

Interactive effects of salinity and plant density on the growth of *Cyperus arenarius*, a sand dune stabilizer

Farhat AGHA^{1,2,*} Muhammad Zaheer AHMED², Bilquees GUL², Muhammad Ajmal KHAN²

¹DHA College for Women, Defense Housing Authority, Karachi, Pakistan

²Dr. Muhammad Ajmal Khan Institute of Sustainable Halophyte Utilization, University of Karachi, Karachi, Pakistan

Received: 25.04.2021 • Accepted/Published Online: 30.11.2021 • Final Version: 28.12.2021

Abstract: Competition and environmental stress are crucial factors for structuring plant population in natural habitats. *Cyperus arenarius*, a sedge of coastal sand dunes habitat, is a suitable species for coastal restoration and dune stabilization, but how salinity and plant density interact in affecting its growth is still unknown. Here, growth, survival, and physiological responses of *C. arenarius* to salinity (sea-salt) and plant density were investigated. A set of growth experiments in which combinations of 4 salinity levels (0, 2, 4, and 6 S m⁻¹ sea-salt) and 3 planting densities (2, 5, 8 plants pot⁻¹) were tested under controlled greenhouse conditions. Plant biomass and height were optimal in 2 S m⁻¹ sea-salt while biomass decreased considerably at 6 S m⁻¹. The inhibitory effect of high salinity was more severe in shoot dry mass relative to that of root dry mass, which resulted in increasing root/shoot dry mass ratio. Tissue succulence declined while the accumulation of Na and Cl increased with the increment of salinity, especially in root. Plant nutrient (K⁺, Ca²⁺, and Mg²⁺) contents decreased under salinity. Plant height was more sensitive with increasing plant density than biomass. High plant density (8 plants pot⁻¹) lowered tissue biomass and water content in non-saline conditions to the similar levels observed under the 6 S m⁻¹ sea-salt salinity. Moreover, the combined effect of high salinity and increasing plant density had highly negative effects on plant growth attributes and water relations than their individual effect.

Key words: Ion-flux, plant density, sand dune vegetation, sea-salt, sedge

1. Introduction

Sand dunes are considered important elements in coastal ecosystems, as they act as protective buffers against storm surge, wave attack, and erosion of the hinterland, and supply a singular habitat for flora and fauna (USACE, 2013). Moreover, the solidity of sand dunes directly links with their level of vegetation cover. Plants that grow on dunes play a pivotal role in dune stabilization, dissipate storm wave energy, and help trap additional wind-blown sediment, which successively lead to continual dune growth. Vegetation of dunes is exposed to a variety of environmental stresses, e.g., summer water shortage, drought due to low water-holding capacity of sandy soils, and continuous seawater spray (Alessio et al., 2004).

High salinity causes hyper-osmotic stress, ion (mostly Na⁺ and Cl⁻) toxicity and nutrient disequilibrium that also produce other secondary effects (Flowers et al., 2015). In general, dune plants mostly survive in high salinity by avoidance or resistance strategies, while rarely depending on tolerance strategies (Glenn and Nagler, 2005; Koyro et al., 2005). Most perennial halophytes alter their response at the organ and cellular levels to deal with the osmotic

and ionic effects of salinity (Glenn and Nagler, 2005; Koyro et al., 2005). Plants use readily available inorganic ions (Na⁺ and Cl⁻ in saline areas) to regulate water potential and ensure sufficient water uptake), while they reduce ion toxicity by salt exclusion, salt sequestration, and salt secretion mechanisms (Flowers et al., 2015). In saline areas, high extracellular Na⁺ negatively affects K⁺ acquisition, while Ca²⁺ helps to reduce Na⁺ entry into cells while enhancing K⁺/Na⁺ selective trans-membrane transport (Shabala et al., 2010; Sun et al., 2010).

The decline in the number of individuals within dune plant populations in the absence of salinity stress is considered density-dependent mortality by Ungar (1992). Moreover, intra-specific competition affects biomass production, reproduction, survival, and growth, particularly in environmental stress conditions (Yu et al., 2019; Wang et al., 2021). Decreases in growth and fecundity have been observed for several halophytic species growing at high densities (Wang et al., 2021).

Cyperus arenarius Retz. is a perennial (0.06–0.30 m in plant height), rhizomatous sedge that covers sand dunes of the Sindh sea-coast as a dominant species (Kukumen,

* Correspondence: farhatagha_1@yahoo.com

2001). This sedge protects soil from wind erosion and is grazed by animals. Furthermore, *C. arenarius* is economically important as a source of essential-oil components, Cyperene and cyperotundone (Feizbakhsh et al., 2012). Because salinity and plant density can be a major determinant of *C. arenarius* in its natural habitat, this research was designed to find out the ability of *C. arenarius* to tolerate sea-water salinity under various levels of intra-specific competition. The working hypothesis of this study was as follows: 1) Increasing salinity inhibits growth, and this effect was more pronounced with high plant density, 2) plant succulence compromised more with high plant density than salinity, and 3) plants maintain nutrient homeostasis under salinity. Therefore, *C. arenarius* exposed with 0, 2, 4, and 6 S m⁻¹ of sea-salt along with 3 planting densities (2, 5, 8 plants per pot) to observe the changes in growth and eco-physiological responses. *Cyperus arenarius* grows optimally at moderate salinity (2 S m⁻¹), but growth inhibits severely due to combined effects of high salinity (6 S m⁻¹) and high plant density rather than their individual effects.

2. Materials and methods

2.1. Experimental design and salinity treatments

Seeds of *C. arenarius* were collected from a population near the coast of Karachi (located at Gizri Creek, Karachi along the Arabian Sea coast) and stored at 4 °C. Seeds were germinated in plastic pots of 0.13 m in diameter and 0.13 m in height (6.9×10⁻³ m³ pot volume) and filled with acid-washed beach sand. Plants were sub-irrigated through holes present in the base of the pots by placing them in the containers with an experimental solution of corresponding salt concentrations. Thinning of seedlings is done by removing extra plants from the pots at the second leaf stage. As a result, three density treatments (2, 5 and 8 plants pot⁻¹) were then supplied with 2, 4, and 6 S m⁻¹ sea-salt solutions fortified with nutrient solution (Popp and Polania, 1989). Salinity concentrations were gradually increased by 0.05 S m⁻¹ after every 12 h intervals (6 days required to achieve the maximum salinity levels of 6 S m⁻¹) to reduce the chances of osmotic shock. The solution was replaced on a weekly basis, and the salinity level of the culture solution was maintained through daily sub-irrigation with tap water. Plants were grown for 2 months (when the growth declined 50% under high salinity in comparison with control conditions) in aforementioned conditions before harvest.

2.2. Growth attributes and water relation

Growth parameters [root length, shoot length, fresh mass (FM)] were recorded immediately after harvest. Tissue dry mass (DM) was recorded after oven drying at 80 °C for 24 h. Leaf succulence on a DM basis was measured using the equation proposed by Delf (1912): Succulence (g H₂O g⁻¹

$$DM) = (FM - DM) / DM.$$

2.3. Cation and anion contents

Hot water extracts of plant samples were prepared with 0.5 g plant material boiled in 10 ml distilled water in sealed test tubes for 2 h using a water bath at 90 °C (Shoukat et al., 2020). The extracts were cooled and filtered using Whatman No. 1 filter paper. The dilutions were made with deionized distilled water for ion analysis. Cations (Na⁺, K⁺, Ca²⁺, Mg²⁺) and anion (Cl⁻) were measured by titration techniques as reported in Vogel and Jeffery (1989). All data were examined in at least four replicates.

2.4. Statistical analysis

Analysis of variance (ANOVA) was performed by SPSS (version 16 for Windows; SPSS 2007) to determine: the effects of sea-salt and plant density on growth and physiological responses of *C. arenarius* at $p < 0.05$ significance level. A Bonferroni post-hoc test was used to determine significant differences between treatment means. Sigma Plot (ver. 12.5 for Windows, Systat Software, San Jose, CA, USA) was used to construct graphs.

3. Results

Plant biomass (FM and DM) was increased in low salinity (2 S m⁻¹), while the growth was inhibited (> 50%) in high salinity (6 S m⁻¹) (Figure 1). High density (8 plants pot⁻¹) decreased biomass (particularly DM) of both root and shoot tissues (particularly shoots) under non-saline and low (< 4 S m⁻¹) salinity levels (Figure 1). Moderate density (5 plants pot⁻¹) resulted in a decline of only shoot DW. Shoot FM and DM were substantially higher than root tissue (Figure 1). The root to shoot DM ratio was significantly increased by high plant density but unaffected by salinity treatment (Figure 2). Plant height decreased ca. 35% at 6 S m⁻¹. High density (5 and 8 plant pot⁻¹) decreased plant height under non-saline and low salinity (< 4 S m⁻¹) conditions, but no difference was found at 6 S m⁻¹ (Figure 3). Succulence decreased with the increment of sea-salt concentration irrespective of plant tissue type. In addition, high plant density led to a decline in plant succulence (Figure 4). Sodium and Cl⁻ content increased, while Ca²⁺, Mg²⁺ and K⁺ decreased with incremental increases in sea-salt concentration (Table).

4. Discussion

This is one of the first few studies on the salt tolerance of sedges in relation with plant density. Approximately 50% growth reduction occurred at 1.2 S m⁻¹ for *Bouteloua dactyloides*, 2.6 S m⁻¹ for *Cynodon dactylon* and > 4.6 S m⁻¹ for *Distichlis spicata* (Wu and Lin, 1994; Marcum, 2002). In the case of *C. arenarius*, biomass (both shoot and root) and length were considerably increased at 2 S m⁻¹, while a 50% growth declined at 6 S m⁻¹ of sea-salt. Shoot growth peaked at 0.8 S m⁻¹ in *Halopyrum mucronatum* (Khan and Ungar,

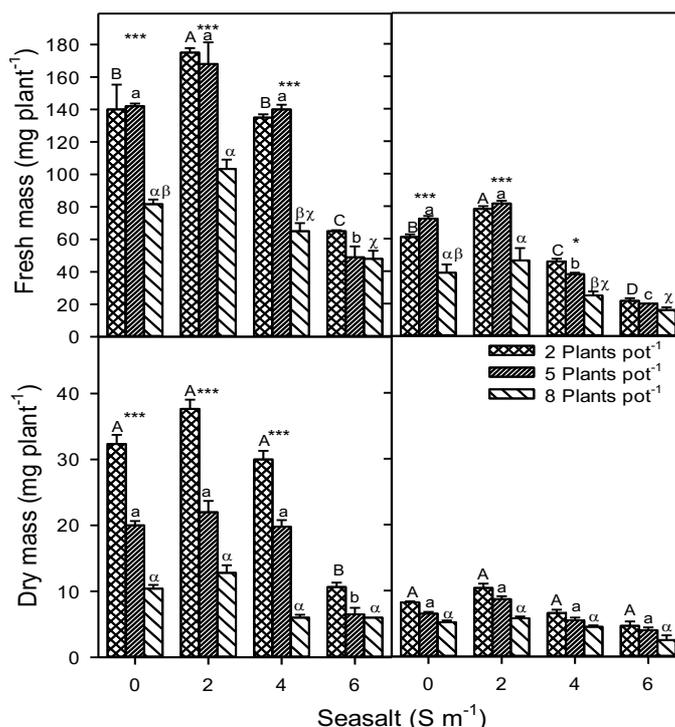


Figure 1. Fresh and dry mass (mg plant^{-1}) of shoot and root tissues of *Cyperus arenarius* raised at different sea-salt concentrations (0, 2, 4, 6 S m^{-1}) and plant densities (2, 5, 8 plants pot^{-1} of $6.9 \times 10^{-3} \text{ m}$ volume). Values are means \pm SE. Significant differences in the Bonferroni multiple comparisons between sea salt concentrations ($p < 0.05$) were shown by different uppercase and lowercase alphabets, and Greek letters for 2, 5, and 8 plants-per-pot conditions, respectively. Asterisks (***) $p < 0.001$, * $p < 0.05$) indicate significant differences within each sea salt concentration (among plant density treatments).

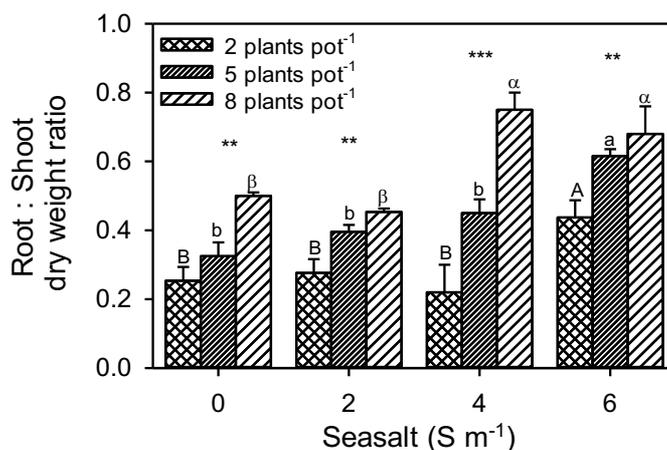


Figure 2. Root to shoot ratio of *Cyperus arenarius* raised at different sea-salt concentrations (0, 2, 4, 6 S m^{-1}) and plant densities (2, 5, 8 plants pot^{-1} $6.9 \times 10^{-3} \text{ m}$ volume). Values are means \pm SE. Significant differences in the Bonferroni multiple comparisons between sea salt concentrations ($p < 0.05$) were shown by different uppercase and lowercase alphabets, and Greek letters for 2, 5, and 8 plants-per-pot conditions, respectively. Asterisks (***) $p < 0.001$, ** $p < 0.01$) indicate significant differences within each sea salt concentration (among plant density treatments).

1999) and at 2 S m^{-1} in *Aeluropus lagopoides* (Gulzar et al., 2003). In contrast, biomass was highest in fresh water and the growth progressively declined with increases in salinity for *Desmostachya bipinnata*, *Urochondra setulosa*, and

Sporobolus ioclados (Gulzar et al., 2003; Adnan et al., 2021). *Cyperus arenarius* increased the root to shoot biomass ratio at high salinity (6 S m^{-1}), which could help in improved water and mineral absorption while reducing water loss.

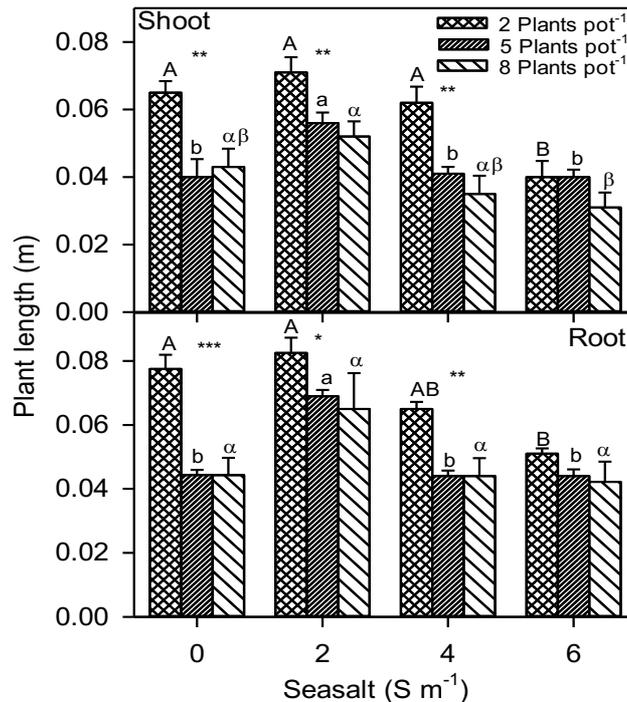


Figure 3. Root and shoot length of *Cyperus arenarius* raised at different sea-salt concentrations (0, 2, 4, 6 S m⁻¹) and plant densities (2, 5, 8 plants pot⁻¹ 6.9×10⁻³ m volume). Values are means ± SE. Significant differences in the Bonferroni multiple comparisons between sea salt concentrations ($p < 0.05$) were shown by different uppercase and lowercase alphabets, and Greek letters for 2, 5, and 8 plants-per-pot conditions, respectively. Asterisks (***) $p < 0.001$, ** $p < 0.01$, * $p < 0.05$) indicate significant differences within each sea salt concentration (among plant density treatments).

Intra-specific competition is a significant ecological factor that determines population survival under saline conditions, and it may influence survival, growth, and fecundity (Ungar, 1992; Zhang and Tielbörger, 2020). In the case of *C. arenarius*, increased density had a negative effect on plant biomass and length, while an increase in the root to shoot ratio is probably the result of competition for resources including water and nutrients as previously reported in another member of cyperaceae *Bolboschoenus yagara* (Yu et al., 2019). The growth of *C. arenarius* was limited due to increasing plant density irrespective of the presence of salinity stress, similar results were also found in other halophytes *Atriplex prostrata* (Wang et al., 2005) and *Suaeda salsa* (Wang et al., 2021). Such morphological plasticity in response to salt and high plant density could be a useful strategy for halophyte for the survival under hard environmental seasons in natural fields (Wang et al., 2021). In *C. arenarius*, planting density was the main environmental factor that restricted growth in comparison with salinity, as previously reported in the case of *Suaeda salsa* (Wang et al., 2021), which reflects plant nature to successfully deal with the toxic ion (Na⁺ and Cl⁻) but susceptible for water and nutrient limitation. Therefore, the first hypothesis “increasing salinity inhibits growth and this effect is more pronounced with high plant density” is accepted.

Succulence substantially decreased during high salinity and high plant density. Among plant tissues, root succulence was more affected than shoot tissue. In general, decreased water percentage results in the reduction of succulence in grasses under stress conditions (Glenn, 1987). In another case, 11 grasses were found to display similar results (Marcum and Murdoch, 1990). Perennial grasses from Karachi, Pakistan were observed to show an irregular pattern of succulence. Succulence increased in *Halophyrum mucronatum* (Khan et al., 1999), while it decreased with increased salinity in *Urochondra setulosa*, *Sporobolus ioclados* and *Aeluropus lagopoides* (Gulzar et al., 2003). The decrease in succulence with salinity could be attributed to controlled ion accumulation in the photosynthetically active plant parts (Gulzar et al., 2003). Plants, especially grasses, possibly maintain their osmotic balance in high salinity by reducing water in the tissues rather than increasing ion content of the tissue (Glenn, 1987). Plants reduce succulence during non-saline and high-density conditions, which represents the xerophytic nature/adaptation of *C. arenarius* for survival in the sand dune habitats. In addition, high density decreases leaf succulence of *C. arenarius* in the absence of salinity stress, and such inhibition was comparable with plants grown at 4 S m⁻¹ with low density. Therefore, our second hypothesis

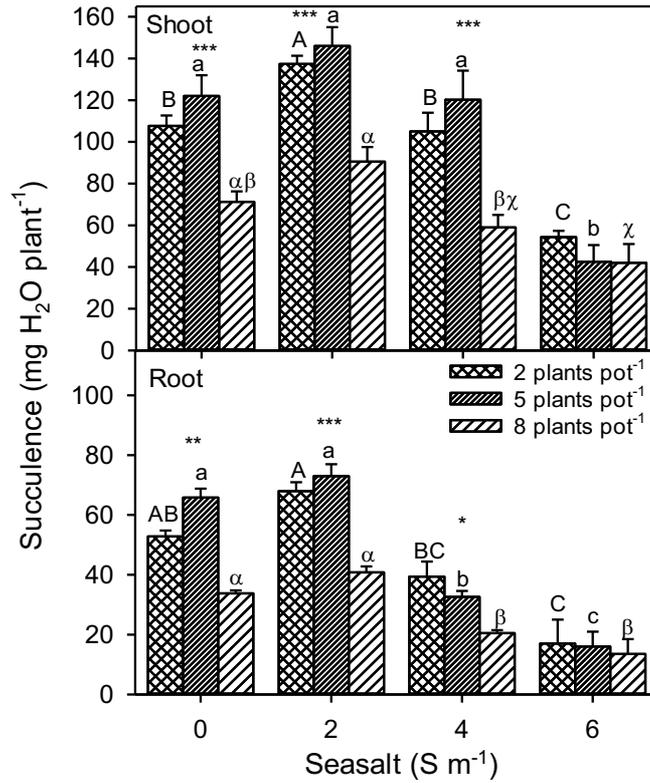


Figure 4. Succulence (mg H₂O per plant tissue) of *Cyperus arenarius* raised at different sea-salt concentrations (0, 2, 4, 6 S m⁻¹) and plant densities (2, 5, 8 plants pot⁻¹ 6.9×10⁻³ m volume). Values are means ± SE. Significant differences in the Bonferroni multiple comparisons between sea salt concentrations ($p < 0.05$) were shown by different uppercase and lowercase alphabets, and Greek letters for 2, 5, and 8 plants-per-pot conditions, respectively. Asterisks (***) $p < 0.001$, ** $p < 0.01$, * $p < 0.05$) indicate significant differences within each sea salt concentration (among plant density treatments).

Table 1. Ion content (μ mol g⁻¹ DW; mean ± SE) in shoot and root tissues of *Cyperus arenarius* grown at different sea-salt concentrations. Different letters based on ANOVA-Bonferroni test represent significant ($p < 0.05$) differences of respective ions between salinity treatments at each plant tissue.

Plant tissue	Sea-salt (S m ⁻¹)	Na ⁺	K ⁺	Ca ²⁺	Mg ²⁺	Cl ⁻	Na ⁺ /K ⁺
Shoot	0	327 ± 43 c	53 ± 6 a	133 ± 3 a	73 ± 4 a	500 ± 55 c	6.16
	2	627 ± 13 b	28 ± 4 b	77 ± 3 b	50 ± 3 b	867 ± 66 b	22.39
	4	787 ± 13 a	24 ± 5 b	60 ± 4 b	37 ± 2 c	1000 ± 69 a	32.79
	6	120 ± 40 d	27 ± 2 b	40 ± 2 c	27 ± 3 c	1109 ± 70 a	4.44
Root	0	400 ± 46 c	67 ± 13 a	87 ± 3 a	63 ± 3 a	620 ± 34 c	5.97
	2	667 ± 13 b	53 ± 13 b	63 ± 3 b	40 ± 6 b	806 ± 43 b	12.58
	4	853 ± 53 a	29 ± 2 c	53 ± 6 bc	30 ± 5 bc	900 ± 45 b	29.41
	6	747 ± 26 ab	20 ± 3 c	43 ± 3 c	27 ± 6 c	1203 ± 49 a	37.35

“succulence compromised more with high plant density than salinity” is also accepted.

In *C. arenarius*, a substantial increase in Na⁺ and Cl⁻ content was found with increased salinity in both roots and shoots, which suggested that *C. arenarius* uses

both salt-excluding and salt-accumulating strategies to protect above-ground plant tissue from ion-toxicity and dehydration, respectively. Moreover, the increase in Na⁺ content was lower than Cl⁻ content, which may help the plant to reduce ionic damage, as it was previously

reported that Na⁺ is a more toxic element than Cl⁻ in most plant species (Maathuis et al., 2014; Wege et al., 2017). However, nutrient (K⁺, Ca²⁺, and Mg²⁺) content decreased in *C. arenarius* with increases in salinity, similar to other grasses like *Cynodon dactylon*, *Zoysia japonica*, and *Zoysia matrella* (Uddin et al., 2012). The imbalanced nutrient homeostasis is probably the result of high influx and uptake of mainly available ions (Na⁺ and Cl⁻ in the case of salinity). The increasing trend of Na⁺/K⁺ is due to high Na⁺ and low K⁺ influx. Glenn (1987) studied the growth of 14 grasses and reported that in response to salt stress, sodium levels increased while potassium decreased. Therefore, the third hypothesis of this study “plants maintain nutrient homeostasis under salinity” is rejected.

In conclusion, *C. arenarius* is a eu-halophyte that grows optimally in moderate salinity (equal to 200 mmol

L⁻¹ NaCl). Moreover, *C. arenarius* is more sensitive to increasing plant density rather than salinity stress. This study indicated that the density-dependent competitive interactions play a major role in shaping the population of *C. arenarius* when soil salinity is low (below 4 S m⁻¹), while plant resists high salinity by efficient toxic ion sequestration in root tissue, alter biomass partitioning between shoot to root and low succulence along with Na⁺ and Cl⁻ accumulation in shoots for better osmotic adjustment.

Acknowledgment

This work is posthumously dedicated to Prof. Dr. Muhammad Ajmal Khan – founder of state-of-the-art halophyte research institute (Institute of Sustainable Halophyte Utilization) in Pakistan.

References

- Adnan MY, Hussain T, Ahmed MZ, Gul B, Khan MA (2021). Growth regulation of *Desmostachya bipinnata* by organ-specific biomass, water relations, and ion allocation responses to improve salt resistance. *Acta Physiologia Plantarum* 43: 1-12.
- Alessio GA, De Lillis M, Brugnoli E, Lauteri M (2004). Water sources and water-use efficiency in Mediterranean coastal dune vegetation. *Plant Biology* 6: 350-357. doi: 10.1055/s-2004-820882
- Delf EM (1912). Transpiration in succulent plants. *Annals of Botany* 26: 409-442. doi.org/10.1093/oxfordjournals.aob.a089398
- Feizbakhsh A, Aghassi A, Naeemy A (2012). Chemical constituents of the essential oils of *Cyperusdifformis* L. and *Cyperusarenarius* Retz from Iran, *Journal of Essential Oil Bearing Plants*, 15:1, 48-52. doi: 10.1080/0972060X.2012.10644018
- Flowers TJ, Munns R, Colmer TD (2015). Sodium chloride toxicity and the cellular basis of salt tolerance in halophytes. *Annals of Botany* 115: 419-431. doi: 10.1093/aob/mcu217
- Glenn EP (1987). Relationship between cation accumulation and water content of salt-tolerant grasses and a sedge. *Plant Cell Environment* 10: 205-212. doi:10.1111/1365-3040.ep11602236
- Glenn EP, Nagler PL (2005). Comparative ecophysiology of *Tamarix ramosissima* and native trees in western U.S. riparian zones. *Journal of Arid Environment* 61: 419-446. doi.org/10.1016/j.jaridenv.2004.09.025
- Gulzar S, Khan MA, Ungar IA (2003). Salt tolerance of a coastal salt marsh grass. *Communications in Soil Science and Plant Analysis* 34: 2595-2605. doi.org/10.1081/CSS-120024787
- Khan MA, Ungar IA (1999). Seed germination and recovery of *Triglochin maritima* from salt stress under different thermoperiods. *Great Basin Naturalist* 59: 144-150.
- Koyro HW, Geissler N, Hussain S, Huchzermeyer B (2005). Mechanisms of cash crop halophytes to maintain yields and reclaim soils in arid areas. In: Khan MA, Weber DJ, editors. *Ecophysiology of high salinity tolerant plants*, Netherlands: Springer Publication, pp. 345-366.
- Kukumen I (2001). *Cyperaceae*. In: Ali SI, Qaiser M, editors. *Flora of Pakistan*. University of Karachi and Missouri Botanical Garden, pp. 277.
- Maathuis FJ, Ahmad I, Patishtan J (2014). Regulation of Na⁺ fluxes in plants. *Frontiers in Plant Science* 5: 467. doi:10.3389/fpls.2014.00467
- Marcum KB (2002). Growth and physiological adaptations of grasses to salinity stress. In: Pessaraki M, editor. *Handbook of plant and crop physiology*. 2nd ed. New York: Marcel Dekker, pp. 623-635.
- Popp M, Polania J (1989). Compatible solutes in different organs of mangrove trees. *Annals of Forest Science* 46: 842-844. doi:10.1051/forest:198905ART0185
- Shabala S, Shabala S, Cuin TA, Pang J, Percey W et al. (2010). Xylem ionic relations and salinity tolerance in barley. *The Plant Journal* 61: 839-853. doi:10.1111/j.1365-313X.2009.04110.x
- Shoukat E, Ahmed MZ, Abideen Z, Azeem M, Ibrahim M et al. (2020). Short and long term salinity induced differences in growth and tissue specific ion regulation of *Phragmites karka*. *Flora* 263: Article 151550. doi:10.1016/j.flora.2020.151550
- SPSS Amos (version 16). (2007). Armonk, NY: IBM.
- Sun JM, Wang J, Ding MQ, Deng SR, Liu MQ et al. (2010). H₂O₂ and cytosolic Ca²⁺ signals triggered by the PM H⁺-coupled transport system mediate K⁺/Na⁺ homeostasis in NaCl stressed *Populus euphratica* cells. *Plant Cell Environment* 33: 943-958.
- Uddin M, Juraimi AS, Ismail M, Hossain M, Othman R et al. (2012). Physiological and growth responses of six turfgrass species relative to salinity tolerance. *The Scientific World Journal*. doi:10.1100/2012/905468
- Ungar IA (1992). The effect of intraspecific competition on growth reproduction and survival of the halophyte *Spergularia marina*. *International Journal of Plant Sciences* 153: 421-424. doi:10.1086/297047

- USACE (U.S. Army Corps of Engineers) (2013). Hurricane sandy coastal projects performance evaluation study: disaster relief appropriations act. Washington, DC: U.S. Army Corps of Engineers.
- Vogel AI, Jeffery GH. 1989. Vogel's textbook of quantitative chemical analysis. Wiley.
- Wang LW, Showalter AM, Ungar IA (2005). Effects of intraspecific competition on growth and photosynthesis of *Atriplex prostrata*. Aquatic Botany 83: 187-192. doi:10.1016/j.aquabot.2005.06.005
- Wang Q, Jiang L, Chen Y, Tian X, Lv G (2021). Abiotic stress-by-competition interactions drive hormone and nutrient changes to regulate *Suaeda salsa* growth. Global Ecology and Conservation, p.e01845.
- Wege S, Gilliam M, Henderson SW (2017). Chloride: not simply a 'cheap osmoticum', but a beneficial plant macronutrient. Journal of Experimental Botany 68: 3057-3069.
- Wu L, Lin H (1994). Salt tolerance and salt uptake in diploid and polyploid buffalo grasses (*Buchloe dactyloides*). Journal of Plant Nutrition 17: 1905-1928. doi.org/10.1080/01904169409364854
- Yu H, Shen N, Yu D, Liu C (2019). Effects of temporal heterogeneity of water supply and spatial heterogeneity of soil nutrients on the growth and intraspecific competition of *Bolboschoenus yagara* depend on plant density. Frontiers in Plant Science 9: 1987. doi: 10.3389/fpls.2018.01987
- Zhang R, Tielbörger K (2020). Density-dependence tips the change of plant–plant interactions under environmental stress. Nature Communications 11: 1-9. doi:10.1038/s41467-020-16286-6