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The differential responses of *Aegiceras corniculatum* and *Kandelia candel* under salt stress and re-watering phase. A study of leaf electrophysiological and growth parameters

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ABSTRACT

This study investigates differential responses of *Aegiceras corniculatum* and *Kandelia candel* mangrove species, using physiological capacitance (CP), photosynthetic, and growth parameters under different salt stress and re-watering conditions. Experiment was conducted at various NaCl levels. The Results indicated that CP was significantly affected in stress phase due to the limitation of salt storage capacity of the vacuole. Although *A. corniculatum* has a secreting effect, the solute concentration in vacuole was significantly higher than *K. candel* at M and H treatment, because their volume of vacuole was lower than *K. candel* species. In the re-watering phase, CP values of both species increased at M-L and H-M treatments respectively. Furthermore, CP was positively correlated with net photosynthesis and stomatal conductance. This finding suggests that the concentration of solute in vacuole is an important factor controlling photosynthesis and growth parameters, and CP can better represent salt concentration in the plant leaf.

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KEYWORDS

Mangroves; physiological capacitance; photosynthetic parameters; salt stress; re-watering phase

1. Introduction

Soil salinity is a serious environmental problem, more than 800 million hectares of land are salt-affected throughout the world (Solangi et al. 2019). Soil salinity is a major issue in the agricultural ecosystems, due to the shortage of fresh-water and subsequent essential to utilize saline water or low-quality water for irrigation (Semiz and Suarez 2015). It would be the most economical approach to improve productivity based on limited water resources. Moreover, the adaptation of salt-tolerant species is the better option to reduce salinity in the soil ecosystem (Hasanuzzaman et al. 2014).

Mangrove species grow in intertidal areas of tropical and subtropical zones of coastlines (García-Samaniego et al. 2017). Mangroves can survive in stressful conditions such as high salinity, low oxygen, tidal floods influence, and low humidity (Feller et al. 2010; Richards and Friess 2016). How mangroves survive in intertidal zones with high salinity in stress conditions and maintained their development? Mangroves have the ability to develop various mechanisms in stress conditions with their anatomic or physiological characteristics to regulate salt absorption and barring, e.g. salt secretion, ultrafiltration, and ion sequestration (Liang et al. 2008). Based on their special characteristics mangrove species are divided into two categories, true mangrove and associate mangrove (Parida and Jha 2010). *Aegiceras corniculatum* (*A. corniculatum*) species belong to true mangrove (Parida et al. 2004). It has salt glands in its leaves, considered as a salt secretor mangrove. Salt secretion increased at night

time, usually in daytime salt is accumulated (Yuan et al. 2016). Salt secretion by salt glands is an important strategy, *A. corniculatum* species secrete the salts from their leaves, to maintain internal ion concentration at the lower level and increase salt tolerance (Parida and Jha 2010). Furthermore, a high concentration of salts could reduce the osmotic potential of water, which decreases the ability of plant roots to uptake water. As result, plants reduce the expansion of their growing leaves and close their stomata to reduce the amount of water loss by transpiration (Munns and Tester 2008). Moreover, *Kandelia candel* (*K. candel*) belongs to true mangrove and a major mangrove species for forestation in coastal areas of southeast China (Wang et al. 2014). *K. candel* known as non-secretor mangroves species, usually one-year-old species is fully covered in sea-water at high tidal conditions (Chen et al. 2005). *K. candel* can survive in field conditions up to 500 mM NaCl range and is considered as a model for studying ecological adaptation and salt tolerance (Hwang and Chen 1995). However, many studies focus on mangrove plants using different salt (NaCl) concentrations (Patil et al. 2015; García-Samaniego et al. 2017). Some species perform well under low salt concentrations, and some have the ability to grow up in moderate to higher concentrations (Parida et al. 2004; Zhu et al. 2011; Bompy et al. 2014).

Usually, salt-tolerant mechanism depends on plant cell and vacuole volume which have the ability to store salts and helps plants regulate their salts through different mechanisms, like salt secretion by *A. corniculatum* and salt accumulation by *K. candel* are important strategies against

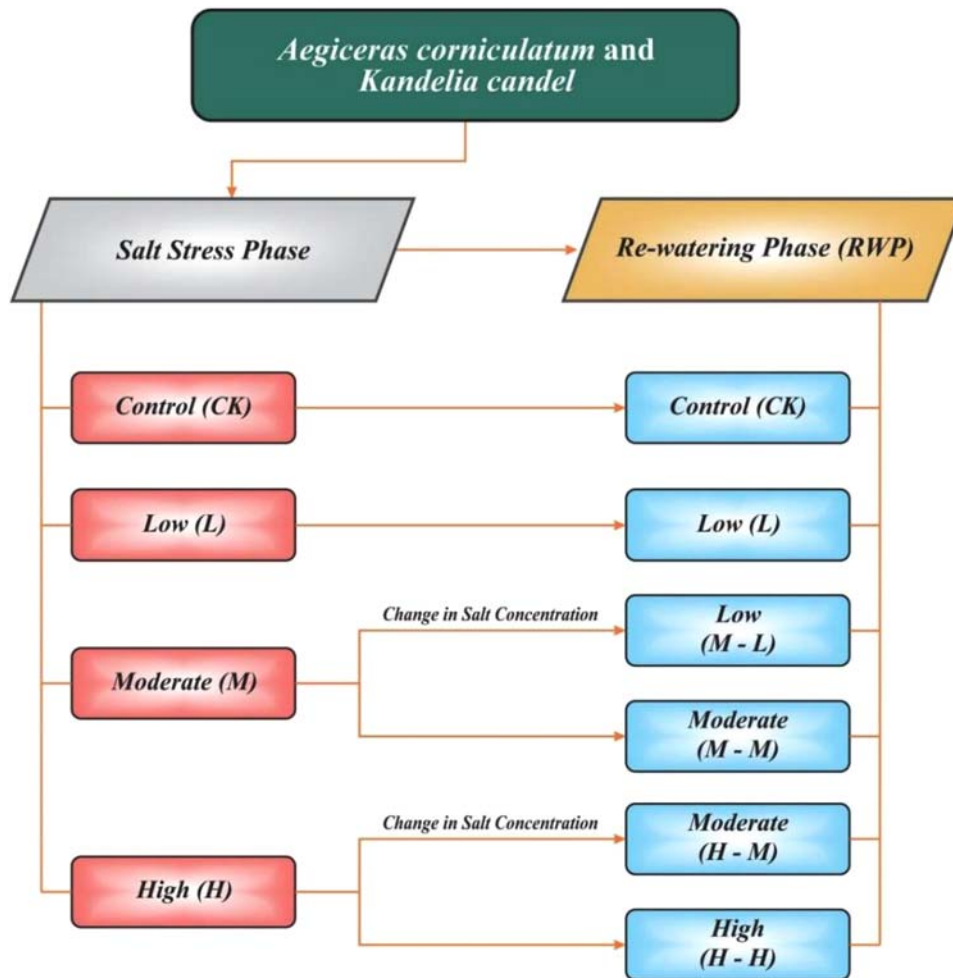


Figure 1. Experiment design of salt stress and RWP.

the salt stress-tolerant (Qiu et al. 2018). A large amount of salt in the cytoplasm is harmful to both glycophytes and halophytes to overcome the problem of plants either restrict the excess salts in the vacuole or compartmentalize the ions in different tissues to facilitate their metabolic functions (Zhao et al. 2020). The net photosynthesis (P_N), stomatal conductance (g_s), transpiration rate (Tr), and leaf water content (WC) considered as the indirect parameters for determining water status in the plant (Milliron et al. 2018).

Water regulation due to changes in cell volume is difficult to analyze by the above-mentioned indirect indexes (Xing et al. 2018). Electrophysiological parameters have been gradually used for diagnosing plant water status since the variation of plant cell volume and cell sap concentration are closely correlated with electrophysiological indexes such as physiological capacitance (CP) and water potential (Ψ) (Zhang et al. 2015; J6cs6k et al. 2019). As we know that the cell sap is related to CP and Ψ . Therefore, these indices can be determined with a non-destructive custom-made parallel-plate capacitor that employs a given frequency and voltage.

Leaf CP is associated with the effective thickness and area of leaves in contact with capacitor plates. The cytosol solute concentration as well as the elasticity and plasticity of leaf cells are highly responsive to the variable gripping forces (F), which are used for clamping a leaf during the measurement (Zhang et al. 2015). The index that is determined using a specific gripping force is an instantaneous value that can only represent an instantaneous water status (Xing et al. 2021). The plant cells are composed of protoplasts and cell walls. Vacuoles and cytoplasm, which are the main electrolytic inclusions in the protoplasts, are surrounded by the tonoplast and plasma membrane, respectively. The cytoplasm contains numerous organelles with specific membranes, and the vacuole contains mainly dissolved inorganic ions and organic acids (Zhang et al. 2015). Electrical characteristics vary between the organelles, the vacuole and the cytoplasm, which occupy most of the space in cells

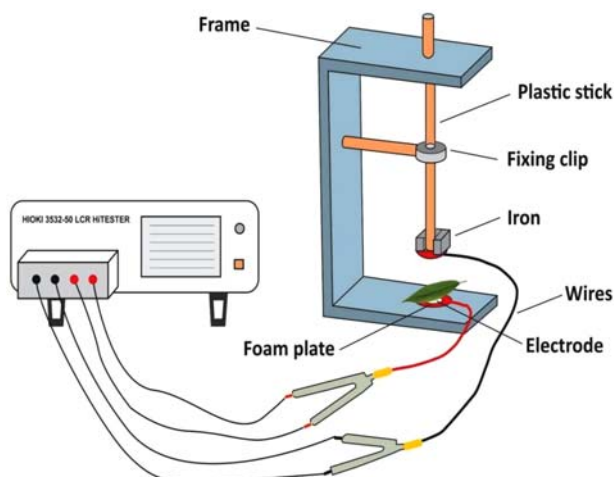


Figure 2. Representation of the parallel-plate capacitor attached with LCR tester (3532–50, HIOKI, Japan).

Table 1. Physiological capacitance of both species in salt stress and RWP ($\mu\text{F} \times 10^{-12}$) (clamping force $F = 0$).

Salt concentrations	Salt stress phase		Salt concentrations	Re-watering phase	
	<i>A. corniculatum</i>	<i>K. candel</i>		<i>A. corniculatum</i>	<i>K. candel</i>
CK (0 mM)	36.1 ± 2.2a	59.5 ± 2.6c	CK	33.2 ± 5.7a	65.2 ± 4.3b
L (100 mM)	21.1 ± 2.1c	74.6 ± 6.7b	L-L	19.8 ± 5.1c	75.7 ± 7.8a
M (200 mM)	16.7 ± 5.4c	37.4 ± 2.1e	M-L	22.2 ± 4.1b	48.4 ± 9.3d
H (400 mM)	8.9 ± 2.3d	16.5 ± 4.4g	M-M	19.9 ± 12.0c	36.7 ± 3.8e
			H-M	14.3 ± 2.8c	31.2 ± 4.0f
			H-H	7.9 ± 0.8d	14.4 ± 6.0g

and can be regarded as resistors, while the plasma membrane has a capacitive characteristic. When the alternating current flow through the plant tissue, the ratio of the passing current between the extracellular and intracellular spaces is influenced by the frequency of the alternating current and tissue features. Therefore, change in leaf water status could be rapidly determined by the variation of physiological capacitance and water potential (Zhang et al. 2015). A significant relationship was observed between WC, Ψ and CP (Javed et al. 2017).

The results of the study will help to understand the relationship between CP, Ψ , and P_N . Moreover, after salt stress, the technique of re-watering phase (RWP) defines dilution of saline water or decreased salt concentration that could be a supportive technique to recover the plant growth and maintained the Ψ and WC. In this study salt stress and RWP are considered as an intertidal environment for mangroves. Javed et al. (2018) studied on *Orychophragmus*

violaceus and found that the best re-watering time is when plants undergo moderate concentration levels and suggested that the RWP technique could be used to maintain the crop productivity. Until now the effects of RWP after salt stress on the secretor and non-secretor mangroves species still unclear. In the view of this scenario, the main objective of the study was: to identify the differential responses of *A. corniculatum* and *K. candel* through CP, photosynthetic and growth parameters in salt stress and RWP. Furthermore, the possible mechanism involves in both mangrove species were also investigated.

2. Material and method

The pot experiment was carried out in the greenhouse at Jiangsu University, Zhenjiang, Jiangsu, China (32.20°N, 119.45°E) from 15th May to 15th July 2019. The climate zone of the district is humid and subtropical monsoon

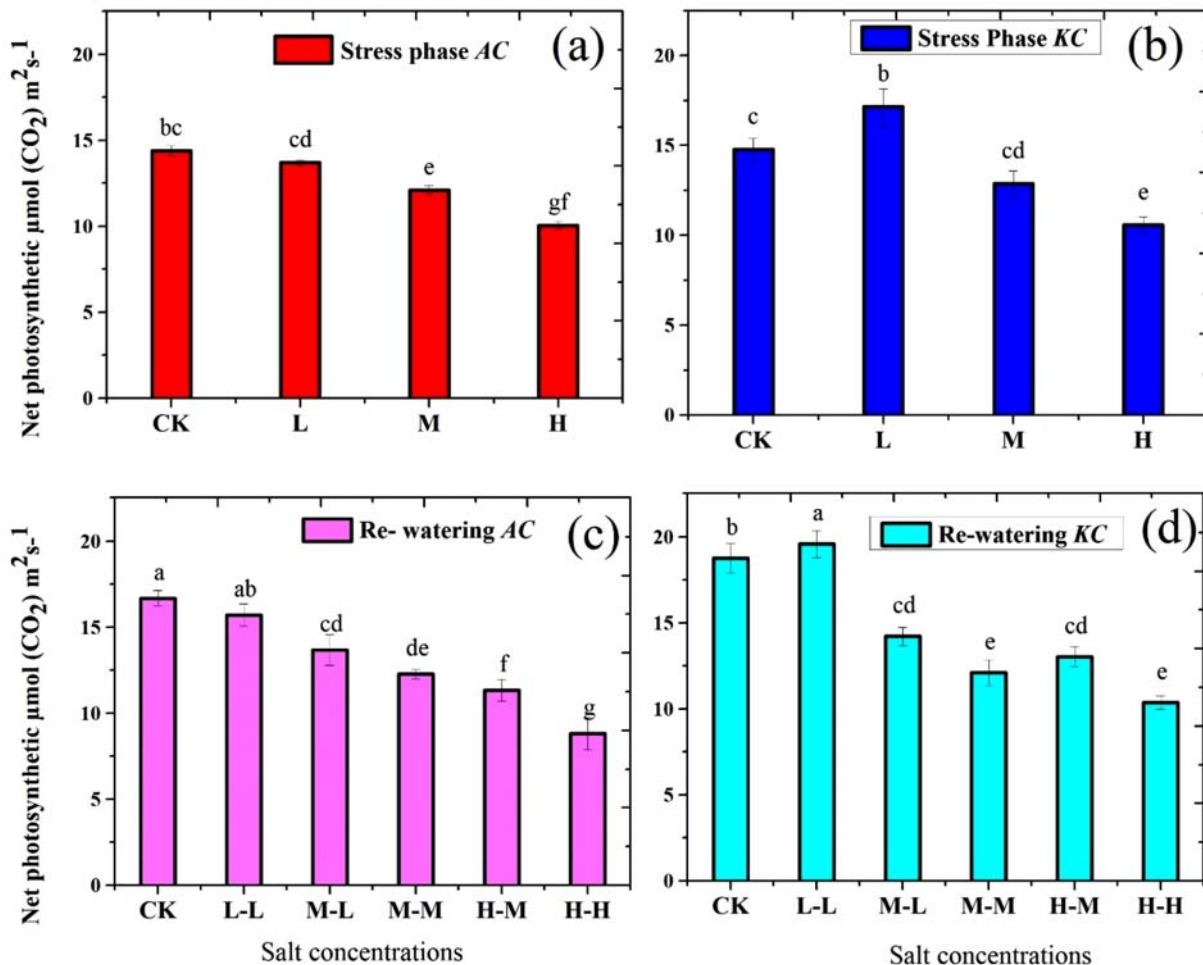


Figure 3. Effect of salt stress and RWP of net Photosynthesis (P_N) on *A. corniculatum* (a, c) and *K. candel* (b, d), the small letter indicates significant difference at ($p < 0.05$) using Duncan's multiple range tests.

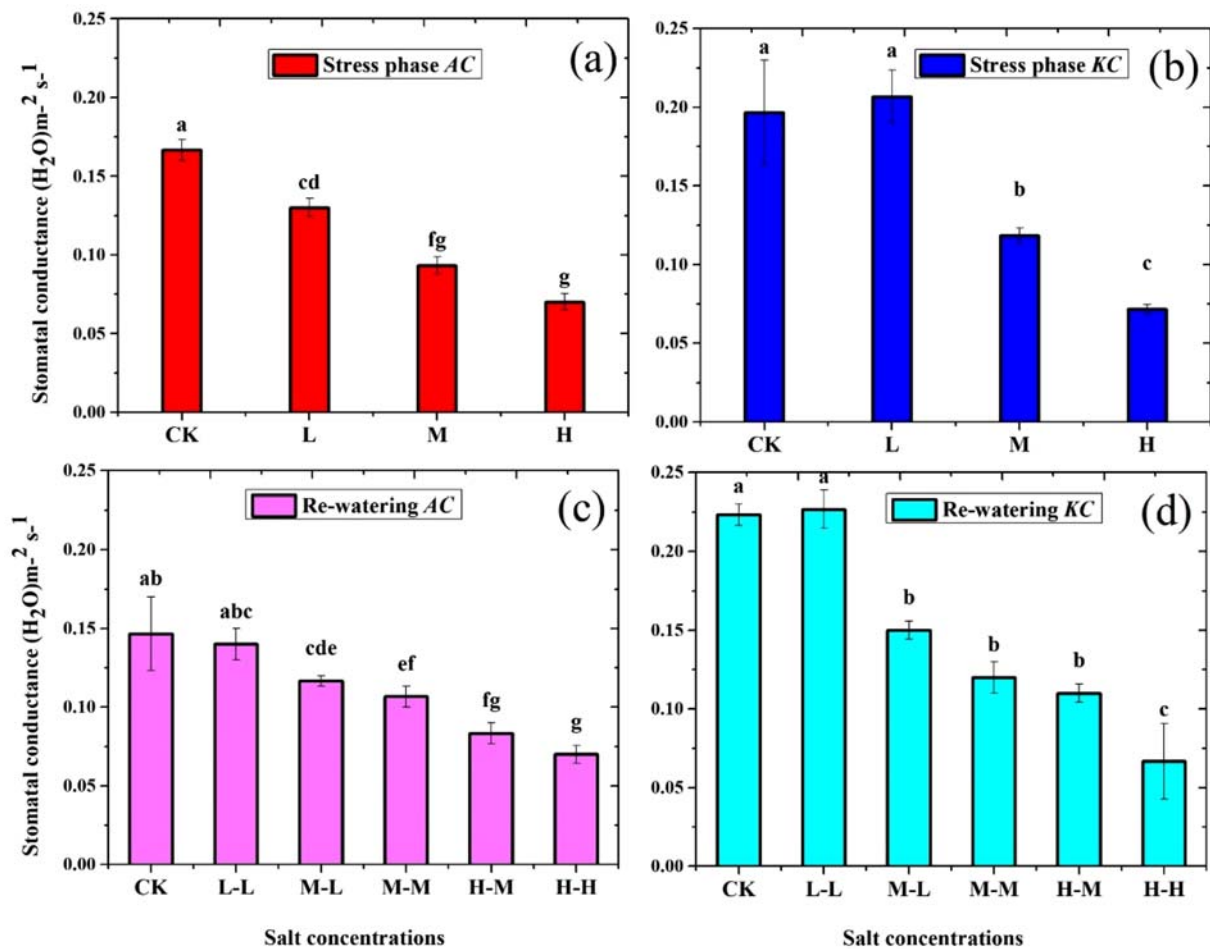


Figure 4. Effect of salt stress and RWP of stomatal conductance (gs) on *A. corniculatum* (a, c) and *K. candel* (b, d), the small letter indicates significant difference at ($p < 0.05$) using Duncan's multiple range tests.

with an average annual air temperature of $15.5^{\circ}C$ and mean annual precipitation was 1058.8 mm y^{-1} (Huang et al. 2019). One-year-old seedling of two mangrove species *A. corniculatum* and *K. candel* were collected from Quanzhou Tongqing mangroves technology Co Ltd, Fujian Province, China. Initially, both species were washed with tap water and kept in 10-liter half-strength nutrients Hoagland solution for one week (Hoagland and Arnon 1950).

2.1. Experimental design

The experiment was conducted in a complete randomized block design with six treatments containing four replicates in each, totally 144 mangrove species were used. Both mangrove species were kept 30 days in the salt stress phase and determine the electrophysiological, photosynthesis and growth parameters. After that, change in salt concentration and mangrove species kept 30 days for re-watering phase (RWP) and obtained the same parameters as the stress phase. Each pot contains 10-liter distilled water with half-strength nutrients Hoagland solution. In salt stress phase, various NaCl concentrations were used as treatments such as; CK:0 mM (control), L:100 mM (low salinity), M:200 mM (moderate salinity), H:400 mM (high salinity) shown in (Figure 1). In the RWP two treatments were changed in moderate to low salt (M-L:200 into 100 mM) and high to moderate salt (H-M: 400 into 200 mM) other treatments were used the same as the salt stress phase shown in (Figure 1).

2.2. Data collection and analysis

The data were recorded at every three days interval under the following parameters: leaf width and height were measured by measuring scale for the estimation of growth rate (GR_{50}). Physiological parameters such as net photosynthesis (P_N), leaf stomatal conductance (gs), leaf intercellular CO_2 concentration (C_i), and transpiration rate (Tr) were measured on weekly basis at each sampling time and every replicate measured from the top of fully plant young leave, further details of physiological parameters mentioned in Section 2.4. Although, every 15 days interval physiological capacitance (CP) and water potential (Ψ) were also measured, during the all-measurement leaf attached to the plant. After that, the same leaf was harvested for the determination of fresh and dry weight. Similar method was used in re-watering phase for determining all parameters which are discussed above in detail with the same time interval.

2.3. Electrophysiological parameter

The variation of leaf physiological capacitance (CP) at increasing F was measured using an LCR tester (3532-50, HIOKI, Japan). The voltage and frequency were used 1 V and 3 kHz, respectively (Xing et al. 2021). Each leaf was clipped onto the custom-made parallel-plate capacitor with a diameter of 10 mm (Figure 2). The relationship curve between CP and F was established using Sigma plot (ver. 12.5, Systat Software, Inc., San Jose, Cal.). The relationship

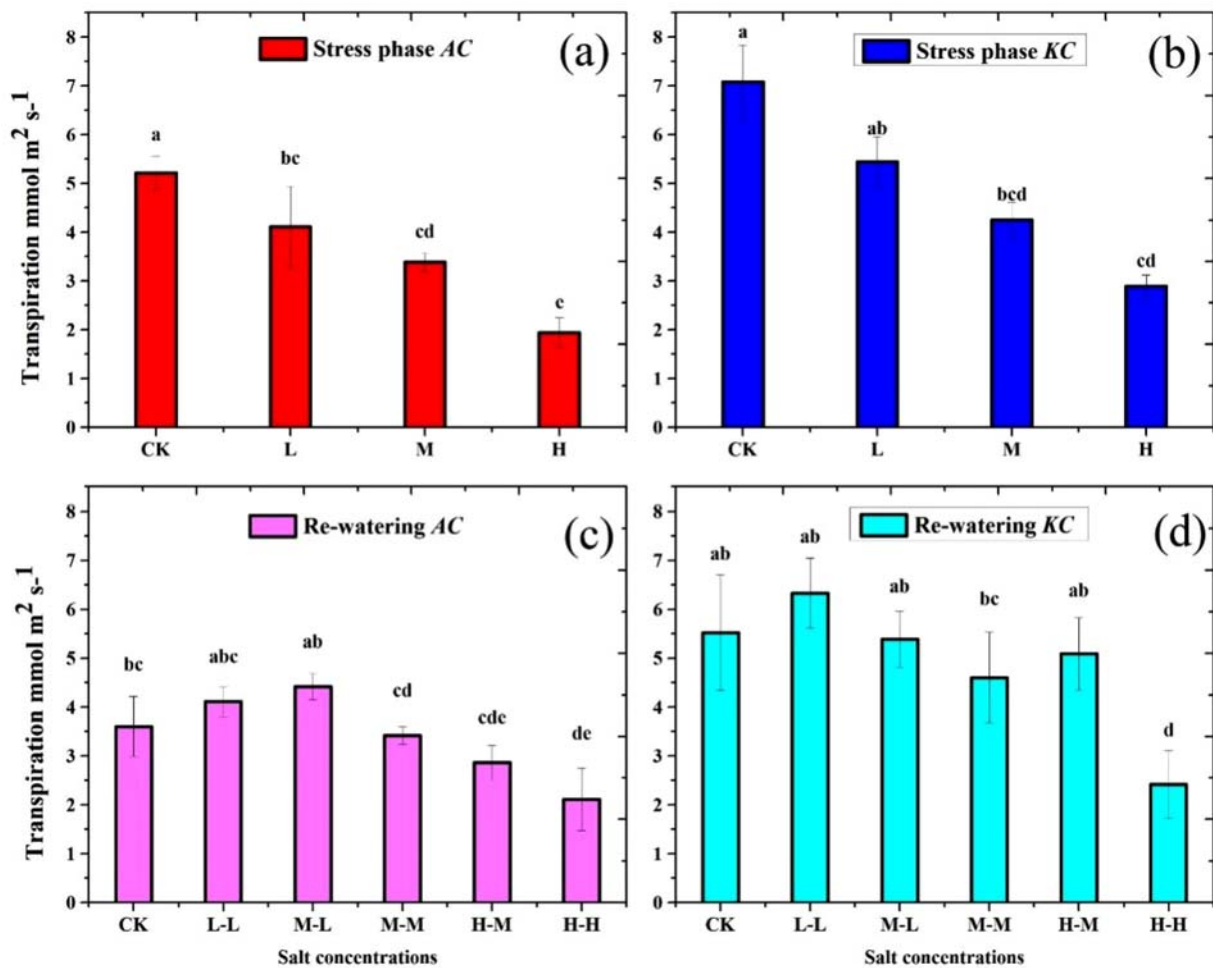


Figure 5. Effect of salt stress and RWP of Transpiration on *A. corniculatum* species (a, c) and *K. candel* species (b, d), the small letter indicates significant difference at ($p < 0.05$) using Duncan's multiple range tests.

between CP and F was fitted, and the model parameters were estimated. Finally, the CP at $F = 0$ could be calculated (Zhang et al. 2020; Xing et al. 2021).

2.4. Photosynthetic traits and water potential

The P_N , g_s , C_i , and Tr were recorded using a portable LI-6400XT photosynthesis measurement system (LI-COR, Lincoln, NE, USA). The leaf of *A. corniculatum* and *K. candel* species were enclosed within the chamber. Five repeated measurements were taken for each parameter, and four plants for each treatment were measured. A fully expanded youngest leaf from the top was used for all these measurements, the experiment was performed during full sunshine from 9.00 am to 11.30 am. (Chen et al. 2016). During the data recording process, the set values were used as follows: atmospheric pressure 99.9 kPa, flow rate inside the chamber, 500 ($\mu\text{mol s}^{-1}$) and photosynthetic active radiation (PAR) 800 ($\mu\text{mol m}^{-2} \text{s}^{-1}$) using its own red and blue light source. Water use efficiency (WUE) was calculated from this equation $WUE = P_N/Tr$, where P_N is the net photosynthetic and Tr is the transpiration rate.

The leaf in salt stress and re-watering phase of both species were used for the determination of Ψ . The leaf Ψ was measured with dew point micro voltmeter in a C-52-SF universal sample room (Psypro, Wescor, USA). Ψ was measured at the same position of the leaves with the above CP testing.

2.5. The growth parameter

Leaf area (cm) was determined with help of the measuring scale and leaf area estimation model according to Xing et al. (2019) as follows:

$$S = a \times (X_1 \times X_2)^b$$

whereas a , b were model parameters and, X_1 was exposed to the maximum leaf width, X_2 was exposed to the maximum leaf length in cm; while S was denoted the leaf area in cm^2 . The growth rate was calculated using a four-parameter logistic equation, the details of the equation are mentioned (Xing et al. 2019).

2.6. Statistical analysis

To assess the significant variations between different salt stresses and re-watering stages, all measurements were subjected to analysis of variance (ANOVA) in SPSS software (version 20.0, SPSS Inc) using Duncan's LSD *post hoc* test at ($p < 0.05$). A correlation matrix of the study was based on Pearson's correlation coefficients using * and ** to indicate the $p < 0.05$ and $p < 0.01$ probability levels, respectively. Graphs were prepared by using Origin Pro. 9.0 (Northampton, MA, USA).

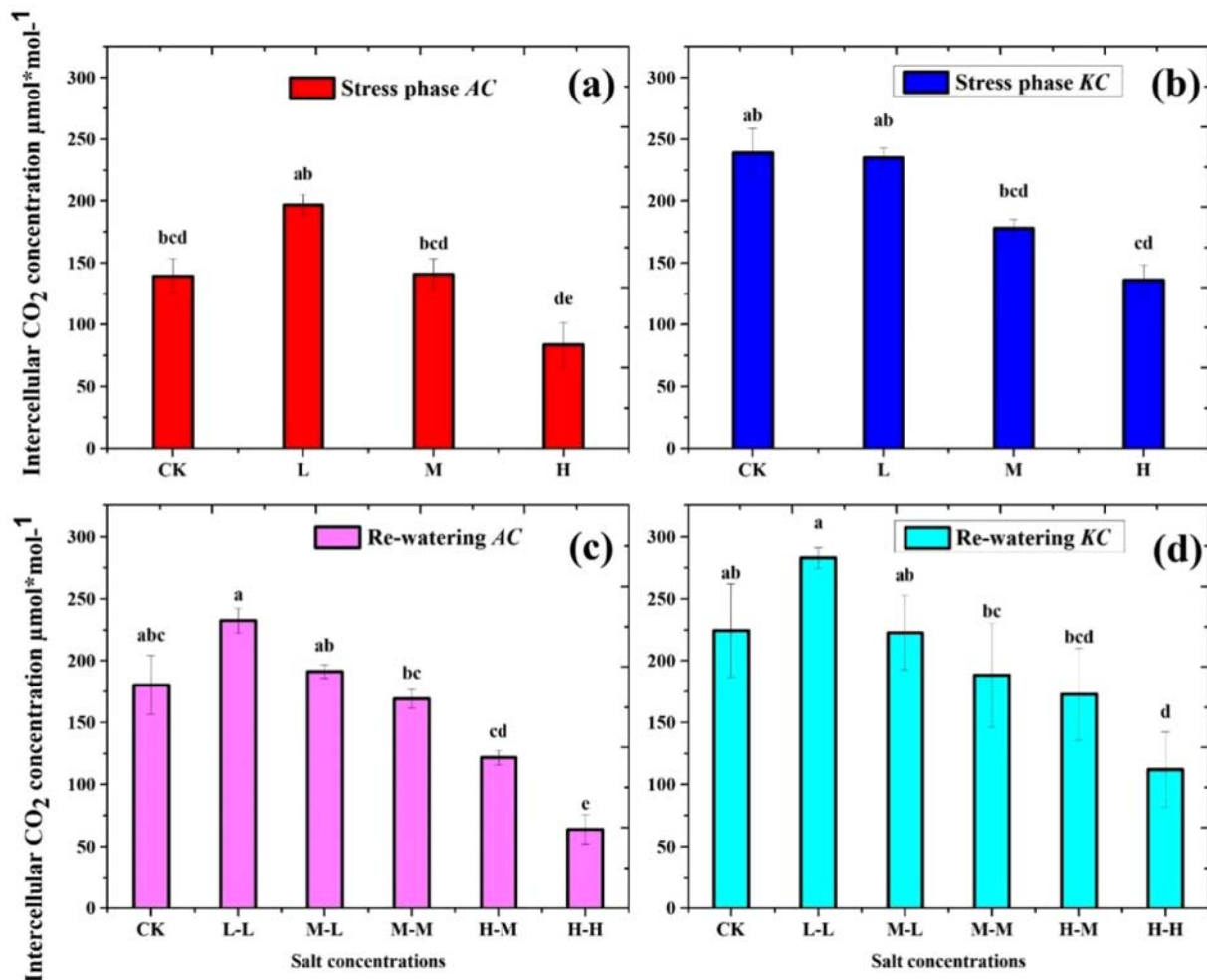


Figure 6. Effect of salt stress and RWP of Intercellular CO₂ on *A. corniculatum* specie (a, c) and *K. candell* (b, d), the small letter indicates significant difference at ($p < 0.05$) using Duncan's multiple range tests.

3. Results

3.1. Physiological capacitance (CP)

Effect of salt stress and re-watering phase of CP on both species were shown in Table 1. The CP values of *A. corniculatum* were significantly decreased by 41.7%, 53.4%, and 75.1% in salt stress phase of low, moderate, and high salt treatments respectively, compared to the control. While, CP values of *K. candell* decreased at moderate by 33.3% and high by 70.2%, but in low treatment the CP values increased by 20.3% than control. Furthermore, in re-watering phase, when salt concentration decreased, the CP values of *A. corniculatum* species increased at moderate to low (M-L) by 23.8% and high to moderate (H-M) by 37.7%, whereas in *K. candell* species increased at M-L by 22.2%, and H-M by 46.7% compared to stress phase. In re-watering phase *K. candell* species obtained higher values in L (100 mM) treatment compared to control as shown in Table 1.

3.2. Net photosynthesis (P_N)

The P_N of both species showed a clear significant difference in salt stress and RWP (Figure 3(a,b)). In higher salt concentration both species show progressive reduction in P_N values. Thus, minimum P_N values of both species were observed in H treatment. During the stress phase, P_N values of *A. corniculatum* were decreased at L by 4.7%, M by 15.7%,

and H by 30.1%, while the P_N values of *K. candell* were decreased at M level by 12.9% and H by 28.9% as compared to control. In addition, P_N values of *K. candell* species were increased in L treatment by 16.1% than control. The P_N values of both species in RWP showed a good response (Figure 3(c,d)). The P_N values of *A. corniculatum* species increased at M-L by 12.8% and H-M by 12.7%, while *K. candell* species increased at M-L by 10.4% and H-M by 23.1% as compared to stress phase. In both phases, the *K. candell* species obtained higher values of P_N than *A. corniculatum* species.

3.3. Stomatal conductance (g_s)

It was observed that stomatal conductance was adversely affected by salt; in both species, the g_s values were significantly decreased in stress phase (Figure 4(a,b)). Lowest g_s values of *A. corniculatum* and *K. candell* species were noted in H treatment. The g_s values of *A. corniculatum* decreased at L by 22%, M by 44%, and H by 58% as compared to control. While the g_s values in *K. candell* decreased by 39% and 63% at M and H level, respectively. On other hand, g_s values increased at L by 4.8% than control of *K. candell* species. Moreover, the values of RWP in *A. corniculatum* species increased at M-L level by 20% and H-M by 16%, and *K. candell* increased under M-L by 21.1% and H-M by 34.8%, as compared to stress phase.

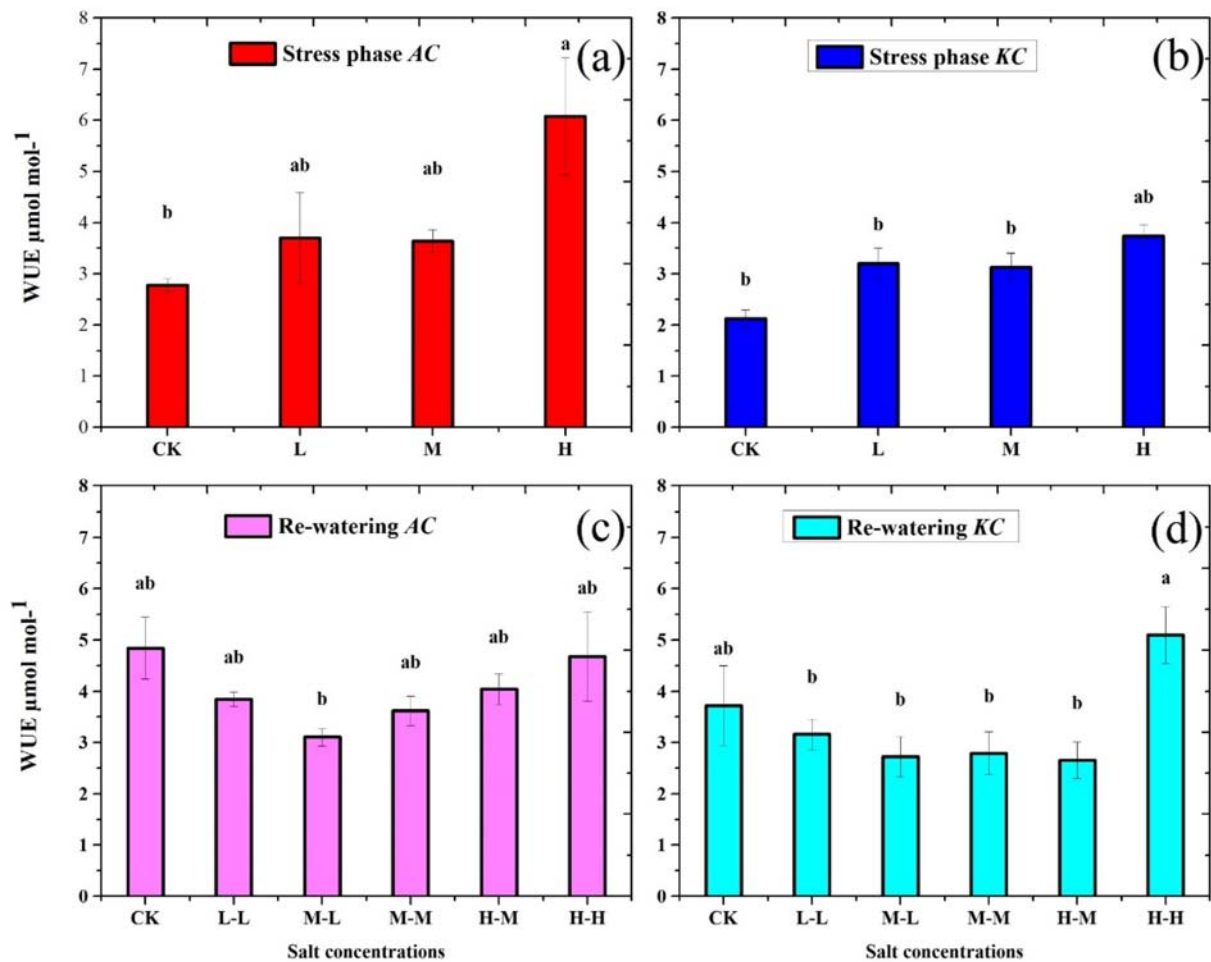


Figure 7. Effect of salt stress and RWP of water use efficiency on *A. corniculatum* species (a, c) and *K. candel* (b, d) the small letter indicates significant difference at ($p < 0.05$) using Duncan's multiple range tests.

3.4. Transpiration (Tr)

Transpiration of both mangrove species was significantly decreased with increasing the salt concentrations (Figure 5 (a,b)). Minimum Tr values of both species were observed in the H treatment. During the stress phase, *A. corniculatum* species decreased at L level by 21.2%, M by 35.1% and H by 62.8%, respectively, whereas, *K. candel* species decreased at L level by 23.1%, M by 39.9% and H by 59.1% compared to control. Subsequently, in the RWP the Tr values of *A. corniculatum* species increased at M-L by 23.3% and H-M by 32.2%, while values of *K. candel* species at M-L by 21.1% and H-M by 43.2% as compared to stress phase.

3.5. Intercellular CO_2 concentration (C_i)

The results of the intercellular CO_2 concentration of both species showed a significant difference in the salt stress phase (Figure 6(a,b)). C_i of both species was highly decreased in H treatment. The *A. corniculatum* decreased by 40.1% and *K. candel* by 43.2% as compared to control. The reduction in C_i could be a limitation of salt storage capacity and stomatal conductance. Furthermore, in the RWP, both species showed a good response (Figure 6(c,d)). The values of *A. corniculatum* species at M-L level increased by 26.4% and H-M by 31.3%, whereas *K. candel* species values increased at M-L by 20.1% and H-M by 21.3% compared to stress phase. In

the comparison of both species, *K. candel* obtained higher values of C_i in both phases.

3.6. Water use efficiency (WUE)

The results of WUE indicate that both species showed non-significant ($p > 0.05$) changes in stress phase. The WUE values of *A. corniculatum* and *K. candel* were increased in H treatment by 54.3% and 43.1%, respectively, as compared to control, while the non-significant results were observed in the remaining treatments. Furthermore, a similar trend was observed in RWP of both species (Figure 7(c,d)).

3.7. Water potential (Ψ)

Water potential of both mangrove species showed significant results in salt stress phase (Figure 8(a,b)). In the stress phase minimum values were observed in H treatment. *A. corniculatum* species values increased at L by 8.1%, M by 23.3%, and H by 35.1%, whereas *K. candel* species increased at L by 9.7%, M by 19.9%, and H by 41.6%, respectively, as compared to control. However, the increment of Ψ indicating that the solute concentration inside the cell could have a threshold value for dysfunction of cells and increased the Ψ of plant. After that in RWP, the Ψ of *A. corniculatum* species increased at M-L by 25.7% and H-M by 13.8%, while *K. candel* species increased at M-L by 9.9% and H-M by 16.8%, compared to the stress condition (Figure 8(c,d)).

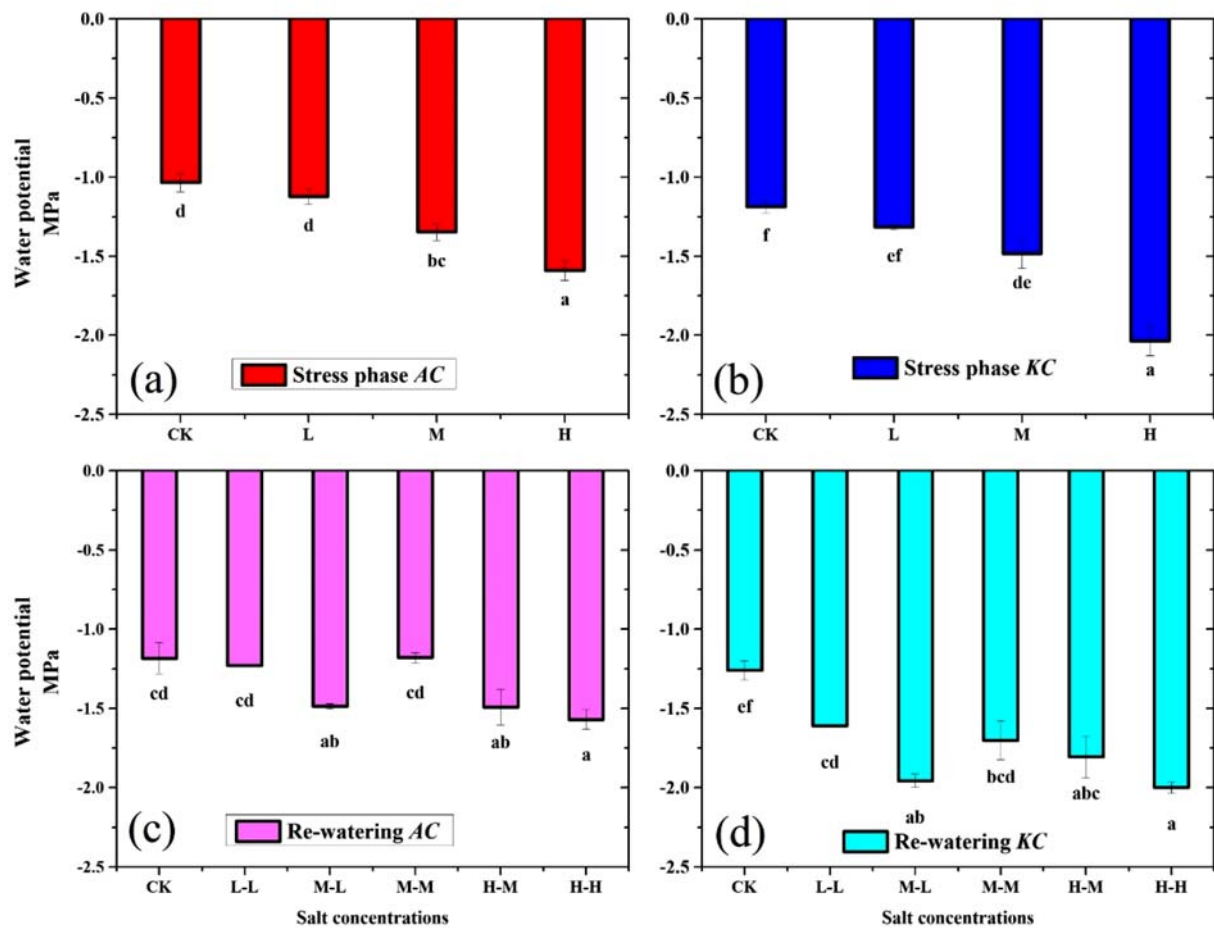


Figure 8. Effect of salt stress and RWP of water potential on *A. corniculatum* (a, c) and *K. candel* (b, d), the small letter indicates significant difference at ($p < 0.05$) using Duncan's multiple range tests.

3.8. Water content (WC)

The WC of both mangrove species significantly decreased with increasing the salt concentrations (Figure 9(a,b)). The WC was highly decreased in H treatment and slightly decreased in L treatment during the stress phase. The WC of *A. corniculatum* species decreased at L level by 2.8%, M by 5.6%, and H by 10.1% as compared to control. While the values of *K. candel* species decreased at L by 4.9%, M by 8.3%, and H by 13.6% than control. During the RWP the *A. corniculatum* species increased at M-L by 6.8% and H-M by 4.9% and the values of *K. candel* increased by M-L by 1.1% and H-M by 4.9% as compared stress phase. (Figure 9(c,d)).

3.9. The growth rate under salt stress and re-watering phase (RWP)

The leaf length and width of mangrove species in stress phase and RWP were calculated according to the above-mentioned leaf area model equation (Section 2.5) and growth rate estimated by using the four-parameter logistic equation (Table 2). *A. corniculatum* species, the $GR_{50} \times DT_{log}$ were decreased at L-L by 28.1%, M-L by 78.4%, M-M by 91.5%, H-M 92.4%, and H-H 95.5%, respectively, as compared to control. The results of *K. candel* species (Table 3), the $GR_{50} \times DT_{log}$ values decreased with increasing the salt concentration, at M-L by 55.9%, M-M by 59.5%, H-M by 63.1%, and H-H by 67.9% correspondingly compared to control. Moreover, it was

also noted that the growth rate of *K. candel* species was increased at L-L by 42.1% than control. The variation in growth rate depends on the species and their different mechanism. In the L treatment, where *K. candel* species kept higher growth rate at same stage CP and P_N values were also higher. These results indicating that in the low salt concentration plant cell maintained their turgor and help to increase their growth, which directly impacts on other related photosynthetic parameters.

3.10. Correlation between CP, P_N , g_s , and Ψ in salt stress and re-watering phase

The physiological capacitance variables appear to be related to photosynthesis, stomatal conductance, and water potential; bivariate correlations were used to determine the relationships among these parameters (Table 4). The result indicating that in stress condition *A. corniculatum* showed positive correlations between CP and g_s ($r = 0.975^*$), while *K. candel* species showed a positive correlation in CP with P_N and g_s (0.994^{**} and 0.982^*), respectively. When the salt concentration was changed in RWP, it was observed that the values of CP, P_N , g_s , and Ψ were increased. The correlation analysis shows that the CP with P_N (0.846^*), P_N with g_s (0.943^{**}), and P_N with Ψ (0.919^{**}) were highly correlated, while, the CP values of *K. candel* species was highly correlated with P_N , g_s , and Ψ ($r = 0.971^{**}$, 0.988^{**} , 0.961^{**}), respectively.

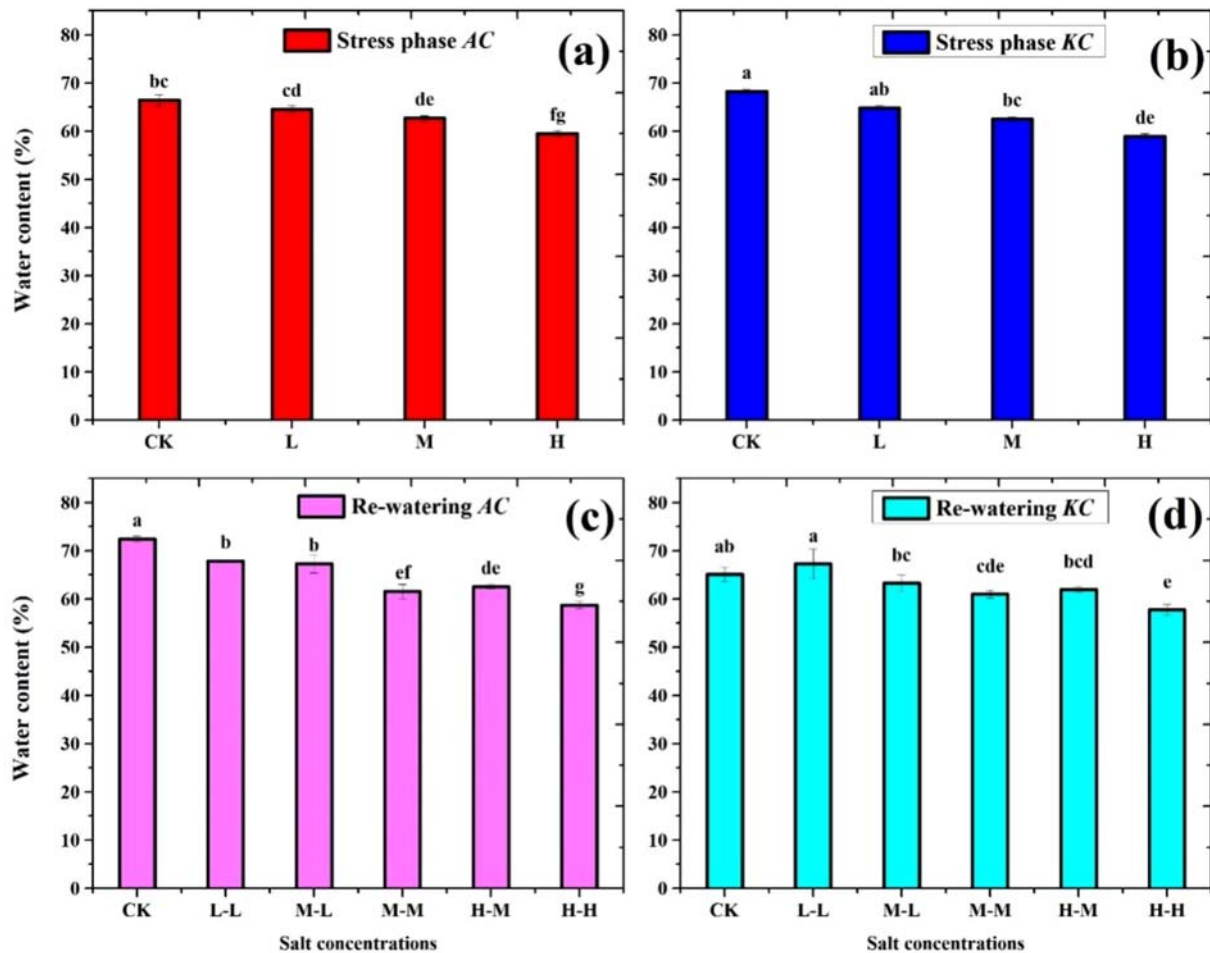


Figure 9. Effect of salt stress and RWP of water content (%) on *A. corniculatum* (a, c) and *K. candel* (b, d), the small letter indicates significant difference at ($p < 0.05$) using Duncan's multiple range tests.

4. Discussion

4.1. The differential responses of *A. corniculatum* and *K. candel*

4.1.1. Responses in salt stress phase

The current study measures the electrophysiological parameter of true mangroves *A. corniculatum* and *K. candel* species. Both species have different mechanisms of salt stress tolerances (Parida and Jha 2010). The CP values depend on plant cell and vacuole volume of species. The plant cell wall plays an important role in the determination of salt stress tolerance and plant growth rate (Feng et al. 2018). Na^+ accumulated in the apoplast may directly bind to cell wall components and affect their chemical properties (Shomer et al. 2003). Because detecting the changes in the cell wall composition is challenging, understanding the mechanisms underlying modifications of the cell walls and salt storage capacity upon exposure to high salinity is limited (Zhao et al. 2020). The *K. candel* species had greater salt storage capacity as compare to *A. corniculatum* species because *K. candel* species cell and vacuoles volume is bigger, so it could be resisted in higher salt stress conditions. Salt storage capacity depends on the volume of vacuole; it is, therefore, if volume of vacuole is smaller it means salt storage capacity is also smaller like *A. corniculatum* species showed in Figure 10. *A. corniculatum* species have smaller vacuole but have a different mechanism like salt secretion. The cell volume is positively correlated with the volume of vacuole, and the

main component of vacuole and cytoplasm is water. The mechanism of vacuolar size is directly associated with plant CP. The dynamic changes in vacuole size rapidly determined from plant CP. In the other words, the water-holding capacity of cells is directly proportional to $v = \alpha\sqrt{\text{CP}^3}$ (Zhang et al. 2020). When salt concentration increased, the CP values significantly decreased. In the present study, it was observed that when higher salt entered into the vacuole, ion concentration was increased and CP values significantly decreased. Therefore, in the above-mentioned equation v is equal to the volume of cell and CP is physiological capacitance. The experimental results showed that, if the volume of vacuoles is bigger CP values is larger and the volume of vacuole is smaller CP value also smaller which is shown in Figure 10. Under the stress phase, at the control level, the CP values of *A. corniculatum* specie were 36.1, which shows that vacuole volume is smaller, because volume of vacuole depends on solute concentration inside the cell (Figure 10(a)). Whereas CP values of *K. candel* species at control level were 59.5, it shows that vacuole was bigger as compared to *A. corniculatum* specie and solute concentration inside was lower as shown in Figure 10(b). Accordingly:

$$\frac{V1}{V2} = \frac{\sqrt{(36)^3}}{\sqrt{(59.5)^3}} = \frac{1}{2.1}$$

Table 2. Estimated leaf area of *A. corniculatum* species using four-parameter logistic equations under different salt concentrations and subsequent RWP.

Salt concentrations	GR ₅₀	DT _{log}	GR ₅₀ × DT _{log}	R ²	Equations
Control	606.9	49.25	29889.8	0.993	$Y = 6.0 + \frac{17.3}{1 + \left(\frac{X}{41.5}\right)^{-3.37}}$ ($n = 8, P = 0.0018$)
L-L	465.9	46.1	21477.9	0.992	$Y = 5.99 + \frac{18.2}{1 + \left(\frac{X}{34.5}\right)^{-2.23}}$ ($n = 8, P = 0.0002$)
M-L	116.8	55.08	6433.3	0.990	$Y = 2.29 + \frac{16.9}{1 + \left(\frac{X}{19.5}\right)^{-1.41}}$ ($n = 8, P = 0.0059$)
M-M	129.4	19.53	2527.1	0.958	$Y = 4.32 + \frac{11.7}{1 + \left(\frac{X}{14.7}\right)^{-3.01}}$ ($n = 8, P = 0.0078$)
H-M	60.64	37.19	2255.2	0.965	$Y = 0.02 + \frac{12.5}{1 + \left(\frac{X}{13.45}\right)^{-1.44}}$ ($n = 8, P = 0.0257$)
H-H	74.81	17.6	1316.6	0.990	$Y = 1.67 + \frac{8.4}{1 + \left(\frac{X}{12.46}\right)^{-2.83}}$ ($n = 8, P = 0.0011$)

Table 3. Estimated leaf area of *K. candel* species using four-parameter logistic equation under different salt concentrations and subsequent RWP.

Salt concentrations	GR ₅₀	DT _{log}	GR ₅₀ × DT _{log}	R ²	Equations
Control	304.7	42.9	13071.6	0.996	$Y = 0.90 + \frac{23.84}{1 + \left(\frac{X}{23.41}\right)^{-2.18}}$ ($n = 8, P = <0.0001$)
L-L	473.3	47.7	22576.4	0.997	$Y = 2.8 + \frac{31.7}{1 + \left(\frac{X}{26.7}\right)^{-2.23}}$ ($n = 8, P = <0.0001$)
M-L	190.8	30.21	5764.1	0.956	$Y = 10.9 + \frac{28}{1 + \left(\frac{X}{14.3}\right)^{-1.9}}$ ($n = 8, P = <0.0241$)
M-M	254.5	20.79	5291.1	0.998	$Y = 2.4 + \frac{12}{1 + \left(\frac{X}{21}\right)^{-4.04}}$ ($n = 8, P = 0.0001$)
H-M	279.4	17.29	4830.8	0.970	$Y = 10.4 + \frac{25.9}{1 + \left(\frac{X}{13.6}\right)^{-3.15}}$ ($n = 8, P = 0.0023$)
H-H	204.78	20.48	4193.8	0.997	$Y = 5.9 + \frac{19.9}{1 + \left(\frac{X}{14.5}\right)^{-2.83}}$ ($n = 8, P = <0.0001$)

As we know that V_1 = cell volume of *A. corniculatum* and V_2 = cell volume of *K. candel* species, solute concentration is equal to number of salt ion/volume. In Figure 10, it could be observed that, whether *A. corniculatum* or *K. candel*, the solute concentration of vacuole at L level was lowest, and at H level was highest among all treatments. It also indicated that the solute concentration of *A. corniculatum* specie was larger than *K. candel* at M and H levels. It means that salt storage capacity of *K. candel* was larger than *A. corniculatum*, although *K. candel* species could not secrete their salt, all salt ion was present in the vacuole. While *A. corniculatum* at L salt level it could resist the salt stress because their mechanism of salt secretion. The present study is consistent with the previous study reported that after capturing hundreds of three-dimensional microscopic images of secretions and shows that the similar secretion rate throughout the profile but ion concentration increased with increasing the NaCl concentration shown in Figure 10 (Tan et al. 2013).

Moreover, at L salt level, the salt secretion of *A. corniculatum* species and bigger volume of vacuole of *K. candel* species help them to maintain the same salt concentration and keep photosynthesis. As the salt concentration increased the bigger volume of vacuole in *K. candel* species is conduct to maintain the lower salt concentration as compared to *A. corniculatum* species, and it shows better salt storage capacity. *K. candel* species exhibited better photosynthesis and growth under high salt concentration. Our results are consistent with the previous study reported by Parida et al. (2004) that *A. corniculatum* species could tolerate up to 250 mM range of NaCl in stress conditions. Whereas under stress phase, the CP values of *K. candel* species at L level increased by 20.3% than control, it shows that the low salt level was more suitable for *K. candel* species, and at the same Level *K. candel* species easily maintained their growth. Similarity was seen in previous work that *K. candel* gave a better performance on low salinity at

Table 4. Correlation between CP, P_N, gs, and Ψ .

Parameters	Aegiceras corniculatum			Kandelia candel		
	P _N	gs	Ψ	P _N	gs	Ψ
Salt stress phase						
CP	0.905	0.975*	0.936	0.994**	0.982*	0.918
P _N	–	0.955*	0.986*	–	0.956*	0.871
Gs	–	–	0.987*	–	–	0.972*
Re-watering phase						
CP	0.846*	0.809	0.913*	0.971**	0.988**	0.961**
P _N	–	0.986**	0.943**	–	0.986**	0.944**
Gs	–	–	0.919**	–	–	0.982**

Note: Correlation significant level at *, ** $p < 0.05$, $p < 0.01$, respectively (two-tailed).

86 mM salt concentration compared to 0 NaCl (Wang et al. 2014). The reduction in CP values could be caused by increasing the concentration of solute salt in the cytosol (Zhang et al. 2015). CP and Ψ are determined simultaneously; both reflect the status of leaf water in plants and their cell volumes. If a large amount of salt (NaCl) is present in water, it increases Ψ in the plant roots and diffusion products in the leaf cell due to turgor loss (Munns and Tester 2008). This process reduced the Ψ , cell growth and finally development of the whole plant, which was observed (Tables 2 and 3). These findings agreed with previous work (Cristóvão et al. 2012). As we know that P_N is a very sensitive parameter in stress conditions, the P_N values of *A. corniculatum* species significantly decreased with increasing the salt concentration, P_N highly

declines in the H treatment by 30.1% as compared to control. Because at H treatment salt ions are present in large amounts in the vacuole so the plant cannot maintain their turgor, therefore the Ψ decreased and the P_N also decreased. While the *K. candel* species P_N values at L treatment increased by 16.1% same as the CP values because where CP values were higher P_N and gs values were also higher. The P_N values more decreased at H level by 28.9% of *K. candel* species as compared to control. The reduction of P_N values was due to the large amount of NaCl present in the water, it increased the osmotic potential hence plants cannot uptake water easily. The reason behind it could be when osmotic stress rapidly closes stomata, it reduced the plant's ability to assimilate CO₂. As reported by Xu et al. (2014) that the

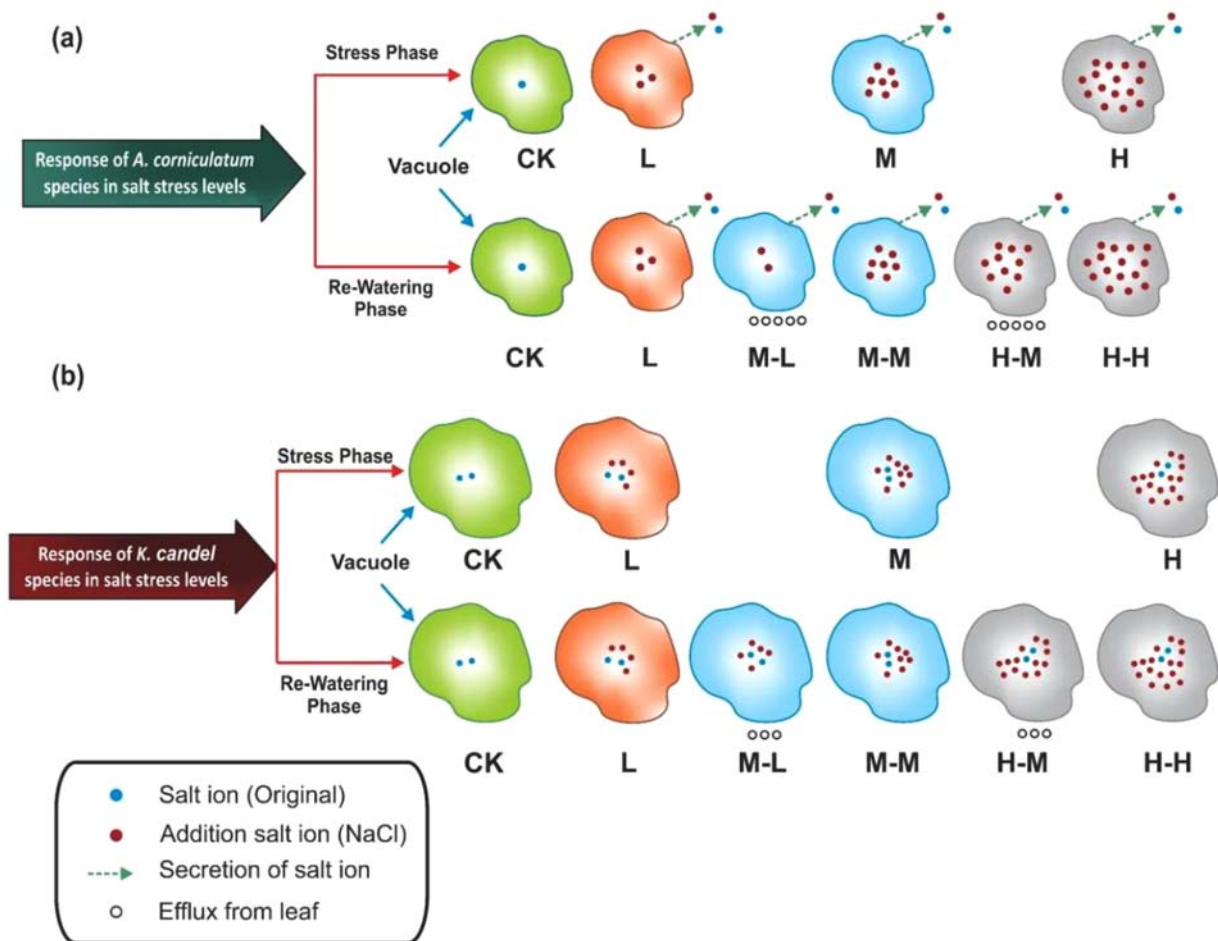


Figure 10. Vacuole volume, ion concentration and salt secretion with the variation of salt concentration. *A. corniculatum* species vacuole volume was smaller than *K. candel* species also *A. corniculatum* had secreting effect during the stress condition. Consequently, salt concentration was low inside the vacuoles at low salt stress level and became higher due to smaller vacuole size at high salt stress. While *K. candel* species vacuoles were bigger, it easily maintained their intracellular ion concentration and growth also increased at low salt stress, but when the salt concentration increased, at that time the solute concentration was also lower due to its bigger vacuole volume in this process. The salt efflux from leaf cells in both *A. corniculatum* and *K. candel* decreased the intracellular salt concentration after re-watering.

high salinity inhibited photosynthesis by the closing of gs and the reduction of CO₂ assimilation, the main cause of salt stress on photosynthetic activity. The CO₂ assimilation rate and gs both decreased when increasing the environmental salinity (García-Samaniego et al. 2017). Similarities were found in another study of mangroves that the high salt stress inhibited photosynthesis because of closing gs (Shiau et al. 2017).

4.1.2. Responses in re-watering phase (RWP)

The present study exposed, both mangrove species had a positive response in RWP, when salt treatments were changed into M-L and H-M treatments. In RWP, the solute concentration of both species M-L < M-M were shown in (Figure 10). When salt concentration decreased, the lower solute concentrations were observed in the M-L level and CP values also increased as compared to the stress phase. In this study, it was observed that the ratio of salt ion decreased the CP values increased, it indicated that plant is under low salt. Under M-L level, the efflux from leaf of *A. corniculatum* was higher than that in *K. candel*, since *K. candel* had a stronger salt storage capacity, and *A. corniculatum* keep significantly lower salt concentration in the vacuole, *A. corniculatum* exhibited a higher growth rate. Under M-M level, although salt secretion happened in *A. corniculatum*, but the salt concentration in the vacuole was still high due to its small cell volume and the growth of *A. corniculatum* was significantly inhibited. Furthermore, the CP values of *A. corniculatum* species increased in M-L by 23.8% and H-M by 37.7%, while *K. candel* increased at M-L by 22.2% and H-M by 46.7% as compared to the stress phase (Table 1). Simultaneously, in RWP the Ψ of *A. corniculatum* were decreased as compared to stress phase. These results are consistent with previous work done by Azeem et al. (2017) and Javed et al. (2018) that after RWP, a positive response was observed which significantly improve plant growth, when decreased the environmental salinity. The change in Ψ due to the opening and closing of gs, which triggers an imbalance of gaseous exchange (Javed et al. 2018). Moreover, in RWP the P_N values of *A. corniculatum* and *K. candel* species increased at H-M level by 12.7% and 23.1% than the stress phase (Figure 3). These results constituted with the former study reported that *K. candel* species can grow up when the salt concentration reached 500 mM NaCl (Parida et al. 2004). Results demonstrating that *K. candel* had more ability to resist the salt stress because the cell and vacuole volume is greater. Furthermore, when salt concentration increased at a level of 250 mM, *A. corniculatum* species could not maintain their growth but at the same level *K. candel* species can grow up well.

4.1.3. Response of growth rate

The growth rate of *A. corniculatum* and *K. candel* in stress and RWP timely increased and decreased was calculated with the help of a four-parameter logistic equation (Table 2). The minimum GR₅₀ × DT_{log} was observed at H-H treatment, *A. corniculatum* by 95.5%, and *K. candel* by 67.9% decreased than control. When solute concentration was higher, the P_N values decreased. Meanwhile, P_N values were directly proportional to the growth rate. The *K. candel* species at L-L level, the growth rate increased by 42.1% in the same treatment, the P_N also increased by 16.1% and solute concentration was lower than other

treatments (Figure 10(b)). Besides, the growth rate of *K. candel* specie at M-L, M-M, and H-M levels, the non-significant difference was observed. While *A. corniculatum* species, growth rate decreased with increasing the salt concentration. A research study reported that carbohydrates were accumulated during the photosynthesis process and play many important roles such as ion absorption and resistance to adversity (Xing et al. 2019). Therefore, in stress phase carbohydrates were produced in the photosynthesis period that were used to respiration and produced energy for plant tolerance in salt stress, which decreased the growth. Moreover, during high salt concentrations, the leaf cells lose water, this loss of cell water and turgor is transient. After some hours cell recovered their original volume of water and turgor, despite the cell elongation rates reduced. Apparently, plant leaves smaller and thicker were observed due to reductions in cell elongations, hence the growth rate was reduced. The previous study reported that P_N and plant growth rate had a strong relationship (Sudhir and Murthy 2004; Tavakkoli et al. 2011). In this study, in the H treatment where P_N obtained a minimum value at the same treatment growth rate was also lowest. The growth rate also concerns gs, lower gs minimized the leaf thickness and decreased the growth rate (Parida and Jha 2010), comparable phenomena were observed in the current study. Furthermore, *K. candel* had better growth in L treatment as compared to other treatments, the similarity was seen in the previous study by Hwang and Chen (1995). The results of WUE were not clear like other parameters, even in low or high salt concentration results were non-significant, the WUE of *A. corniculatum* was slightly higher at H treatment, but *K. candel* species was almost similar even at low or high salt concentrations.

4.1.4. Correlation between CP, P_N, gs, and Ψ

In the current study, it was observed that there is no correlation between CP and Ψ in salt stress phase, but it is positively correlated in RWP, which indicates that CP can better represent water status (Zhang et al. 2015), while RWP can improve CP and water potential at some time. The P_N, and gs values were decreased significantly in the stress phase (Figures 3 and 4), and these parameters had a strong relationship with CP in Table 4. Our result supports a previous study by Wang et al. (2018) reported that water potential and gas exchange parameters have a positive relationship and another researcher reported that P_N values significantly correlated with gs and Ψ (Xing et al. 2018). In RWP, when changed the salt concentration from high to moderate, the *A. corniculatum* and *K. candel* species gave a positive response. When the CP values increased at H-M treatment by 49% at the same level P_N values also increased by 12.7% of *A. corniculatum* species, while *K. candel* species at H-M level increased by 46.7% at the same level P_N 23.1% increased than stress phase. These findings support the previous study that after RWP okra cultivars recovered and increased their growth and CP values (Azeem et al. 2017).

5. Conclusion

The differential responses of *A. corniculatum* in stress phase indicating that the CP was significantly decreased with increasing the salt concentrations. While *K. candel* species at M and H treatments were slightly decreased compared

to control, but at L level, the CP values were higher as compared to control. In the low salt concentration *K. candel* species showed a higher growth rate as compared to *A. corniculatum* species and low salt level was suitable for *K. candel* species. Furthermore, *K. candel* species did not secrete their salt, all salt ions present in the vacuole, so vacuole volume was bigger but solute concentration was lower than *A. corniculatum* species. Salt storage capacity depends on vacuole volume and vacuole volume directly linked with CP, therefore variation in cell volume could be rapidly determined from CP; *A. corniculatum* had a smaller vacuole volume but at L level *A. corniculatum* species secrete the salt through the mechanism of salt secretion and maintained their growth. In the RWP, when the salt concentration decreased, *K. candel* species showed a good response especially at H-M treatment as compared to *A. corniculatum*. According to the growth rate, *A. corniculatum* and *K. candel* decreased by 95.5% and 67.9%, respectively, in H-H treatment compared to control. Moreover, in the current study the determination of CP, in which a leaf was placed between two parallel electrode plates, hence this method provided rapid response as compared to traditional methods. It was concluded that both species have a different mechanism of salt tolerant *A. corniculatum* species by salt secretion and *K. candel* species by bigger vacuole volume to maintained their growth. The above-mentioned conclusions were obtained only for *A. corniculatum* and *K. candel* species, both are true mangrove species but both have a different mechanism of adaptations. Other mangrove species like associate mangrove response in re-watering after salt stress conditions needs to be further investigated.

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