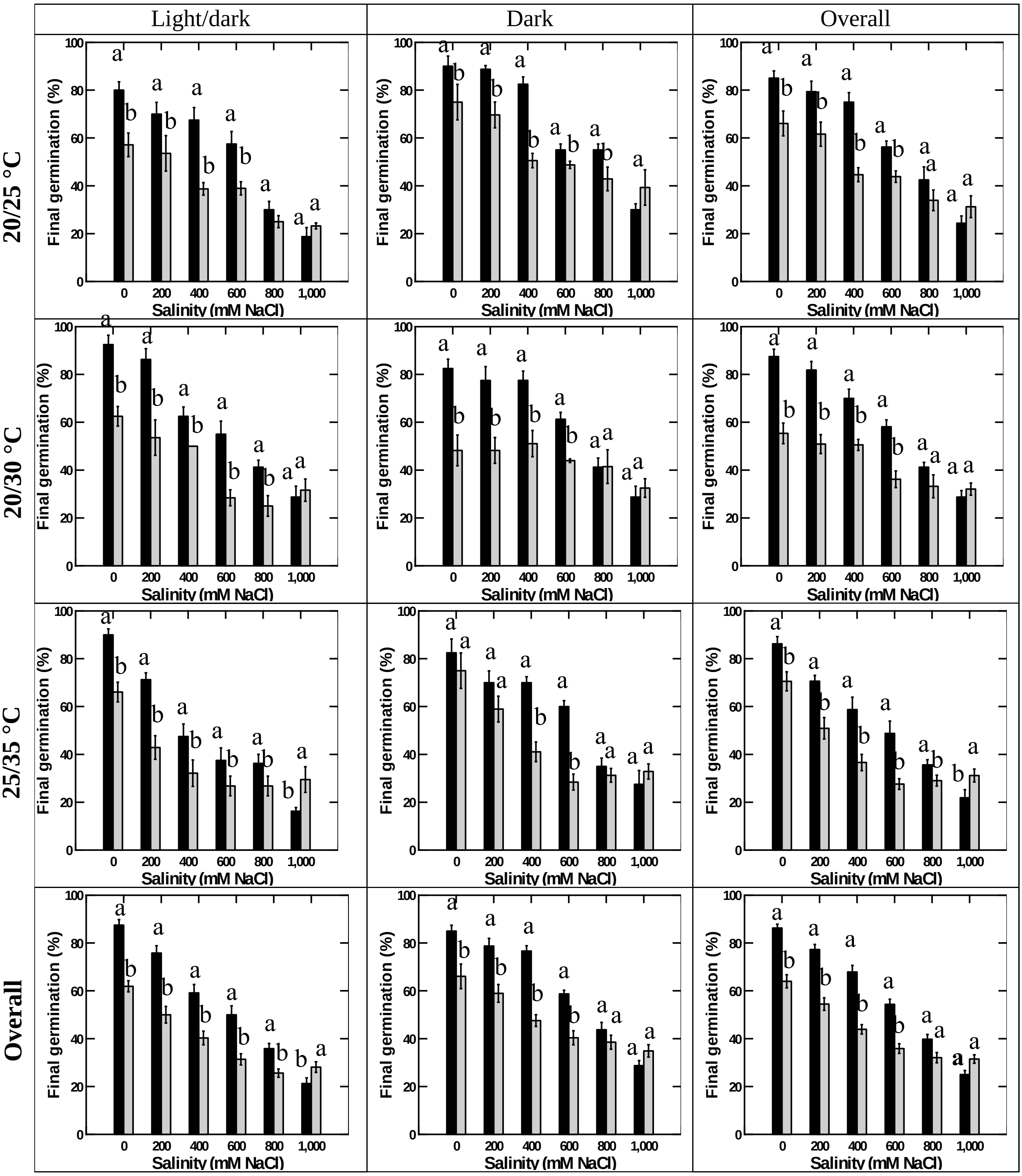


Figure 21. Effects of maternal salinity, and environmental factors during seed incubation (salinity, temperature and light) on final germination percentage (mean ± SE) of *Salsola drummondii* Ulbr., seeds. Dark and light bars are for seeds of non-saline and saline habitats, respectively.

Three-way ANOVA indicated significant effects for the three factors (maternal salinity, NaCl concentration and thermoperiod of seed incubation) and most of their interactions on GRI of *S. drummondii* ($P < 0.05$, Table 11). In control (0 mM NaCl), seeds from both saline and non-saline soils germinated within 48 hours, in all temperatures. In the different NaCl concentration, however, there were no significant differences in GRI between seeds from saline and those from non-saline soils in NaCl ≥ 600 mM at 15/25 °C. At 20/30 °C and 25/35 °C, seeds from the saline soils germinated faster than those from non-saline soils (Fig. 22). There were insignificant negative relationships between germination rate index (GRI) and salinity of seeds from both saline and non-saline soils at the different thermoperiods ($P > 0.05$, Table 10). The insignificant relationship between GRI and NaCl concentration indicates that GRI was not affected greatly with the increase of salinity levels.

ANOVA test showed significant effects for maternal salinity and NaCl concentration on germination rate index (GRI) of recovered seeds ($P < 0.001$, Table 9). The overall GRI of seeds from the non-saline soils was 28.2, but that of seeds from saline soils was 20.3. In addition, seeds incubated in the higher NaCl concentration (≥ 600 mM) recovered faster than those at lower NaCl concentrations; germination recovery for seeds germinated at higher NaCl concentrations occurred within 24 hours after their transfer to distilled water (data not shown). The relationships between NaCl concentration and GRI of germination recovery were significantly positive at the different temperatures ($P < 0.001$, Table 10).

Table 10. Correlation coefficient values between concentrations of salinity and different germination attributes of *Salsola drummondii* Ulbr., seeds from saline and non-saline habitats germinated at different temperatures. *: P ≤ 0.05, **: P ≤ 0.01 and ***: P ≤ 0.001.

Maternal salinity	**Temp. (°C)**	**Final germination**	**GRI**	**Germination recovery %**	**GRI of germination recovery**	**Total germination**
Non-saline habitats	15/25	-0.858***	-0.104	0.822***	0.810***	-0.380**
	20/30	-0.922***	-0.151	0.735***	0.712***	-0.666***
	25/35	-0.863***	-0.126	0.757***	0.806***	-0.697***
	Overall	-0.879***	-0.127	0.748***	0.775***	-0.574***
Saline habitats	15/25	-0.647***	-0.134	0.589***	0.651***	-0.284
	20/30	-0.178	-0.127	0.510***	0.535***	0.093
	25/35	-0.503***	-0.113	0.526***	0.545***	-0.360*
	Overall	-0.451***	-0.124	0.525***	0.577***	-0.173***

Table 11. Results of three-way ANOVA showing the effects of maternal salinity and NaCl concentration and temperature on germination rate index of *Salsola drummondii* Ulbr., ns = not significant.

Source of variation	**df**	**Mean squares**	**F-Ratio**	**P-value**
Maternal salinity (MS)	1	0.633	45.357	<0.001
Salinity (S)	5	0.783	56.118	<0.001
Temperature (T)	2	0.002	0.110	Ns
MS * S	5	0.050	3.552	<0.01
MS * T	2	0.029	2.053	ns
S * T	10	0.030	2.123	<0.05
MS * S * T	10	0.036	2.550	<0.01
Error	108	0.014		

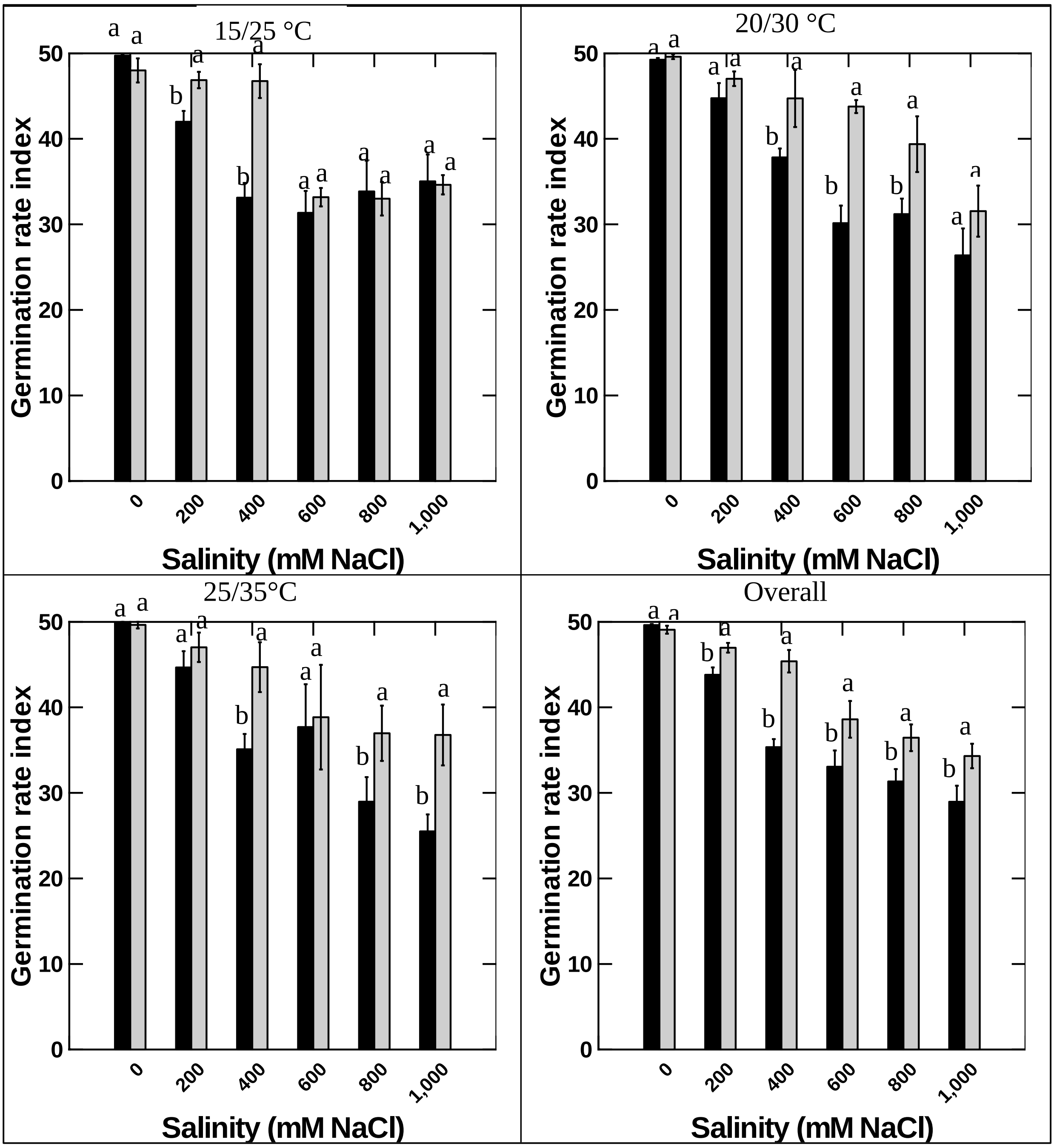


Figure 22. Effects of maternal salinity, and salinity and temperature of incubation on germination rate index (mean ± SE) of *Salsola drummondii* Ulbr., seeds. Dark and light bars are for seeds of non-saline and saline habitats, respectively.

3.3.3. Seed germination recovery

There were significant effects for the main factors and most of their interactions on the ability of seeds failed to germinate in different NaCl solution to recover their germination when transferred to distilled water (P < 0.05, Table 9). Seeds collected from non-saline soils attained significantly greater overall germination recovery than those from saline soils. This was particularly obvious in light and at both lower and moderate thermoperiods. Most of the recovery occurred for seeds failed to germinate at higher NaCl concentration. In light, recovery of seeds from non-saline soils was significantly greater than those from saline soils in all salinities. In dark, however, the recovery of seeds from the non-saline soils was significantly greater than those from saline soils in only 1000 Mm; there were no significant differences in all lower NaCl concentrations (≤ 800 mM). The recovery was significantly lower at 25/35 °C; still was higher in seeds from the non-saline than those from saline soils in 1000 mM (Fig. 23). There were significant positive relationships between salinity concentration and germination recovery at the different temperatures (P < 0.001, Table 10). Viability test for non-recovered seeds from the different NaCl concentrations indicated that seeds from the saline soils were more viable (20%) than those from non-saline soils (5%).

3.3.4. Total seed germination

All the main four factors and their interactions showed significant effects on the total seed germination (i.e., germination in saline solution plus germination recovery) of *S. drummondii* (P < 0.05, Table 9). The total germination has a trend similar to that observed for germination in NaCl solutions (data not shown). Interestingly, there was no significant relationships between total germination and NaCl concentrations for seeds from saline soils at 15/25 °C and 20/30 °C (P > 0.05, Table 10). However, the relationships were significantly positive at the same temperatures for seeds from the non-saline soils. This indicates that the germination of *S. drummondii* seeds from saline soils was less affected by the increase in NaCl concentration at both low and moderate temperatures, but seeds from non-saline soils were negatively affected by the increase in the NaCl concentrations.

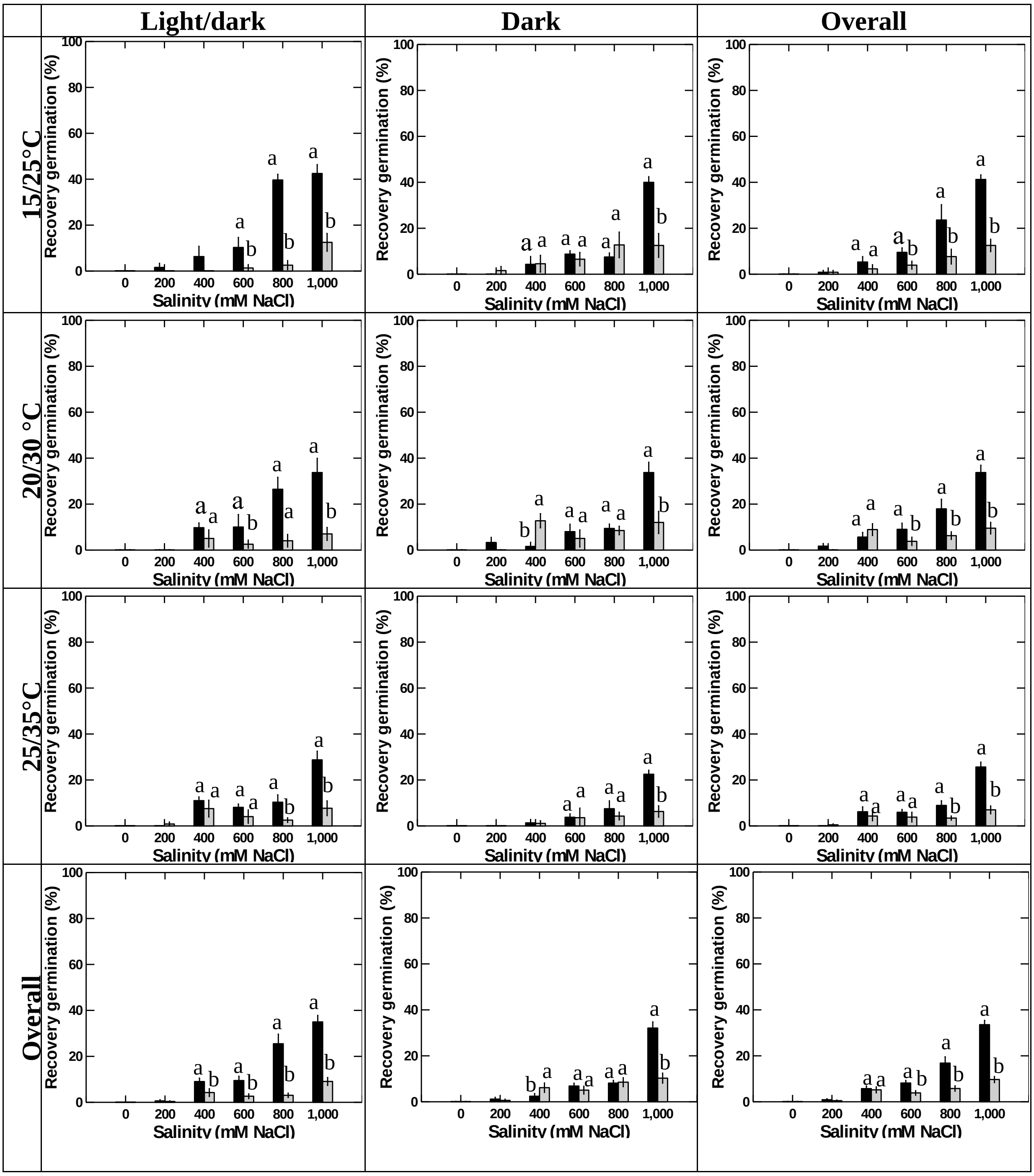


Figure 23. Effects of maternal salinity (non-saline or saline habitat), and salinity (different concentrations of sodium chloride (NaCl)), temperature and light of incubation on germination recovery percentage (mean ± SE) of *Salsola drummondii* Ulbr., seeds. Dark and light bars are for seeds of non-saline and saline habitats, respectively.

3.4. Ecophysiological adaptations of *Salsola drummondii* Ulbr., plants in natural saline and non-saline habitats

3.4.1. Soil and plant organs (leaves, stems, roots) elemental analysis

Sodium (Na^+) attained significantly higher values ($P < 0.05$, Table 12) in soils and all organs of plants from saline habitats, as compared to soils and organs of plants of non-saline habitat. The Na^+ concentration in saline habitat soil was around 9.5 times greater than that of the non-saline habitat (Table 13). Leaves had the highest Na^+ accumulation, but both roots and stems had the lower concentration. The concentration of Na^+ was greater in roots, stems and leaves of the saline habitat by 50%, 91% and 26%; the concentrations of Na^+ in these organs were 7.01, 24.7 and 98.4 mg/g, respectively in plants of saline habitats, but were 4.67, 12.9 and 78 mg/g, respectively in plants of non-saline habitat (Fig. 24A).

It is clear that *S. drummondii* have great abilities to accumulate Na^+ in leaves in both saline and non-saline habitats. The bioaccumulation factor of Na^+ (concentration in plant organ/concentration in soil) was 0.73 and 4.62 in roots of plants from saline and non-saline habitats, respectively, 2.57 and 11.96 in stems of plants from saline and non-saline habitat, respectively and 10.24 and 77.14 in leaves of plants from saline and non-saline habitats, respectively. The bioaccumulation factors were also very high in K^+, but was low in other elements such as Ca^{2+}, Mg^{2+} and Fe^{2+}. There was no significant difference between saline and non-saline soils in all elements, except Na^+. In the different plant organs, there was no significant difference between saline and non-saline habitat for elements such as Ca^{2+}, Mg^{2+} and Fe^{2+} (Fig. 24). The exception was roots in which Fe^{2+} was significantly greater in plants of the saline (0.21 mg/g) than in plants of the non-saline habitats (0.07 mg/g, Fig. 24E).

Table 12. Results of one-way ANOVA showing the effect of habitat (saline and non-saline) on elemental composition in soils and different plant organs of *Salsola drummondii* Ulbr. The table also showing effect of habitat type on soil attributes such as soil salinity, electrical conductivity (EC) and pH.

Elemental composition/ soil attributes	**Soil/ plant organs**	**Mean squares**	**F-Ratio**	**P-value**
Na$^+$	Soil	222.161	10.319	< 0.01
Na$^+$	Roots	8.171	14.487	< 0.05
Na$^+$	Stem	354.102	5.836	< 0.05
Na$^+$	Leaves	838.400	5.533	< 0.05
Ca^{2+}	Soil	1,344.284	0.207	ns
Ca^{2+}	Roots	4.546	0.229	ns
Ca^{2+}	Stem	27.231	1.736	ns
Ca^{2+}	Leaves	87.321	1.593	ns
K$^+$	Soil	0.049	0.234	ns
K$^+$	Roots	0.441	0.254	ns
K$^+$	Stem	18.748	0.814	ns
K$^+$	Leaves	153.198	4.354	ns
Mg^{2+}	Soil	3.901	0.452	ns
Mg^{2+}	Roots	24.309	2.622	ns
Mg^{2+}	Stem	0.259	0.119	ns
Mg^{2+}	Leaves	3.890	0.487	ns
-Fe^{2+}	Soil	3.314	2.322	ns
Fe^{2+}	Roots	0.032	8.291	< 0.05
Fe^{2+}	Stem	0.001	0.200	ns
Fe^{2+}	Leaves	0.001	0.067	ns
Soil salinity	Soils	1.168E+008	11.115	0.013
EC	Soils	305.854	8.646	0.026
pH	Soils	0.014	0.257	0.628

Table 13. Different soil traits (soil salinity (mg/l), Electrical conductivity (EC (mS/cm)), and pH from non-saline and saline habitats. Every value in the column represents the mean ± standard error (n = 6). Values with different letters indicate significant differences between the two habitat types at $P \leq 0.05$.

Soil traits	**Salinity (mg/l)**	**EC (mS/cm)**	**pH**
Non-saline habitats	340.68±121.9b	0.77±0.3b	8.30±0.1a
Saline habitats	7592.00±1915.8a	13.54±3.2a	8.22±0.1a

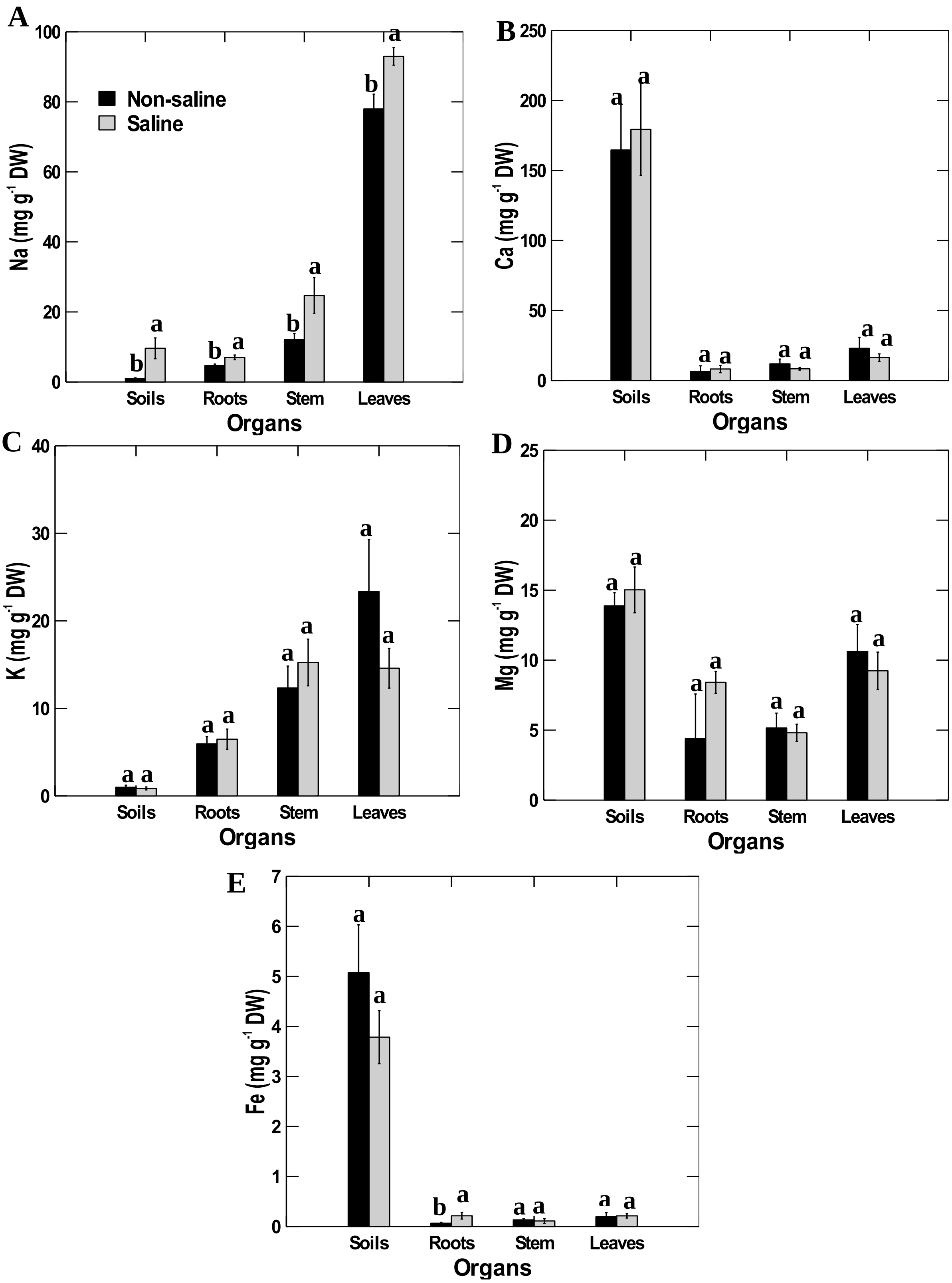


Figure 24. Effect of habitat type on concentrations of different elements in plant organs (roots, stems and leaves) of *Salsola drummondii* Ulbr. Bars represent mean ± standard error (n = 6). Bars with different letters are significantly different from each other at $P \leq 0.05$ [Tukey's test, $P < 0.05$].

3.4.2. Effects of the habitat type (saline and non-saline) on leaf pigments, leaf biomass and leaf succulence

There were significant effects for the habitat type on the different types of pigments (chlorophylls *a*, *b*) and total chlorophyll and carotenoids ($P \leq 0.01$, Table 14). All pigments values were significantly higher in plants from the non-saline, compared to those from the saline habitats (Table 15). The values of chlorophylls *a*, *b*, total chlorophyll and carotenoids in non-saline habitat were greater than those in saline habitat by 78%, 104%, 74% and 77%, respectively (Table 15). The habitat had insignificant effect on fresh and dry weights as well as on the leaf succulence (Table 14).

Table 14. Results of one-way ANOVA showing the effect of habitat (saline and non-saline) on some morphological and physiological traits of *Salsola drummondii* Ulbr., leaves.

Morphological and physiological traits	Mean squares	F-Ratio	P-value
Chlorophyll *a*	0.016	17.762	< 0.01
Chlorophyll *b*	0.002	14.282	< 0.01
Total Chlorophyll	0.026	13.031	< 0.01
Carotenoids	0.002	12.963	< 0.01
Fresh weight of leaves	0.270	0.551	ns
Dry weight of leaves	0.016	2.860	ns
Fresh: dry weight ratio of leaves	0.932	1.883	ns
Leaf succulence	0.934	1.883	ns
Carbon isotope composition	0.976	37.019	< 0.01
Carbon isotope discrimination	1.025	38.877	< 0.01

Table 15. Variations in leaf pigment contents, fresh (FW) and dry leaf weights (DW) and leaf succulence (SWC). Values represent mean ± SE of six replicates. Means with different letters indicate significant differences at $P \leq 0.05$ with respect to control.

Traits	Habitat	
	Non-saline	**Saline**
Chl *a* (mg/g FW)	0.20±0.01a	0.11±0.00b
Chl *b* (mg/g FW)	0.07±0.01a	0.03±0.00b
Total Chl (mg/g FW)	0.27±0.02a	0.15±0.01b
Carot. (mg/g FW)	0.08±0.01a	0.04±0.00b
FW (g/100 leaf)	2.78±0.24a	3.14±0.43a
DW (g/100 leaf)	0.38±0.02a	0.46±0.05a
FD ratio	7.38±0.42a	6.70±0.26a
SWC	6.38±0.42a	5.70±0.27a

3.4.3 Effects of the habitat type (saline and non-saline) on oxidative damage signals (MDA and H_2O_2) and proline production

There was no significant difference in the level of lipid peroxidation (MDA) in plants from saline and those from non-saline habitats ($P > 0.05$, Table 16). The difference in H_2O_2 level was significant only in the roots ($P < 0.001$, Table 16). The values of H_2O_2 in the roots were greater in saline than in non-saline habitats by 0.6 fold (Fig. 25B). However, proline was greater in both root and shoot systems of the non-saline than in saline ($P < 0.05$, Table 16). Proline was greater in roots and shoots of plants from the non-saline habitat than from the saline habitat by 142% and 367%, respectively (Fig. 25C).

Table 16. Results of one-way ANOVA showing the effect of habitat (saline and non-saline) on some antioxidants (GPX, CAT and APX), damage signals (MDA and H_2O_2) and proline in shoots and roots of *Salsola drummondii* Ulbr.

Biochemical traits	Organs	MS	F-Ratio	p- value
GPX	Shoot	0.115	0.597	ns
GPX	Root	0.010	0.100	ns
CAT	Root	0.159	3.818	ns
CAT	Shoot	3.454	34.235	< 0.001
APX	Root	625.153	129.803	< 0.001
APX	Shoot	3.172	0.630	ns
MDA	Root	9.824	2.037	ns
MDA	Shoot	7.495	1.203	ns
H_2O_2	Root	2.372	25.658	< 0.001
H_2O_2	Shoot	0.084	0.050	ns
Proline	Root	13.883	58.136	< 0.001
Proline	Shoot	41.104	1,440.084	< 0.001

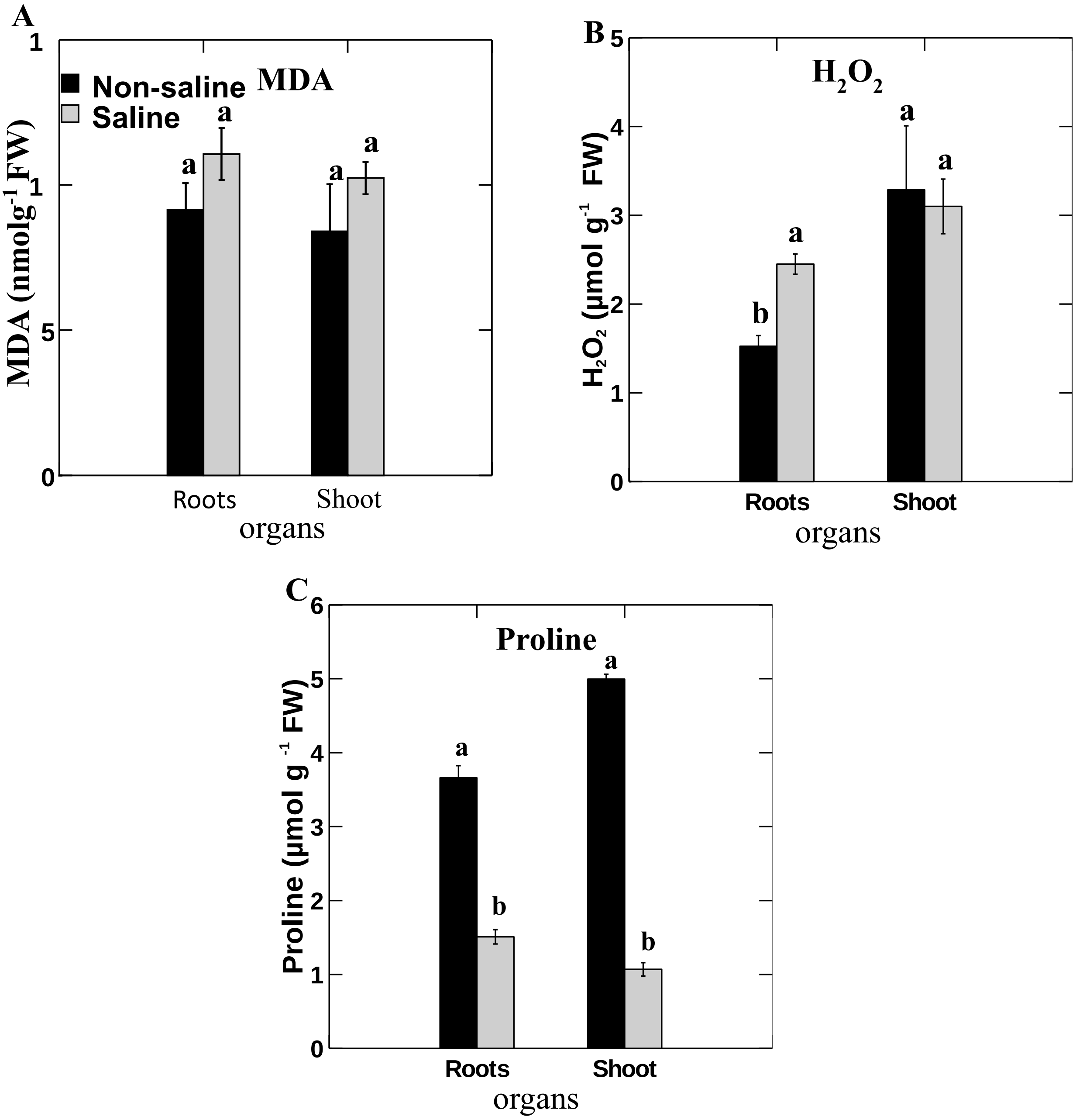


Figure 25. Effect of habitat types on oxidative damage signals (A) lipid peroxidation; MDA and (B) hydrogen peroxide; H_2O_2 and (C) proline concentrations in different organs of *Salsola drummondii* Ulbr. Bars represent mean ± standard error (n = 6). Bars with same alphabet are not significantly different from each other [Tukey's test, $P < 0.05$].

3.4.4. Effects of the habitat type (saline and non-saline) on antioxidant enzymes activity

Generally, antioxidant enzymes (CAT: catalase, GPX: guaiacol peroxidase and APX: ascorbate peroxidase) attained higher values in plants from the saline than those from non-saline habitat. This difference was significant only for APX in the roots and CAT in the shoots ($P < 0.001$, Table 16). The values of APX in the roots were higher in saline than in non-saline habitats by two-folds. Similarly, CAT in shoots was greater in saline than in non-saline by 0.75-fold (Fig. 26).

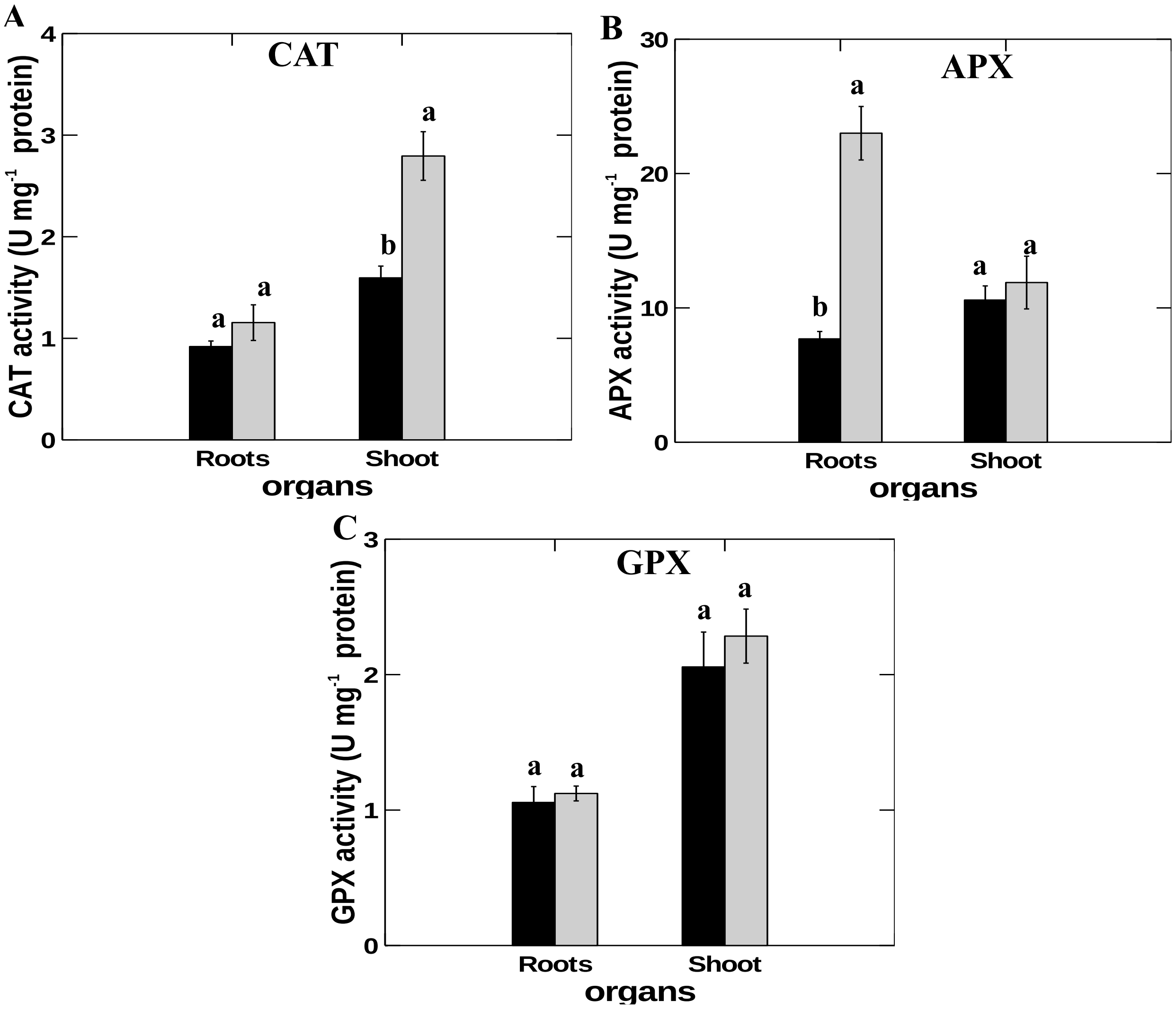


Figure 26. Effect of habitat types (saline and non-saline) on antioxidant enzymes: catalase (CAT), guaiacol peroxidase (GPX), and ascorbate peroxidase (APX), in different organs of *Salsola drummondii* Ulbr. Bars represent mean ± standard error ($n = 6$). Bars with same alphabet are not significantly different from each other [Tukey's test, $P < 0.05$].

3.4.5. Effects of the habitat type (saline and non-saline) on carbon isotope discrimination

There were significant effects for the habitat type on both carbon isotope composition and discrimination ($P < 0.01$, Table 13). The $\delta^{13}C$ was significantly less negative in leaves of *S. drummondii* Ulbr., plants from the saline (-13.06‰), as compared to those from the non-saline habitat (-13.87‰). Similarly, $\Delta^{13}C$ was significantly higher in non-saline (4.71‰), as compared to saline habitat (3.88‰) (Fig. 27).

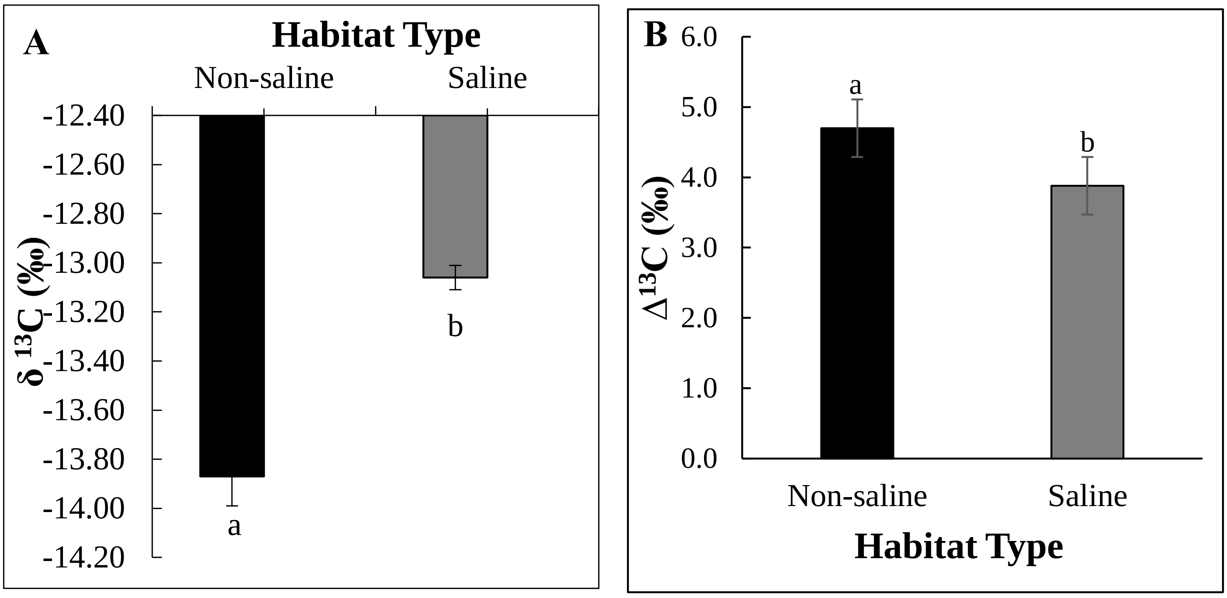


Figure 27. Changes in carbon isotope composition ($\delta^{13}C$) (A), and carbon isotopes discrimination ($\Delta^{13}C$) (B) in leaves of *Salsola drummondii* Ulbr., following exposure to different habitats (non-saline and saline). Bars represent mean ± standard error (n = 6). Bars with same alphabet are not significantly different from each other [Tukey's test, $P < 0.05$].

3.4.6. Correlations between studied traits

Under non-saline habitat, Pearson's correlations analysis showed that Na^+ attained a significant positive correlation with CAT, APX, proline, and leaf DW while a significant negative relation with chlorophyll *b* contents. Na^+ exhibited significant positive correlation with other nutrient elements such as K^+, Ca^{2+}, Mg^{2+} and Fe^{2+}. In the saline habitat, the Na^+ exhibited significant positive correlation with Ca^{2+}, CAT, GPX, while a significant negative correlation with APX and proline (Table 17).

Table 17. Pearson's correlations among sodium (Na^{+}) and other elements, physiological and biochemical traits of *Salsola drummondii* Ulbr., from saline and non-saline habitats. *: $P \leq 0.05$, **: $P \leq 0.01$ and ***: $P \leq 0.001$. Values between brackets are number of samples (n).

Traits	**Habitat**	
	Non-saline	**Saline**
Ca^{2+}	0.715(13)**	0.673(20)***
K^{+}	0.811(13)***	0.367(20)
Mg^{2+}	0.767(13)**	0.421(20)
Fe^{2+}	0.555(13)*	0.263(20)
Chlorophyll *a*	-0.883(3)	0.991(3)
Chlorophyll *b*	-0.999(3)*	-0.381(3)
Total chlorophyll	-0.919(3)	0.610(3)
Carotenoids	-0.883(3)	0.991(3)
Leaf fresh weight	-0.937(3)	-0.142(4)
Leaf dry weight	-0.99 (3)**	-0.125(4)
Catalase	0.913(5)*	0.973(7)***
Guaiacol peroxidase	0.781(6)	0.950(7)***
Ascorbate peroxidase	0.99 (3)**	-0.869(6)*
Malondialdehyde	0.500(5)	-0.025(7)
Hydrogen peroxide	-0.041(4)	0.583(7)
Proline	0.814(6)*	-0.879(7)**
Leaf succulence	-0.490(3)	-0.062(4)
Carbon isotope composition	0.469(3)	0.692(3)
Carbon isotope discrimination	-0.469(3)	-0.692(3)

3.5. Effect of salt stress on physiological and biochemical traits in *Salsola drummondii* Ulbr., at seedling stage under experimental conditions

3.5.1. Effect of sodium chloride (NaCl) on plant growth and biomass from different plant organs

There were no significant differences in the fresh weights of shoots and leaves between control (non-treated) plants and those treated with 200 mM and 500 mM NaCl respectively. However, at 800 mM NaCl, a significant decrease in the fresh weight of shoots and leaves was observed (Fig. 28A). Moreover, there were no significant differences in root fresh weight between control and plants treated with different concentrations of NaCl (Fig. 28C).

For shoot succulence, control plants do not differ significantly from those treated with 200 and 500 mM NaCl, but attained significantly greater succulence than plants treated with 800 mM NaCl (Fig. 29A). Additionally, there was a significant decrease in leaf succulence for plants treated with 500 and 800mM NaCl, compared with control and plants treated with 200 mm NaCl (Fig. 29B). For root succulence, control plants do not differ significantly from those treated with 200, 500 and 800 mM NaCl (Fig. 29C)

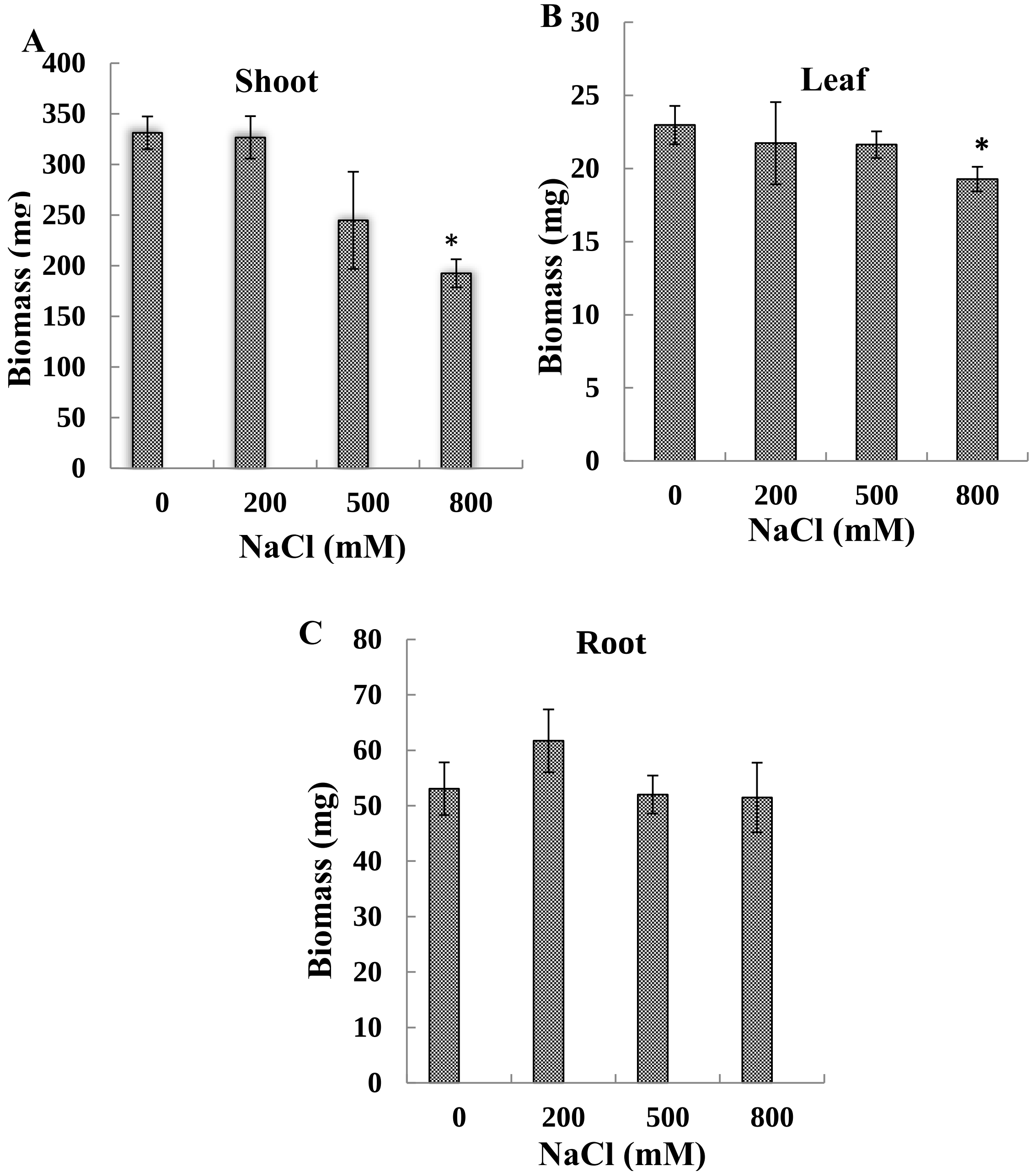


Figure 28. Effect of different sodium chloride (NaCl) concentrations on (A) shoot biomass, (B) root biomass and (C) leaf biomass of *Salsola drummondii* Ulbr. Error bars represent standard errors of mean values of three replicates. Biomass is measured as mg/plant. Statistically significant difference was calculated at *: P ≤ 0.05, **: P ≤ 0.01.

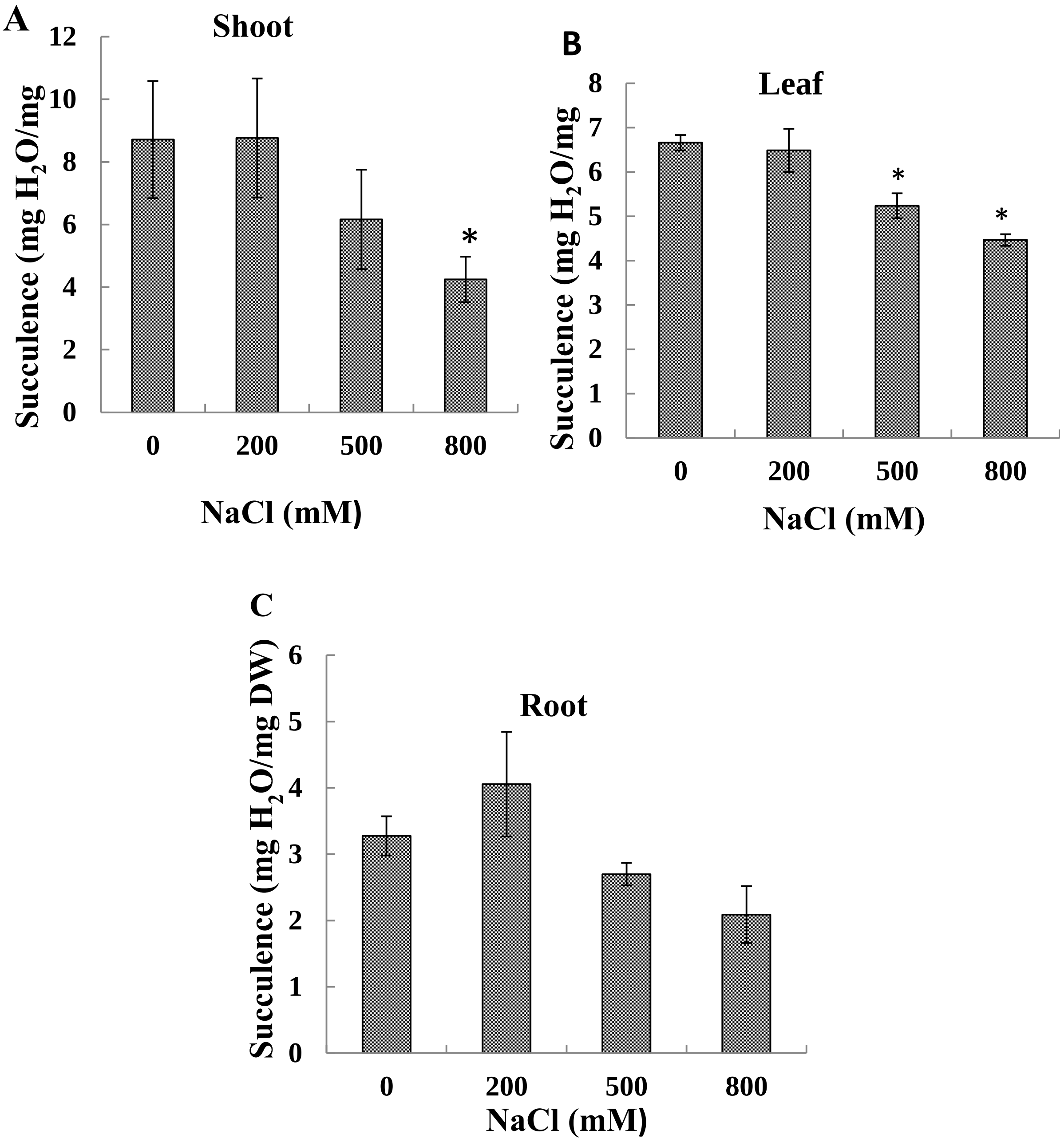


Figure 29. Leaf succulence of *Salsola drummondii* Ulbr., shoot (A), leaf (B) and root (C) under the effect of different concentrations of sodium chloride (NaCl). Error bars represent standard errors of mean values of three replicates. Statistically significant difference was calculated at *: $P \leq 0.05$, **: $P \leq 0.01$.

3.5.2. Effect of sodium chloride (NaCl) on leaf pigment contents

When *S. drummondii* plants were treated with NaCl for 20 days, an induced senescence was observed on plants treated with high levels of NaCl, compared to control. To quantify the levels of senescence, the contents of chlorophyll *a* and *b* were measured. Compared to the control plants, leaves of plants treated with 200 mM NaCl had a significantly higher level in chlorophyll *b*, but concentrations of chlorophyll *a*, total chlorophyll and carotenoid were not affected (Fig. 30). However, leaves of plants treated with 500 and 800 mM NaCl showed significantly lower levels of chlorophyll *a*, *b*, total chlorophyll, and carotenoids, compared with control plants (Fig. 30).

3.5.3. Sodium influx, accumulation and ion composition (Na^+, K^+, Cl^-, Mg^{+2} and Ca^{+2})

In relation to short-term sodium influx analysis, *S. drummondii* samples grown under high salinity (1200 mM NaCl) showed a significant increase in sodium accumulation in roots at exposure time (0, 0.5, 1, 2, 4, 8 hrs) (Fig. 31A).

Interestingly, plants grown under higher salinity for 20 days exhibited significantly higher sodium accumulation in shoots in comparison to roots (Fig. 31B and C). Shoots treated with 200 mM, 500 mM and 800 mM NaCl accumulated 3-, 6- and 4-fold more Na^+ than roots, respectively (Fig. 31B and C). There was a corresponding increase in the sodium (Na^+) accumulation in plant tissues with the concentration of sodium in the culture medium. Additionally, XRF analysis showed that as sodium increased in plant tissues (stems, leaves and roots), the mass % of sodium and chloride increased, but the mass % of calcium, potassium and magnesium decreased (Fig. 32).

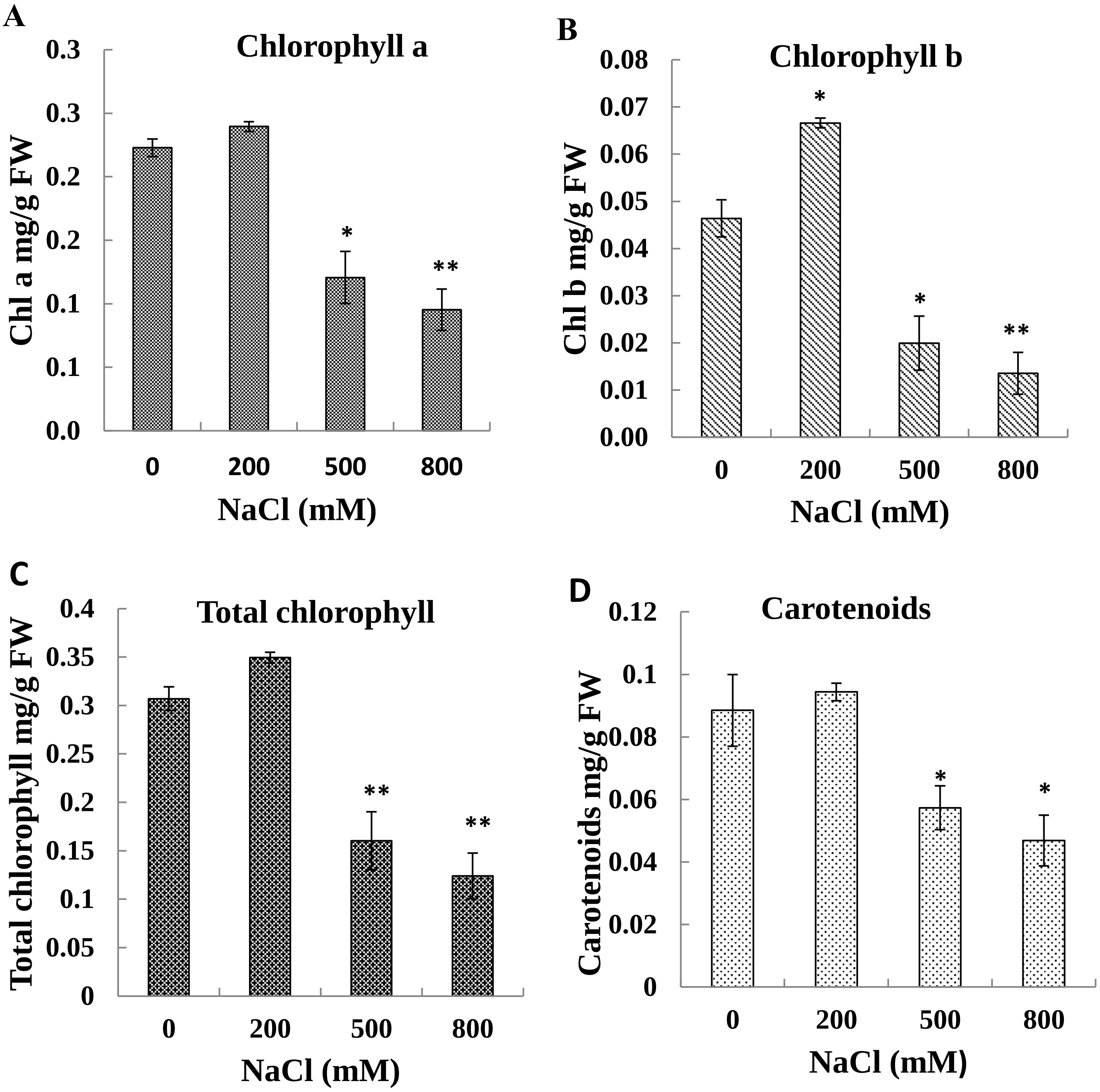


Figure 30. Chlorophyll content of control and sodium chloride (NaCl) leaves of *Salsola drummondii* Ulbr. (A) Chlorophyll *a*, (B) Chlorophyll *b*, (C) Total chlorophyll and (D) Carotenoids. Error bars represent standard errors of mean values of three replicates. Statistically significant difference was calculated at *: $P \leq 0.05$, **: $P \leq 0.01$.

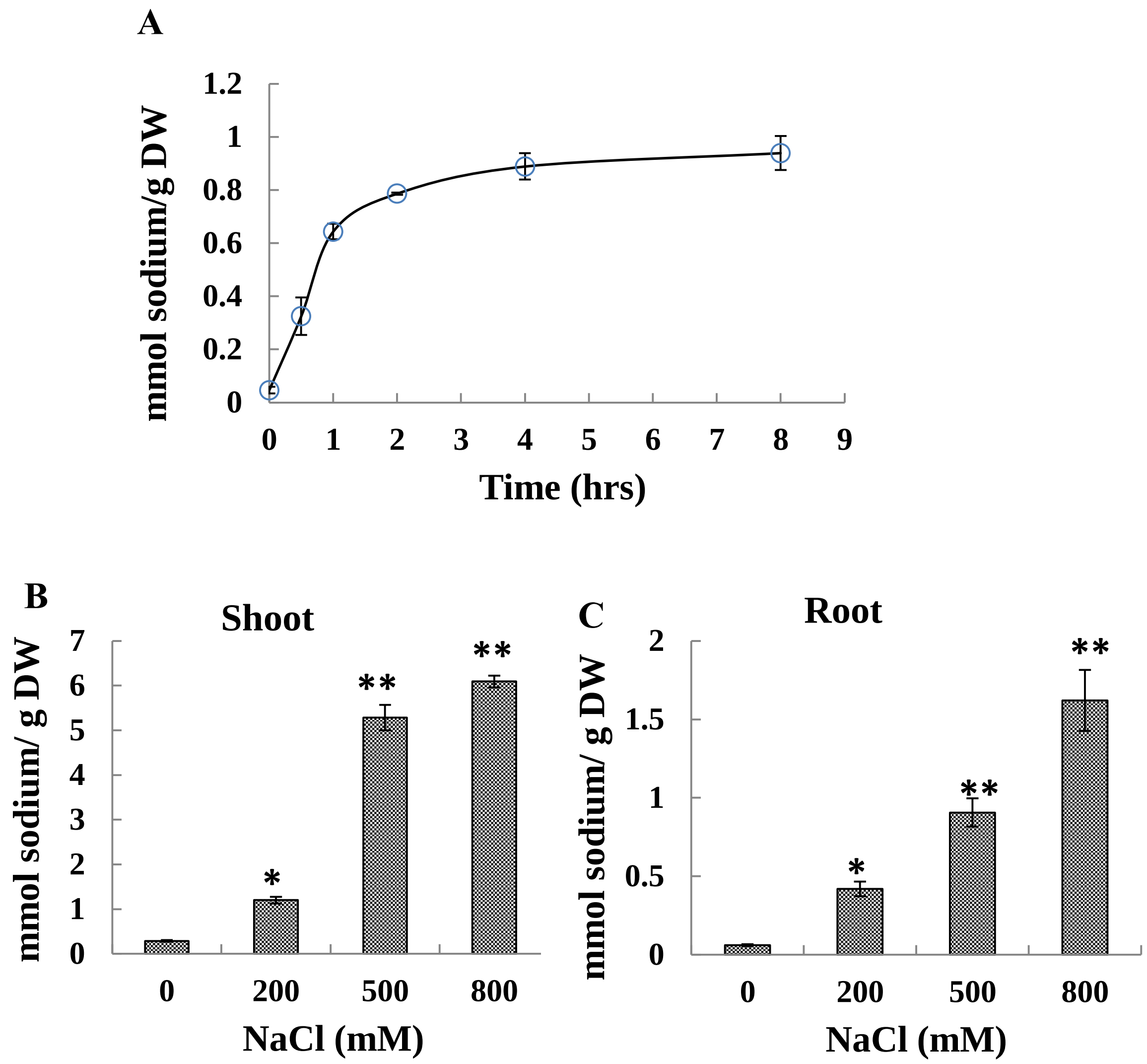


Figure 31. *Salsola drummondii* Ulbr., Na^+ transport and accumulation. (A) Na^+ transport in roots of *S. drummondii* during eight hours treatment with 1200 mM NaCl in hydroponic growth solution. Changes in Na^+ concentrations in shoots (B) and roots (C) of *S. drummondii* after 20 days without and with salt treatment 200, 500, 800 mM NaCl in sandy soil. Na^+ contents were determined by atomic absorption spectroscopy (AAS). Data shown are averages of three experimental replicates. Ten plants were pooled in each replicate. Error bars represent standard errors of mean values of six replicates. Statistically significant difference was calculated at *: $P \leq 0.05$, **: $P \leq 0.01$.

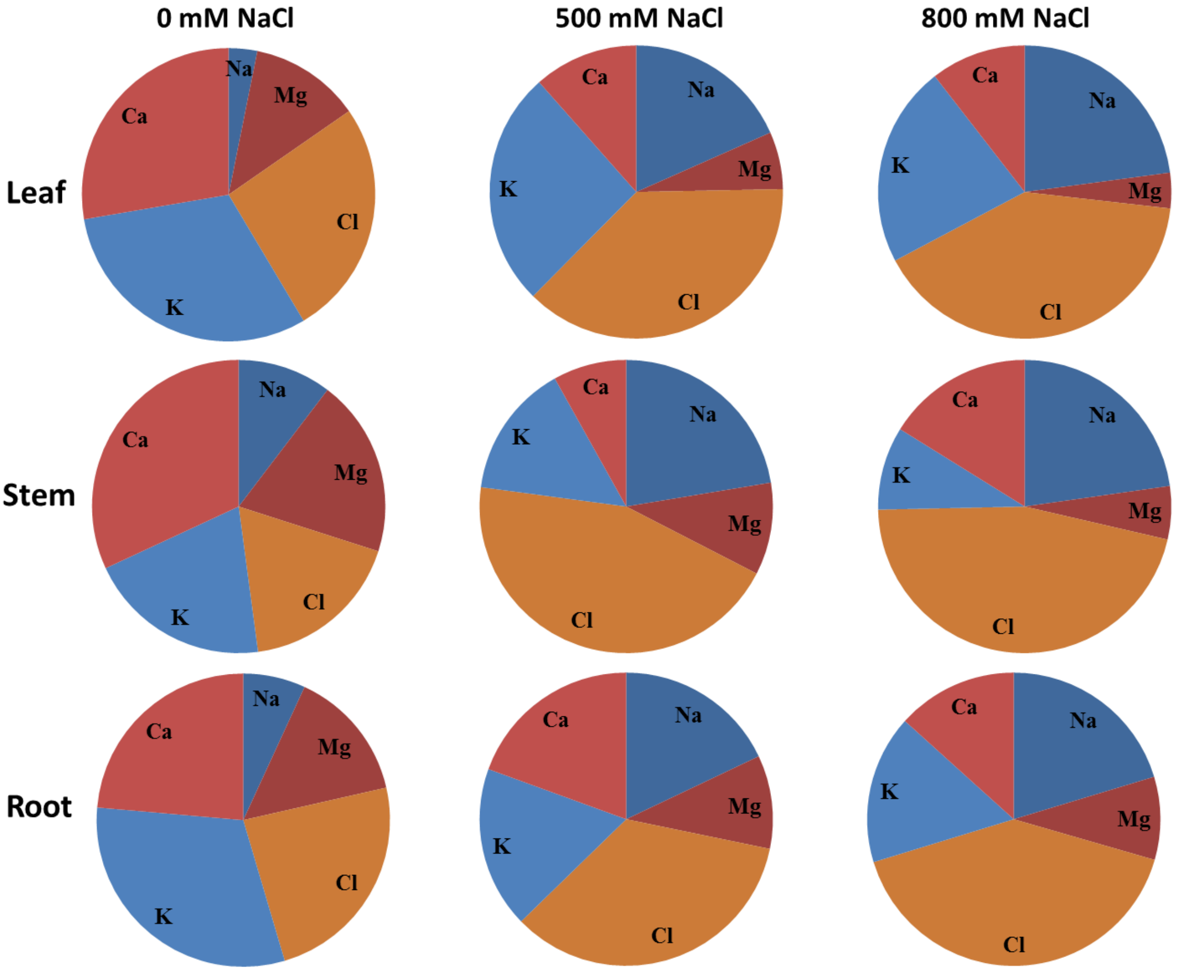


Figure 32. X-ray fluorescence (XRF) analysis of Na^+, K^+, Cl^-, Mg^{+2} and Ca^{+2} concentrations (mass%) in leaf, stem and root of *Salsola drummondii* Ulbr., in response to sodium chloride (NaCl) treatment (0, 500, 800 mM NaCl).

3.5.4. Sodium chloride (NaCl) induced oxidative damage in *Salsola drummondii*

Oxidative damage caused by NaCl was assessed by measuring malondialdehyde (MDA) and hydrogen peroxide (H_2O_2) production. In shoots, MDA concentration increased significantly at 500 mM and 800 mM, but decreased significantly at 200 mM NaCl, as compared with control (Fig. 33A). Salt stress had no significant effects on root MDA content at the higher concentrations of 500 and 800 mM NaCl relative to the control. However, there was a significant reduction in MDA levels at 200 mM NaCl (Fig. 33B). Furthermore, salt stress had no significant effects on shoot hydrogen peroxide levels in *S. drummondii* plants treated with 200 and 500 mM NaCl respectively. However, shoot hydrogen peroxide (H_2O_2) concentration increased significantly at 800 mM (Fig. 33C). In contrast, there were no significant differences between control and treated plants in levels of root hydrogen peroxide at all NaCl concentrations (Fig. 33D).

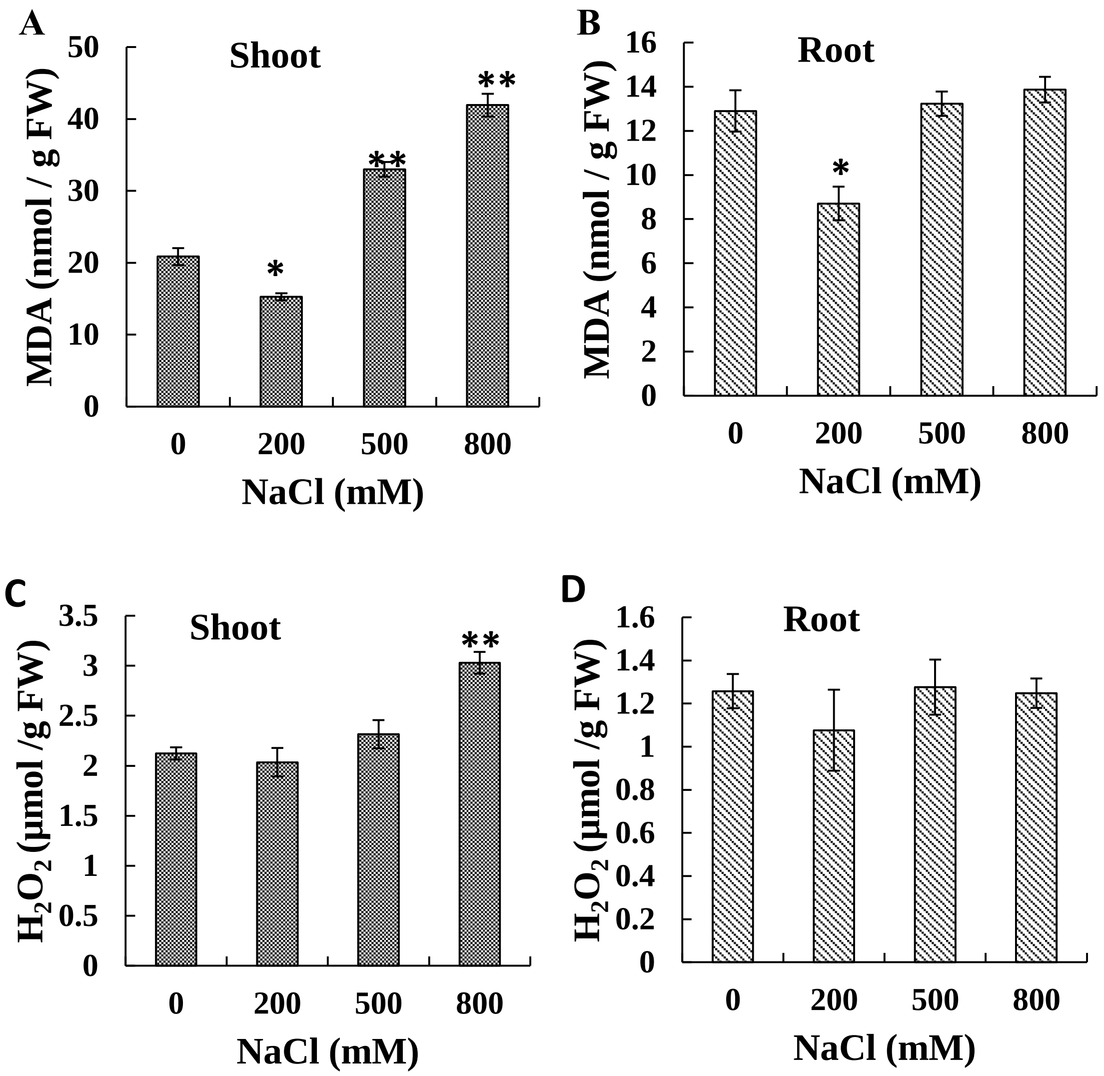


Figure 33. Effect of sodium chloride (NaCl) on MDA (nmol g^{-1} FW) concentrations in *S. drummondii* Ulbr., shoots (A) and roots (B), and effect of sodium chloride (NaCl) on hydrogen peroxide (H_2O_2) (µmol H_2O_2/g FW) contents in shoots (C) and roots (D). Error bars represent standard errors of mean values of six replicates. Statistically significant difference was calculated at *: $P \leq 0.05$, **: $P \leq 0.01$.

3.5.5. Effect of sodium chloride (NaCl) on proline content in shoots and roots

Under non-saline conditions (control) and in 200 mM NaCl treated plants, proline levels were low. However, shoot and root proline levels increased as the salinity increased (Fig. 34). The levels of proline in *S. drummondii* treated with 500 and 800 mM NaCl increased significantly in both shoots and roots comparing to control plants (Fig. 34A and B).

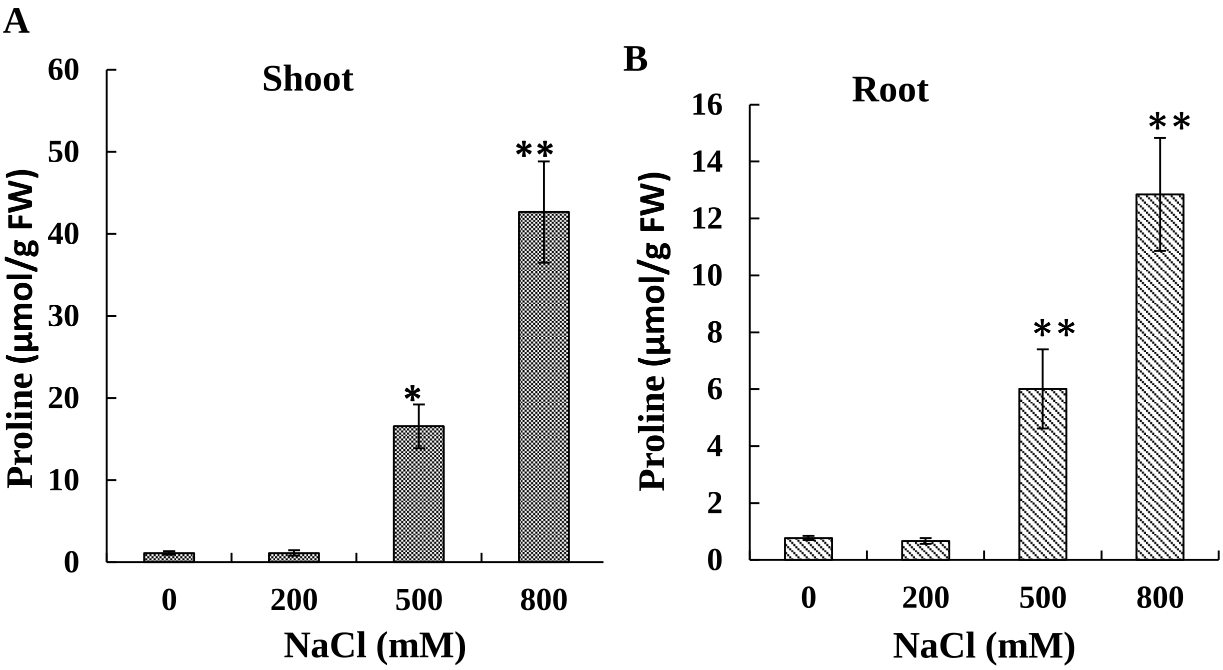


Figure 34. Changes in proline concentration expressed as µmol/g FW of *Salsola drummondii* Ulbr., shoot (A) and root (B) in response to sodium chloride (NaCl) treatment. Error bars represent standard errors of mean values of six replicates. Statistically significant difference was calculated at *: $P \leq 0.05$, **: $P \leq 0.01$.

3.5.6. Changes in antioxidant enzymes activity (catalase, ascorbate peroxidase and guaiacol peroxidase) in roots and shoots of *Salsola drummondii* Ulbr., treated with sodium chloride.

There were no significant changes in catalase (CAT) enzyme levels in the shoots of all sodium chloride (NaCl) treated plants in comparison to control plants even at high salinity (Fig. 35A). Similarly, roots of 200 and 500 mM NaCl treated plants revealed no significant changes in CAT activity in comparison to control plant roots. However, at high NaCl concentration (800 mM), a significant increase in CAT activity was observed (Fig. 35B). Ascorbate peroxidase (APX) enzyme increased significantly in shoots, while the activity of APX in roots decreased significantly with rising NaCl concentrations (Fig. 35C and D). Guaiacol peroxidase (GPX) activity increased significantly in both shoot and root tissues, with enhanced NaCl levels observed in the growth medium of *S. drummondii*. GPX activity levels in treated roots were much higher in comparison with shoots (Fig. 35E and F).

3.5.7. Effect of sodium chloride (NaCl) on total glutathione content

In response to salinity, the total glutathione contents in shoot was significantly increased in 500 and 800 mM NaCl treated *S. drummondii,* while in root there was no significant difference between control plants and plants treated with 500 mM NaCl. However, at 800 mM NaCl there was a significant decrease in total glutathione contents. The production of total glutathione was dose and plant organ dependent as shown in (Fig. 36). Additionally, concentration of total glutathione in shoots was higher than roots.

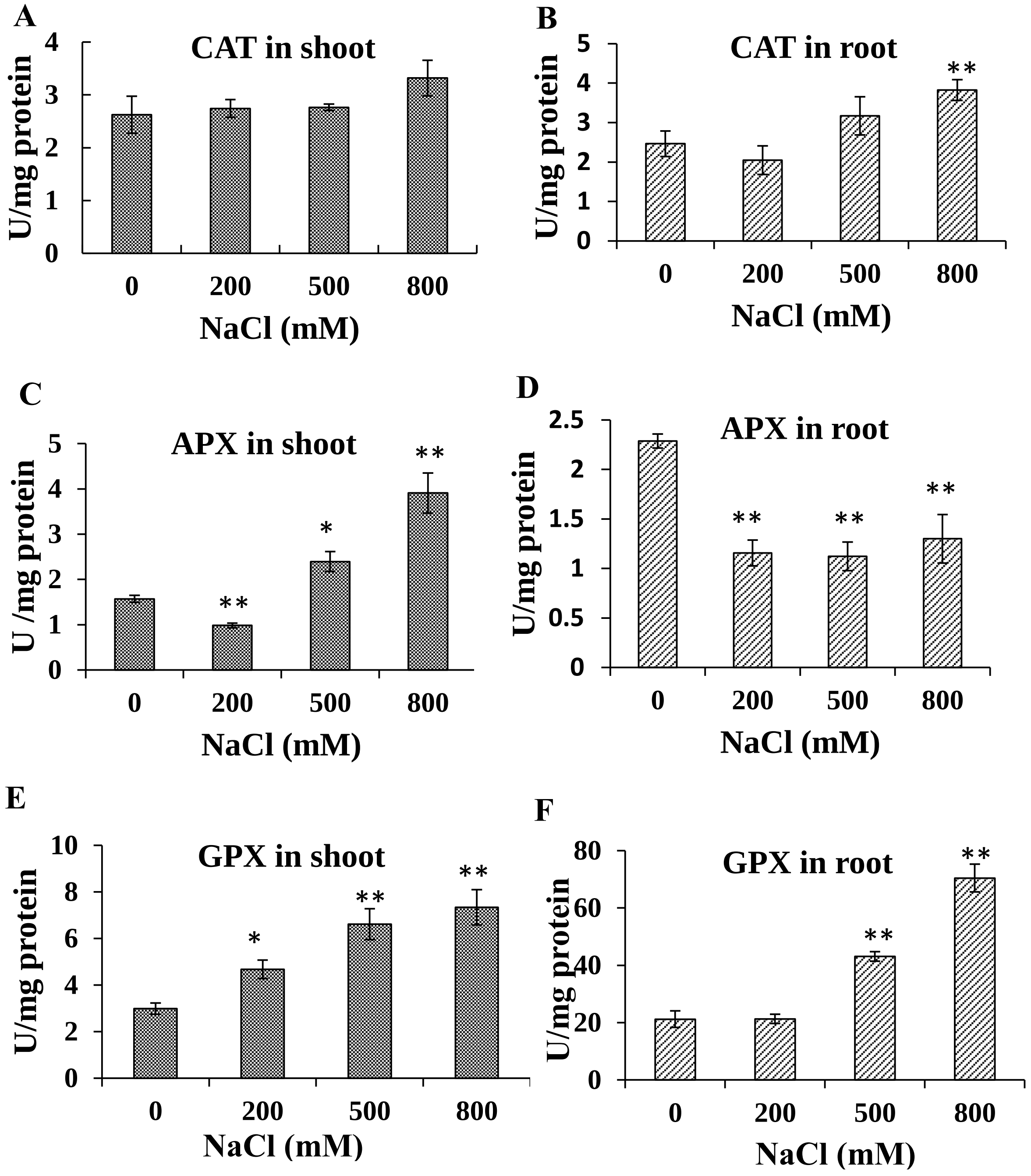


Figure 35. Effect of different sodium chloride (NaCl) concentrations on catalase (CAT) activity (unit. mg^{-1} protein) of shoot (A) and root (B), ascorbate peroxidase (APX) activity (unit. mg^{-1} protein) of shoots (C) and roots (D) and guaiacol peroxidase (GPX) activity (unit. mg^{-1} protein) of shoot (E) and roots (F) of *Salsola drummondii* Ulbr. Error bars represent standard errors of mean values of six replicates. Statistically significant difference was calculated at *: $P \leq 0.05$, **: $P \leq 0.01$.

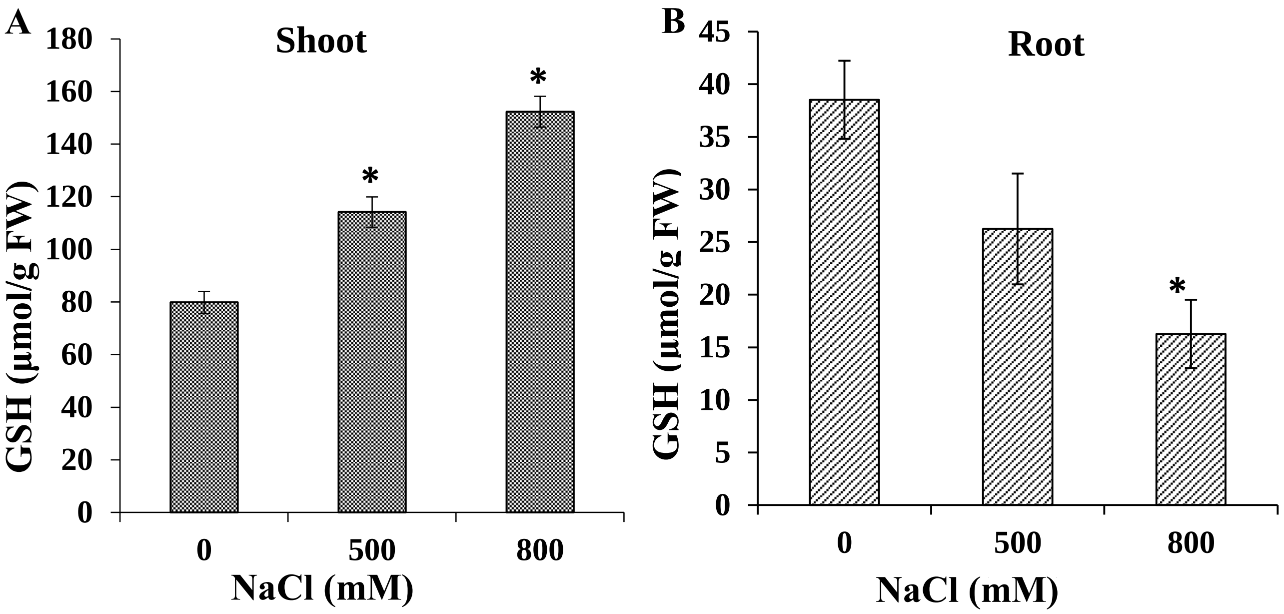


Figure 36. Changes in total glutathione content of *Salsola drummondii* Ulbr., shoot and roots in response to sodium chloride (NaCl) (A). Error bars represent standard errors of mean values of 6 replicates. Statistically significant difference was calculated at *: P ≤ 0.05, **: P ≤ 0.01.

3.6. Transcriptomic analysis of *Salsola drummondii* Ulbr., under salt stress

3.6.1. RNA Sequencing and *de novo* transcriptome assembly

Transcriptome libraries were prepared from the control and salt treated *Salsola drummondii* seedlings. RNA-seq analysis was performed using Illumna Hi-Seq2000 device. RNA sequencing and further bioinformatics analysis resulted in millions of sequence reads. The total numbers of raw and clean reads are summarized in (Table 18) and the average base quality is above Q30 (error-probability ≥ 0.001) for 92.25% of bases. Number of Assembled reads before and after cd-hit-est are summarized in (Table 19). Length distribution of the transcripts and unigenes of the *de novo* assembly are shown in (Fig. 37). Guanine-Cytosine (GC) summary of the number of unigenes and assembled transcripts in *S. drummondii* are shown in (Fig. 38). The *de novo* assembly were made using 1509047 transcripts form all the data files and their average GC% was 43.05 (Table 19). The numbers of transcripts shared between different groups of tissues (control roots, treated roots, control shoots and treated shoots) of *Salsola drummondii* Ulbr., have been shown by using comprehensive venn diagram (Fig. 39).

Table 18. Total raw and clean reads for transcriptome assembly of *Salsola drummondii* Ulbr.

Sample Name	**Raw reads**	**Clean reads**	**GC_perc (%) of Clean reads**	**Base quality score Q_30 of clean reads**
Control-Shoot 1	112052706	108729456	41.925	96.435
Control-Shoot 2	89803448	87931968	41.815	96.01
Control-Shoot 3	110644316	107521028	41.935	95.705
Control- Root 1	95624532	92562572	45.5	96.545
Control- Root 2	79500996	77893790	44.855	96.585
Control- Root 3	88264288	85406850	46.5	95.36
Treated- Shoot 1	69646476	67761214	42.145	95.8
Treated- Shoot 2	128798320	124097624	42.025	95.68
Treated- Shoot 3	92992834	90388068	41.845	94.48
Treated- Root 1	111473604	97194942	47.3	95.895
Treated- Root 2	82551406	79531820	45.345	94.755
Treated- Root 3	137220060	76698880	51.065	94.69

Control = (0 mM NaCl); Treated = (1200 mM NaCl)

Table 19. Assembly of *Salsola drummondii* Ulbr., transcriptome summary.

Description	**Number of assembled transcripts**	**Number of assembled transcripts after cd-hit-est**
Number of assembled transcripts	1509047	1314598
Longest transcript length (bp)	29878	29878
Mean GC % of transcripts	43.05%	43.57%

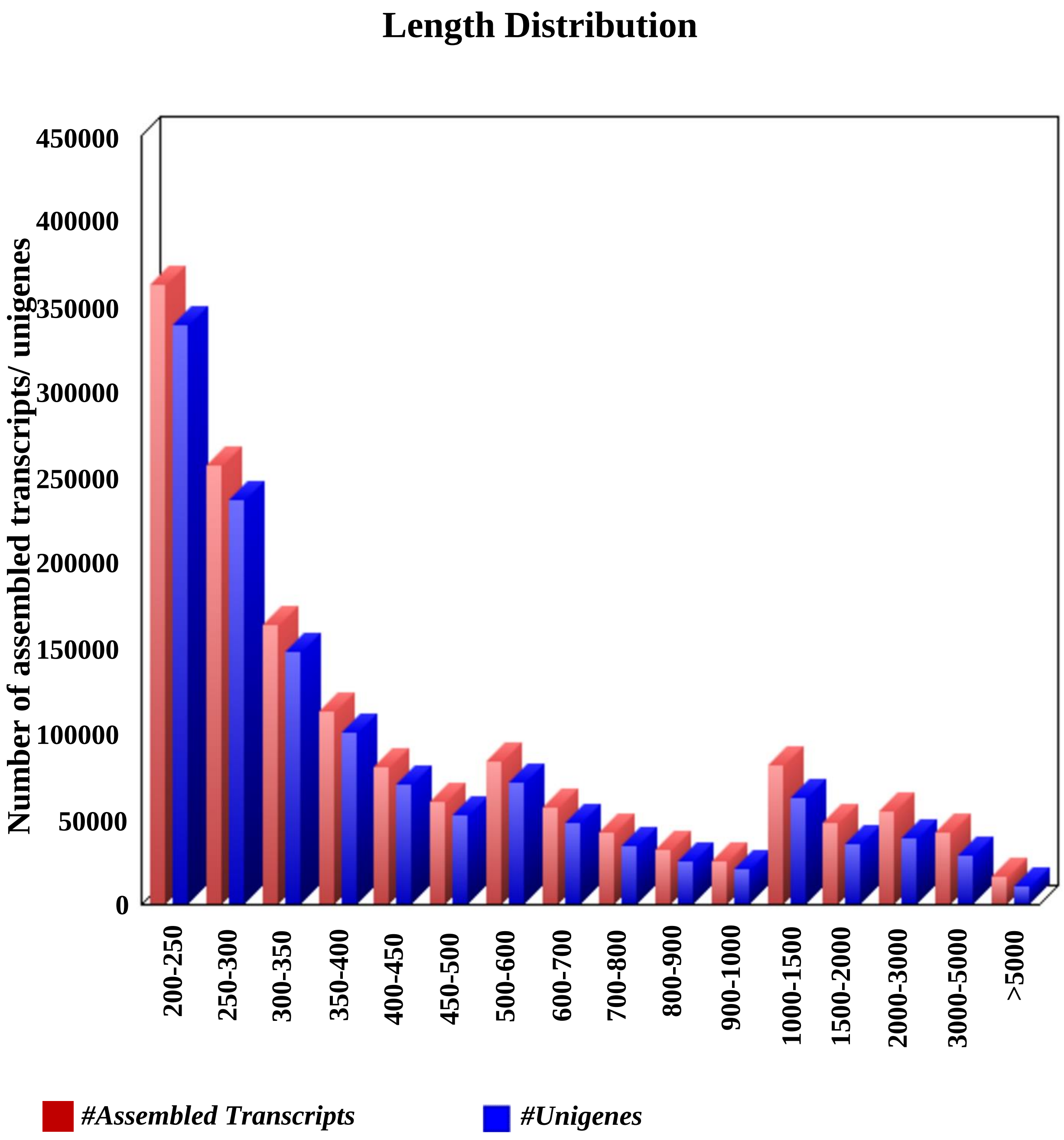


Figure 37. Length distribution of the transcripts and unigenes of the *de novo* assembly of *Salsola drummondii* Ulbr.

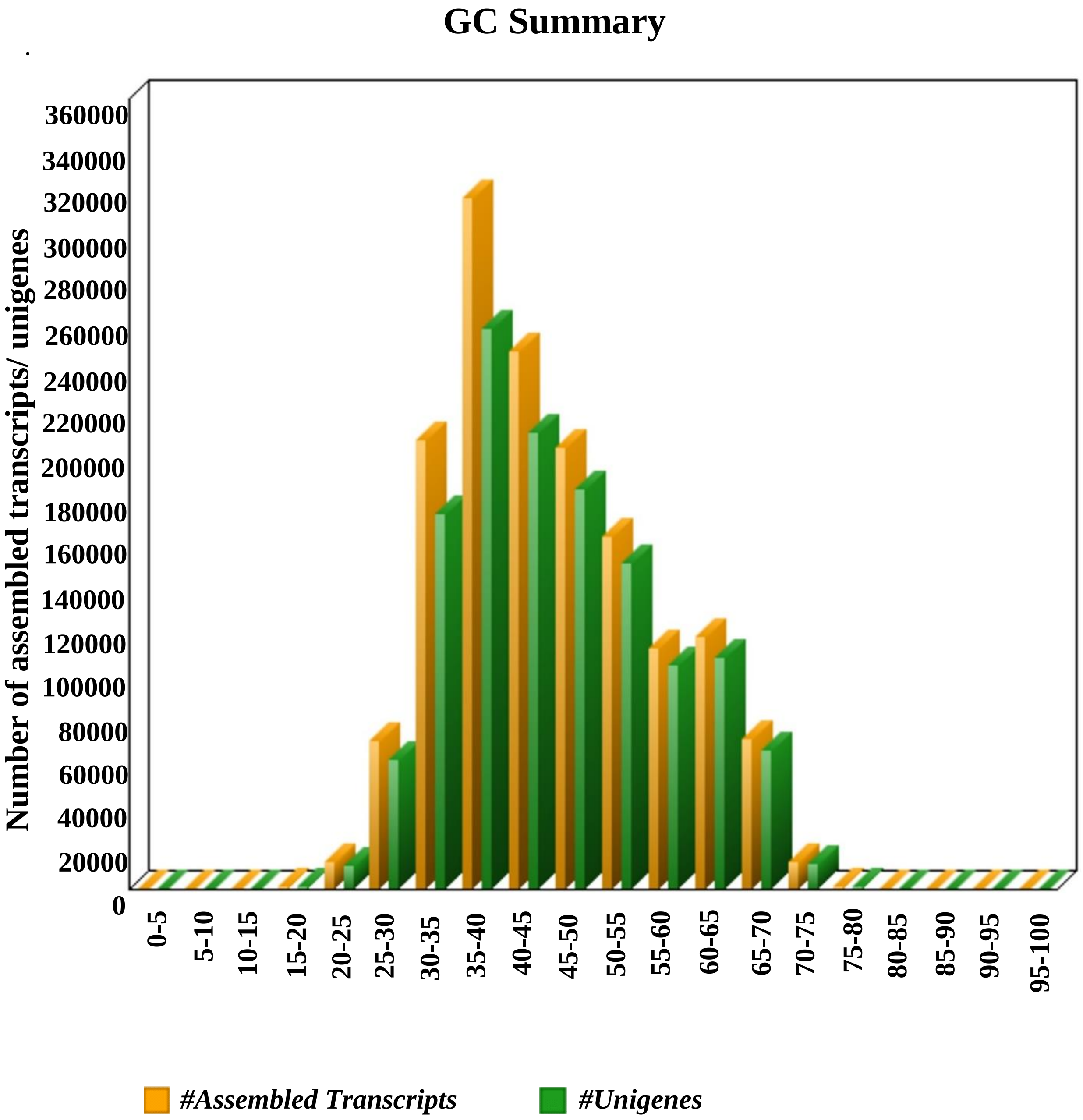


Figure 38. Guanine-Cytosine (GC) summary of the number of unigenes and assembled transcripts in *Salsola drummondii* Ulbr.

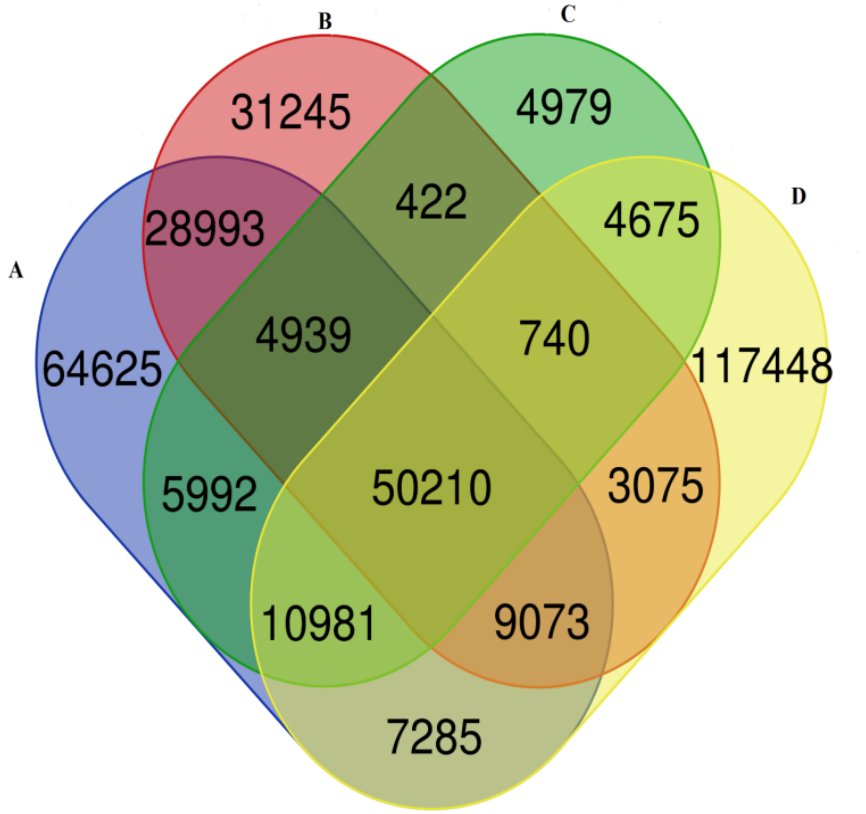


Figure 39. Comprehensive venn diagram shows the number of transcripts shared between different groups of tissues (A) control roots, (B) treated roots, (C) control shoots and (D) treated shoots of *Salsola drummondii* Ulbr.

3.6.2. Annotation of unigenes and their functional categorization

All the identified unigenes were searched against nucleotide and protein databases with an e-value cutoff of 10^{-5} for gene ontology classification. Of the **272643** unigenes, **125918** had top hits in the BLASTX (nucleotide) sequence database. Based on the gene ontology classification with sequences of the different species, the majority of hits **16907 (6.2%)** were found against *Theobroma cacao* (Cacao) (Cocoa), followed by *Eucalyptus grandis* (Flooded gum) **10116 (3.7%)** (Fig. 40).

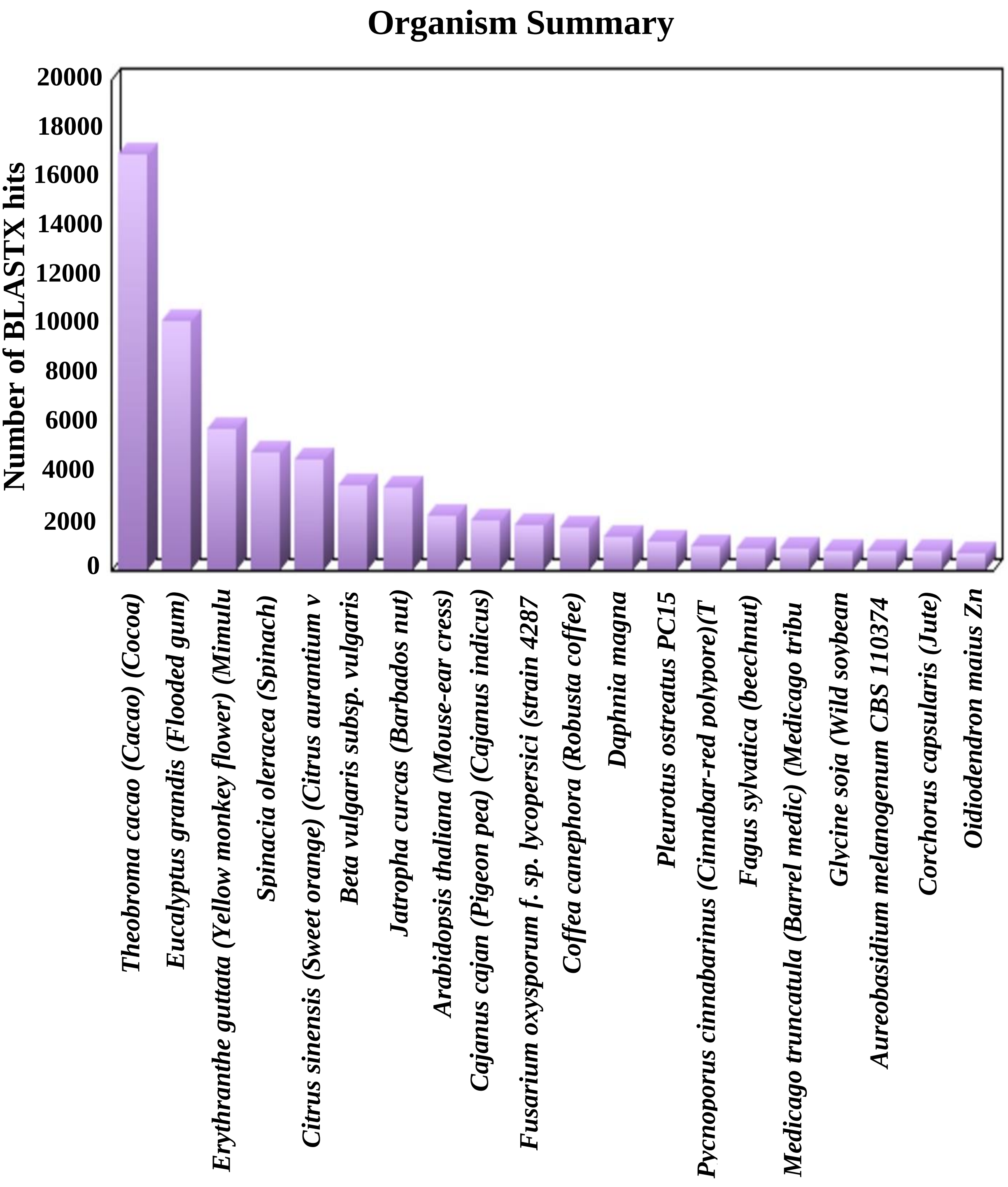


Figure 40. Top 20 hit organism distribution of transcriptome of *Salsola drummondii* Ulbr., using BLASTX.

Gene ontology analysis were performed for all identified unique transcripts to characterize the transcriptome data. Among the **272643** unigenes, **6434** were assigned to different GO terms, including **3213** in the biological processes category, **2329** in the molecular functions and **892** in the cellular components category (Fig. 41). The gene ontology (GO) analysis of the transcripts of the *de novo* assembly of *Salsola drummondii* Ulbr., shows the top 20 hit GO terms of biological process (Fig.42), molecular function (Fig. 43) and Cellular component (Fig. 44).

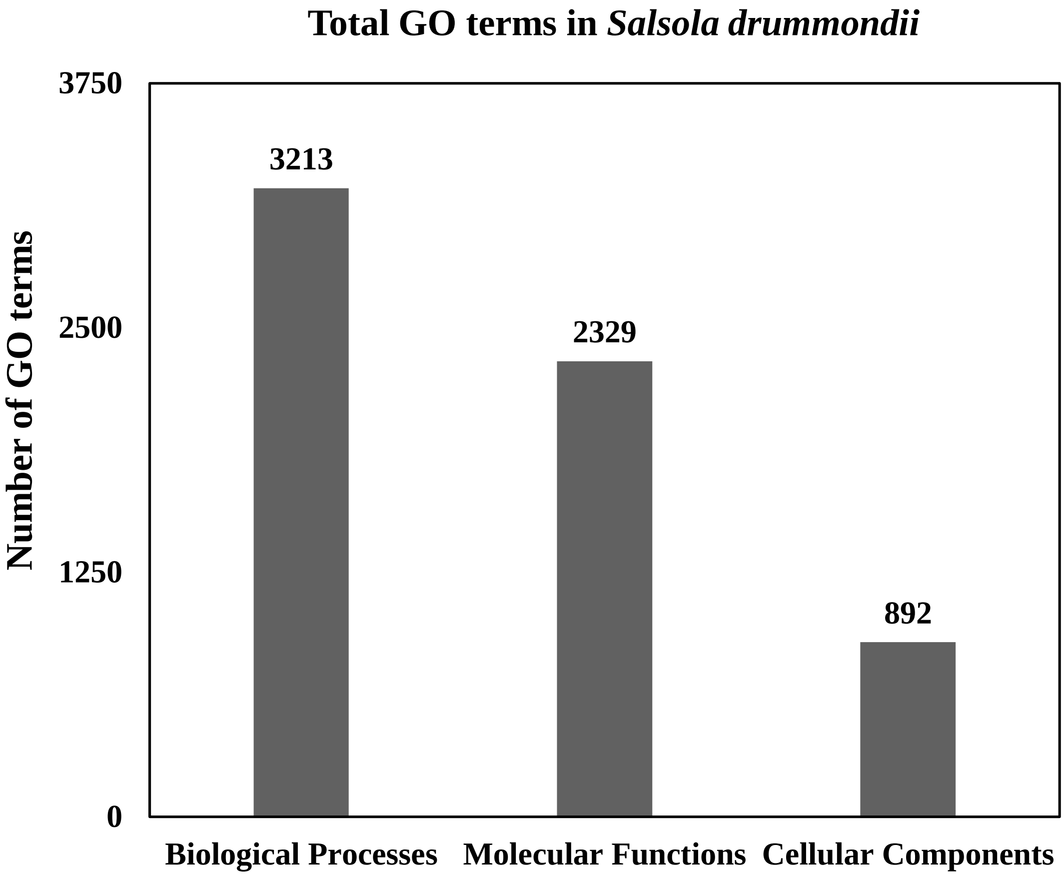


Figure 41. Number of gene ontology (GO) terms identified in each category biological process, molecular function and cellular component in *Salsola drummondii* Ulbr.

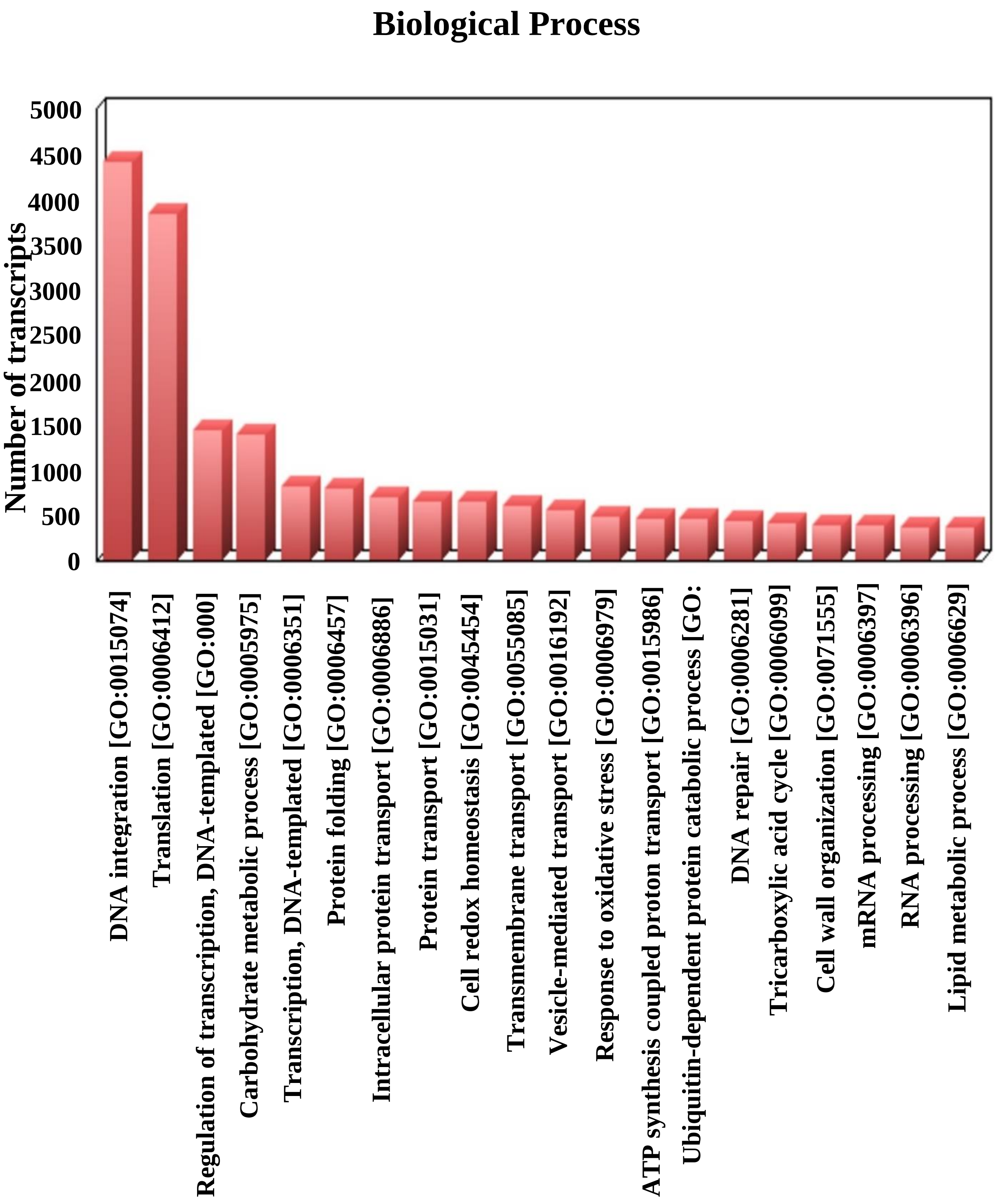


Figure 42. Gene ontology (GO) analysis of the transcripts of the *de novo* assembly of *Salsola drummondii* Ulbr., shows the top 20 hit GO terms of biological process.

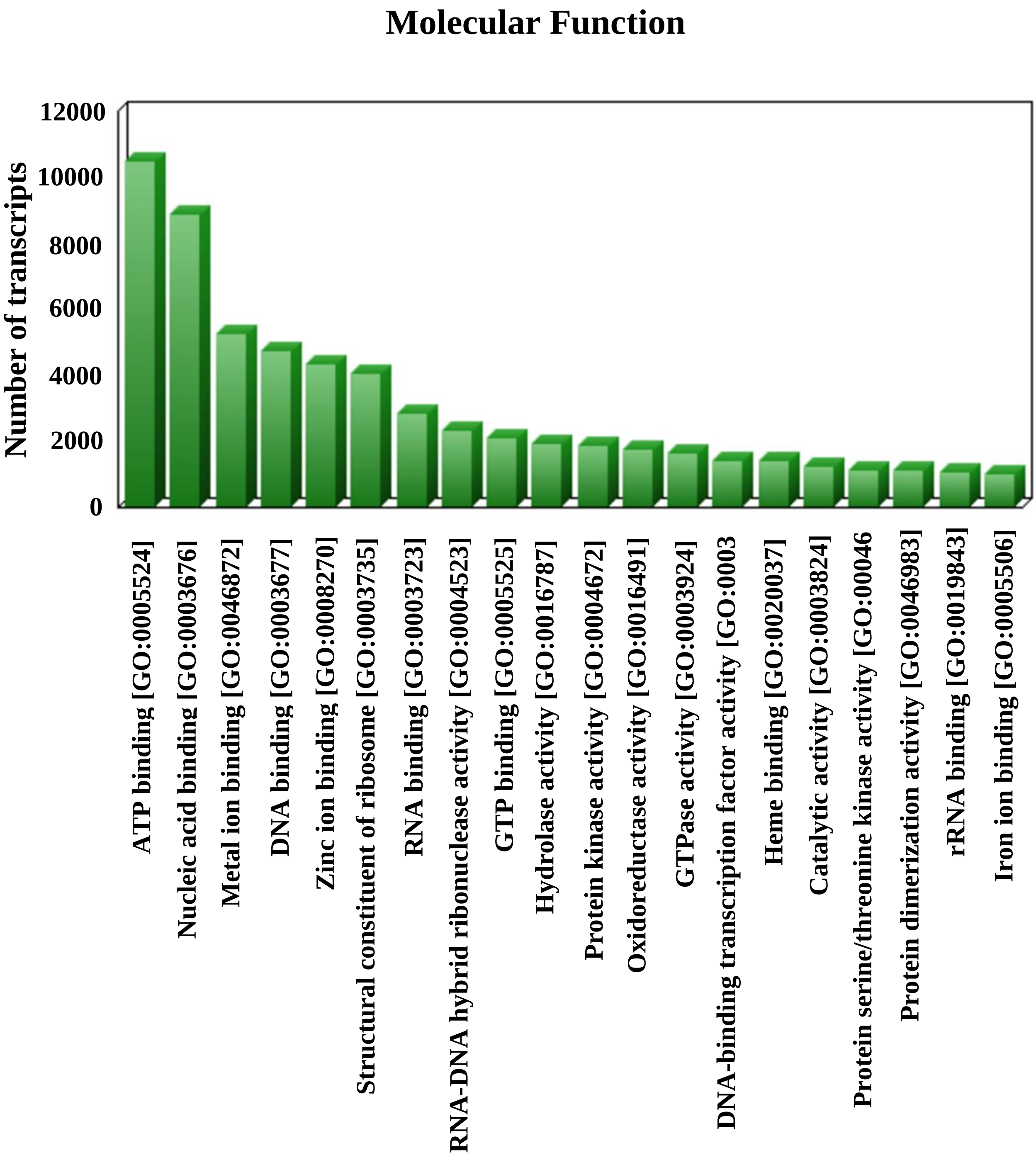


Figure 43. Gene ontology (GO) analysis of the transcripts of the *de novo* assembly of *Salsola drummondii* Ulbr., shows the top 20 hit GO terms of molecular function.

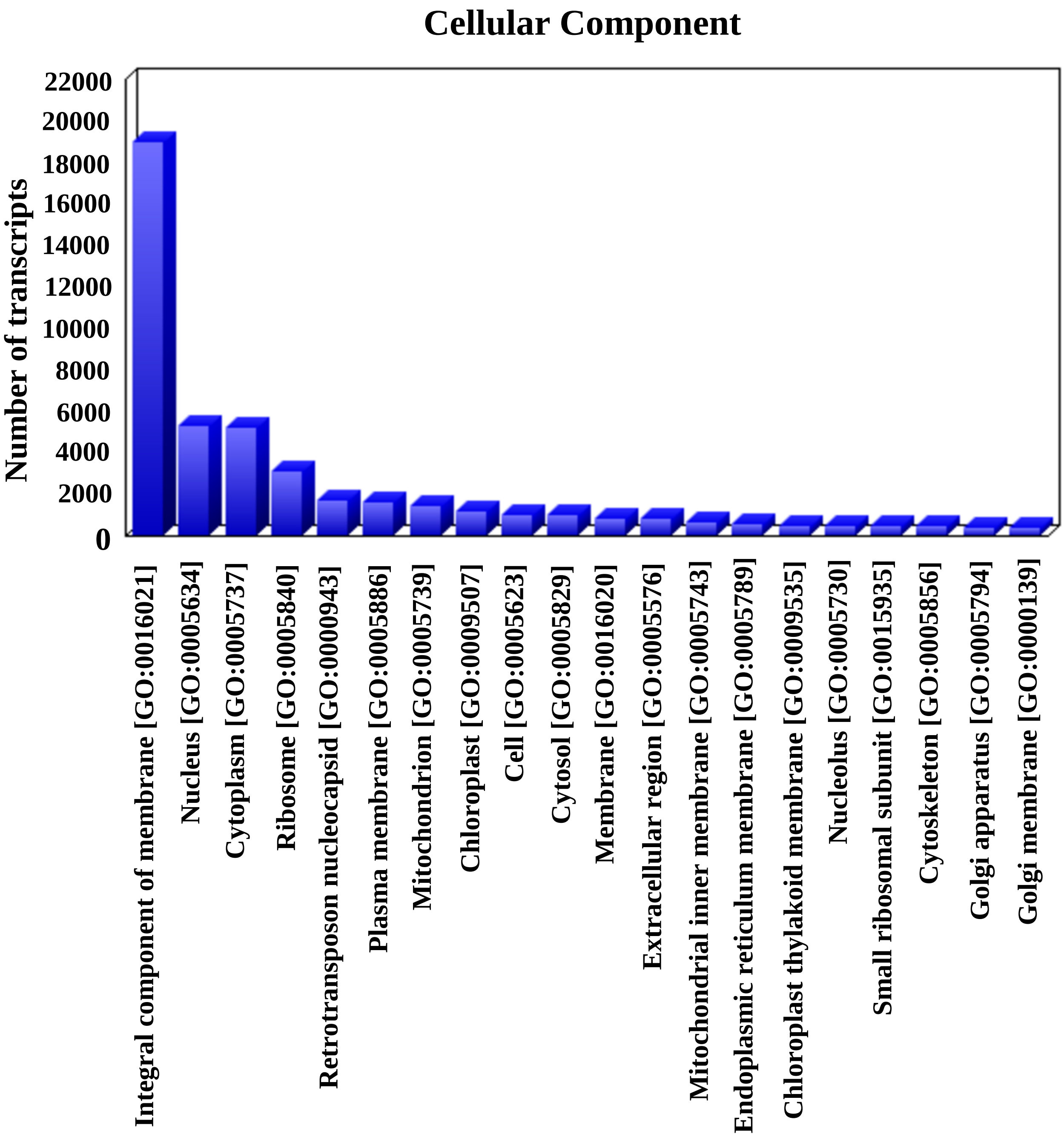


Figure 44. Gene ontology (GO) analysis of the transcripts of the *de novo* assembly of *Salsola drummondii* Ulbr., shows the top 20 hit GO terms of cellular component.

3.6.3. Identification of salt-responsive transcripts

FPKM (fragments per kilobase per million mapped reads) values of each unigenes were calculated to find out the salt responsive transcripts. Comparison of the expression values FPKM between control and salt treated plants showed that the expression levels of 17361(6.36 %) unigenes were significantly (>2 fold, FDR<0.05) altered at salt stress. From the transcriptome assembly, salt responsive genes were calculated based on their expression levels. The number of differentially expressed genes in root and shoot upon salt treatment are shown in (Table 20). In roots of *S. drummondii* Ulbr., total number of differentially expressed gene contigs (contig is a contiguous length of genomic sequence in which the order of bases is known) are represented by volcano plot change as shown in (Fig. 45) and histogram showed the log2 fold change with annotation (Fig. 46). Furthermore, in shoots of *S. drummondii*, volcano plot showed the total number of differentially expressed gene contigs (Fig. 47), and also histogram represented the log2 fold change with annotation (Fig. 48).

Table 20. Total number of differentially expressed genes (DEGs) in *Salsola drummondii* Ulbr., root and shoot tissues under salt treatment with 1200 mM NaCl. Down = downregulated and Up = upregulated.

Plant organ	**DEG contigs with adj p value ≤ 0.05**		**DEGs with adj p value ≤ 0.05**		**DEG contigs with p value ≤ 0.05**		**DEGs with p value ≤ 0.05**	
	Down	Up	Down	Up	Down	Up	Down	Up
Root	4258	7870	3327	6134	28735	33745	22138	25437
Shoot	1105	4130	736	2944	4931	15062	3304	10632

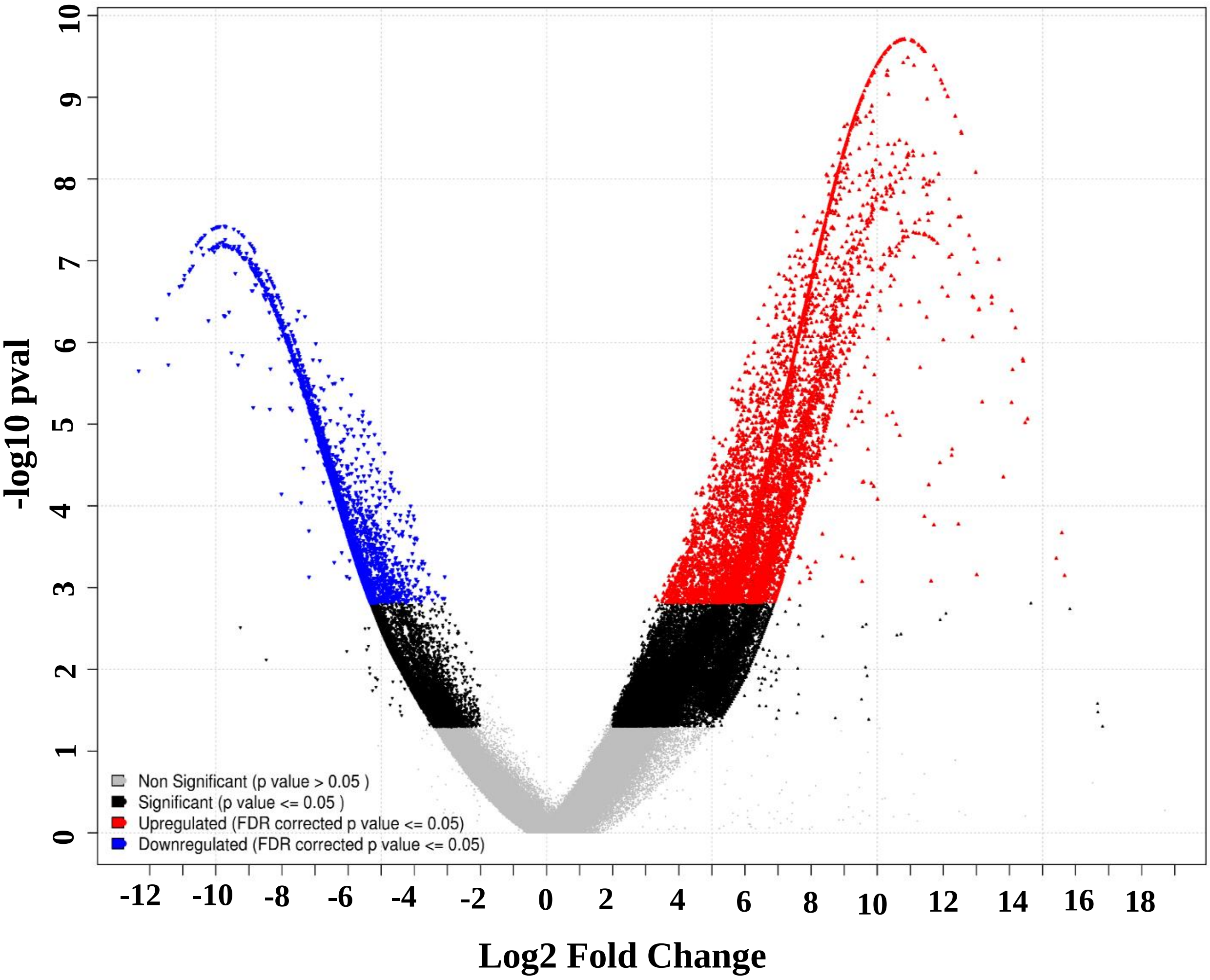


Figure 45. Volcano plot shows the differential gene expression of *S. drummondii* Ulbr., roots upon 1200 mM NaCl treatment (upregulated transcripts represented as red dots and downregulated transcripts represented as blue dots).

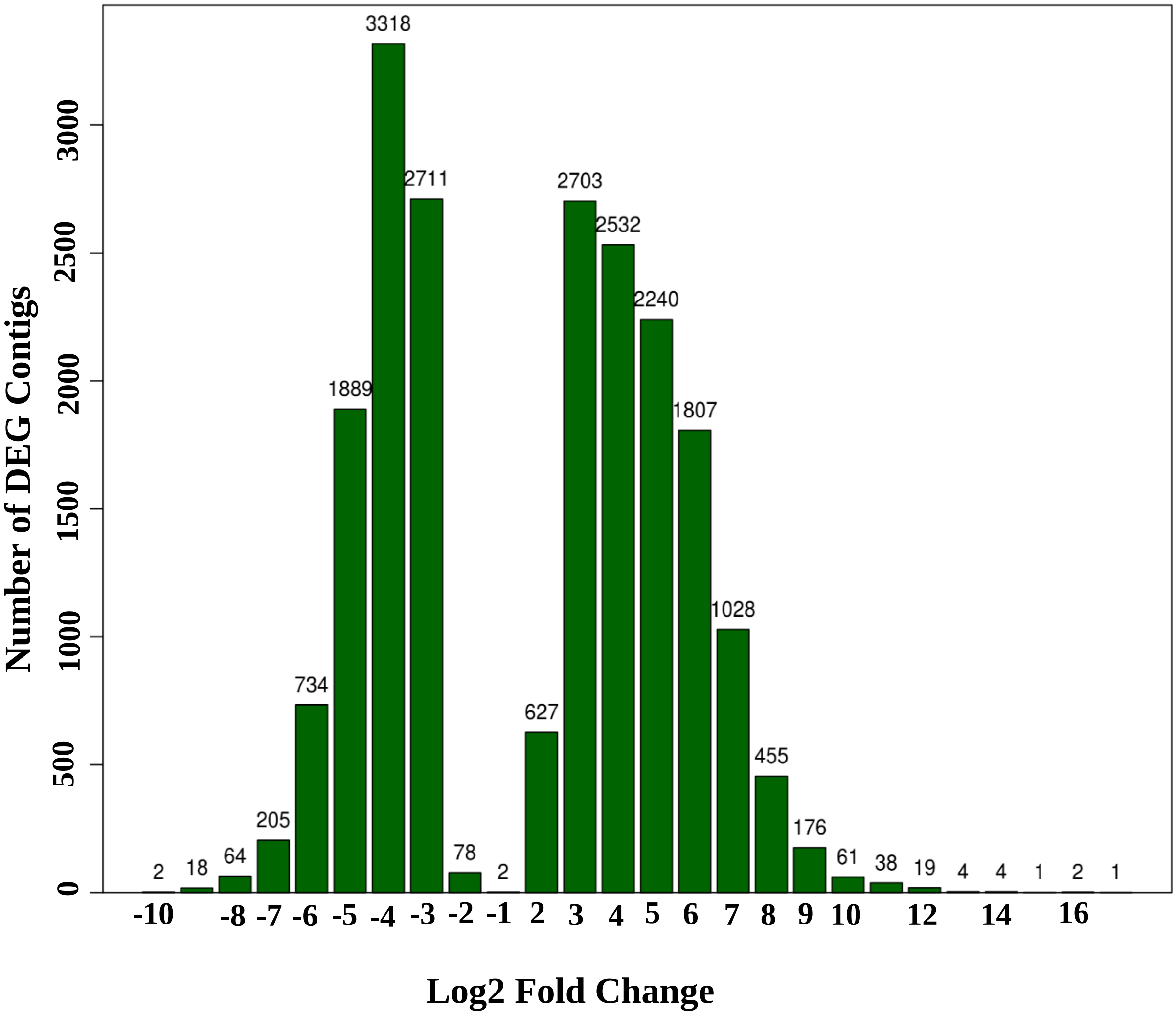


Figure 46. Histogram represents number of differentially expressed gene (DEG) contigs and log2 fold change with annotation in *Salsola drummondii* Ulbr., roots upon 1200 mM NaCl.

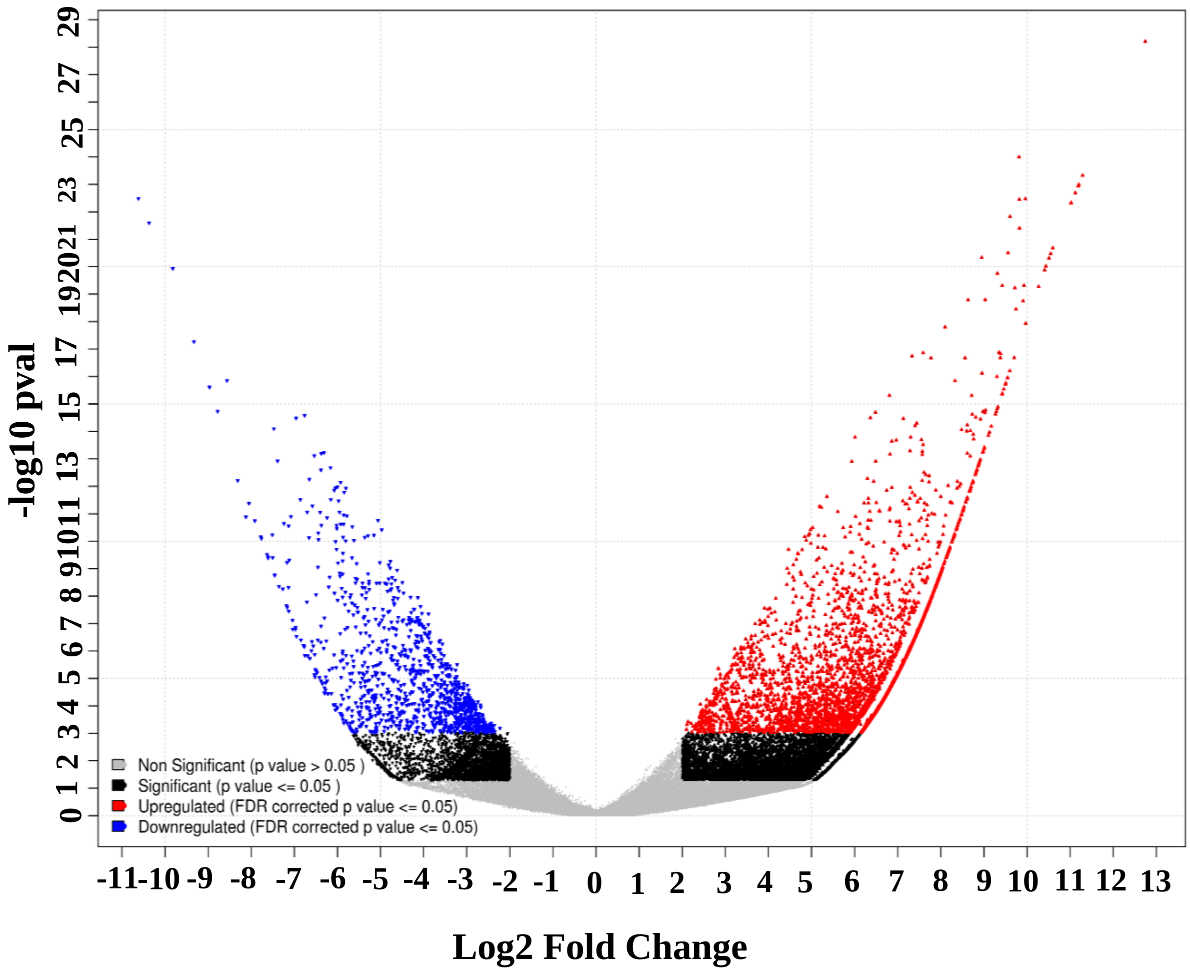


Figure 47. Volcano plot shows the differential gene expression of *Salsola drummondii* Ulbr., shoots upon 1200 mM NaCl treatment (upregulated transcripts represented as red dots and down regulated transcripts represented as blue dots).

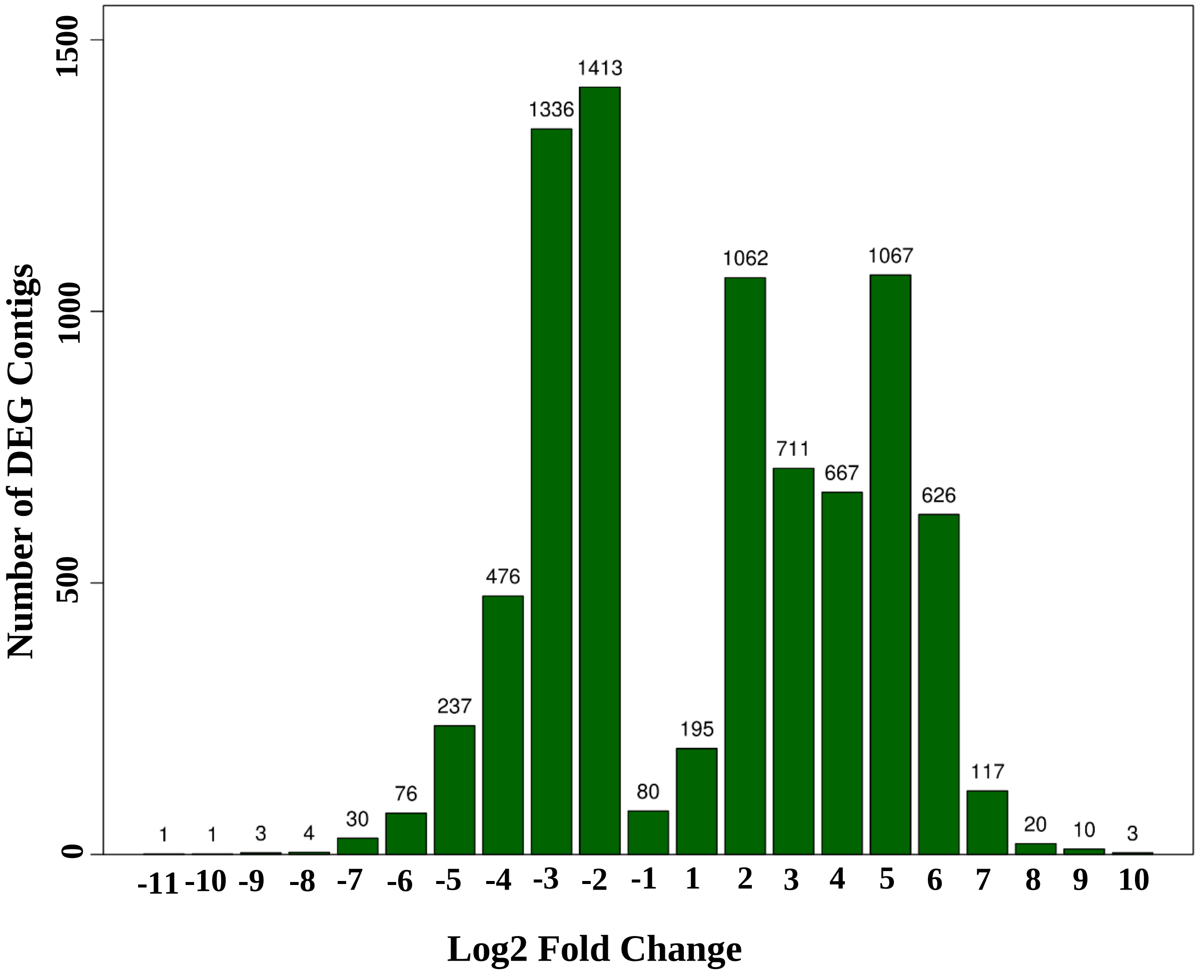


Figure 48. Histogram represents number of differentially expressed genes (DEG) contigs and Log2 fold change with annotation in *Salsola drummondii* Ulbr., shoots upon 1200 mM NaCl treatment.

3.6.4. Differentially regulated transcripts in *Salsola drummondii* Ulbr., under salt stress

Heat maps of top 100 annotated DEGs which are downregulated and upregulated in root of *S. drummondii* under salt stress were shown in (Fig. 49) and (Fig. 50) respectively. Also Heat maps of top 100 annotated DEGs which are downregulated and upregulated in shoot of *S. drummondii* under salt stress were shown in (Fig. 51) and (Fig. 52) respectively.

Downregulated and upregulated transcripts in treated vs control root of *S. drummondii* that were chosen from the top 100 downregulated and top 100 upregulated annotated transcripts were listed in (Table 21) and (Table 22). Also downregulated and upregulated transcripts in treated vs control shoot of *S. drummondii* that were chosen from the top 100 down-regulated and top 100 upregulated annotated transcripts were listed in (Table 23) and (Table 24) respectively.

In *S. drummondii* the differentially expressed genes (DEGs) under salt stress (1200 mM NaCl for 24hrs) include functional categories like transcription factors, regulatory process, signal transduction, defense metabolism, transporters, cell wall metabolism, respiration, chaperons and ubiquitination which may have specific biological function in salt tolerance mechanism of *S. drummondii* (Fig. 53).

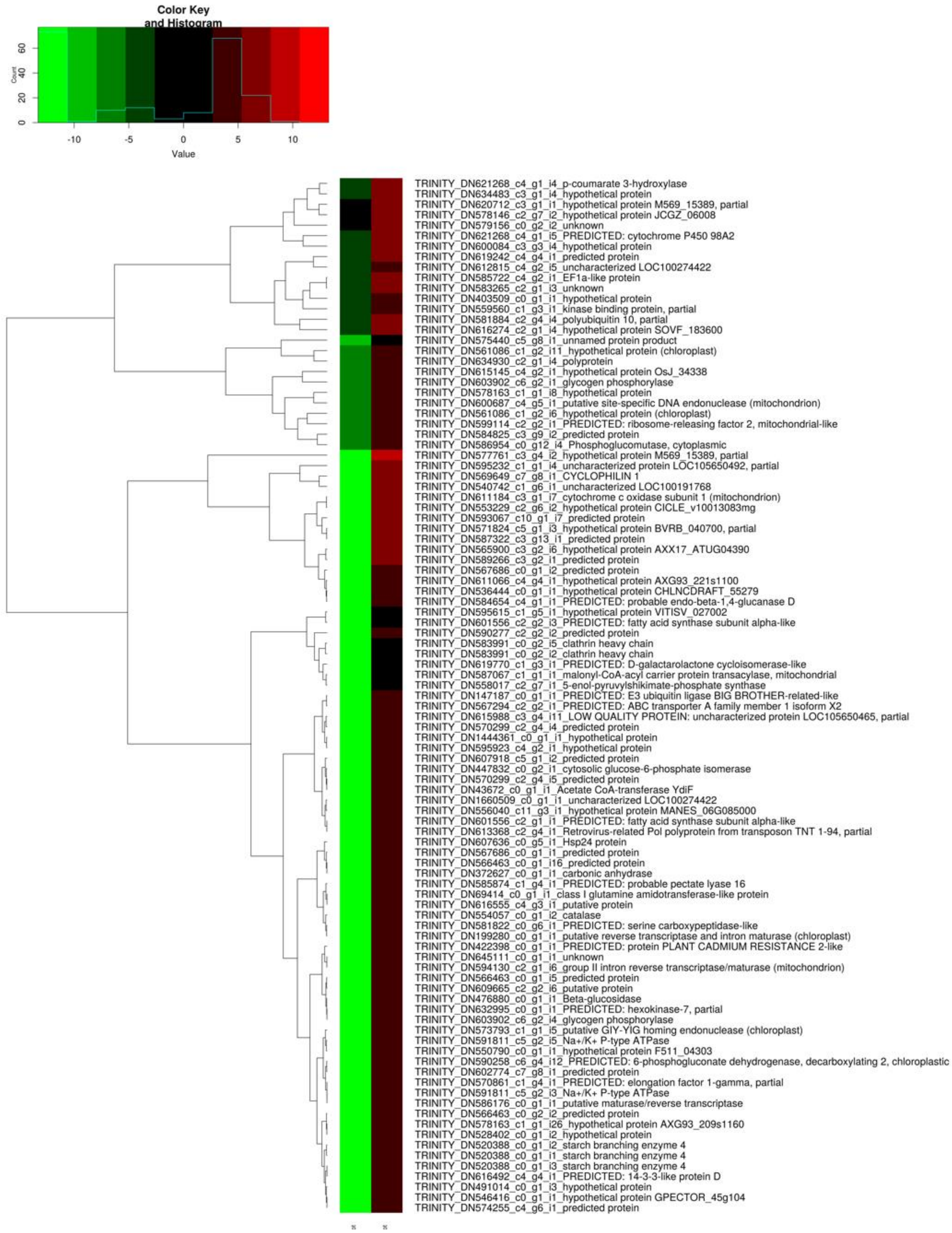


Figure 49. Heat map of top hundred downregulated transcripts in roots of *Salsola drummondii* Ulbr., upon 1200 mM NaCl treatment.

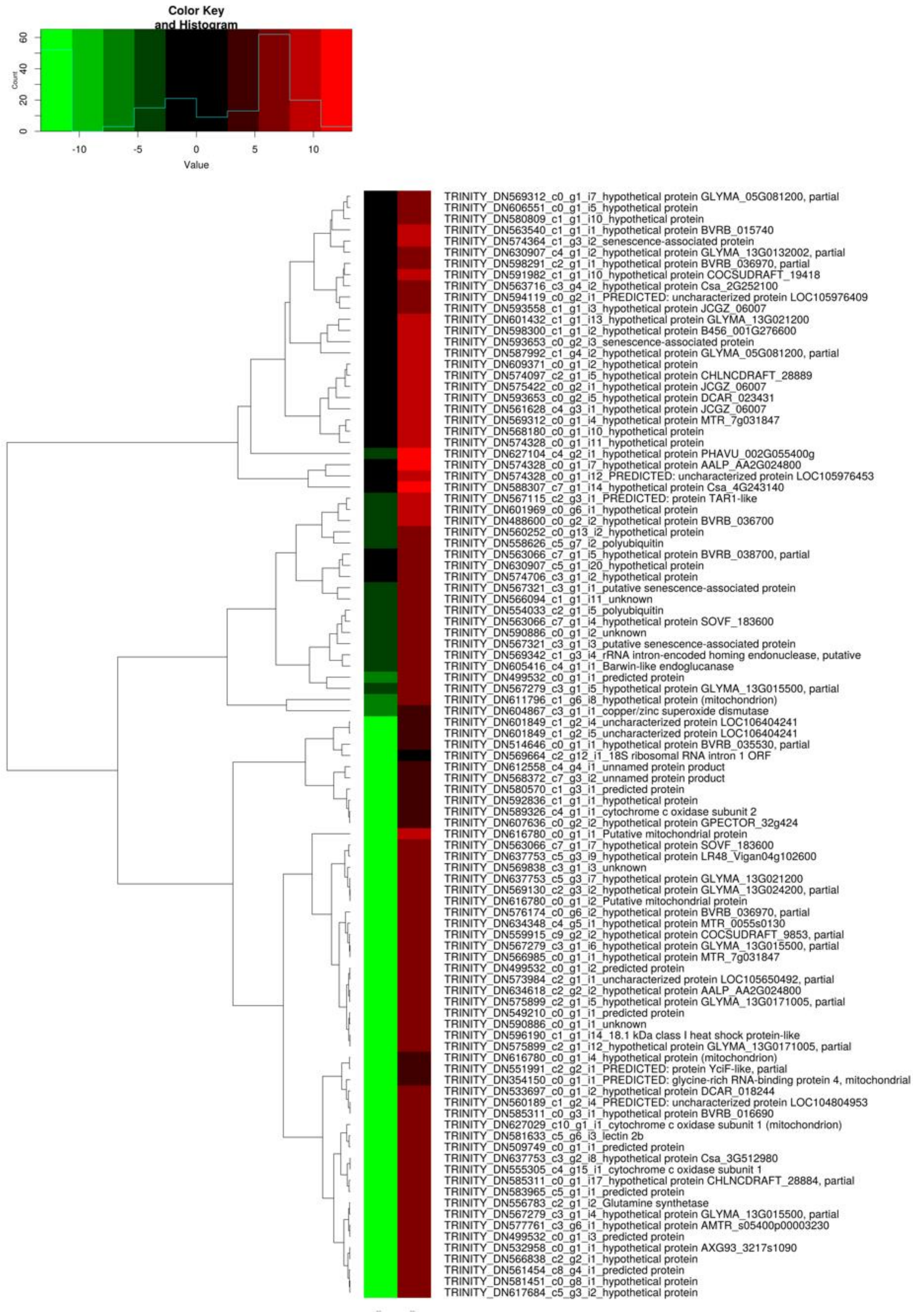


Figure 50. Heat map of top hundred upregulated transcripts in roots of *Salsola drummondii* Ulbr., upon 1200 mM NaCl treatment.

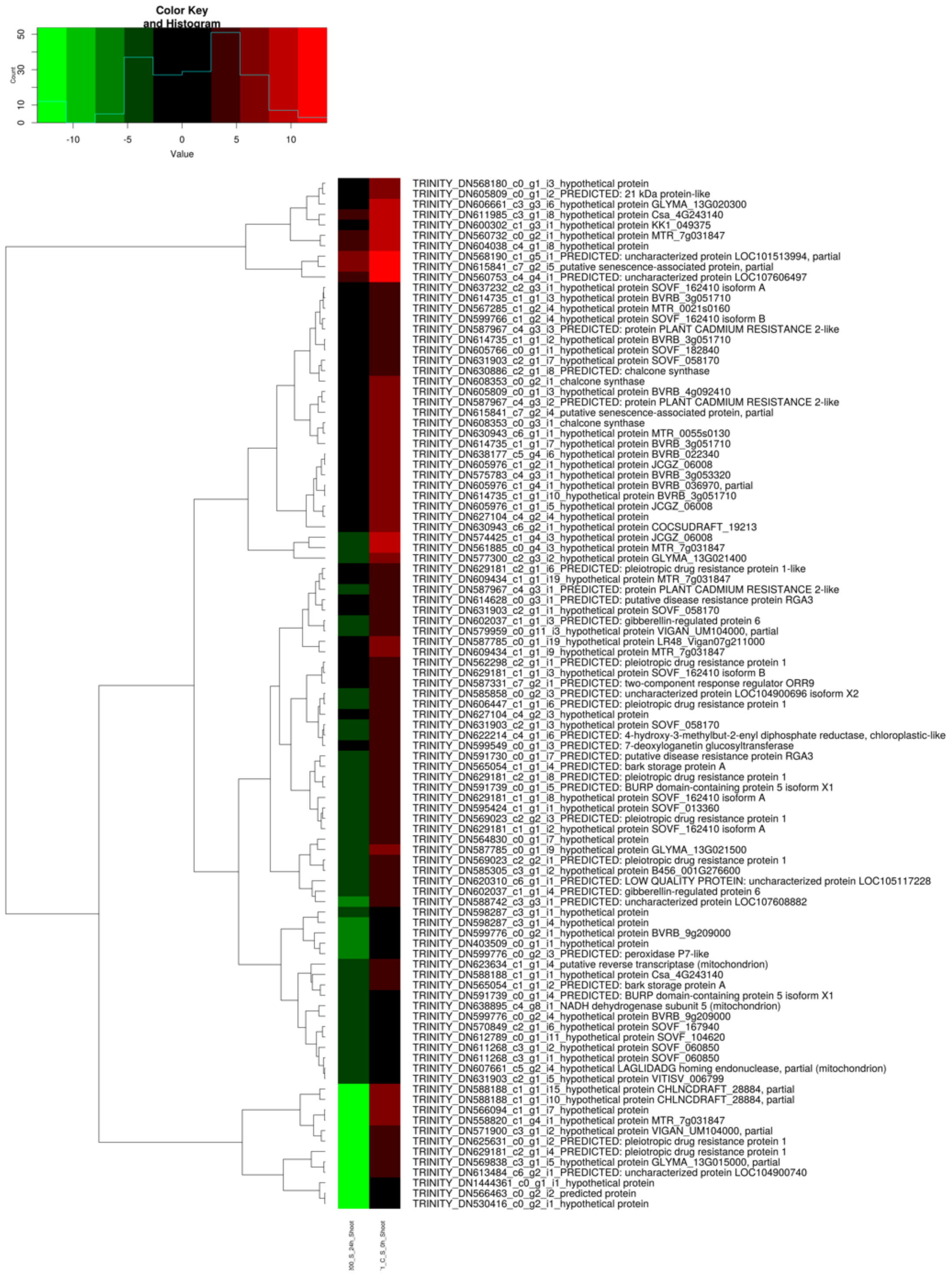


Figure 51. Heat map of top hundred downregulated transcripts in shoots of *Salsola drummondii* Ulbr., upon 1200 mM NaCl treatment.

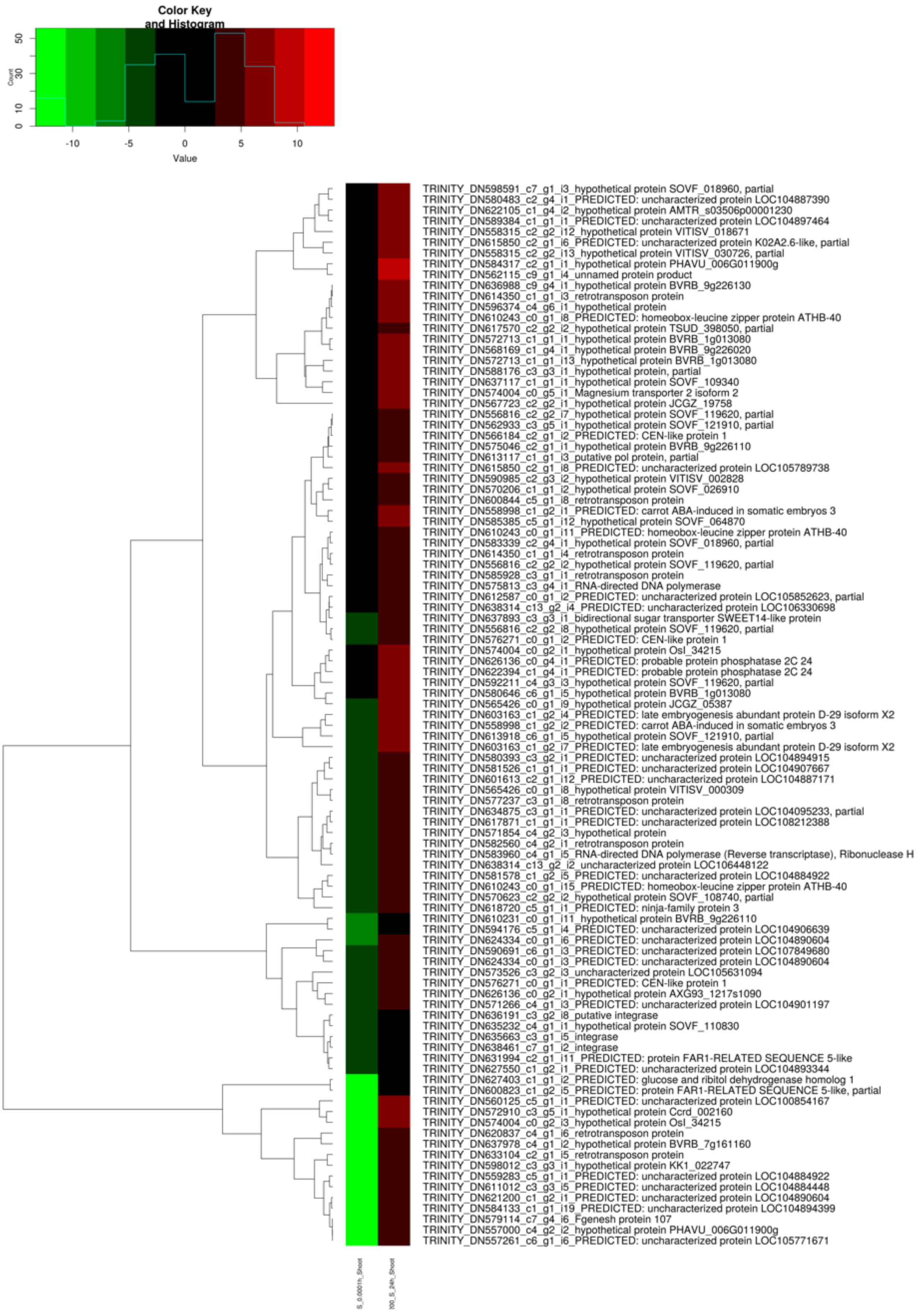


Figure 52. Heat map of top hundred upregulated transcripts in shoots of *Salsola drummondii* Ulbr., upon 1200 mM NaCl treatment.

Table 21. Downregulated transcripts with functional annotation in salt treated vs control roots of *Salsola drummondii* Ulbr. The transcripts were selected from the list of top hundred downregulated annotated transcript.

Transcript ID	**Log2 Fold Change**	**Gene Description**	**Function**
TRINITY_DN567294_c2_g2_i1	-8.623404	ABC transporter A family member 1 isoform X2 [*Vigna radiata* var. radiata]	Protein transporter
TRINITY_DN581884_c2_g4_i4	-7.851605	Polyubiquitin 10, partial [*Arachis hypogaea*]	Protein degradation (Regulation of transcription)
TRINITY_DN634930_c2_g1_i4	-7.819368	Polyprotein [*Citrus sinensis*]	Nucleic acid binding, zinc ion binding and DNA integration
TRINITY_DN583991_c0_g2_i5	-7.65339	Clathrin heavy chain [*Klebsormidium nitens*]	Clathrin coat assembly, intracellular protein transport, and vesicle-mediated transport.
TRINITY_DN590258_c6_g4_i12	-7.569336	6-phosphogluconate dehydrogenase, decarboxylating 2, chloroplastic [*Capsicum annuum*]	Carbohydrate metabolism (pentose phosphate pathways)
TRINITY_DN616492_c4_g4_i1	-7.534436	14-3-3-like protein D [*Elaeis guineensis*]	Regulating cell-signalling
TRINITY_DN422398_c0_g1_i1	-7.402281	Plant cadmium resistance 2-like [*Citrus sinensis*]	Ion transporter
TRINITY_DN581822_c0_g6_i1	-8.561079	Serine carboxypeptidase-like [*Musa acuminata* subsp. malaccensis]	Secondary metabolism and plant defense
TRINITY_DN569649_c7_g8_i1	-8.558728	Cyclophilin 1 [Oryza punctata]	Chaperons (signaling and regulatory pathways)
TRINITY_DN621268_c4_g1_i4	-9.329824	p-coumarate 3-hydroxylase [*Fagopyrum tataricum*]	Metabolic process (lignin pathway)
TRINITY_DN520388_c0_g1_i3	-8.283499	Starch branching enzyme 4 [*Klebsormidium nitens*]	Carbohydrate metabolism (starch biosynthesis)
TRINITY_DN520388_c0_g1_i2	-8.229546	Starch branching enzyme 4 [*Klebsormidium nitens*]	Carbohydrate metabolism (starch biosynthesis)
TRINITY_DN520388_c0_g1_i1	-8.208332	Starch branching enzyme 4	Carbohydrate metabolism (starch

		[*Klebsormidium nitens*]	biosynthesis)
TRINITY_DN476880_c0_g1_i1	-8.020764	Beta-glucosidase [*Klebsormidium nitens*]	Carbohydrate metabolism (cellulose hydrolysis)
TRINITY_DN585874_c1_g4_i1	-7.858918	Probable pectate lyase 16 [*Nicotiana tabacum*]	Carbohydrate metabolism (degradation of pectin)
TRINITY_DN554057_c0_g1_i2	-7.838221	catalase [*Klebsormidium nitens*]	Antioxidant enzyme
TRINITY_DN603902_c6_g2_i1	-8.976779	Glycogen phosphorylase [*Klebsormidium nitens*]	Carbohydrate metabolism
TRINITY_DN601556_c2_g1_i1	-8.966767	fatty acid synthase subunit alpha-like [*Pyrus x bretschneider*i]	Lipid metabolism
TRINITY_DN43672_c0_g1_i1	-8.754053	Acetate CoA-transferase YdiF [*Auxenochlorella protothecoides*]	Lipid metabolism (propanoate metabolism)
TRINITY_DN619770_c1_g3_i1	-8.418675	D-galactarolactone cycloisomerase-like [*Ziziphus jujuba*]	Carbohydrate acid metabolism (pathway D-galacturonate degradation)
TRINITY_DN559560_c1_g3_i1	-8.292916	kinase binding protein, partial [*Oryza sativa* Japonica Group]	Cellular activation and regulatory processes
TRINITY_DN584654_c4_g1_i1	-8.12868	Endo-beta-1,4-glucanase D [Pyrus x bretschneideri]	Carbohydrate metabolism (cellulose degradation, polysaccharide degradation)
TRINITY_DN476880_c0_g1_i1	-8.020764	Beta-glucosidase [*Klebsormidium nitens*]	Carbohydrate metabolism (completes the final step during cellulose hydrolysis by converting the cellobiose to glucose)
TRINITY_DN587067_c1_g1_i1	-8.013305	Malonyl-CoA-acyl carrier protein transacylase, mitochondrial [*Dorcoceras hygrometricum*]	Lipid metabolism
TRINITY_DN594130_c2_g1_i6	-7.895692	Group II intron reverse transcriptase/maturase (mitochondrion) [*Prasiola crispa*]	Intron mobility and also as Maturases to promote RNA splicing

TRINITY_DN69414_c0_g1_i1	-7.801652	Class I glutamine amidotransferase-like protein [*Coccomyxa subellipsoidea* C-169]	Glutamine metabolic process
TRINITY_DN147187_c0_g1_i1	-7.797919	E3 ubiquitin ligase BIG BROTHER-related-like [*Tarenaya hassleriana*]	Protein degradation
TRINITY_DN585874_c1_g4_i1	-7.858918	Pectate lyase 16 [*Nicotiana tabacum*]	Carbohydrate metabolism (degradation of pectin)
TRINITY_DN558017_c2_g7_i1	-7.661515	5-enol-pyruvylshikimate-phosphate synthase [*Conyza sumatrensis*]	Carbohydrate metabolism (shikimate pathway)
TRINITY_DN447832_c0_g2_i1	-7.623212	Cytosolic glucose-6-phosphate isomerase [*Chara vulgaris*]	carbohydrate metabolism (glycolysis)
TRINITY_DN372627_c0_g1_i1	-7.611874	Carbonic anhydrase [*Klebsormidium nitens*]	Carbohydrate metabolism
TRINITY_DN601556_c2_g2_i3	-7.387662	fatty acid synthase subunit alpha-like [*Pyrus x bretschneider*i]	Fatty acid biosynthetic process
TRINITY_DN586954_c0_g12_i4	-7.384198	Phosphoglucomutase, cytoplasmic [*Gossypium arboreum*]	Carbohydrate metabolism
TRINITY_DN621268_c4_g1_i5	-8.63385	cytochrome P450 98A2 [Beta vulgaris subsp. vulgaris]	Phenolic metabolism
TRINITY_DN607636_c0_g5_i1	-8.328508	Hsp24 protein [*Populus davidiana* x *Populus alba* var. pyramidalis]	Chaperones
TRINITY_DN613368_c2_g4_i1	-7.801827	Retrovirus-related Pol polyprotein from transposon TNT 1-94, partial [*Cajanus cajan*]	DNA integration
TRINITY_DN599114_c2_g2_i1	-7.767014	Ribosome-releasing factor 2, mitochondrial-like [*Populus euphratica*]	Mitochondrial translation

Table 22. Upregulated transcripts with functional annotation in salt treated vs control roots of *Salsola drummondii* Ulbr. The transcripts were selected from the list of top hundred upregulated annotated transcript.

Transcript ID	**Log2 Fold Change**	**Gene Description**	**Function**
TRINITY_DN567115_c2_g3_i1	13.81481241	Protein TAR1-like [*Cicer arietinum*]	Hormone metabolism (pathway auxin biosynthesis)
TRINITY_DN593653_c0_g2_i3	13.17583408	Senescence-associated protein [*Medicago truncatula*]	Cellular signal transduction and cell viability
TRINITY_DN574364_c1_g3_i2	11.29722955	Senescence-associated protein	Cellular signal transduction and cell viability
TRINITY_DN556783_c2_g1_i2	11.24672453	Glutamine synthetase [*Klebsormidium nitens*]	Glutamine biosynthetic process
TRINITY_DN604867_c3_g1_i1	10.92713864	Copper/zinc superoxide dismutase [*Klebsormidium nitens*]	Antioxidant enzyme
TRINITY_DN555305_c4_g15_i1	10.34676503	cytochrome c oxidase subunit 1	
TRINITY_DN596190_c1_g1_i14	10.32927904	18.1 kDa class I heat shock protein-like [*Dorcoceras hygrometricum*]	Chaperons (protein folding)
TRINITY_DN558626_c5_g7_i2	10.24505127	Polyubiquitin	Protein degradation
TRINITY_DN589326_c4_g1_i1	10.05225997	Cytochrome c oxidase subunit 2	
TRINITY_DN627029_c10_g1_i1	10.04959256	Cytochrome c oxidase subunit 1 (mitochondrion) [*Schrenkiella parvula*]	
TRINITY_DN354150_c0_g1_i1	10.0007162	Glycine-rich RNA-binding protein 4, mitochondrial [*Oryza sativa* Japonica Group]	RNA binding
TRINITY_DN554033_c2_g1_i5	9.858374003	polyubiquitin	Protein degradation
TRINITY_DN551991_c2_g2_i1	9.837489627	Protein YciF-like, partial [*Ziziphus jujuba*]	Stress protein
TRINITY_DN605416_c4_g1_i1	9.820250094	Barwin-like endoglucanase [*Cynara cardunculus* var. scolymus]	Polysaccharide metabolism and transport

Table 23. Downregulated transcripts with functional annotation in salt treated vs control shoots of *Salsola drummondii* Ulbr. The transcripts were selected from the list of top hundred downregulated annotated transcripts.

Transcript Id	**Log2 Fold Change**	**Gene Description**	**Group Function**
TRINITY_DN602037_c1_g1_i4	-8.314012419	Gibberellin-regulated protein 6 [*Beta vulgaris* subsp. vulgaris]	Hormone signalling transduction
TRINITY_DN602037_c1_g1_i3	-7.474357045	Gibberellin-regulated protein 6 [*Beta vulgaris* subsp. vulgaris]	Hormone signalling transduction
TRINITY_DN569023_c2_g2_i1	-7.267231516	Pleiotropic drug resistance protein 1 [*Beta vulgaris* subsp. vulgaris]	ABC transporters
TRINITY_DN591739_c0_g1_i5	-7.17077495	BURP domain-containing protein 5 isoform X1 [*Beta vulgaris* subsp. vulgaris]	Defense Metabolism
TRINITY_DN629181_c2_g1_i6	-7.135629422	pleiotropic drug resistance protein 1-like [*Prunus mume*]	ABC transporters
TRINITY_DN565054_c1_g1_i4	-7.133438709	Bark storage protein A [*Beta vulgaris* subsp. vulgaris]	Nitrogen storage, catalytic activity and nutrient reservoir activity
TRINITY_DN625631_c0_g1_i2	-7.037158789	Pleiotropic drug resistance protein 1 [*Beta vulgaris* subsp. vulgaris]	ABC transporters
TRINITY_DN608353_c0_g2_i1	-6.860032509	Chalcone synthase [*Morus alba* var. multicaulis]	Transferase activity and metabolism (the flavonoid/isoflavonoid biosynthesis pathway)
TRINITY_DN629181_c2_g1_i8	-6.756601378	Pleiotropic drug resistance protein 1 [*Beta vulgaris* subsp. vulgaris]	ABC transporters
TRINITY_DN587967_c4_g3_i1	-6.56033105	Plant cadmium resistance 2-like [*Beta vulgaris* subsp. vulgaris]	Response to oxidative stress and ion transporter

TRINITY_DN599776_c0_g2_i3	-6.533006633	Peroxidase P7-like [*Beta vulgaris* subsp. vulgaris]	Response to oxidative stress
TRINITY_DN591739_c0_g1_i4	-6.520834472	BURP domain-containing protein 5 isoform X1 [*Beta vulgaris* subsp. vulgaris]	Defense metabolism
TRINITY_DN630886_c2_g1_i8	-6.496620982	Chalcone synthase [*Beta vulgaris* subsp. vulgaris]	Transferase activity and metabolism (the flavonoid/ isoflavonoid biosynthesis pathway)
TRINITY_DN606447_c1_g1_i6	-6.400322909	Pleiotropic drug resistance protein 1 [*Beta vulgaris* subsp. vulgaris]	ABC transporters
TRINITY_DN565054_c1_g1_i2	6.386076613	Bark storage protein A [*Beta vulgaris* subsp. vulgaris]	Nitrogen storage, catalytic activity and nutrient reservoir activity
TRINITY_DN622214_c4_g1_i6	-6.181749682	4-hydroxy-3-methylbut-2-enyl diphosphate reductase, chloroplastic-like [*Cicer arietinum*]	Chloroplast development
TRINITY_DN569023_c2_g2_i3	-6.139944146	Pleiotropic drug resistance protein 1 [*Beta vulgaris* subsp. vulgaris]	ABC transporter
TRINITY_DN605809_c0_g1_i2	-6.074136346	21 kDa protein-like [*Beta vulgaris* subsp. vulgaris]	Enzyme inhibitor activity and regulation of cell wall extension
TRINITY_DN587967_c4_g3_i2	-6.068822492	Protein PLANT CADMIUM RESISTANCE 2-like [*Beta vulgaris* subsp. vulgaris]	Response to oxidative stress
TRINITY_DN599549_c0_g1_i3	-5.939491367	7-deoxyloganetin glucosyltransferase [*Beta vulgaris* subsp. vulgaris]	Biosynthesis of monoterpene indole alkaloids and quinoline alkaloids (secologanin biosynthesis)
TRINITY_DN587331_c7_g2_i1	-5.879902932	Two-component response regulator ORR9 [*Beta vulgaris* subsp. vulgaris]	Signal transduction (cytokinin-activated signalling pathway)

TRINITY_DN629181_c2_g1_i4	-5.852165224	Pleiotropic drug resistance protein 1 [*Beta vulgaris* subsp. vulgaris]	ABC transporter
TRINITY_DN562298_c2_g1_i1	-5.707783672	Pleiotropic drug resistance protein 1 [*Beta vulgaris* subsp. vulgaris]	ABC transporter
TRINITY_DN608353_c0_g3_i1	-5.662797644	Chalcone synthase [*Acacia confusa*]	Transferase activity and metabolism (the flavonoid/ isoflavonoid biosynthesis pathway)
TRINITY_DN638895_c4_g8_i1	-5.643113137	NADH dehydrogenase subunit 5 (mitochondrion) [*Roya obtusa*]	Carbohydrate metabolism and mitochondrial electron transport chain
TRINITY_DN587967_c4_g3_i3	-5.630730199	Plant cadmium resistance 2-like [*Beta vulgaris* subsp. vulgaris]	Response to oxidative stress and ion transporter

Table 24. Upregulated transcripts with functional annotation in salt treated vs control shoots of *Salsola drummondii* Ulbr. The transcripts were selected from the list of top hundred upregulated annotated transcripts.

Transcript Id	**Log2 Fold Change**	**Gene Description**	**Group Function**
TRINITY_DN603163_c1_g2_i4	9.815318338	Late embryogenesis abundant protein D-29 isoform X2 [*Beta vulgaris* subsp. vulgaris]	Response to stimulus (chaperons)
TRINITY_DN558998_c1_g2_i2	8.614282772	Carrot ABA-induced in somatic embryos 3 [*Beta vulgaris* subsp. vulgaris]	ABA Signal Transduction
TRINITY_DN622394_c1_g4_i1	7.883703289	Protein phosphatase 2C 24 [*Beta vulgaris* subsp. vulgaris]	ABA Signal Transduction
TRINITY_DN626136_c0_g4_i1	7.770725338	Protein phosphatase 2C 24 [*Beta vulgaris* subsp. vulgaris]	ABA Signal Transduction
TRINITY_DN576271_c0_g1_i1	7.643210231	CEN-like protein 1 [*Beta vulgaris* subsp. vulgaris]	Involved in the control of shoot meristem identity and flowering time
TRINITY_DN574004_c0_g5_i1	7.607620942	Magnesium transporter 2 isoform 2 [*Dorcoceras hygrometricum*]	Ion transporter
TRINITY_DN637893_c3_g3_i1	7.56815089	Bidirectional sugar transporter SWEET14-like protein [*Suaeda glauca*]	Carbohydrate transport
TRINITY_DN627403_c1_g1_i2	7.48193581	Glucose and ribitol dehydrogenase homolog 1 [*Beta vulgaris* subsp. vulgaris]	Carbohydrate metabolism, signal transduction and oxidoreductase activity
TRINITY_DN576271_c0_g1_i2	7.397980963	CEN-like protein 1 [*Beta vulgaris* subsp. vulgaris]	Involved in the control of shoot meristem identity and flowering time

TRINITY_DN610243_c0_g1_i11	7.332514952	Homeobox-leucine zipper protein ATHB-40 [*Beta vulgaris* subsp. vulgaris]	Transcription factors
TRINITY_DN566184_c2_g1_i2	7.289282965	CEN-like protein 1 [*Beta vulgaris* subsp. vulgaris]	Involved in the control of shoot meristem identity and flowering time
TRINITY_DN618720_c5_g1_i1	7.281835182	Ninja-family protein 3 [*Beta vulgaris* subsp. vulgaris]	Signal transduction
TRINITY_DN585928_c3_g1_i1	7.278614771	Retrotransposon protein [*Beta vulgaris*]	Nucleic acid binding
TRINITY_DN638461_c7_g1_i2	7.270530441	Integrase [*Beta vulgaris*]	Transcription factors
TRINITY_DN614350_c1_g1_i3	7.2629674	Retrotransposon protein [*Beta vulgaris*]	Nucleic acid binding
TRINITY_DN610243_c0_g1_i15	7.259729423	Homeobox-leucine zipper protein ATHB-40 [*Beta vulgaris* subsp. vulgaris]	Transcription factors
TRINITY_DN614350_c1_g1_i4	7.251502744	Retrotransposon protein [*Beta vulgaris*]	Nucleic acid binding
TRINITY_DN577237_c3_g1_i8	7.243909811	Retrotransposon protein [*Beta vulgaris*]	Nucleic acid binding
TRINITY_DN575813_c3_g4_i1	7.22948932	RNA-directed DNA polymerase [*Theobroma cacao*]	RNA-directed DNA polymerase activity
TRINITY_DN633104_c2_g1_i5	7.224047425	Retrotransposon protein [*Beta vulgaris*]	Nucleic acid binding
TRINITY_DN610243_c0_g1_i8	7.129534335	Homeobox-leucine zipper protein ATHB-40 [*Beta vulgaris* subsp. vulgaris]	Transcription factors
TRINITY_DN635663_c3_g1_i5	7.102771485	Integrase [*Beta vulgaris*]	Transcription factors

TRINITY_DN558998_c1_g2_i1	7.055931414	Carrot ABA-induced in somatic embryos 3 [*Beta vulgaris* subsp. vulgaris]	Signal transduction and Transcription factor
TRINITY_DN631994_c2_g1_i11	6.949479476	Protein FAR1-RELATED SEQUENCE 5-like [*Beta vulgaris* subsp. vulgaris]	Transcription factor
TRINITY_DN600823_c1_g2_i5	6.931774069	Protein FAR1-RELATED SEQUENCE 5-like, partial [*Beta vulgaris* subsp. vulgaris]	Transcription factor
TRINITY_DN620837_c4_g1_i6	6.919476276	Retrotransposon protein [*Beta vulgaris*]	Nucleic acid binding
TRINITY_DN583960_c4_g1_i5	6.909051038	RNA-directed DNA polymerase (Reverse transcriptase), Ribonuclease H [*Theobroma cacao*]	RNA-directed DNA polymerase activity
TRINITY_DN579114_c7_g4_i6	6.878185985	Fgenesh protein 107 [*Beta vulgaris*]	Cell redox homeostasis
TRINITY_DN600844_c5_g1_i8	6.863579045	Retrotransposon protein [*Beta vulgaris*]	Nucleic acid binding
TRINITY_DN582560_c4_g2_i1	6.822530359	Retrotransposon protein [*Beta vulgaris*]	Nucleic acid binding

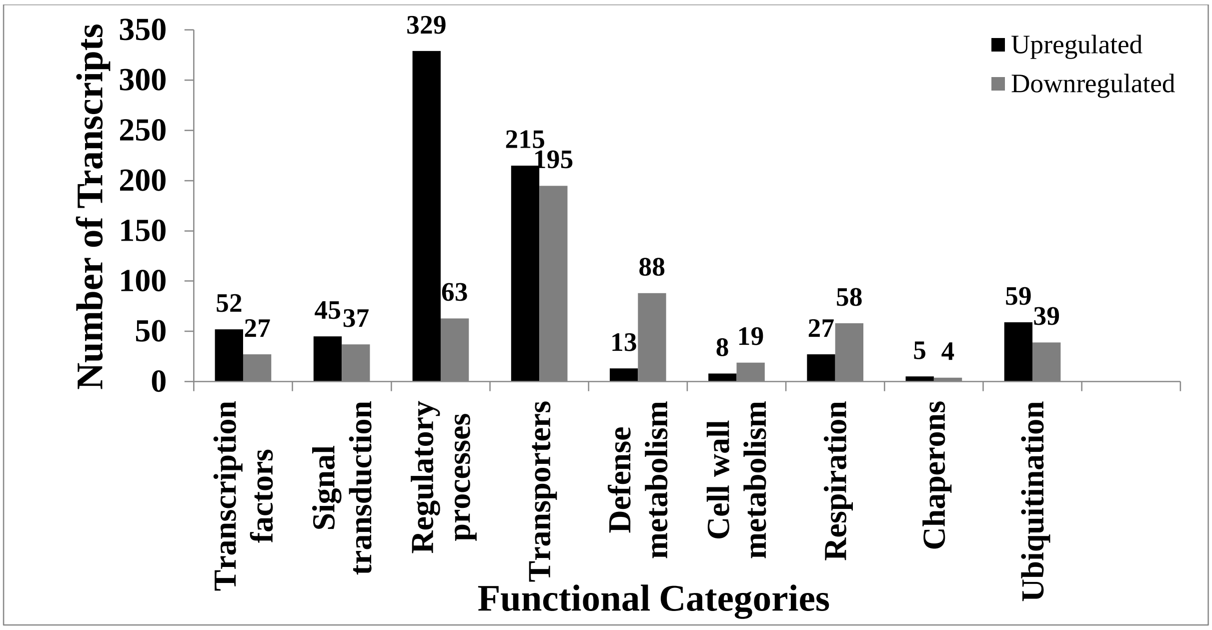


Figure 53. Clustered bar graph shows candidates salt stress related functional categories of upregulated and downregulated transcripts in *Salsola drummondii* Ulbr., treated with 1200 mM NaCl.

3.6.5. Validation of differentially expressed genes (DEGs) in *Salsola drummondii* under salt by real time polymerase chain reaction (qRT-PCR)

To validate the *de novo* transcriptome results, quantitative real time PCR (qRT-PCR) analysis was performed for selected differentially expressed genes (DEGs) candidates using specific primers. The qRT-PCR data were calculated using ddCT method (Livak and Schmittgen, 2001). The qRT-PCR results were highly correlated with the *de novo* transcriptome data, All the tested genes were showed similar trend as transcriptome analysis. The same pattern of differential expression for 4 transcripts in root and 5 transcripts in shoot were confirmed by qRT-PCR analysis, which each showed similar levels of up- or down-regulation. In roots of *Salsola drummondii* Ulbr., (Cyclophilin 1 and Malonyl-CoA-acyl carrier protein transacylase, mitochondrial) showed downregulation (Fig. 54) and (Glycine-rich RNA-binding protein 4, mitochondrial and Glutamine synthetase) showed upregulation (Fig. 55) at 1200 mM NaCl in comparison with control (0 mM NaCl) in both qRT-PCR and *de novo* transcriptome. In shoots of S*alsola drummondii* Ulbr., (Peroxidase P7-like and Gibberellin-regulated protein 6.) showed downregulation (Fig. 56) and (Carrot ABA-induced in somatic embryos, 3 Magnesium transporter 2 isoform 2 and Homeobox-leucine zipper protein ATHB-40) showed upregulation (Fig. 57) at 1200 mM NaCl in comparison with control in both qRT-PCR and *de novo* transcriptome.

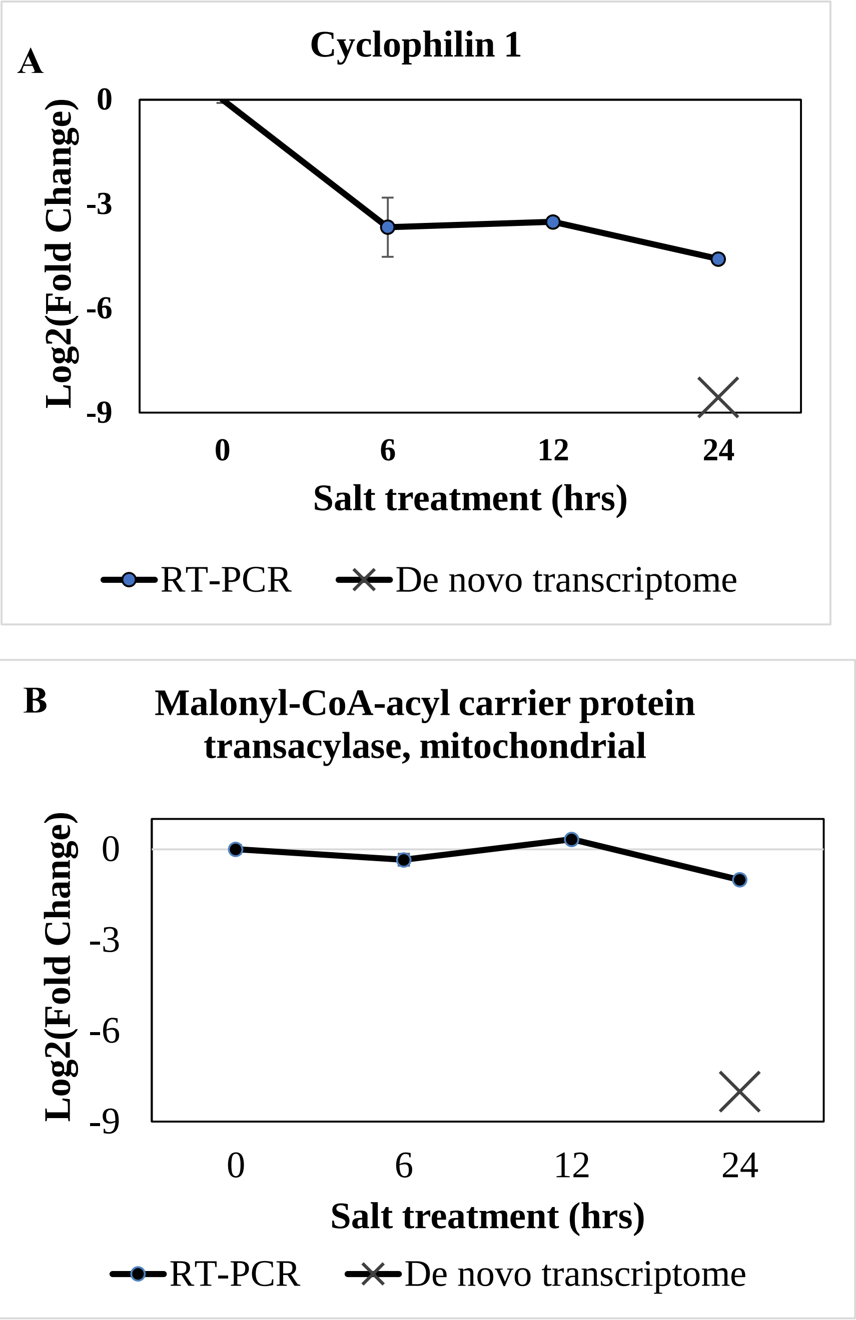
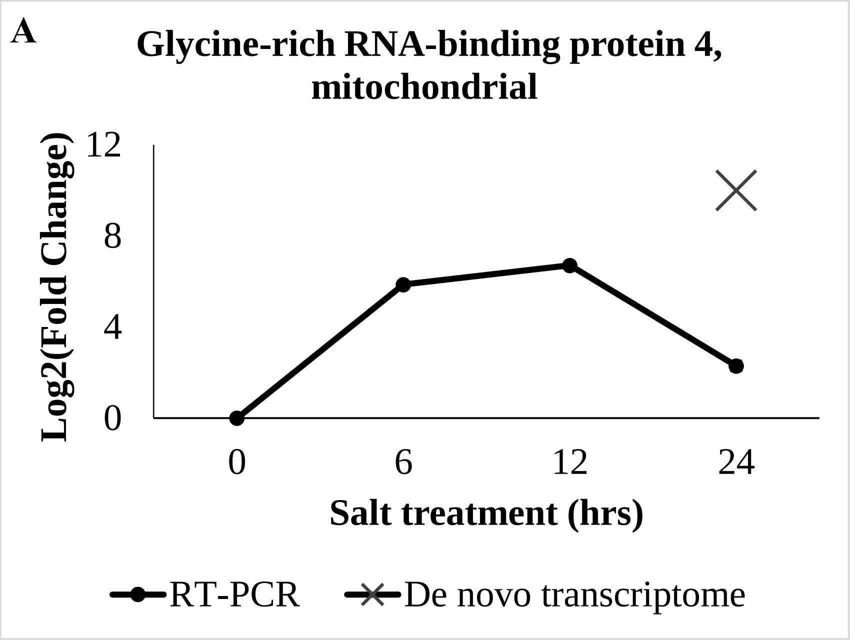


Figure 54. Validation of *de novo* transcriptome results by quantitative real time - PCR. Downregulated transcripts (A) Cyclophilin 1 and (B) Malonyl-CoA-acyl carrier protein transacylase, mitochondrial) in roots of *Salsola drummondii* Ulbr., treated with 1200 mM NaCl at different time points (0, 6, 12, 24 hrs).



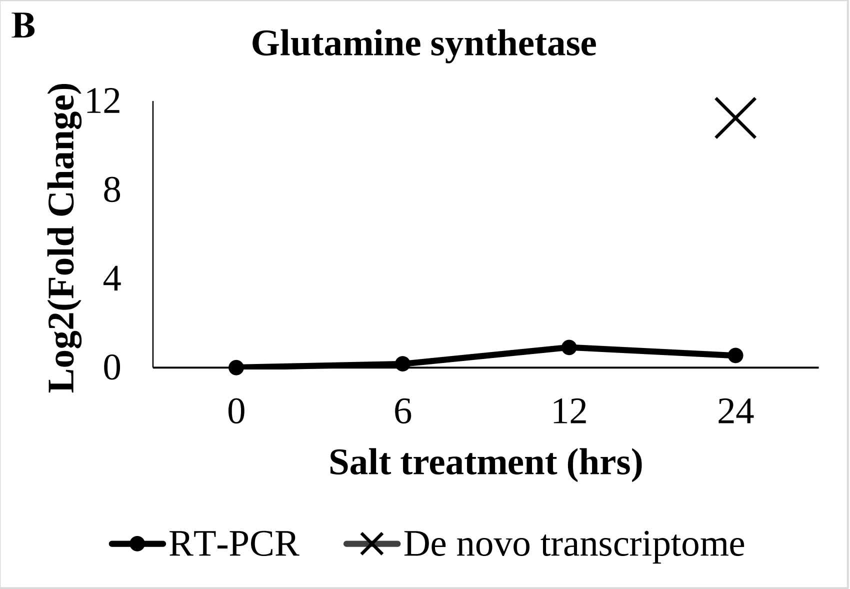
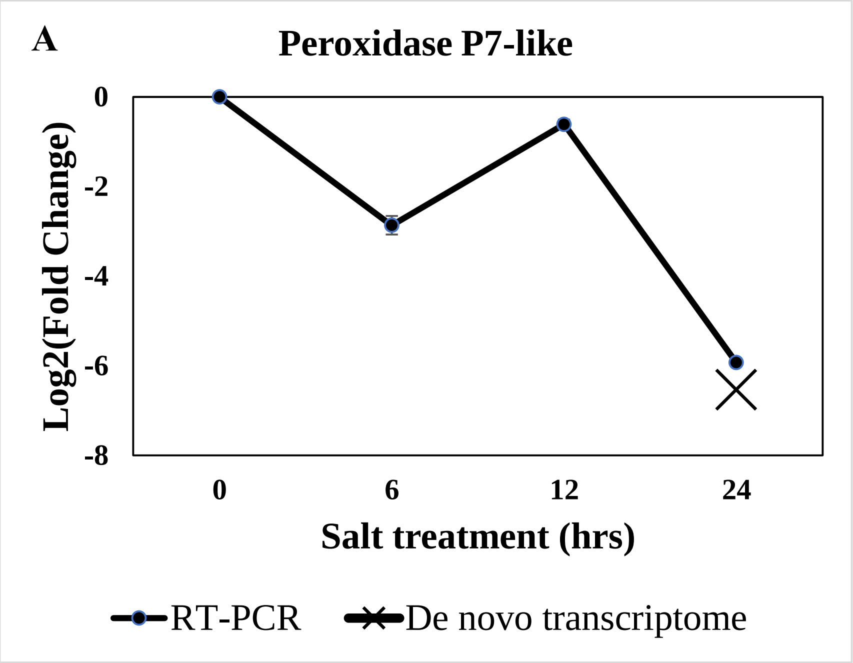


Figure 55. Validation of *de novo* transcriptome results by quantitative real time - PCR. Upregulated transcripts (A) Glycine-rich RNA-binding protein 4, mitochondrial and (B) Glutamine synthetase in roots of *Salsola drummondii* Ulbr., treated with 1200 mM NaCl at different time points (0, 6, 12, 24 hrs).



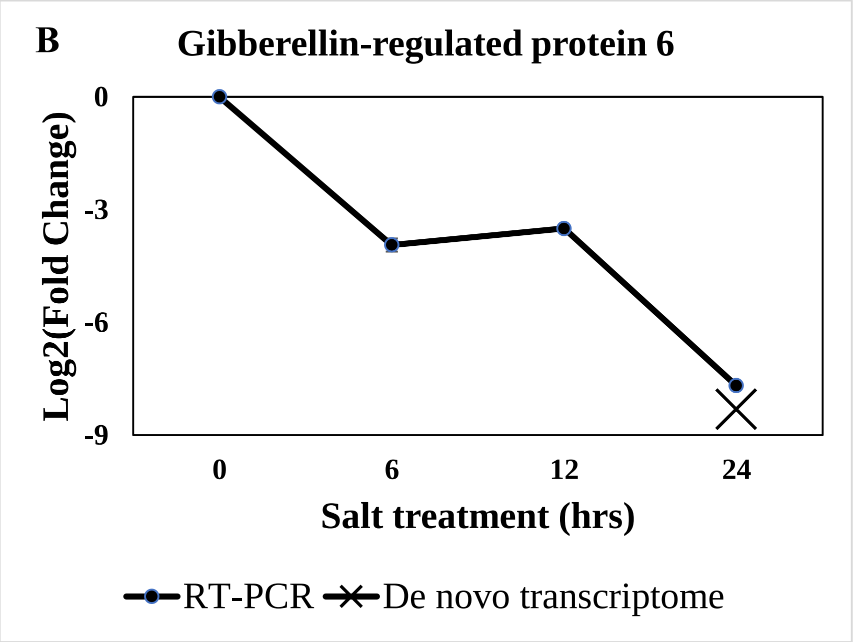


Figure 56. Validation of *de novo* transcriptome results by quantitative real time - PCR. Downregulated transcripts (A) Peroxidase P7-like and (B) Gibberellin-regulated protein 6 in shoot of *Salsola drummondii* Ulbr., treated with 1200 mM NaCl at different time points (0, 6, 12, 24 hrs).

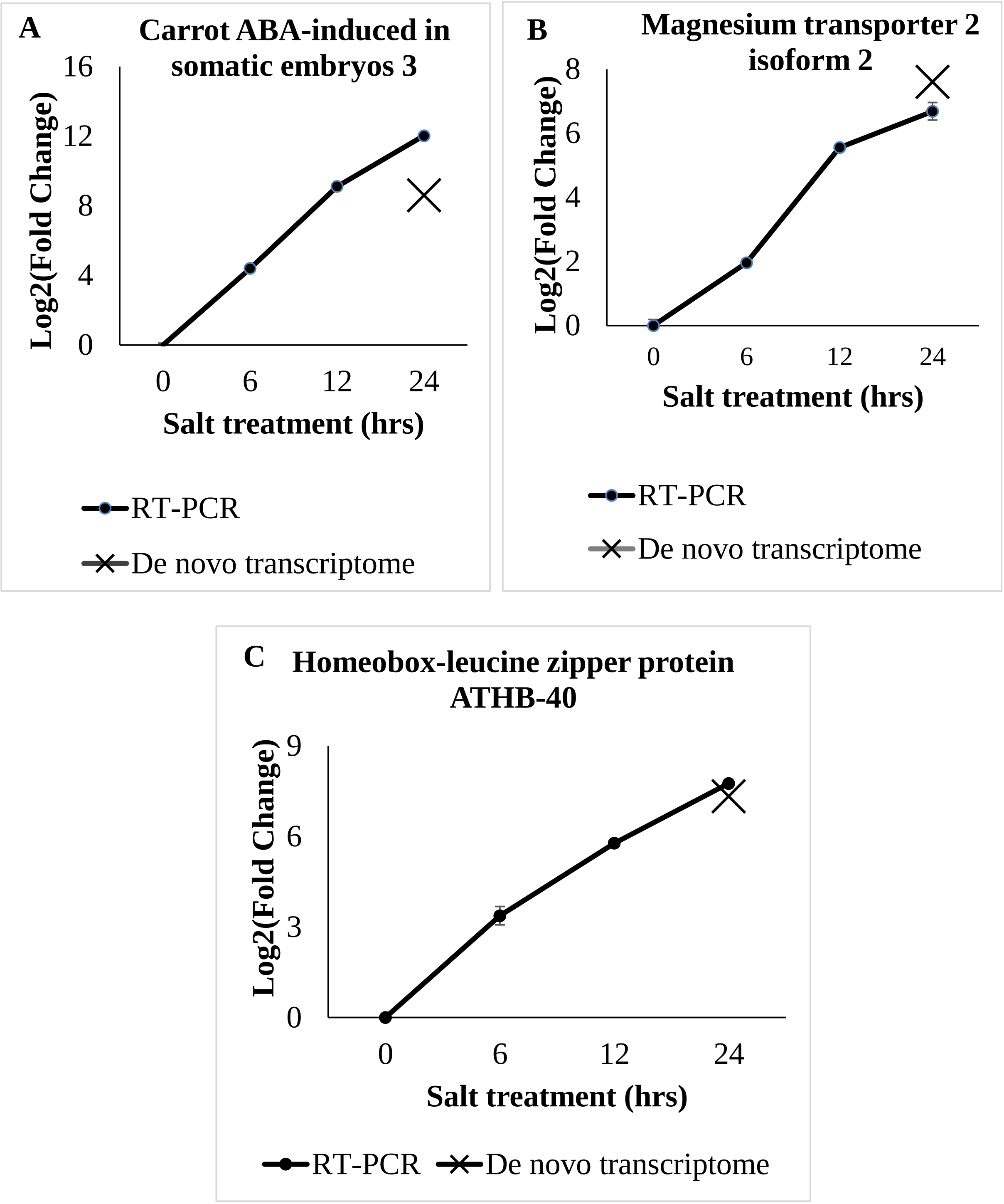


Figure 57. Validation of *de novo* transcriptome results by quantitative real time - PCR. Upregulated transcripts (A) Carrot ABA-induced in somatic embryos 3, (B) Magnesium transporter 2 isoform 2 and (C) Homeobox-leucine zipper protein ATHB-40 in shoots of *Salsola drummondii* Ulbr., treated with 1200 mM NaCl at different time points (0, 6, 12, 24 hrs).

4. DISCUSSION

4. DISCUSSION

4.1. Effects of temperature and light on drought tolerance during seed germination of *Salsola imbricata* Forssk.

Salsola imbricata produces and disperses a large number of ready-to-germinate fruits during December and January (Mehrun-Nisa et al., 2007; El-Keblawy, 2014). Our study showed that the highest germination of this species under experimental conditions occurred in both light and darkness at lower and moderate temperatures (15/25 and 20/30 °C). This trend has been reported in other succulent halophytes of subtropical regions, such as *Zygophyllum propinquum* Decne., (Manzoor et al., 2017) and *Suaeda vermiculata* Forssk. ex. J. F. Gmel (El-Keblawy et al., 2018). Such low and moderate temperatures usually prevail in the natural habitats during the time of effective rainfalls (December–February) that encourage successful germination and seedling establishment (El-Keblawy, 2014). The average minimum and maximum temperatures are 13.8 and 26.5 °C, respectively, in December and 12.1 and 24.4 °C, respectively, in January (Feulner, 2006). The immediate germination after seed dispersal at the favourable time of the year could result in an earlier establishment of seedlings that might have greater competitive ability (Castellanos et al., 1994). Conversely, as *S. imbricata* has a transient seed bank, failure to germinate would expose seeds to death during summer storage at soil high temperatures. It has been reported that few seeds of this species can retain their viability after few months under natural habitats (El-Keblawy et al., 2007; Mehrun-Nisa et al., 2007). Our study also showed that the germination was very fast (i.e., Germination Rate Index (GRI) was close to 50) in distilled water and moderate polyethylene glycol (PEG) osmotic potentials ($\leq$ -0.8 MPa), especially at lower and moderate temperatures, a trend similar to that in *Salsola drummondii* Ulbr., (see section 3.2). This indicates that seeds can germinate within 24 hrs following imbibition. The faster germination at moderate osmotic potential has been considered as a strategy for seedling establishment when little rainfalls are received early in the growing season (Kasera and Mohammed, 2010; Liu et al., 2013). At higher temperatures (25/35 °C), however, both final germination and GRI were significantly lower at lower osmotic potentials ($\leq$ -1.4 MPa), indicating a lower chance for germination and seedling establishment when little rain precipitates late in the growing seasons.

Seed germination and seedling emergence are critical phases for seedling establishment in the unpredictable arid deserts. In these deserts, emergence often fails, especially if rainfall is not enough to support plant requirements (Lewandrowski et al., 2017).

Our results showed little germination of *S. imbricata* seeds in lower osmotic potential at lower temperatures (4% and 14% germinated at -2.2 and -1.8 MPa, respectively) and moderate temperatures (12% germinated at -1.8 MPa). No germination occurred in these osmotic potentials at the higher temperatures (Fig. 14). The ability of seeds to germinate under such lower osmotic potential further support the hypothesis that some of them might germinate in years that receive rainfalls less than average (i.e. dry years). According to climatic data available from the study region, Feulner (2006) reported that 27 years received 50 mm or less annual average rainfalls, out of 71 years of rainfall records in Sharjah Airport meteorological station in the UAE. Consequently, some seeds of *S. imbricata* could contribute for the future generation even in the very dry years. The potential of little rainfalls to contribute to regeneration of *S. imbricata* is particularly important when rainfalls occur at lower temperatures; i.e. December and January. The chance of successful seedling recruitment is higher when rainfalls occur early in the growing season. *S. imbricata* plants have a shallow root system, yet produce flowers and fruits during September-November; i.e. before the arrival of any rainfalls (Jongbloed et al., 2003). This indicates that *S. imbricata* can efficiently use the atmospheric moisture in the form of dew and fog as a non-conventional water source. This also implies that if seed passed the germination stage, seedlings of this species would likely complete their life cycle.

Higher tolerance to water deficiency at the germination stage has been regarded as an evolutionary strategy for xerophytes in arid hot deserts and is regulated by temperatures (e.g. Fyfield and Gregory, 1989; Zeng et al., 2010). In our study, higher temperatures exacerbated simulated drought stress in *S. imbricata*; germination was significantly lower in all tested polyethylene glycol levels (PEG) at higher temperature, compared to lower and moderate temperatures. This trend was most obvious at the lowest osmotic potentials (Fig. 14). Similar results have been reported in other species such as sugar-beet (Gummerson, 1986) and *Artemisia sphaerocephala* Krasch. (Zheng et al., 2005).

Most non-germinated seeds of *S. imbricata* at lowest osmotic potentials (-1.8 and -2.2 MPa PEG) recovered their germination immediately once they were transferred to distilled water (Fig. 16). In fact, there was no significant difference in total germination (i.e. in PEG and after seeds transferred to distilled water) between higher and lower osmotic potentials (-2.2 MPa) at the lower temperatures (Fig. 17). This result indicates that osmopriming with PEG could be used to enhance germination level and speed of *S. imbricata* seeds upon the arrival of effective rainfalls, which usually come after long periods of drought in arid deserts. In addition, osmopriming could be applied for *S. imbricata* seeds before their use for restoration of degraded deserts of the arid regions. Germination speed might play a highly adaptive role under harsh environmental conditions, such as in arid deserts, where time favourable for seedling establishment is short and unpredictable (Kadereit et al., 2017). Rogers et al. (1995) suggested that fast germination ensures rapid seedling establishment, which can minimize competition with other associated plants, especially in years that receive less than average rainfalls. The result also indicates the seeds are showing resilience to drought, or low moisture conditions. As seed survival in deserts is important, the result also demonstrates a sort of bet hedging occurrence, whereby seeds do not risk germination at dry years. This in turn will have implications for seed persistence, but yet to be tested with field studies.

In contrast to the findings of Mehrun-Nisa et al. (2007) in a Pakistani population, our results showed that seed germination of *S. imbricata* was significantly greater at lower, as compared to higher temperatures. The difference in the time of effective rainfalls could explain the difference in temperature requirements for germination in the two geographical regions. The UAE population receives rainfalls mainly during winter (i.e. December–February), when temperature is lower (Feulner, 2006). The subtropical Pakistan, however, receive effective rainfalls at both cooler time of winter and warmer time of summer (i.e. monsoon rainfalls; Saeed et al., 2011). Such difference in the germination temperatures between the Pakistani and the UAE populations has ecological significances. The lower temperature requirement in the UAE indicates that germination should happen at the moist period of the year that allows successful seedling establishment. In the Pakistani population, however, there are two episodes for seedling emergence and recruitment: the first during the cooler winter and the second during the warmer summer.

Soil moisture regime can affect dormancy of seeds and their sensitivity to environmental signals that promote germination (Mollard and Insausti, 2009). For example, light and temperature interacted to regulate seed germination at lower osmotic potentials of sodium chloride (NaCl) in several species (Khan and Weber, 1986; Li et al., 2005; El-Keblawy et al., 2015). Germination inhibition in darkness was greater in saline solutions at higher temperatures in several species, including *Salicornia pacifica* Standl. (Khan and Weber, 1986), *Sarcocornia fruticosa* (L.) A.J.Scott. (Redondo et al., 2004), *Limonium stocksii* (Boiss.) Kuntze (Zia and Khan, 2004), *Haloxylon recurvum* Bunge ex Boiss. and *Zygophyllum simplex* L. (Khan and Ungar, 1997), black, but not brown seeds of *Suaeda salsa* (L.) Pall. (Li et al., 2005) and *Halopeplis perfoliata* (Forssk.) Bunge (El-Keblawy et al., 2015). Our results indicate that germination of *S. imbricata* seeds was significantly lower in darkness than in light, at lower osmotic potentials (≤ -0.6 MPa PEG) at moderate temperatures (20/30 °C) and most of PEG levels at the higher temperatures (25/35 °C). This result indicates that dark inhibition is likely happening in *S. imbricata* under drought and temperature stresses. It also implies that buried seeds prefer not to germinate if little rainfalls are received at higher temperature, i.e. by the end of the growing season, if seeds are still viable. Emergence of buried seeds requires more energy and time (Chen and Maun, 1999), which would be very limited by the end of the seasons in the presence of limited rainfalls. As light sensitivity of seeds depends on phytochrome and this sensitivity is modulated by temperature and drought (Mollard and Insausti, 2009; Ballaré, 1994), further studies are needed to assess the role of phytochromes in dark dormancy induction of *S. imbricata* at lower osmotic potentials.

Climate has a large influence on plant recruitment and survival (Gurvich et al., 2017). In particular, temperature and water availability are critical drivers for seed dormancy and germination. Consequently, projected climate change will undoubtedly affect recruitment of plants population dynamics (Walck et al., 2011). In many studies, greater tolerance to water limitation at the germination stage was regarded as an evolutionary strategy of xerophytes to arid hot desert (e.g. Zeng et al., 2010). Our results showed that tolerance of *S. imbricata* to simulated drought seed germination was relatively moderate at lower osmotic potential, but lower at higher temperatures, as compared to many other desert plants. Seeds germinated in up to -1.8 MPa PEG at lower temperatures, but few seeds germinated at -1.4 MPa at higher temperatures (Fig. 14). In the desert grass *Allenrolfea occidentalis* (S.Wats.) Kuntze, germination tolerated water potentials of -4.0 MPa (Blank et al., 1994), but that of two desert shrubs (*Ephedra alata* Decne., and *Artemisia sphaerocephala* Krasch.) tolerated only -1.0 and -1.5 MPa PEG, respectively (Wafa'a et al., 2010; Zheng et al., 2005). In these studies, however, the interactive effect between salinity and osmotic potential was not assessed. As global climate change is expected to increase temperatures and decrease the frequency and amount of rainfalls (Gurvich et al., 2017), *S. imbricata* seed germination could be negatively affected by climate change. The projected global change would restrict germination to a narrower window and consequently reduce the successful recruitment. Definitely, this would affect local abundance of *S. imbricata*, especially in the hyper-arid desert of the UAE that currently receives on average less than 100 mm annual rainfall and has extremely high temperatures (Feulner, 2006). This is also expected to happen in several species of cacti, where germination was significantly reduced in a combination of low water potentials and high temperatures (Gurvich et al., 2017).

4.2. Effects of temperature, light and maternal salinity on drought tolerance during germination of *Salsola drummondii* Ulbr.

The results of our study showed significantly greater germination of seeds from the non-saline habitat as compared with those from saline habitat in all polyethylene glycol (PEG) concentrations up to -1.2 MPa. At -1.5 MPa; however, there were non-significant differences in the final germination of the two seed lots. The results also showed insignificant differences in the viability of the seeds from the non-saline and saline habitats. This indicates that seeds from the saline habitat are more dormant, as compared to those from the non-saline habitats when germinated in lower osmotic potential solutions of polyethylene glycol (PEG). Maruyama et al. (2016) explained the higher dormancy observed in *Impatiens capensis* Meerb., seeds produced under maternal drought stress to be a mechanism for desiccation avoidance/drought tolerance in heterogeneously dry sites. The greater dormancy of the saline habitat seeds of *S. drummondii* helps them postpone their germination until the onset of favorable conditions for seedling establishment. Such conditions usually occur when effective rainfall happens at lower temperatures during winter (e.g., during November-February, El-Keblawy, 2004, 2017).

The combined effect of soil temperature and water content on seed germination is an environmental signal that could determine the germination time (Fyfield and Gregory, 1989). Our results showed non-significant differences between the germination of seeds at the three temperatures, when *S. drummondii* seeds were incubated at low levels of drought (0 and -0.4 MPa). At higher drought levels, however, germination was significantly reduced at high temperatures (25/35 °C) as compared to lower temperatures (15/25 °C). This could be an ecological adaptation to reduce germination at the end of the growing season, when conditions are not favorable for seedling establishment (Hameed et al., 2013; El-Keblawy et al., 2015; Rasheed et al., 2015). In general, exposing seeds to two stress factors (drought and high temperatures) would affect the integrity of cell membranes (Raison, 1986). Electrolyte leakage resulting from loss of membrane integrity at higher temperatures reduced germination in several species, such as Brassica spp. (Thornton et al., 1990) and *Brassica olearcea* L. (Jett et al., 1996).

Drought lowers the plant water potential by reducing the free energy of water available for the plant to be below that of pure free water. To avoid desiccation, the water potential of the symplast must be adjusted (Flowers and Yeo, 1986). Osmotic adjustment could be through ion contents or production of organic osmolytes (Ghoulam et al., 2002). The result also indicates that polyethylene glycol (PEG) might cause irreversible damage to the cells (Yu and Rengel, 1999). The rehydration of desiccated seeds after being treated with polyethylene glycol (PEG) could be associated with damage of the plasma lemma, and consequently leakage of cell solutes (Hendricks and Taylorson, 1976; Yu and Rengel, 1999). Changes in organelle morphology and function, and disruption of organelle membranes due to desiccation associated with water stress have been also reported in other species (Dhindsa and Bewley, 1977).

Climatic factors, in particular temperature and water availability, have a considerable influence on plant recruitment and survival (Gurvich et al., 2017). These factors are critical drivers for seed dormancy and germination. Consequently, plant recruitment and population dynamics will certainly be affected by projected climate change (Walck et al., 2011). Evans (2009) used 18 global climate models and predicted an overall temperature increase of ∼1.4 K by mid-century, increasing to almost 4 K by late-century for the Middle East. In addition, he also predicted increases in the length of the dry season and changes in the timing of the maximum precipitation that will impact the growing season (Evan, 2009). Our results showed that seeds of *S. drummondii* from both saline and non-saline habitats germinated to more than 40% under high levels of drought (-1.2 MPa). In addition, more than 25% of the seeds germinated at high temperatures (i.e. above the average of the growing season; Böer, 1997) (Fig. 18 A and B). The broad windows of germination under different temperature and light regimes and the ability of seeds to germinate under relatively lower osmotic potentials indicate that *S. drummondii* is less threatened by the projected climate change in the Middle East.

4.3. Effects of temperature, light and maternal salinity on salinity tolerance during germination of *Salsola drummondii* Ulbr.

Seeds of *S. drummondii* from the saline soils showed relatively greater dormancy than those from the non-saline soils; maximum germination for seeds of non-saline and saline soils was about 85% and 70%, respectively in distilled water and low temperatures. Such dormancy level is relatively lower than that of most of Arabian desert glycophytes (El-Keblawy and Gairola, 2017; El-Keblawy, 2017), but comparable to many halophytes of the same region (e.g., *Halocnemum strobilaceum* (Pall.) Bieb., *Halopeplis perfoliata* (Forssk.)

Bunge (El-Keblawy and Bhatt, 2015), *Haloxylon salicornicum* (Moq.) Bunge ex Boiss., (El-Keblawy and Al-Shamsi, 2008) and *Salsola imbricata* Forssk., (El-Keblawy et al., 2007) and habitat-indifferent halophytes (e.g., *Anabasis setifera* Moq. (El-Keblawy et al., 2016b), *Suaeda aegyptiaca* (Hasselq.) Zohary, (El-Keblawy et al., 2017a), *Suaeda vermiculata* Forssk. ex. J. F. Gmel., (El-Keblawy et al., 2018)). Gul et al. (2013) indicated that the low innate dormancy in seeds of perennial halophytes might be an adaptive strategy to postpone their germination till the arrival of effective rainfalls that could dilute high salinity of salty soils (Song et al., 2005). The insignificant difference in viability of seeds from plants of the two habitat types (Table 8) confirms that the difference in germination of the seed lots from the two habitats is attributed to the greater dormancy of seeds from saline soils. The greater dormancy of seeds from saline soils is further confirmed by the greater dormancy of seeds failed to recover their germination after their transfer from sodium chloride (NaCl) solutions to distilled water; seeds of saline habitats that did not recover their germination, after being transferred to distilled water, were more viable (20%) than those of non-salty seeds (5%). The higher dormancy of the saline habitat seeds could be ecologically important in a temporally and spatially arid unpredictable environment.

Seeds of many halophytes have the ability to germinate and to keep their viability under high levels of salinity; a phenomenon distinguishes halophytes from glycophytes (Khan and Gul, 2006). Our study showed the ability of *S. drummondii* seeds to germinate and recover their germination in up to 1000 mM of sodium chloride (NaCl). This indicates that this species is among the most salt tolerant halophytes (Khan and Gul, 2006); up to 25 and 31.5% of seeds from the non-saline and saline soils germinated in 1000 mM NaCl, respectively. In a Pakistani population, only few seeds germinated in 1000 mM NaCl (Rasheed et al., 2015), indicating that the maternal environment under which seeds developed and matured in the subtropical arid deserts of the United Arab Emirates (UAE) might enhanced the seed salt tolerance. In the UAE, the limited amount of rainfalls (annual average is <100 mm, (Böer, 1997)) coupled with higher temperatures would increase salt tolerance in halophytes. In several studies, the increase in salinity stress on maternal plants resulted in an increase in salt tolerance of the produced seeds. For example, Van Zandt and Mopper (2004) examined the maternal effect on germination of *Iris hexagona* Walter by growing plants in three different salt levels in a common garden and found that seeds produced by plants grown under higher salinity germinated faster and to high level, compared to seeds from plants grown under lower salinity. Similarly, plants of *Chenopodium album* L. exposed to higher salt stress produced larger, more salt-tolerant seeds, compared to plants exposed to lower salinities (Yao et al., 2010).

In Pakistani population, Rasheed et al. (2015) reported almost no recovery for *S. drummondii* seeds germinated in darkness and low recovery for seed germinated in light. The recovery was greater at moderate than at both lower and higher thermoperiods (Rasheed et al., 2015). In the present study, germination recovery was around 40% for seeds from the non-saline soils, but was about 10% for seeds from salty soils. Interestingly, the recovery from higher salinities (>800 mM NaCl) was greater at lower, than at higher thermoperiods for seeds from the two habitat types, but the response to the photoperiod did not differ between the two habitats (Fig. 3). The differences in the recovery between the Pakistani and the two Arabian habitat types could be considered as an ecological adaptation to the local environments. The Pakistani populations receive heavy monsoon rainfalls during summers that could significantly dilute soil salinity (Saeed et al., 2011). At that time, temperatures are usually moderate and light intensity is higher. Recovery of some seeds at the monsoon time could ensure some successful recruitment. In the UAE, however, no monsoon rainfall could happen in summer and germination of this species only happen after the first effective rainfall following seed dispersal, which usually happen in December-January, when temperature is low and salinity is diluted (El-Keblawy, 2014).

Halophytes of the arid deserts are exposed to various levels of water osmotic potential, such as soil moisture and salinity stresses (El-Keblawy and Bhatt, 2015). In addition, the position of seeds to soil surface is an environmental cue that determines light and temperature requirements for seed germination (El-Keblawy et al., 2018). Consequently, the proper water osmotic potential coupled with suitable light and temperatures could regulate the time of seedling emergence that would result in successful recruitments (Qu et al., 2008; El-Keblawy and Bhatt, 2015). Our results indicated that *S. drummondii* germinated significantly greater at the lower thermoperiods (15/25 °C) than at the higher thermoperiods (25/35 °C). Similar results have been reported for other halophytes of the Arabian deserts, such as *Suaeda aegyptiaca* (Hasselq.) Zohary (El-Keblawy et al., 2017a) *Salsola imbricata* Forssk. (El-Keblawy et al., 2007) and *Haloxylon salicornicum* (Moq.) Bunge ex Boiss. (El-Keblawy and Al-Shamsi, 2008). In the subtropical region of Pakistan, however, halophytes such as *Aeluropus lagopoides* (L.) Thwaites, *Halopyrum mucronatum* (L.) Stapf, *Limonium vulgare* Mill., *Salsola imbricata* Forssk., and *Sporobolus ioclados* (Nees ex Trin.) Nees showed optimal germination at moderate temperatures (20-30 °C), but any further increase or decrease in thermoperiods reduced seed germination (Khan and Gul, 2006). The difference in the time of germination between the two subtropical regions would depend on the temperatures at the time of effective precipitation. In the Arabian deserts, seed germination of halophytes mainly occurs immediately after effective rainfalls, when soil salinity levels are usually low (El-Keblawy et al., 2007; El-Keblawy and Al-Shamsi, 2008; El-Keblawy, 2014). The effective rainfall that can dilute soil salinity is usually happen during cooler time of the year (December and January, (Böer, 1997)). However, little rainfall might happen by the end of the season, when temperatures are higher. So, high temperatures by the end of the season in the Arabian desert might be an environmental cue to prevent germination to happen when soil salinity is increasing and the amount of available water would not help seedling establishment. In the subtropical Pakistani region, germination occurs during monsoon time; when temperature is moderate (Khan and Gul, 2006).

Results of our study indicated that seeds of plants from non-saline soil attained significantly better germination in sodium chloride (NaCl) solutions up to 800 mM, compared to seeds of plants from saline soils. Similar results have been reported in two habitat-indifferent halophytes of the Gulf region, *Anabasis setifera* Moq. (El-Keblawy et al., 2016b) and *Suaeda aegyptiaca* (Hasselq.) Zohary (El-Keblawy et al., 2017a). The results of germination speed in *S. drummondii* showed that seeds from plants of the saline soils germinated faster than those from non-saline soils. Similar results have been reported for seeds of other two habitat-indifferent halophytes inhabiting the Gulf desert (*Suaeda aegyptiaca* (Hasselq.) Zohary; El-Keblawy et al., 2017a; *Anabasis setifera*; El-Keblawy et al., 2016b). In the saline habitats, the death rate of emerged seedlings could be very high if they not established within a short period after rainfalls; evaporation could increase salinity level again. The fast germination for seeds in the saline soils confers advantage to seedlings growing in a saline substrate that change rapidly with time. The fast germination is a strategy for seedling establishment during the brief period of lower salinity levels after rainfall (Zia and Khan, 2004; El-Keblawy et al., 2016b).

Germination inhibition induced by higher salinity could be ascribed to either osmotic or ion-specific toxicity effect. However, drought induced germination inhibition is usually attributed to osmotic effect (Almansouri et al., 2001). High salinity could be injurious to most glycophytes; however, seeds of many halophytes could maintain their viability for longer period of exposure to hypersaline conditions and recover germination when conditions are favourable for seedling establishment (Khan and Ungar, 1997; El-Keblawy et al., 2016b; El-Keblawy et al., 2017a). In the present study, around 25% and 32% of seeds from the non-saline and saline soils, respectively, germinated in 1000 mM NaCl. However, seeds of the same habitats were able to germinate only to less than 20% in -1.5 MPa PEG solutions (see section 3.2 above). The greater tolerance to lower osmotic potential resulted from NaCl than that from polyethylene glycol (PEG) has been reported in several other species. In *Ceratonia siliqua* L., for example, germination was significantly reduced by a water stress simulated by a moderate level of PEG (-0.5 MPa), but it occurred in higher levels of NaCl (-1.0 MPa, Cavallaro et al., 2016). Similarly, the effects of NaCl on both germination and seedling growth of three pea cultivars was significantly less, compared to the effect of PEG (Okçu et al., 2005). Furthermore, germination of *Henophyton deserti* (Coss. and Durieu) Coss. and Durieu seeds was less affected by NaCl, as compared with polyethylene glycol (PEG) (Gorai et al., 2014). The ability of *S. drummondii* seeds to germinate in 1000 mM NaCl (around -5.0 MPa), but only in less than -1.5 MPa PEG indicates that the failure of germination in saline solutions could be osmotic, rather than ion-specific toxicity effect. This is further confirmed by the greater ability of *S. drummondii* seeds to recover from 1000 mM NaCl, but not from -1.5 MPa PEG; less than 25% of PEG treated seeds recovered their germination from -1.5 MPa PEG (see section 3.2 above). Also this ability indicates that this species is more adapted to saline than drought conditions. In fact, this species produce flowers and fruits before the onset of the rainy season (October-November), despite the fact that it has a very shallow root system to tap groundwater, indicating that it depends on atmospheric moisture as a non-conventional source for water, in absence of soil water during the dry summer (Dirks et al., 2016).The ability of the plants of *S. drummondii* to flower and fruit in the absence of conventional soil water indicates that they are relying on moisture absorption from air rather than soil. Consequently, as seeds have a limited ability to absorb atmospheric moisture, they cannot tolerate soil moisture deficiency as adult plants do.

Plants are sedentary organisms that have little choice for the suitable environment where they can grow and reproduce. Environmental stresses that are experienced by paternal plants can induce phenotypic changes that span multiple generations (Münzbergová and Hadincová, 2017). Transgenerational plasticity provides phenotypic variation that contributes to adaptation to environmental stresses (Vu et al., 2015). Transgenerational phenotypic plasticity in progeny traits can occur through maternal and/or epigenetic effects (Soliman et al., 2018). Maternal effects in plants include the maternal genetic effects caused by maternal inheritance of plastids in addition to non-inheritance effect of endosperm, seed coat, resource provisioning of nutrient resources, hormones, proteins and transcripts (Vu et al., 2015; Verslues, 2016). Whereas environmental maternal effects are usually diminished in the first generation, epigenetic effects transmit heritable plastic responses to environmental cues (Uller et al., 2008). In our study, it is not clear whether the differences in seed dormancy, germination responses, drought tolerance and salinity tolerance between seeds from saline and those from non-saline habitats are due to maternal and/or epigenetic effects. Therefore, further studies are needed to separate epigenetic effect from maternal salinity effect in habitat-indifferent halophytes, such as *S. drummondii*. For example, reciprocal transplant experiments between the two populations should be conducted and seed germination response and drought tolerance from these plants should be compared. Another approach could be through growing micro propagated plants from the two populations in both habitat types.

4.4. Ecophysiological adaptations of *Salsola drummondii* Ulbr. at adult stage under natural saline and non-saline habitats

Study of salt tolerance under natural habitat has been considered to be important for understanding salt tolerance mechanisms of plants under natural, and ecologically relevant circumstances. Therefore, this section assesses some morphological, physiological and biochemical responses of *S. drummondii* to two different habitats differ in salinity levels (i.e. saline and non-saline habitat). Interestingly, the results showed insignificant difference in many of the studied attributes between plants grown in saline and those grown in non-saline habitats. Among the attributes that had insignificant differences are fresh and dry weight, concentrations of essential elements such as K^+, Ca^{2+}, Mg^{2+}, Fe^{2+}, malondialdehyde concentration and guaiacol peroxidase activity. This indicates that *Salsola drummondii* plants from saline habitat adopted physiological and biochemical attributes enabled them to tolerate the high salinity level of the saline habitat and to grow well as plants from the non-saline habitat.

Halophytes are a group of plants that tolerate higher salinity, which would otherwise cause death in most glycophytes (Flowers and Colmer, 2008). In contrast, *Salsola drummondii* a habitat-indifferent halophyte, can grow and complete their life cycle successfully in both non-saline and saline habitats. Halophytes have developed several mechanisms that help them adapting the survival in the saline and hypersaline soils. For example, it has been suggested that phenotypic plasticity, especially leaf size and succulence, is an important mechanism in plant adaptation to salt stress (Richard et al., 2005). Our results showed insignificant difference in leaf biomass and leaf succulence of *S. drummondii* between the non-saline and saline habitat. However, salinity has increased biomass of other halophytic plants. For example, both fresh and dry weight of both *Salsola soda* L. and *Portulaca oleracea* L. were greater in saline, as compared to non-saline treatments (Karakaş et al., 2017). However, other studies indicated a decrease in plant biomass in some halophyte grasses following salinity exposure (e.g., Muscolo et al., 2013). Phenotypic plasticity has been widely recognized as an important aspect of how organisms develop, function and evolve in their environments. This biological characteristic corresponds to the ability of an organism to adjust its performance by altering its morphology, physiology and life-history in response to varying environmental conditions (Castillo et al., 2018; Tucić et al., 2018). Moreover, plasticity in phenotypic traits is necessary for the survival and development of halophytes under harsh and severe desert conditions.

The pigment contents are good indicators for stress detection and tolerance (Barbagallo et al., 2003). Our results indicated that leaves of plants from the saline habitats had lower concentrations of all pigments (chlorophyll a, b, total chlorophyll and carotenoids), as compared to leaves of plants from the non-saline. The decrease of chlorophyll a and b contents demonstrate a significant inhibition in chlorophyll a/b-binding proteins that are direct relationship with the photosystem II- light-harvesting complex II (PSII (LHCII)) to transfer excitation energy to the PSII core complex (Xu et al., 2011). The decrease in LHCII showed interference with photosynthetic machinery which allows plants to survive in unfavourable conditions (Spundova´ et al., 2003). The salinity stress modifies the chlorophyll a content more than chlorophyll b, which appears to be less sensitive to saline habitat. A higher level of carotenoids was found in halophytic *Chloris virgate* under control conditions compared to wheat. However, following exposure to salt stress, there was slighter decrease in carotenoid contents in halophyte *Chloris virgate* than wheat (Yang et al., 2009).

In the present study, we found that plant have highest Na^+ concentration in leaves and lowest in roots (Fig. 24). Na^+ accumulated more in stems and leaves of *S. drummondii* from saline than non-saline habitats. Still, plants showed normal growth; the average dry weight of leaves of plants from the saline habitats were even insignificantly heavier (0.46 g/100 leaves), as compared to leaves from the non-saline habitats (0.38 g/100 leaves) (Table 16). This is a distinct feature of halophytes that make them suitable plants for rehabilitation of saline lands where glycophytes are not able to grow. To surviving the high Na^+ accumulation, plant cells reduce their osmotic potential to maintain water uptake and cell turgor, which are important for normal physiological processes (Bose et al., 2014a). However, ion accumulation could be very toxic and one of the major causes of salt stress in the cell. Ion toxicity can affect membrane function and activities of enzymes (Munns and Tester, 2008; Hussain et al., 2016; Negrão et al., 2017).

In halophytes, osmotic adjustment through sodium ion accumulations (Na^+) in the vacuole requires less energy, as compared to synthesizing compatible organic solutes (Yang et al., 2007; Shabala and Mackay, 2011; Flowers and Colmer, 2015). The low energy cost associated with osmotic adjustment through ion accumulation, as compared to the costly production of organic osmolytes, could explain the insignificant heavier leaves of plants from the saline habitats. On the other hand, lower Na^+ accumulation and the greater production of organic osmolytes (proline) in the leaves of plants from non-saline habitat, as compared to those from saline habitats (Fig. 25), might explain the insignificant smaller leaf mass of plants from the non-saline habitat.

Our results showed that greater accumulation of Na^+ in saline habitat was not accompanied by any changes in K^+ contents. Similarly, some other halophytes such as *Sarcocornia fruticosa* (L.) A. J. Scott. and *Inula crithmoides* L., did not show any variation in K^+ contents in various plant organs, although at seasonal salinity fluctuations (Gil et al., 2014). It was demonstrated by other researchers that presence of Na^+ in the soil and its absorption will hinder the absorption of K^+ by plant roots (Rodriguez-Navarro, 2000; Souid et al., 2016). Gil et al. (2014) has reported that the level of K^+ in plant tissue of *Juncus maritimus* Lam., and *Juncus acutus* L., was elevated with increasing Na^+ in the soil. The Ca^{2+}, Mg^{2+} and Fe^{2+} content was statistically unaffected in leaves, stems and roots of *S. drummondii* collected from both saline and non-saline natural habitats (Fig. 24) and this indicates that *Salsola drummondii*, a habitat-indifferent halophyte can maintain ion homeostasis even under high salinity in saline natural habitat. Several researchers reported that presence of Na^+ in the cytoplasm significantly decreased the absorption of the macronutrients such as Ca^{2+}, Mg^{2+} and Fe^{2+} (Khan et al., 2000b; Koyro, 2006; Elouzi et al., 2011). The bioaccumulation factors were also high in $K^{+,}$ but was low in Ca^{2+}, Mg^{2+} and Fe^{2+}. Potassium is necessary for different enzymatic reactions, membrane stability, pH and ionic homeostasis in plant cell (Ahmad and Maathuis, 2014). The higher bioaccumulation of K^+ in *Salsola drummondii* plants collected from natural habitats might be related with salt tolerance mechanism as K^+ has a pivotal role in osmoregulation and considered as osmolyte and osmoprotector under salinity (Isayenkov and Maathuis, 2019)

Our results indicated that the concentration of proline in both roots and shoots was significantly greater in non-saline as compared with the saline while more proline was accumulated in shoots than roots (Fig. 25). This result indicates that plants of the non-saline habitat rely more on proline as an osmoregulator to maintain lower osmotic potential within both roots and shoots. The results indicated that plants of the saline habitat accumulated significantly more sodium in all organs, as compared to plants of non-saline habitat. Such higher accumulation of sodium might help the plants in maintaining lower osmotic potential. However, the lower Na^+ accumulation in plants of non-saline habitat indicates that they rely more on the production of proline. As the production of proline costs more resources, the plants of saline habitat attained greater average fresh and dry weight of leaves, as compared to plants from non-saline habitat. Several researchers documented the valuable effect of proline buildup in halophytes (Radyukina et al., 2007; Szabados and Savoure, 2010). In another study, Ghars et al. (2008), reported the accumulation of more proline in two halophytes (*Thellungiella salsuginea* and *Lepidium crassifolium.*) under salt stress condition higher proline production is coincident with synthesis of pyrroline-5-carboxylate synthetase (P5CS) and reduced proline catabolism by PDH (Taji et al., 2004; Kant et al., 2006).

Several researchers documented that proline helps in scavenger the ROS (Ashraf et al., 2012; Kaul et al., 2008). Meanwhile, increased in the synthesis of proline also contribute in the reduction of ROS production and redox homeostasis (Verbruggen and Hermans, 2008). According to the hypothesis supported by Taji et al. (2004) and Kant et al. (2006), there was suppression of proline dehydrogenase in halophytic *Thellungiella salsuginea* L., but it was not the case with *Arabidopsis thaliana*. They suggested that the possible mechanism behind this is *T. salsuginea* is a hyper-accumulating halophyte plant.

Results of our study indicated an insignificant difference in Oxidative Stress Markers (ROS) in the shoots of *S. drummondii* malondialdehyde and hydrogen peroxide (MDA and H_2O_2). This indicate that plants scavenge or detoxify these ROS under the high salt stress in the saline habitat. However, Ozgur et al. (2013), reported a significant boost in lipid peroxidation in shoots following augmentation in salt level in soil solution beyond 150 mM. The MDA contents in the plant tissue demonstrate the production and release of superoxide, and hydroxyl radicals that will ultimately damage the cell integrity and loss of essential fatty acids (Montillet et al., 2005; Rodrigo-Moreno et al., 2013b). Halophytes possess enzymatic and non-enzymatic antioxidant system against ROS that make them superior than glycophytes and thus can tolerate the salinity (Jithesh et al., 2006; Flowers and Colmer, 2008; Ellouzi et al., 2011). The halophytes trigger the formation of H_2O_2 under high salinity through the production of enzymatic antioxidant such as catalase, ascorbate peroxidase and glutathione reductase and non-enzymatic molecules such as ascorbate, glutathione, tocopherol, carotenoids that protect the plants against the cellular damage that salinity might cause due to ionic, tissue toxicity and osmotic stress (Koyro et al., 2013; Munns and Tester, 2008; Hussain et al., 2016; Negrão et al., 2017). The results showed that the only antioxidant enzymes that was increased in the shoots of plants from the saline habitats was catalase (CAT). In addition, ascorbate peroxidase (APX) level was also increased in the roots of plants from the saline habitats (Fig. 26). The higher CAT activity in *S. drummondii*, reaffirming the importance of CATs in scavenging reactive oxygen species (ROS) during stresses. According to reports of other researchers (Shigeoka et al., 2002; Jithesh et al., 2006), the increase in antioxidant activity, especially, APX helps the plants in tolerance of different stresses. The results demonstrate that CAT and APX are fast responders and may act as first-line defenses against salt stress. Those antioxidant enzymes might partially responsible about the capturing the ROS in plants of the saline. However, there are different reports in literature (increase, decrease and no change) regarding CAT expression in different halophytes following salinity exposure (Jithesh et al., 2006; Souid et al., 2018). Several other mechanisms such as accumulation of organic osmolytes (soluble sugars, amino acids, proline, and betaines) and non-enzymes antioxidants could be responsible about detoxifying the ROS of plants under salt stress (Munns and Tester, 2008; Ashraf et al., 2012; Koyro et al., 2013; Negrão et al., 2017).

Salsola drummondii is a C_4 plant (Squires and Ayoub, 2012). Plants of C_4 photosynthesis pathway can use very low concentration of CO_2 in palisade mesophyll tissue. In addition, C_4plants minimize photorespiration by separating initial CO_2 fixation and the Calvin cycle in space; CO_2 fixation occurs inside the mesophyll cell, but Calvin cycle takes place in bundle sheath cells. The separation for Calvin cycle enzyme rubisco bundle sheath cells help plants of C_4 pathway to avoid the photorespiration by keeping the rubisco away from the oxygen present in the mesophyll cell (Moore, 1999). Our results showed less negative (greater) carbon isotope composition ($\delta^{13}C$) value in leaves of *S. drummondii* from saline as compared to non-saline habitat. In *S. drummondii,* carbon isotope discrimination ($\Delta^{13}C$) values decreased in leaf samples of plants from the saline habitat, but elevated in the plants from the non-saline habitat (Fig. 27). Similar results have been reported in the C_4 plants *Atriplex vesicaria* and *A. stipitata*; carbon isotope discrimination decreased in leaves with increasing soil salinity (Walker and Sinclair, 1992). Similarly, Carbon isotope discrimination ($\Delta^{13}C$) decreased with the salinity stress increase in other C_3 plants such as the halophyte *Mesembryanthemum crystallinum* (also use CAM pathway) (Winter and Holtum, 2005), *Gossypium hirsutum* L., and *Phaseolus vulgaris* L., (Brugnoli and Lauteri, 1991). Jiang et al. (2006) reported that carbon isotope discrimination (Δ) attained also lower values under saline conditions in 14 barley genotypes. The increase in δ (less negative) with salt and drought stress observed in other halophytes (Guy et al., 1980; Winter et al., 1981). Some studies have showed that $\delta^{13}C$ increased with salinity increase whether the plants are halophytes or not (Farquhar et al., 1989; Yang et al., 2006). Opposite results have been reported in *Spartina* spp (C_4) as Δ increased of up to 2‰ with increasing salinity (Maricle and Lee, 2006). Also the increase in Δ has been reported in *Atriplex lentiformis* (C_4) (Meinzer and Zhu, 1999), *Atriplex confertifolia* (C_4) (Sandquist and Ehleringer, 1995) and *Zea mays* (C_4) (Bowman et al., 1989). Salt stress could affect photosynthesis by decreasing the stomatal conductance required to prevent loss of water vapor (Brugnoli and Lauteri, 1991).

In C_3 plants there is a negative correlation between $\delta^{13}C$ value of plant and CO_2 mole fraction in the intercellular air space (Ci). It is evident that high salinity causes reduction in stomatal conductance (to decrease the water loss), which lead to an indirect reduction in CO_2 assimilation rate, a decrease Ci and an increase in δ. Ratio of CO_2 from inside to outside atmosphere (Ci/Ca) decreased when $\delta^{13}C$ decreased in most C_3 plants (Farquhar et al., 1982b; Brugnoli et al., 1988). Drought increased $\delta^{13}C$, i.e., increased water use efficiency (WUE) (Farquhar et al., 1989; Brugnoli et al. 1998). Increasing salinity levels declined the net photosynthesis and leaf conductance but increased water use efficiency in *Abronia maritima* (C_3 plant) (De Jong, 1978)

In C_4 plants, the correlation between $\delta^{13}C$ and Ci/Ca ratio and stomatal conductance (gs) can theoretically be positive, zero, or negative, depending on the extent of leakiness (Hubick et al., 1990; Sandquist and Ehleringer, 1995). In C_4 plants, CO_2 leaking from the bundle sheath back to the mesophyll (bundle-sheath leakiness, φ) also affects $\delta^{13}C$ (Avramova et al., 2019). Water use efficiency can provide information about the adaptation of plants into their environment (Walker and Sinclair, 1992). Carbon isotope composition can be used to estimate the water use efficiency easily in C3 plants (Ehleringer et al., 1992). In C_4 plants such as *Salsola drummondii*, more information on bundle-sheath leakiness (φ) is needed to estimate the water use efficiency.

4.5. Effect of salt stress on physiological and biochemical traits in *Salsola drummondii* Ulbr., at seedling stage under experimental conditions

The comparisons of morphological, physiological and biochemical attributes of *S. drummondii* plants from saline and non-saline habitats (see the previous sections) indicated that the plants from saline habitat adapted and survived well; there were insignificant differences in many of the studied attributes between plants of the two habitat types. This was attributed to transgenerational phenotypic plasticity that enables plants of the saline habitats to adapt high levels of Na^+. However, the response of young plants from a specific habitat to salinity levels is not clear. In this section, we are assessing the salinity tolerance and possible mechanisms for such tolerance in small potted plants growing under controlled experimental conditions. Specifically, we assessed the effect of salt stress on the growth parameters, sodium accumulation, elemental composition, antioxidant enzymes activities, Oxidative Stress Markers (ROS) of *S. drummondii* plants during the vegetative stage under different levels of NaCl under controlled experimental conditions.

Our results showed that *S. drummondii* grew successfully very well in up to 500 mM NaCl. In fact, there were no significant differences in the biomass of shoots, roots and leaves between untreated plants and plants treated with 500 mM NaCl (equivalent to sea water salinity) (Fig. 28). Such results confirm the hypothesis that *S. drummondii* are habitat-indifferent halophytes (Cushman, 2001). Similarly, in true halophytes, such as *Suaeda fruticosa* Forssk. ex J. F. Gmel., seedlings fresh weight was enhanced at moderate salinity (200 mM) NaCl, but decreased significantly at higher salinity (up to 1000 mM NaCl) (Khan et al., 2000a). In addition, there were no significant changes in growth parameters between the control and the plants treated with 250 mM NaCl in *Salvadora persica* L., but the growth was significantly decreased at higher NaCl concentrations (500, 750, and 1000 mM) (Rangani et al., 2016). However, in *Crithmum maritimum* L., another halophyte, 50 mM NaCl treatment had enhanced the growth, but 200 mM decreased it (Amor et al., 2005).

The salinity threshold (initial significant reduction in the maximum expected yield) of *S. drummondii* calculated after Shannon and Grieve (1998), was 41% at 800 mM NaCl in relation to shoot fresh weight while it was 17% for leaf fresh weight compared with control (Fig. 28). Interestingly, this reduction in leaf biomass was not associated with reduction in root biomass at high salinity. The shoot biomass decreased at higher salinity significantly, and this might be due to fall in turgor pressure (Clipson et al., 1985; Rozema, 1991; Balnokin et al., 2005), reduced carbon fixation and the imbalance of photosynthesis and respiration (Ball, 1988; Lovelock and Ball, 2002). Such decrease in shoot growth at higher salinity might be an adaptive mechanism to survive under high salinity condition. The growth reduction can reduce the oxidative damage, provide more free amino acids for osmotic adjustment, and save energy (Sobhanian et al., 2010; Yu et al., 2011; Rangani et al., 2016). Additionally, the succulence was not affected in both shoot and root of *S. drummondii* at 200 and 500 mM NaCl, but was significantly reduced at higher salt concentrations (800 mM NaCl) (Fig. 29). Similar results were reported in *Crithmum maritimum* (Amor et al., 2005) and *Suaeda fruticosa* (Khan et al., 2000a), and the decrease in tissue water content was related to decreasing plant growth at high salinity.

Plants treated with 500 and 800 mM NaCl showed significant a reduction in the content of chlorophyll *a*, *b* and total chlorophyll, which might result in photo inhibition at higher salinity levels (Fig. 30). Similar results were reported in other halophytes, such as *Acacia ampliceps* (Theerawitaya et al., 2015), *Plantago coronopus* L. (Koyro, 2006) and *Salicornia rubra* A. Nelson (Tiku, 1976), where increased NaCl concentrations led to decreased chlorophyll concentrations. Furthermore, a significant decrease in chlorophyll and carotenoid contents due to NaCl stress were reported in the halophytes *Salicornia persica* Akhani and *Salicornia europaea* L. (Aghaleh et al., 2009). Additionally, reduced levels of carotenoids were demonstrated in *Halimione portulacoides* (L.) Aellen and *Sarcocornia fruticosa* (L.) A. J. Scott. due to salt stress (Duarte et al., 2013; Duarte et al., 2014). Our results indicate that the decrease in the chlorophyll content at higher salinity was associated with a significant increase in hydrogen peroxide and MDA that are responsible for chlorophyll degradation (Verma and Mishra, 2005; Taïbi et al., 2016). The negative effect of high salinity on chlorophyll content has been ascribed to negative effect of Na^+ on uptake of some important elements, especially Mg^{2+} (Parida and Das, 2005). Our results indicated a significant reduction in Mg^{2+} in *S. drummondii* leaves treated with higher levels of NaCl (Fig. 32).

Our short-term sodium influx analysis revealed that plants grown under high salinity (1200 mM) showed a significant increase in sodium accumulation in roots after 0, 0.5, 1, 2, 4, 8 hrs of NaCl tratment (Fig. 31A). *S. drummondii* plants were exposed to short term (0-8 hrs) NaCl treatment using the highest concentration that can tolerate (1200 mM), so the changes in the sodium accumulation could be detected by AAS. During the long term exposure of *S. drummondii* to the moderate salinity levels, sodium will be accumulated gradually with the increasing time, so the sodium accumulation could be detected easily by AAS. In contrast, in the short term assay due to the limited treatment time, sodium levels could not be detected accurately and might give a false indication that sodium influx might not be occurred through the plant roots. For this reason we used the highest concentration of sodium chloride (1200 mM) in the influx short term assay to help us to follow the changes in sodium concentration inside root tissues of *S. drummondii* plants precisely. Furthermore, the same concentration (1200 mM NaCl) was used to treat the *S. drummondii* for 24 hours for the transcriptomic analysis as to identify the transcripts that are associated with high level of salinity stress.

Our Atomic Absorption Spectroscopy (AAS) results showed a progressive increase in Na^+ accumulation in shoots and roots of plants with the increase in NaCl concentration (Fig. 31). This was also reported in *Crithmum maritimum* L. (Amor et al., 2005) and *Suaeda fruticosa Forssk. ex J.F.Gmel.* (Khan et al., 2000a). The higher Na^+ accumulation levels in *S. drummondii* shoots compared to roots is due to the increased Na^+ translocation from roots to shoots which is a possible adaptive mechanism in halophytes as reported in *Suaeda altissima* (L.) Pall. (Balnokin et al., 2005), *Mesembryanthemum crystallinum* L. (Agarie et al., 2007), and *Salicornia europea* L. (Lv et al., 2012). Upregulation of SOS1, HKT and HAK transporters to translocate Na^+ from root to shoot tissues in different halophytes have been reported (Chauhan et al., 2000; Shi et al., 2002; Su et al., 2002; Lv et al., 2012). However, Na^+ accumulation could affect the uptake and/or distribute essential nutrients or synthesized organic solutes (Britto and Kronzucker, 2006). Our results showed that *S. drummondii* plants treated with NaCl exhibited significant reduction in the percent of essential ions in different plant organs under salinity stress (Fig. 32). It has been reported that major essential ions including Ca^{2+}, K^+ and Mg^{2+} were decreased in different halophytes such as *Atriplex griffithii* Moq. (Khan et al., 2000b), *Plantago coronopus* L. (Koyro, 2006), and *Cakile maritima* Scop. (Megdiche et al., 2007; Ellouzi et al., 2011) under salinity treatment.

Salt accumulation in vacuoles is particularly obvious in some dicotyledonous halophytes, such as *Salicornia maritima* Wolff and Jefferies (Harvey et al., 1981), *Salicornia bigelovii* Torr. (Ayala and O'Leary, 1995), *Salicornia europea* L. (Park et al., 2013) and is characterized by leaf and stem succulence. The dicotyledonous halophytes have the ability to prevent cytoplasm dehydration by accumulating high concentrations of Na^+ and Cl^- that may exceed 1000 mM in cell vacuoles as well as compatible osmotica (e.g. proline) in the cytoplasm (Gorham, 1995; Park et al., 2013). For osmotic adjustment at higher salinities, Marcum and Murdoch (1992) suggested that 200 to 300 mM of organic osmotica in the cytoplasm is sufficient. *S. drummondii* produces about 42 mM proline in shoots and about 13 mM in roots (as the capacity to accumulate proline is correlated with salt tolerance) (Fig. 34), which is theoretically not sufficient to balance the high accumulation of salt in the vacuoles. In this case, the plants examined in our study may have utilized other organic osmotica, such as glycine betaine, and inorganic osmotica such as sodium and chloride for osmotic adjustment. Elevated salinity can cause ionic and osmotic stress; halophytes can avoid water stress by decreasing the stomatal conductance to decrease water loss and/or can tolerate it through osmotic adjustment by accumulation of inorganic ions or organic osmolytes (Touchette et al., 2009). Our results indicated that there were no significant differences in shoot and root succulence of *S. drummondii* plants treated with 500 mM NaCl which suggests that *S. drummondii* plants are developing avoidance strategy by having succulent leaves and might be through closing their stomata to decrease the water loss and maintain stable water content inside their tissues. Furthermore, *S. drummondii* plants are tolerating the osmotic effect of salt stress by producing proline as our results showed an increase in proline levels with the salinity increase.

Secondary oxidative stress can occur as a result of salt stress by production of excess ROS, e.g. H_2O_2, O_2^- and OH (Hernández et al., 2001; Xiong and Zhu, 2002; Zheng et al., 2009). In our study, the concentration of H_2O_2 increased significantly only in shoots at the highest salinity levels (Fig. 3.20 C and D). Similar results were reported in *Gypsophila oblanceolate* (Sekmen et al., 2012). Additionally, our results showed that the concentration of the well-known oxidative stress biomarker lipid peroxidation-MDA was significantly increased under high salt concentrations in the shoots of *S. drummondii* plants. Similar trends were also reported in *Crithimum maritimum* L. (Amor et al., 2005), *Nitraria retusa* and *Atriplex halimus* (Boughalleb and Denden, 2011). Aghaleh et al. (2009) also reported that MDA content remained close to control levels under moderate NaCl treatments (100 and 200 mM) and increased at higher concentrations (400 and 600 mM NaCl) in *Salicornia persica* Akhani and *Salicornia europea* L. It seems that the higher sodium accumulation in shoots of plants treated with higher salinity levels stimulated higher accumulations of Oxidative Stress Markers (ROS) (H_2O_2 and MDA) that may cause injury to the cellular membranes. This also suggests that antioxidant compounds must function actively to scavenge the excess ROS produced under higher salt stress.

Generally, under environmental stresses, the rate of ROS production is dependent on the plant species, the age of plants, and the stress intensity and period (Navari-Izzo et al., 1996). The membrane damage under salt stress is related to a higher production of toxic ROS (Hernandez et al., 1995; Gossett et al., 1996; Miszalski et al., 1998; Hernández et al., 2001;

Sairam and Srivastava, 2002; Amor et al., 2005; Ellouzi et al., 2011). In the roots, however, our results showed that 800 mM NaCl did not induce membrane damage (membrane lipid peroxidation), where the MDA concentration remained unchanged (Fig. 33B), agreeing with previous findings were unchanged membrane lipid peroxidation levels were a characteristic of tolerant plants coping with salinity (Shalata et al., 2001; Seckin et al., 2009; Yıldıztugay et al., 2011).

It is well known that CAT and APX play a crucial role in plant defense against salt-induced oxidative stress to scavenge hydrogen peroxide (H_2O_2) (Miller et al., 2010). In the roots of *S. drummondii*, high salinity increased significantly the CAT activity. Furthermore, in our study, the observed changes in hydrogen peroxide and CAT levels may be directly related. High NaCl concentration (800 mM) significantly increased CAT activity to detoxify the produced hydrogen peroxide under high salinity. As such, changes in *Salsola drummondii* root hydrogen peroxide levels were not observed. It has been reported that activity of APX and CAT was not changed in the storage parenchyma of salt-treated plants of succulent halophyte *Carpobrotus rosii* (Haw.) Schwantes (Zeng et al., 2018).

Our results showed that APX increased significantly in the shoots of *S. drummondii* plants treated with 500 and 800 mM NaCl (Fig. 35). Similar results were reported in leaves of lentil (Bandeoğlu et al., 2004), shoots of the euhalophyte *Salicornia brachiata* Roxb. (Parida and Jha, 2010), *Sesuvium portulacastrum* (L.) L. plants (Srivastava et al., 2015), and leaves of *Phaseolus vulgaris* L. (Taïbi et al., 2016). In contrast, APX levels were decreased significantly in the roots of *S. drummondii*, which was in accordance with a previous report in the roots of cv. Adamello of *Triticum durum* Desf. (Meneguzzo et al., 1999) and roots of the sunflower *Helianthus annuus* L., ecotype K. Piacenza irrigated 20% sea water concentrations (Di Baccio et al., 2004).

Halophyte plants can respond to salinity oxidative stress by increasing the activity of antioxidant enzymes, which was obvious in the present study where high activities of GPX at high salinity levels were observed in both shoots and roots, with higher levels in roots in comparison to shoots (Fig. 35 E and F). This was also observed in some salt tolerant plants such as *C. maritimum* L. (Amor et al., 2005). Additionally, GPX activity increased under salt stress as reported in other halophytes such as *Suaeda nudiflora* Thw. (Cherian and Reddy, 2000), *Hordeum marinum* (Seckin et al., 2010), *Halimione portulacoides* (L.) Aellen and *Sarcocornia fruticosa* (L.) A. J. Scott. (Duarte et al., 2013) and *Limonium delicatulum* (Girard) Kuntze (Souid et al., 2016). Our results indicated that H_2O_2, which is an important mediator of cellular toxicity during environmental stress, is scavenged effectively by induced levels of GPX in roots. The level of H_2O_2 in roots was unchanged due to the high level of GPX in this region, while GPX activity in shoots was not high enough to scavenge the produced H_2O_2. GPX were observed to be increased in *S. drummondii* roots under salt stress, similarly observed in *Suaeda nudiflora* Thw., roots (Cherian and Reddy, 2000). In *S. drummondii* roots, the activity of GPX at 800 mM NaCl was found to be increased by 3-fold more than control plants, while CAT increased by around 1.5-fold. This may explain why our results did not demonstrate significant changes in root MDA and hydrogen peroxide levels, possibly due to the induced compensatory mechanisms suggested by (Apel and Hirt, 2004) when the balance of scavenging enzymes is altered. APX was found to be decreased under increased salinity levels, possibly due to unchanged H_2O_2 and MDA levels reflecting the high tolerance of *S. drummondii*. Additionally, the resulting oxidative damage may not be sufficient to warrant APX activity. Our data also demonstrated that CAT and GPX enzymes had the greatest H_2O_2 scavenger activity in roots.

Glutathione is one of the most important antioxidants and could decrease the oxidative stress either via scavenging the toxic ROS or by the ascorbate-glutathione cycle (Foyer et al. 1997; Ashraf 2009). Total Glutathione significantly increased in the shoot of *S. drummondii* at the highest salinity level as reported in the halophyte *Cakile maritima* Scop., (jerba accession) under salt stress (Amor et al., 2006) while it decreased in root as reported in wheat under drought stress (Loggini et al., 1999) and in *Cakile maritima* Scop. (Tabarka accession) under salt stress (Amor et al., 2006). We suggested that total glutathione increased in shoot might be due to the high accumulation of sodium in shoot and the oxidative damage happened in shoot i.e. the high stressed part in *S. drummondii* is the shoot part while the root have less sodium accumulation, no changes in MDA and hydrogen peroxide i.e. not stressed and this might be the reason in the decline of total glutathione in root. Noteworthy, the Na^+ translocation rate is very high, as many of the responses occur in the shoot while roots appear to be more homeostatic.

Adult plants collected from field accumulated around 120 mg/g dry weight Na^+, which is approximately 600 times more than that accumulated in four-months old plants exposed to 800 mM NaCl for 20 days in the laboratory. This big difference in Na^+ accumulation between adult plants from natural habitats and those grew in the lab could be attributed to the age and time of exposure to salinity. Plants in field might be spent years under the high salinity and accumulated high level of Na^+ for osmotic regulation (Table 16). Yet, there was no significant differences in sizes and growth of *S. drummondii* growing in saline and non-saline habitats. However, plants grown in the lab for four months and then exposed to 800 mM NaCl for 20 days showed a significant reduction in growth (Fig. 28 and Fig. 29) and showed some toxicity symptoms (Fig. 33 A and C), despite they produced more proline and antioxidants (Fig 34, 35 and 36) to overcome the sodium toxicity. This means that salt adaptation of the habitat-indifferent halophyte, *S. drummondii* in field under natural conditions might be due to transgenerational plasticity which provides phenotypic variation that contributes to salinity adaptation and can occur through maternal and/or epigenetic effects (Vu et al., 2015; Soliman et al., 2018).

4.6. Transcriptomic analysis of *Salsola drummondii* Ulbr. under salt stress

Identification of differentially expressed genes under salt stress

S. drummondii has high salt tolerance and represents an excellent source for studying salt stress tolerance mechanisms, and may provide a valued source for salinity tolerance-related potential genes. Transcriptome analysis for salt tolerance in *S. drummondii*, identified 17361 differentially expressed genes (DEGs). Within DEGs, about 1283 (7.3%) genes can be assembled into 9 functional categories (including transcription factors, signal transduction, defense metabolism, transporters, cell wall metabolism, regulatory processes, respiration, chaperons and ubiquitination) which may hold specific biological functions in salt tolerance mechanisms of *S. drummondii*. The putative functional roles of the candidate genes are discussed below and summarized in (Table 25)

Transcription factors

TRINITY_DN610243_c0_g1_i11 and TRINITY_DN610243_c0_g1_i15: homeobox-leucine zipper protein (ATHB-40) was up-regulated in the shoots of *S. drummondii* under salt stress. Transcription factors such as homeobox 6 (ATHB 6), ATHB12 and HD-Zip have been reported to be involved in many physiological functions as well as the mediation of growth responses to water deficits (Tan and Irish, 2006; Gharat et al., 2016), the regulation of floral development (Olsson et al., 2004), and cell cycle regulation (Hur et al., 2015). Upregulation of members of the HD-Zip transcription factors in *Suaeda maritima* L., in response to salt treatment also indicated their necessary role in abiotic stress tolerance (Gharat et al., 2016). *Arabidopsis thaliana* homeobox 12 (ATHB12) regulates leaf growth (specifically adaxial leaf fates) by promoting cell expansion and endo-reduplication (Hur et al., 2015). In our analysis, *S. drummondii* homeobox-leucine zipper protein ATHB-40 transcription factor, which has been implicated in stress tolerance (van Muijen et al., 2013), was upregulated under salt stress. Similar to our results, homeobox-leucine zipper protein ATHB-40-like was also upregulated in the early blight resistant genotype of tomatoes treated with *Alternaria solani*. Additionally, it was identified as cathepsins, which are involved in the lysosome pathway (Upadhyay et al., 2016), and was upregulated in the roots of *Prunus persica* under drought stress (Ksouri, 2016).

Another transcription factor was upregulated in shoots under salt stress is TRINITY_DN631994_c2_g1_i11: protein FAR1-RELATED SEQUENCE 5-like. Protein FAR1-RELATED SEQUENCE 5-like is involved in the regulation of numerous functions including light control of development, zinc ion binding, the DNA-template and transcription. (Yang et al., 2018b) reported that Sb09g006170, involved in encoding FAR1 and suberin synthesis, was upregulated significantly in two genotypes of sweet sorghum inbred lines which differ in salinity tolerance (i.e. salt sensitive and salt tolerant respectively). Moreover, FAR1-related Sb04g022400 was observed to be downregulated only in salt sensitive genotype roots. Hence, FAR1-RELATED SEQUENCE 5-like transcription factor may play a key role in the salt tolerance mechanisms of *S. drummondii.*

Signal transduction

Signal transduction plays an important role for plant tolerance to abiotic stresses such as salt stress (Huang et al., 2012; Seyfferth and Tsuda, 2014). In the current study, genes involved in signal transduction pathways were differentially expressed under salt stress.

In *S. drummondii*, carrot ABA-induced in somatic embryos 3 (TRINITY_DN558998_c1_g2_i2) demonstrated upregulation in the shoots treated with 1200 mM NaCl. Carrot ABA-induced in somatic embryos 3 (CAISE3) was also reported to be expressed in embryogenic cells, somatic embryos and seeds in the later stages of development (Shiota et al., 2004). CAISEs were induced by abscisic acid treatment and might be involved the desiccation tolerance in carrot somatic embryo (Shiota et al., 2004). Upregulation of CAISE3 may be the result of ABA production induced by salt stress in *S. drummondii*, where the ABA signal transduction pathway contributes in the salt tolerance process.

The present study also highlighted that the gene encodes for (protein phosphatase 2C 24 (PP2Cs): TRINITY_DN558998_c1_g2_i2) was up-regulated in response to salinity in *S. drummondii* shoots. Members of plant PP2Cs form a unique class of enzymes, where some members counteract mitogen-activated protein kinase pathways whereas other members act as co-receptors for abscisic acid phytohormone. Therefore, plant PP2Cs function as regulators of various signal transduction pathways (Rodriguez, 1998; Wang et al., 2007; Fuchs et al., 2013). Protein phosphatase 2C is involved in ABA signal transduction and plays a notable role in stress signaling (Meyer et al., 1994). Similar results were obtained from *Suaeda fruticosa* (Diray-Arce et al., 2015) and *Suaeda glauca* (Jin et al., 2016), where PP2C was up-regulated under salt stress. Our transcriptomic results in the current study revealed that salt stress-induced abscisic acid signaling was evident as demonstrated previously in the two halophytes *S. glacua* (Jin et al., 2016) and *S. fruticosa* (Diray-Arce et al., 2015).

The transcriptomic analysis of *S. drummondii* roots under salt stress showed down-regulation of 14-3-3-like protein D (TRINITY_DN616492_c4_g4_i1). The 14-3-3 proteins are regulatory proteins which can bind several signaling proteins, regulate the activity of plasma membrane H^+-ATPases by interacting with the MAPK kinase cascade, as well as contribute to maintenance of ion homeostasis and ion transporters (H^+-ATPase, K^+ channels) depending upon their phosphorylation status (Kosová et al., 2015). Evidence has also shown that 14-3-3 proteins regulate the plant stress response (Denison et al., 2011). 14-3-3-like protein increased under salt stress in mangrove (*Kandelia candel*) leaves (Wang et al., 2014). 14-3-3-like protein increased under salt in *Brachypodium distachyon* seedling leaves (Lv et al., 2014).14-3-3-like protein decreased under hydrogen peroxide and osmotic stress in the roots of *Brachypodium distachyon* seedling (Bian et al., 2015; Chen et al., 2018). ABA affects both the expression and protein levels of 14-3-3 isoforms in plants (Schoonheim et al., 2007; Wasilewska et al., 2008). Plants that have downregulated 14-3-3 levels show altered expression of ABA-regulated genes (Schoonheim et al., 2007). One effect of ABA signaling is closure of the stomata to prevent water loss, which includes a decrease in H^+-ATPase (a 14-3-3 client) activity (Merlot et al., 2007). In this case, downregulation of the H^+-ATPase pump during salt and drought stress is a crucial step in membrane depolarization to initiate stomatal closure (Merlot et al., 2007). This process may also be a possible explanation for the down-regulation of 14-3-3 transcript in *S. drummondii* under salt stress.

Gibberellin-regulated family proteins are associated with plant growth and development. In the present study, salt stress decreased the expression levels of gibberellin-regulated protein 6 (TRINITY_DN602037_c1_g1_i4 and TRINITY_DN602037_c1_g1_i3), a factor known to be involved in gibberellin biosynthesis in plants growing under salt stress (Jithesh et al., 2019). Gibberellin production during abiotic stress also modulated the biosynthesis of antioxidant enzymes and sugar signaling (Fahad et al., 2015). GA signaling regulates stomatal closure (a typical ABA signaling response) (Du et al., 2015), where GA application induced a transient opening of stomata as reported by (Göring et al., 1990). Similar trends to our results have also been previously reported, where the Gibberellin-regulated protein 6 transcript was downregulated in potatoes in response to drought (Gong et al., 2015) and in Kenaf (*Hibiscus cannabinus* L.) in response to salt stress, respectively (Li et al., 2017). In contrast, transcriptomic analysis of epidermal bladder cells of the halophyte *Mesembryanthemum crystallinum* in response to salt stress exhibited upregulation of the gibberellin regulated family (Oh et al., 2015).

TRINITY_DN627403_c1_g1_i2: glucose and ribitol dehydrogenase homolog 1 was upregulated in the shoots of *S. drummondii* under salt stress. Glucose and ribitol dehydrogenase homolog 1 (Glc/RibDH) may act as a short alcohol-polyol-sugar dehydrogenase, probably in relation to carbohydrate metabolism and drought tolerance. Glc/RibDH may also be involved in signal transduction and oxidoreductase activity (Alexander et al., 1994; Shiota et al., 2004; Kawahara et al., 2013). Similar to our results, it has been reported that glucose/ribitol dehydrogenase (Glc/RibDH) was upregulated in the mature grains of salt tolerant barley lines compared to salt sensitive lines under salt stress (Witzel et al., 2010). The protein level of Glc/RibDH represented conflicting accumulation way in alfalfa (*Medicago sativa* L. cv. Gabe`s) when the untreated control compared with the osmoprimed seeds under salt stress (Yacoubi et al., 2013).

Transcript TRINITY_DN556783_c2_g1_i2, which corresponds to glutamine synthetase (GS), was upregulated in root tissues. GS is a key enzyme in nitrogen assimilation that assimilates ammonia into amino acids where it catalyzes the reaction of ammonium and glutamate to produce glutamine (Bernard and Habash, 2009; Bao et al., 2015). Glutamine is a vital nutrient and important amino acid in plants. Glutamine may function as a signaling molecule and interact with the other signal transduction pathways to regulate expression of genes involved in plant growth and stress responses (Kan et al., 2015). In general, plants have two isoforms of GS. GS1 is involved in primary nitrogen assimilation and nitrogen remobilization during developmental processes or leaf senescence (Bernard et al., 2008), whereas GS2 is involved in the re-assimilation of photorespiratory ammonium (Igamberdiev et al., 2014). In triticale (× Triticosecale Wittm. ex A. Camus.) seedlings, GS activity was induced under 100 mM NaCl enriched medium for 7 days (Kwinta and Cal, 2005). Similarly, our analysis showed that GS was upregulated upon 1200 mM NaCl treatment in *S. drummondii* seedlings.

Regulatory processes

Another transcript (TRINITY_DN354150_c0_g1_i1) encodes, glycine-rich RNA-binding protein 4, mitochondrial was also observed to be up-regulated in roots. Glycine-rich RNA-binding proteins are involved in vernalization responses and in promoting floral transition in *Arabidopsis thaliana* (Streitner et al., 2008). GRPs have been involved in plant responses to alterations in environmental conditions (Kim et al., 2006; Wang et al., 2012). GRPs play a role in the post-transcriptional regulation of genes, and are known to be involved in responses to environmental stresses such as salt stress (Kim et al., 2006; Wang et al., 2012). GRPs were reported within salt tolerance genes in the halophyte *Sporobolus virginicus* and upregulated in *Arabidopsis thaliana* salt tolerant lines expressing GRP from *S. virginicus* (SvGRP1) compared with wild type under salt stress (Tada et al., 2019). In particular, glycine-rich RNA-binding protein7 (GRP7) is involved in abiotic stress responses through the regulation of stomata opening and closure in *A. thaliana* (Kim et al., 2008). Cao et al. (2006) reported that Glycine-rich RNA-binding protein7 is also involved in regulating stress responses and abscisic acid (ABA) signaling in *Arabidopsis*. Thus, GRPs seem to play a major role in *S. drummondii* tolerance, possibly by regulating stomata opening and closure under salinity stress.

The transcript TRINITY_DN583991_c0_g2_i5, which encodes for clathrin heavy chain, was found to be downregulated in the roots of *S. drummondii* under salt stress. Clathrin heavy chains (CHCs) are components of clathrin (Brodsky et al., 2001; Fotin et al., 2004). Clathrin heavy chain subunits affect stomatal regulation, coordinate endo-and exocytic traffic gas exchange, vegetative growth and PIN Auxin transporters in *Arabidopsis* (Kitakura et al., 2011; Larson et al., 2017). Clathrin heavy chain 2 dependent endocytosis influences the incorporation of activated receptors and is necessary for protection mediated by pattern recognition receptor kinases (Mbengue et al., 2016). Similar to our results, CHC was downregulated in the halophyte *Thellungiella halophila* under salt stress (Pang et al., 2010).

Our differential expression analysis revealed that three transcripts of senescence associated protein (TRINITY_DN593653_c0_g2_i3, TRINITY_DN574364_c1_g3_i2) were upregulated in root tissues. These proteins have also been found to be involved in regulatory processes and cellular signal transduction (Gupta and Huang, 2014). It has been reported that during drought stress, senescence-associated protein is downregulated in leaf tissue from *Mentzelia filifolia* (Devitt, 2018). senescence-associated protein has also been found to be down-regulated in the halophyte *Suaeda fruticosa* under salt stress (Diray-Arce et al., 2015). However, senescence-associated SAG13 that was upregulated in *Arabidopsis,* mostly unaffected in *Thellungiella halophila* under salinity stress (Gong et al., 2005). In *Arabidopsis*, SAG29 regulates cell viability under high salt stress along with a cell plasma membrane localized MtN3 protein (Seo et al., 2011). The SAG29 gene is primarily expressed in senescing plant tissues. This gene is known to be induced upon osmotic stresses through an abscisic acid-dependent pathway (Seo et al., 2011). The upregulation of SAG (senescence-associated gene) indicated that the ABA pathway controls the salt tolerance mechanism in *S. drummondii*. SAG21 is also enhanced during natural and stress conditions such as ozone, drought, cold and salt stresses. SAG21 is not directly involved in senescence, but is also considered as a marker for stresses related to cellular degradation and senescence (Weaver et al., 1998; Hundertmark and Hincha, 2008).

Transporters

Ion homeostasis and ion transporters

Our results demonstrated upregulation of the magnesium transporter 2 isoform 2 (MGT2 isoform 2) (TRINITY_DN574004_c0_g5_i1) in *S. drummondii* shoots. Magnesium transporter 2 isoform 2 is a magnesium ion transmembrane transporter and can also transport other divalent cations. Magnesium transporter plays a vital role in salt tolerance in plants (Chen et al., 2017b). It has been identified as one of the salt tolerance response genes in the salt-treated halophyte *Suaeda asparagoides* (Ayarpadikannan et al., 2012). In contrast, it has been also reported that magnesium transporter NIPA2 was downregulated under salt stress in the halophyte *Suaeda fruticosa* (Diray-Arce et al., 2015). The observed upregulation of magnesium transporter 2 isoform 2 in *S. drummondii* is an indication of its important role in salt tolerance.

Three transcripts (TRINITY_DN587967_c4_g3_i3, TRINITY_DN587967_c4_g3_i2 and TRINITY_DN587967_c4_g3_i1) belonging to protein plant cadmium resistance 2-like (PCR2) were downregulated in *S. drummondii* shoots, while TRINITY_DN422398_c0_g1_i1 was downregulated in roots. Protein PCR2 reduced cadmium accumulation, defended against pathogens and responded to oxidative stress (Song et al., 2004; Song et al., 2010).

Protein transporters

The transcript TRINITY_DN567294_c2_g2_i1 (ABC transporter A family member 1 isoform X2) was downregulated in *S. drummondii* roots under salt stress. ABCA1 isoform X2 is a member of the ATP-binding cassette (ABC) transporter superfamily, which is one of the biggest transporter gene families and energizes the transport of molecules across the cell membrane by hydrolyzing ATP (Leslie et al., 2005). Members of the ABC family were reported to be involved in detoxification processes as well as plant growth, plant development, plant nutrition, interaction of the plant with its environment and response to biotic and abiotic stresses (Kang et al., 2011). ABC transporter A family member 2-like has been found to be involved in nitrogen transport in tea plants (Yang et al., 2018a). ABC transporters were also observed to improve drought and salt stress tolerances in *Arabidopsis* (Kim et al., 2010). In contrast to our results, ABC transporter was upregulated in the halophyte *Salicornia brachiate* under salt and elevated CO_2 conditions (Benjamin et al., 2018).

Our results showed downregulation of ABC (ATP binding cassette) transporter pleiotropic drug resistance 1 (TRINITY_DN629181_c2_g1_i6), (TRINITY_DN625631_c0_g1_i2), (TRINITY_DN629181_c2_g1_i8), (TRINITY_DN606447_c1_g1_i6), (TRINITY_DN569023_c2_g2_i3), (TRINITY_DN629181_c2_g1_i4) and (TRINITY_DN562298_c2_g1_i1) in the shoot and known as a general defense protein. Opposite results have been reported in the roots of the salt-tolerant rice cultivar FL478 in response to salt stress (Senadheera et al., 2009). Pleiotropic drug resistance 5-like (PDR5-like ABC) was also shown to be upregulated in barley leaves during the first 24h of salt stress (Ueda et al., 2006). As such, it is possible that ABC transporter does not play a vital role in the salt tolerance mechanisms of *S. drummondii*.

Sugar transporter

TRINITY_DN637893_c3_g3_i1: bidirectional sugar transporter SWEET14-like protein was up-regulated in the shoots of *S. drummondii*. SWEET genes are involved in sugar diffusion across cell membranes and act as key players in sucrose phloem transport (Daba et al., 2019). SWEET 14 is needed for optimum development of anthers, seeds and seedlings, and in regulating the gibberellic acid response (Kanno et al., 2016). Bidirectional sugar transporter SWEET3, which is involved in low affinity influx and efflux of sugars across the cell plasma membrane, was up-regulated under salt stress in the halophyte *Suaeda fruticosa* (Diray-Arce et al., 2015).

Plant defense metabolism

Salt stress enhances the production of reactive oxygen species (ROS) which cause oxidative stress in plant cells. Plants remove the oxidative stress by production of enzymatic and non-enzymatic antioxidants to detoxify the ROS in order to maintain redox homeostasis. Antioxidant enzymes include SOD, POX, APX, CAT and GR. In our analysis, the transcript TRINITY_DN604867_c3_g1_i1, which codes for copper/zinc superoxide dismutase (SOD), was upregulated in *S. drummondii* roots Therefore, SOD may play a critical role in ROS scavenging under salinity stress in *S. drummondii* as the first line of defense against oxidative stresses by catalyzing $-O_2$ molecules to form H_2O_2 (Alscher et al., 2002). Similar results have been reported that Cu/Zn-SOD increased under salt stress in the seedling of the halophyte *Suaeda maritima* L., (Mallik et al., 2011)

In *S. drummondii*, the transcript TRINITY_DN554057_c0_g1_i2, which is a homologue of catalase (CAT), was downregulated in roots, while the transcript TRINITY_DN599776_c0_g2_i3, which is a homologue of peroxidase P7-like, was also down-regulated in the shoots after salt treatment. CAT enzyme catalyzes the breakdown of H_2O_2 into water and oxygen (Willekens et al., 1997) and was up-regulated in cotton roots and leaves under salt stress (Zhang et al., 2016). Peroxidase P7-like is one of the key enzymes controlling plant growth and development. It has been reported that peroxidase p7-like was downregulated in the roots of peach exposed to drought stress (Ksouri, 2016). In contrast, it has been shown that peroxidase P7-like was upregulated under alkali and salt stress in tobacco and involved in the tolerance process (Xu et al., 2019). Based on our results, we hypothesize that ROS produced due to high salt concentration could be mainly controlled by SOD.

Flavonoids are known to be involved in defense metabolism against many stresses, such as salt stress, wounding and UV-B (Mechri et al., 2015; Murai et al., 2015). In the present study, TRINITY_DN630886_c2_g1_i8 and TRINITY_DN608353_c0_g2_i1: which correspond to chalcone synthase (CHS), was downregulated in the shoots of *S. drummondii*. CHS has been reported as a salt responsive candidate gene in the halophytes *Atriplex nummularia* and *A. leucoclada* (Sayed-Hussin, 2007), and is the first key enzyme in the flavonoid/isoflavonoid biosynthesis pathway. The accumulation of many metabolites such as flavonols, isoflavones, flavones and anthocyanins have been suggested to be affected by the changes in CHS gene expression levels (Domitrovic´ et al., 2015). Upregulation of the CHS gene would increase the accumulation of flavonoids while lower expression would lead to decrease in flavonoid accumulation and increase in the production of metabolites derived from the phenylpropanoid pathway, leading to the production of different phenolic compounds such as lignins and phytoalexins (Domitrović et al., 2015). Flavonoids have been considered as antioxidants and play a role in plant defense against salt stress (Agati et al., 2012). In the present study, the expression level of the CHS gene was inhibited in shoots by salt-stress, which suggests that salt-stress can regulate the expression of chalcone synthase gene in *S. drummondii.* Additionally, treatment with 1200mM NaCl for 24h did not induce the production of flavonoids in *S. drummondii*. Similar results have been reported in the roots of the medicinal halophyte *Limonium bicolor,* while the opposite trend has been seen in the leaves of the same plant (Wang et al., 2016). Similar to our results, CHS was reported to be downregulated at high salinity-flooding combined stress in soyabean (Glycine max L. Merr. cv. Taegwang) roots and hypocotyls (Alam et al., 2011) and in *Salix matsudana* Koidz roots under salt stress (Qiao et al., 2014). In *Amaranthus hypochondriacus* L., root transcripts involved in flavonoid biosynthesis was decreased under drought stress (Huerta-Ocampo et al., 2011).

The transcripts TRINITY_DN591739_c0_g1_i5 and TRINITY_DN591739_c0_g1_i4 (which encode BURP domain-containing protein 5 isoform X1) were observed to be downregulated in *S. drummondii* shoots under salt stress. BURP domain-containing proteins play a vital role in plant development, metabolism and defense against environmental stresses (Shunwu et al., 2004). The plant-specific BURP domain family was also found to play a role in *Arabidopsis thaliana* drought tolerance (Harshavardhan et al., 2014). Similar results have been reported by (Miyama and Hanagata, 2007), where the expression of BURP-domain containing protein was severely downregulated in *burma* mangrove *Bruguiera gymnorhiza* (L.) Savigny leaves under salt stress.

Cell wall metabolism

The cell wall of the plant cell is the first place to receive and respond to abiotic stress (Wimmer and Eichert, 2013). The stress signal induces cell wall remodeling to preserve flexibility and protect the plant cell against ionic disturbances (Hofmann, 2016). Different transcripts associated with cell wall metabolism have been identified in *S. drummondii* under salt stress as discussed below.

Lignin biosynthesis pathway

TRINITY_DN621268_c4_g1_i4: p-coumarate 3-hydroxylase was downregulated in the roots of *S. drummondii* under salt stress. p-coumarate 3-hydroxylase (C3H) is known to be involved in the lignin biosynthesis pathway. Lignin is one of the most important compounds in vascular plants, required in structural support and water transport (Xu et al. 2009). Lignin content and composition in plants may be changed by environmental stresses (Silva-Moura et al. 2010). Drought stress inhibited the expression of ZmC3H of *Zea mays* in leaves whereas it increased its expression in roots (Ludidi et al., 2015). Downregulation of p-coumarate 3-hydroxylase (C3H) in *S. drummondii* roots could lead to a decrease in root lignification (where root growth diminishes), which is considered as an adaptive mechanism to harsh conditions as reported previously in the roots of *Amaranthus hypochondriacus* L., under drought stress (Huerta-Ocampo et al., 2011).

Cellulose and hemicellulose degradation

TRINITY_DN476880_c0_g1_i1 and TRINITY_DN476880_c0_g1_i1: Beta-glucosidase were downregulated in roots of *S. drummondii* under salt stress. β-glucosidases have been found to play a role in abiotic stresses, especially dehydration through abscisic acid. Beta-glucosidase is the key enzyme present in cellulase as it converts cellobiose to glucose during cellulose hydrolysis (Singhania et al., 2013). It has been suggested that downregulation of β-glucosidase might be linked with the inhibition of cell wall elongation under stress, which decreases the growth of plant roots (Kong et al., 2010). Beta-glucosidase gene was upregulated by salt stress *Thellungiella halophila* (Taji et al 2004; Wong et al., 2006).

Furthermore, endo-beta-1,4-glucanase D (TRINITY_DN584654_c4_g1_i1) involved in cellulose degradation was also downregulated in *S. drummondii* roots. Probable endo-beta-1,4-glucanase D was reported to be involved in carbohydrate metabolism, cellulose degradation and polysaccharide degradation (Le Gall et al., 2015). Endo-b-1,4-glucanases affect plant cell wall development by affecting cellulose crystallization (Glass et al., 2015). Several studies have suggested that beta-1,3-glucanase–related proteins are involved in salinity responses, including in salt tolerant tomato line (Sadder et al., 2014), *Sorghum* *bicolor* leaves (Swami et al., 2011) and grapes (Daldoul et al., 2008). It has been suggested that downregulation of beta-1,4-glucanase could lead to changes in the cell wall structure and root growth as part of an adaptive mechanism to reduce the root surface area exposed to stress (Nanjo et al., 2013; Le Gall et al., 2015).

In *S. drummondii* roots, transcripts involved in lignin biosynthesis (p-coumarate 3-hydroxylase), cellulose and hemicellulose degradation (Beta-glucosidase and endo-beta-1,4-glucanase D) were downregulated under salinity. These results suggest that changes in cell wall metabolism might be one of the salt tolerance mechanisms in *S. drummondii*. In this case, decreasing the lignification and cell wall degradation might lead to reduction in root growth which could diminishes the root surface area exposed to salt stress.

Respiration

In the present study, the transcripts cytochrome c oxidase subunit 1 and cytochrome c oxidase subunit 2 (TRINITY_DN555305_c4_g15_i: cytochrome c oxidase subunit 1, TRINITY_DN589326_c4_g1_i1: cytochrome c oxidase subunit 2 and TRINITY_DN627029_c10_g1_i1: cytochrome c oxidase subunit 1), which are involved in the respiratory pathway and sucrose metabolism (Pang et al., 2010), were upregulated in *S. drummondii* roots under salt stress. Cytochrome c oxidase (COX) is involved in the reduction of O_2 to H_2O and is the last electron acceptor of the mitochondrial respiratory chain (Mansilla et al., 2018). COX is a complex comprising of around 10 polypeptides encoded in the nucleus and three protein subunits encoded in the genome of the mitochondria of most organisms (Barrientos et al., 2002; Richter and Ludwig, 2003). Similar to our results, it has been reported that cytochrome c oxidase subunit 1 was upregulated in wheat (*Triticum aestivum* L.) under salt stress (Singh et al., 2017). Cytochrome c oxidase subunit 6b-1 was also induced in salt-treated rice roots (Yan et al., 2005) as well as in response to salt stress in the roots of the halophyte *Tamarix hispida* (Li et al., 2009). Cytochrome c oxidase subunit 1 was also observed to be upregulated under salt stress in many other plants including *Arabidopsis* and rice (Yan et al., 2005; Pang et al., 2010; Barkla et al., 2013). However, we have observed a downregulation of the transcript TRINITY_DN611184_c3_g1_i7 in *S. drummondii* roots under salt stress. This transcript is corresponding to cytochrome c oxidase subunit 1. Downregulation of mitochondrial cytochrome c oxidase (COX5b) was also reported in *Medicago truncatula* Gaertn. cv. Jemalong line M9-10a under water deficiency (Trindade et al., 2010).

Chaperons

TRINITY_DN603163_c1_g2_i7 and TRINITY_DN603163_c1_g2_i4 are two transcripts which encode late embryogenesis abundant protein D-29 isoform X2. The two transcripts were highly upregulated in the shoots of *S. drummondii* under salt treatment. These factors play a vital role in cellular dehydration tolerance, protecting cells against abiotic stresses such as freezing, high temperature, drought and salinity. These transcripts are amongst genes that are highly induced by ABA, which is produced under salt stress to protect the plant against dehydration (Hundertmark and Hincha, 2008). Late embryogenesis abundant protein D-29 isoform X2 is one of the putative stress proteins that reflect tolerance to salt stress in the halophyte *Thellungiella halophila* (Zhang et al., 2008b). Similar results have been reported in the halophyte *Suaeda fruticosa* (Diray-Arce et al., 2015).

TRINITY_DN596190_c1_g1_i14, which encodes 18.1 kDa Class 1 heat shock protein-like, was upregulated in roots upon salt stress. Heat shock proteins are involved in protein metabolism and have the ability to correct protein folding and inhibit toxic aggregate formation (Teyssier et al., 2014; Domżalska et al., 2017). Heat shock protein (HSP70) worked as molecular chaperon and has been implicated in resisting salt stress in the halophyte *Suaeda maritima* L. (Sahu and Shaw, 2009). Another transcript, TRINITY_DN607636_c0_g5_i1: Hsp24 protein, was downregulated in the roots of *S. drummondii*. Similar results have been reported in *Suaeda fruticosa,* where the HSP20-like chaperone superfamily of proteins was down-regulated under salt stress (Diray-Arce et al., 2015).

Ubiquitination

Ubiquitination is a process to degrade harmful cellular proteins and regulate the involved regulatory elements. It is one of the mechanisms for abiotic stress tolerance in plants (Cheng, 2012). E3 ligases serve as a main determinant of substrate specificity and may be involved in the regulation of signal transduction of abiotic stresses such as salt and drought in *Arabidopsis thaliana* (Lee and Kim, 2011). Transcriptomic analysis of *S. drummondii* roots showed upregulation of polyubiquitin TRINITY_DN558626_c5_g7_i2 and TRINITY_DN554033_c2_g1_i5 under salt stress. Polyubiquitin genes are involved in the regulation of a wide array of biological processes, including cell-cycle control, gene silencing, DNA repair, transcription, protein processing, endocytosis, apoptosis, signal transduction and stress response (Lyzenga and Stone, 2011; Kommaddi and Shenoy, 2013). Similar results demonstrated that polyubiquitin was upregulated under salt stress in the roots of woody halophyte *Tamarix hispida* and may be involved in salt tolerance mechanisms (Li et al., 2009). Gharat and Shaw (2015) reported that genes involved in ubiquitination have been suggested to be related with the halophytes response to salinity.

TRINITY_DN147187_c0_g1_i1: E3 ubiquitin ligase BIG BROTHER-related-like was downregulated in the root tissues of *S. drummondii*. E3 ubiquitin ligase BIG BROTHER-related-like is involved in several plant developmental processes (Zhang et al., 2008a), plant response to abiotic stress and reduction in cellular oxidative stress (Park et al., 2011; Chen et al., 2017a).

Table 25. Summary of the differentially expressed candidate genes in *Salsola drummondii* Ulbr., upon 1200 mM NaCl treatment.

↑= upregulated and ↓= downregulated

	Transcript ID	**Gene description**	**Function**	**Expression in *S. drummondii* – Salt stress**	**Expression in other plant species**	**Stress**	**Reference**
1	TRINITY_DN610243_c0_g1_i11 and TRINITY_DN610243_c0_g1_i15	Homeobox-leucine zipper protein (ATHB-40)	Transcription factor	↑ Shoots	↑*Prunus persica* roots	Drought	(Ksouri, 2016)
2	TRINITY_DN631994_c2_g1_i11	FAR1-RELATED SEQUENCE 5-like	Transcription factor	↑Shoots	↑Sweet sorghum inbred line root	Salt	(Yang et al., 2018b)
3	TRINITY_DN558998_c1_g2_i2	Carrot ABA-induced in somatic embryos 3	ABA signal transduction	↑Shoots	↑ induced in ABA-treated carrot somatic embryos (*Daucus carota* L.) somatic	Desiccation	(Shiota et al., 2004)
4	TRINITY_DN558998_c1_g2_i2	Protein phosphatase 2C 24 (PP2Cs)	ABA signal transduction	↑Shoots	↑*Suaeda fruticosa* shoots and roots ↑*Suaeda glauca* Shoots	Salt Salt	(Diray-Arce et al., 2015) (Jin et al., 2016)

5	TRINITY_DN616492_c4_g4_i1	14-3-3-like protein D	ABA signal transduction	↓Roots	↑Mangrove leaves ↑*Brachypodium distachyon* leaves ↓*Brachypodium distachyon* roots ↓ *Brachypodium distachyon* (seedling roots)	Salt Salt H_2O_2 Drought	(Wang et al., 2014) (Lv et al., 2014) (Bian et al., 2015) (Chen et al., 2018)
	TRINITY_DN602037_c1_g1_i4 and TRINITY_DN602037_c1_g1_i3	Gibberellin-regulated protein 6	Signal transduction	↓Shoots	↓*Solanum tuberosum* L. plants at tuber bulking stage ↓ *Hibiscus cannabinus* L. seedlings ↑*Mesembryanthemum crystallinum* epidermal bladder cell	Drought Salt Salt	(Gong et al., 2015) (Li et al., 2017) (Oh et al., 2015)
7	TRINITY_DN574004_c0_g5_i1	Magnesium transporter 2 isoform 2	Ion transporter	↑Shoots	↑ *Suaeda asparagoides* leaves ↓ *Suaeda*	Salt	(Ayarpadikannan et al., 2012)

					fruticosa shoots and roots	Salt	(Diray-Arce et al., 2015)
8	TRINITY_DN587967_c4_g3_i3, TRINITY_DN587967_c4_g3_i2 and TRINITY_DN587967_c4_g3_i1, TRINITY_DN422398_c0_g1_i1	Plant cadmium resistance 2-like	Ion transporter	↓Roots ↓Shoots	↑ *Suaeda fruticosa* shoots and roots	Salt	(Diray-Arce et al 2015)
9	TRINITY_DN567294_c2_g2_i1	ABC transporter A family member 1 isoform X2	ABC transporter	↓Shoots	↑*Salicornia brachiata* shoots	Salt and elevated CO_2	(Benjamin et al., 2018)
10	TRINITY_DN629181_c2_g1_i6, TRINITY_DN625631_c0_g1_i2, TRINITY_DN629181_c2_g1_i8, TRINITY_DN606447_c1_g1_i6, TRINITY_DN569023_c2_g2_i3, TRINITY_DN629181_c2_g1_i4 and TRINITY_DN562298_c2_g1_i1	Pleiotropic drug resistance 1	ABC transporter	↓Shoots	↑ Salt-tolerant rice cultivar FL478 roots ↑ *Hordeum vulgare* L. leaves	Salt Salt	(Senadheera et al., 2009) (Ueda et al., 2006)
11	TRINITY_DN637893_c3_g3_i1	Bidirectional sugar transporter SWEET14-like	Sugar transporter	↑Shoot	↑*Suaeda fruticosa* shoots and	Salt	(Diray-Arce et al., 2015)

					roots		
12	TRINITY_DN604867_c3_g1_i1	Copper/zinc superoxide dismutase (SOD)	Plant defense metabolism	↑Root	↑*Suaeda maritima* seedling	Salt	(Mallik et al., 2011)
13	TRINITY_DN599776_c0_g2_i3	Catalase (CAT)	Plant defense metabolism	↓Root	↑ Cotton roots and leaves	Salt	(Zhang et al., 2016)
14	TRINITY_DN599776_c0_g2_i3	Peroxidase P7-like	Plant defense metabolism	↓Shoot	↓ Peach roots ↑*Nictotiana tabacum* ecotype K326 seedlings	Drought Alkali and salt stress	(Ksouri, 2016) (Xu et al., 2019)
15	TRINITY_DN630886_c2_g1_i8 and TRINITY_DN608353_c0_g2_i1	Chalcone synthase (CHS)	Plant defense metabolism (flavonoid pathway)	↓Shoot	↑*Atriplex nummularia* Lind. leaves and *Atriplex leucoclada* Boiss. leaves ↓Soyabean roots and hypocotyls ↓*Salix matsudana* Koidz roots	Salt Saline-flooding combined stress Salt	(Sayed-Hussin, 2007) (Alam et al., 2011) (Qiao et al., 2014)
16	TRINITY_DN591739_c0_g1_i5 and TRINITY_DN591739_c0_	BURP domain-containing protein 5 isoform X1	Plant defense metabolism	↓Shoot	↓*Bruguiera gymnorhiza* leaves	Salt	(Miyama and Hanagata, 2007)

	g1_i4						
17	TRINITY_DN354150_c0_g1_i1	Glycine-rich RNA-binding protein 4, mitochondrial	Regulatory process	↑ Root	↑*Arabidopsis* salt tolerant lines seedlings expressing *GRP from Sporobolus virginicus*	Salt	(Tada et al., 2019)
18	TRINITY_DN583991_c0_g2_i5	Clathrin heavy chain	Regulatory process	↓ Root	↓*Thellungiella halophila* seedlings	Salt	(Pang et al., 2010)
19	TRINITY_DN593653_c0_g2_i3, TRINITY_DN574364_c1_g3_i2	Senescence associated protein	Regulatory process	↑Root	↑*Arabidopsis thaliana* seedling ↓*Mentzelia filifolia* leaves ↓*Suaeda fruticosa* shoots and roots	Salt Drought Salt	(Gong et al., 2005) (Devitt, 2018) (Diray-Arce et al., 2015)
20	TRINITY_DN621268_c4_g1_i4	p-coumarate 3-hydroxylase	Lignin biosynthesis	↓Root	*Zea mays* ↓leaves and ↑ roots	Drought	(Ludidi et al., 2015)
21	TRINITY_DN476880_c0_g1_i1 and TRINITY_DN476880_c0_g1_i1	Beta-glucosidase	Cellulose and hemicellulose degradation	↓Root	↑*Thellungiella halophila* seedlings	Salt	(Taji et al 2004; Wong et al., 2006)

22	TRINITY_DN584654_c4_g1_i1	Probable endo-beta-1,4-glucanase D	Cellulose and hemicellulose degradation	↓Root	↑*Sorghum bicolor* leaves	Salt	(Swami et al., 2011)
23	TRINITY_DN627403_c1_g1_i2	Glucose and ribitol dehydrogenase homolog 1	carbohydrate metabolism and signalling	↑Shoot	↑The mature grain of salinity tolerant barley lines (REC, OWB34, OWB59)	Salt	(Witzel et al., 2010)
24	TRINITY_DN556783_c2_g1_i2	Glutamine synthetase	Nitrogen assimilation and signalling	↑Root	↑Triticale seedlings	Salt	(Kwinta and Cal, 2005)
25	TRINITY_DN555305_c4_g15_i and TRINITY_DN627029_c10_g1_i1 and TRINITY_DN555305_c4_g15_i	Cytochrome c oxidase subunit 1 and cytochrome c oxidase subunit 2	Cellular respiration (Electron transport chain)	↑Root	↑*Triticum aestivum L.*) seedling ↑Oryza sativa root ↑*Tamarix hispida* roots	Salt Salt Salt	(Singh et al., 2017) (Yan et al., 2005) (Li et al., 2009)
26	TRINITY_DN611184_c3_g1_i7	Cytochrome c oxidase subunit 1	Cellular respiration (Electron transport chain)	↓Root	↓*Medicago truncatula* Gaertn. shoots and roots	Drought	(Trindade et al., 2010)
27	TRINITY_DN603163_c1_g2_i7 and TRINITY_DN603163_c1_g2_i4	Late embryogenesis abundant protein D-29 isoform X2	Chaperons	↑Shoot	↑*Suaeda fruticosa* shoots and roots	Salt	(Diray-Arce et al., 2015)

28	TRINITY_DN596190_c1_g1_i14	18.1 kDa Class 1 heat shock protein-like	Chaperons	↑Root	↑*Suaeda maritima* leaves	Salt	(Sahu and Shaw, 2009)
29	TRINITY_DN607636_c0_g5_i1	Hsp24	Chaperons	↓Root	↓*Suaeda fruticose* shoots and roots	Salt	(Diray-Arce et al., 2015)
30	TRINITY_DN558626_c5_g7_i2 and TRINITY_DN554033_c2_g1_i5	Polyubiquitin	Protein degradation	↑Root	↑*Tamarix hispida* roots	Salt	(Li et al., 2009)

5. CONCLUSIONS

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1. Light and temperature regulate differently the tolerance to drought and salinity stress during germination of both *Salsola drummondii* Ulbr., and *S. imbricata* Forssk., two Amaranthaceae halophytes species from United Arab Emirates (UAE).

2. The tolerance of *S. imbricata* Forssk., seeds to lower levels of osmotic potentials (up to -2.2 MPa) compared to *S. drummondii* Ulbr., (up to -1.5 MPa) indicates that the former one tolerates severer drought than the latter.

3. The fast germination (germination rate index (GRI) values c. 50) in the two *Salsola* L., species indicates that they are opportunistic species; i.e., germinate immediately once rains occur; a survival adaptation to the unpredicted desert climate of the United Arab Emirates (UAE).

4. *Salsola imbricata* Forssk., can germinate at a wide range of temperatures (15-35 °C) indicating the potential germination at different seasons.

5. *Salsola imbricata* Ulbr., germinated at a higher level at low (15/25 °C) and moderate temperatures (20/30 °C) in osmotic potentials up to -0.8 MPa, indicating the ability to germinate below the minimum rainfall (1000 mM) in the United Arab Emirates (UAE).

6. *Salsola drummondii* Ulbr., can be considered among the most salt tolerant halophytes; germinating twice as salinity as seawater (1000 mM of sodium chloride).

7. The maximum germination of *S. drummondii* Ulbr., from non-saline soils was c. 85% and from saline was c. 70% in distilled water under low temperatures, showing a higher dormancy from the saline habitats. This indicates that prefers to postpone their germination until arrival of winter rainfalls to ensure seedling establishment.

8. Germination of *S. drummondii* Ulbr., was significantly lower in all tested polyethylene glycol and sodium chloride levels under higher temperatures (25/35 °C). This indicates that higher temperatures exacerbate the effect of drought and salinity stresses.

9. *S. drummondii* Ulbr., from the saline habitats exposed to double stresses (salinity and drought) postpone their germination when rainfall is low.

10. *S. drummondii* Ulbr., that failed to germinate in different saline solutions recovered their germination within 24 hours when were transferred to distilled water. This indicates that exposure of the seeds to saline solution not kill them and that germination can be favored when it rains.

11. *Salsola drummondii* Ulbr., has a greater tolerance to lower osmotic potentials resulted from sodium chloride concentrations (c. -5.0 MPa) than that from polyethylene glycol (< -1.5 MPa), which indicates that the ion toxicity effect would be responsible for the failure of germination in saline solutions.

12. The biochemical analysis showed that the salt tolerance of *S. drummondii* Ulbr., under saline conditions depended on osmotic adjustments driven by cellular accumulation of sodium ion and proline. Salt tolerance of *S. drummondii* Ulbr., treated with sodium chloride was associated with accumulation of antioxidants such as ascorbate peroxidase, catalase, guaiacol peroxidase and total glutathione to scavenge the reactive oxygen species such as hydrogen peroxide that are produced as a result of salt stress.

13. The carbon isotope discrimination ($\Delta^{13}C$) was lower in *S. drummondii* Ulbr., plants collected from saline soils than those from non-saline, indicating uninterrupted stomatal conductance in plants from non-saline habitats.

14. The transcriptomic analysis indicates that salt tolerance in *S. drummondii* Ulbr., occurred by the interaction of multiple genes that regulate many physiological, biochemical, and molecular processes.

15. The transcriptomic analysis identified potential transcripts that could be involved in salt tolerance in *S. drummondii* Ulbr., such as transcripts of abscisic acid pathway, ion transporters, sucrose transporters, carbohydrate metabolism, transcription factors, chaperons, nitrogen assimilation, redox homeostasis, cellular respiration and auxin biosynthesis pathway.

16. *Salsola drummondii* Ulbr., demonstrates eco-physiological and phenotypic plasticity, which are distinguished characteristics of halophytes plants, when compared to glycophytes.

6. REFERENCES

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