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Trade-off between shoot and root dry weight along with a steady CO_2 assimilation rate ensures the survival of *Eucalyptus camaldulensis* under salt stress

Fahad Rasheed[1], Rasool Bakhsh[1], Ihsan Qadir[2]*

[1]Department of Forestry and Range Management, University of Agriculture, Faisalabad, Pakistan
[2]Department of Forestry and Range Management, Bahaudin Zikaria University, Multan, Pakistan

**Corresponding author: fahad.rasheed@uaf.edu.pk*

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Abstract: Salt stress is a major challenge for reforestation in arid to semi-arid regions. Therefore the effect of salt stress was tested in 4-months-old saplings of *Eucalyptus camaldulensis* under controlled conditions. Individuals were subjected to three levels of salt stress (2, 8, 16 $d{\cdot}Sm^{-1}$) and several traits describing growth and dry weight production/allocation, as well as physiological attributes were measured. The results showed that salt stress had no impact on plant height or stem diameter. Number of leaves, number of branches, and leaf chlorophyll content decreased significantly under high salt stress treatment. Leaf dry weight decreased significantly, but root dry weight increased significantly from 6.22 to 8.24 g under high salt stress treatment. Total plant dry weight remained similar while the root/shoot ratio increased significantly under high salt stress treatment. The net CO_2 assimilation rate remained stable at ~ 10.1 $mmol{\cdot}m^{-2}{\cdot}s^{-1}$ and stomatal conductance decreased significantly to 79 $mmol{\cdot}m^{-2}{\cdot}s^{-1}$ under high salt stress. Consequently, water use efficiency increased significantly to 3.25 $mmol{\cdot}mol^{-1}$ under high salt stress. Therefore we may conclude that the young Eucalyptus camaldulensis saplings can tolerate moderate salt stress by increasing dry weight allocation towards the root system and sustaining the CO_2 assimilation rate.

Keywords: tolerance; salinity; dry weight production and allocation; stomatal conductance; water use efficiency

Forests generally provide more than 80% of the consumable biomass and cater to more than 50% of the terrestrial biodiversity (Neale, Kremer 2011). Forests not only help reduce the atmospheric pollution but also they provide a variety of other products such as wood biomass, paper, and fuel (Harfoche et al. 2012). In the context of climate change, forest plantations are facing different types of environmental stresses. Global climate is predicted to change towards longer periods of drought spells, increased soil salinity, low water availability and temperature extremes. Such factors are liable to result in a worldwide decrease in forest production, tree growth and survival rate. According to the report presented by IPCC (http://www.ipcc.ch), all these environmental factors are going to change for the worse in the future due to global warming (Shakoor et al. 2011).

Salt stress has become a major abiotic factor that has reduced the plant growth and productivity of tree plantations over the past few years (Meloni et al. 2003; Zhu et al. 2012). The natural response of autotrophs to high salt stress has been reported for many decades and many studies have reported the

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salt tolerance mechanism in higher plants (Meloni et al. 2003; Wang et al. 2011). Previous reports have revealed that salt stress has negatively affected almost 20% of the global cultivated land and about half of the irrigated lands (Zhu 2001). Increased salt stress disrupts the photosynthetic system that may result in retardation of plant productivity (Ioannidis et al. 2009; Ashraf, Harris 2013). Essah et al. (2003) reported that plants exposed to salt stress showed symptoms of metabolic toxicity, nutrient deficiency and oxidative stress that damaged leaf tissues and ultimately resulted in early leaf senescence (Zafar et al. 2019). In mature plants, salt stress can cause hyperosmotic and ionic stress that causes a significant negative impact on plant morphology and physiology (Ashraf, Harris 2013). Furthermore, prolonged exposure to high salt stress may result in plant death as water availability decreases under salt stress (Hasegawa et al. 2000; Chaves et al. 2009). Numerous adaptive strategies to survive under high salt stress have also been reported that include modifications in growth regulators, metabolic/osmotic adjustments and altered cellular signalling (Bartels, Sunkar 2005). However, such strategies vary across species and under varying degrees of stress.

Eucalyptus is native to Australia and has become an important tree species in Pakistan. A mature tree stem of *Eucalyptus* produces reddish-brown rounded scales that frequently fall off during later growth stages of tree development. Heartwood is silver in colour and leaves are long and pointed in shape with the length varying from 10 to 20 cm (Flexas et al. 2004). This species has shown an immense growth potential under harsh environmental conditions around the globe. Pakistan is an arid to semiarid country with almost 6.67 Mha of land affected by salinization, which is almost 25% of the total cultivated area of the country (Ahmad et al. 2012). Almost 40% of the salt-affected area is saline (increased level of soluble salt; EC ≥ 4 $dS \cdot m^{-1}$), and 60% is saline-sodic (EC ≥ 4 $dS \cdot m^{-1}$) to sodic (EC < 4 $dS \cdot m^{-1}$) in nature that are high in Na^+ ions (Qureshi et al. 2007). Regarding these circumstances, vigilant selection of salt-tolerant species is of pivotal importance especially in arid to semiarid areas. Species vary in the degree of tolerance towards specific abiotic stress, however, during the early establishment stage, species are generally much more susceptible. Therefore, the present study was conducted to investigate the effect of salinity stress on dry weight production, morphological and physiological adjustments of *Eucalyptus camaldulensis* during the sapling stage.

MATERIAL AND METHODS

Planting material and growth condition. The experiment was carried out in a greenhouse of Forest Nursery, Department of Forestry & Range Management, (31°26'N, 73°06'E; 184.4 m), University of Agriculture Faisalabad, Pakistan. The temperature in the greenhouse was around 25 °C and humidity was 55–60% throughout the experiment. Sixty individuals of uniform size (4-months-old healthy saplings) were taken from the nursery. They were shifted under the shade for one week and then transplanted into the earthen pots (14 cm and 22 cm depth). Pots were filled with substrate composed of peat and sand at a 2:1 ratio. The physicochemical properties of the substrate used in the experiment are shown in Table 1. Three levels of artificial salinity, i.e. 2, 8, and 16 $dS \cdot m^{-1}$, were developed using commercially available salt NaCl. These levels of salinity stress (2, 8, and 16 $dS \cdot m^{-1}$) were developed adding commercial NaCl on a weight basis, as 8 kg of soil was added into each earthen pot and salinity was measured using an EC meter (accuracy ± 1%; FIELD SCOUT EC 450). In the control treatment (2 $dS \cdot m^{-1}$) no additional commercial salt (NaCl) was added. In moderate salt stress treatment (8 $dS \cdot m^{-1}$) and high salt stress treatment (16 $dS \cdot m^{-1}$) about 8.424 g and 19.68 g salt were added per kg of substrate, respectively. During the experiment, each pot was irrigated with 100 ml of tap water

Table 1. Physicochemical properties of substrate used in this study

Properties	Values
pH (H_2O)	6.5
Electrical conductivity ($dS \cdot m^{-1}$)	2.5
Total soluble solids (TSS)	14.2
Soil nitrogen (m/m%)	0.046
Phosphorus (ppm)	9.8
Organic matter content (m/m%)	0.91
Base saturation (%)	36
Percentage of sand (%)	69
Percentage of silt (%)	18.5
Percentage of clay (%)	12.5
Texture class	loam

(TDS < 1 000 mgl^{-1}; EC 0.15 dS·m^{-1}) every day and was rotated to compensate for the climatic variations of the greenhouse.

Growth parameters and dry weight production analysis. Growth parameters like plant height (cm) and stem diameter (mm) were measured using a measuring tape and digital Vernier calliper (to the nearest 0.02 mm), respectively. Leaf chlorophyll content was measured using a chlorophyll meter (SPAD, 502Plus, USA), and the number of leaves and branches was counted twice a week during the experiment. At the end of the experiment (after 60 days), plants were harvested and divided into three sections: leaves, stems and roots. All the plant samples were packed in plastic bags and fresh weight was measured (Electronica Balance PCE-JS 100). Subsequently, all samples were oven-dried (DGH-9202 Thermal Electric Thermostat drying oven) at 70 °C to constant weight and oven-dried weight of each plant section along with total dry weight was calculated. The root/shoot ratio was also calculated by dividing the root dry weight by the leaf + stem dry weight. The biomass allocation percentage in all the plant sections, e.g. leaves, stem and roots, was calculated using the following formula

Leaf gas exchange parameters. One fully developed and healthy leaf per plant was selected per treatment and the following leaf gas exchange parameters were measured: net CO_2 assimilation rate (A; µmol CO_2 m^{-2}·s^{-1}), transpiration rate (E; mmol H_2O m^{-2}·s^{-1}) and stomatal conductance (g_s; µmol·m^{-2}·s^{-1}), using portable Infrared Gas Analyzer CIRAS-3 (Amesbury, USA). The temperature of the leaf chamber was adjusted at 27 °C before the measurement. Relative humidity was at 64% and the CO_2 reference was kept at 400 µmol·mol^{-1}. Measurements were done under natural sunlight between 10:00 AM to 2:00 PM. Water use efficiency was calculated as the ratio between the carbon dioxide assimilation rate and the rate of transpiration (Rasheed et al. 2015).

Statistical analysis. Normality of the data was tested using Q-Q plots and homoscedasticity was checked by plotting residuals vs predicted values. The data was analysed using one-way ANOVA (STATISTICA 12.1, Satatsoft). Means and standard error (SE) were calculated, while the significant differences between treatments were tested using *post-hoc* Tukey's HSD. All tests and correlations were taken as significant at $P < 0.05$.

RESULTS AND DISCUSSION

Effect of salt stress on plant growth

Salinity stress had a significant negative impact on plant growth during the experiment. Treatment means of growth traits and leaf chlorophyll content under salt stress are presented in Table 2. No significant decrease was evidenced in plant height and stem diameter under salt stress ($P = 0.424$ and $P = 0.649$, respectively). However, the number of leaves significantly decreased by 11.2% ($P < 0.001$) and 27% ($P < 0.001$) under moderate and high salt stress treatments, respectively. The number of branches also decreased significantly ($P = 0.023$) by 8.03% and 25% under moderate and high salt stress, respectively. Leaf chlorophyll content remained similar to the control under moderate stress but it decreased significantly by 13.6% under high stress treatment (Table 2).

The effect of salinity stress on plant growth includes changes in morphological attributes such as plant height, stem diameter, number of leaves. Plants respond to salt stress in two distinct phases with time or age. The first phase is marked by os-

Table 2. Growth parameters and leaf chlorophyll content in *Eucalyptus camaldulensis* examined under three levels of salt stress (2, 8, and 16 dS·m^{-1})

Parameters	Control	Moderate stress	High Stress	*F*-value	*P*-value
Plant height (cm)	48.1 ± 3.78^{a}	46.8 ± 3.48^{a}	44.3 ± 2.76^{a}	2.04	$P = 0.148$
Stem diameter (mm)	2.10 ± 0.67^{a}	2.22 ± 0.76^{a}	1.98 ± 0.20^{a}	0.438	$P = 0.649$
Number of leaves	26.6 ± 2.40^{a}	23.6 ± 1.89^{a}	19.4 ± 2.11^{b}	4.76	$P < 0.001$
Number of branches	4.23 ± 0.27^{a}	3.89 ± 0.13^{b}	3.17 ± 0.22^{c}	2.74	$P = 0.023$
Leaf chlorophyll content	51.5 ± 0.85^{a}	50.9 ± 0.61^{a}	44.5 ± 0.45^{b}	11.9	$P < 0.001$

Variability of parameters was analysed using one-way ANOVA; means are presented with their standard errors and small letters represent differences between treatments tested using *post-hoc* Tukey's test; all tests were taken significant at $P < 0.05$

Table 3. Dry weight production (leaves, stem and roots) of *Eucalyptus camaldulensis* saplings examined under three levels of salt stress (2, 8, and 16 dS·m^{-1})

Parameters	Control	Moderate stress	High stress	*F*-value	*P*-value
Leaf fresh weight (g)	16.1 ± 1.32^{a}	15.5 ± 1.23^{a}	12.2 ± 1.28^{b}	4.23	$P = 0.025$
Leaf moisture content (m/m %)	45.0 ± 0.75^{a}	43.8 ± 0.56^{b}	42.6 ± 0.34^{b}	4.92	$P < 0.001$
Leaf dry weight (g)	8.85 ± 0.67^{a}	8.71 ± 0.58^{a}	6.85 ± 0.75^{b}	4.82	$P = 0.018$
Stem fresh weight (g)	18.8 ± 1.84^{a}	16.5 ± 1.85^{a}	16.1 ± 1.83^{a}	3.03	$P = 0.064$
Stem moisture content (m/m %)	48.1 ± 0.57a	45.8 ± 0.48^{b}	44.9 ± 0.31^{b}	4.31	$P = 0.016$
Stem dry weight (g)	9.75 ± 0.84^{a}	8.93 ± 0.87^{a}	8.86 ± 0.43^{a}	3.33	$P = 0.056$
Root fresh weight (g)	11.8 ± 1.94^{a}	13.2 ± 0.97^{a}	14.8 ± 0.88^{a}	2.75	$P = 0.081$
Root moisture content (m/m %)	47.2 ± 0.22^{a}	41.1 ± 0.78^{b}	43.8 ± 0.52^{b}	3.87	$P = 0.035$
Root dry weight (g)	6.22 ± 0.89^{a}	7.78 ± 0.56^{a}	8.34 ± 0.66^{b}	4.92	$P = 0.005$

Variability of parameters was analysed using one-way ANOVA, means are presented with their standard errors and small letters represent differences between treatments tested using *post-hoc* Tukey's test, all tests were taken significant at $P < 0.05$

motic changes and the second phase is the phase of ionic changes (Munns, Tester 2008). The osmotic stress directly affects plant growth parameters as the salt concentration increases the threshold limits around the root zone. Previous studies have demonstrated that in some species, osmotic stress of 40 mM NaCl induces Na^+ toxicity that influences leaf growth especially in old leaves (Munns, Tester 2008). Decreases in the thickness of periderm, phloem tissue, and xylem tissue as well as in the diameter of the pith were also demonstrated under salt stress (Boughalleb et al. 2009). In *Populus deltoides*, 25% decrease in total dry weight was evidenced under high salt stress treatment (Zafar et al. 2018). Similarly, Niazi et al. (1985) reported the inhibitory effect on the growth of *Leucaena* due to a high salt concentration. Moreover, studies have reported that NaCl concentrations of 1 500, 3 000 and 6 000 ppm significantly decreased the growth parameters of *Leucaena* plants e.g. up to 50% under high concentrations (Hansen, Munns 1988). In *Terminalia arjuna*, plant height decreased by 8.6% and 22.9% under moderate and high salt stress conditions, which is in contrast with the findings of the present study where *Eucalyptus camaldulensis* showed no significant decrease in plant height in moderate or high salt stress treatment. As explained by Munns et al. (2006), the decrease in plant growth under salt stress is due to the following two factors: the first is the intensity of salt stress, and the second is the salt-specific or ion excess effect. In order to survive under different intensities of salt stress, various plant species have developed various mechanisms (Munns 2002). Mass and Hoffman (1977) showed that the plants do not decrease their biomass until the threshold level of salt stress is reached, after which the biomass decreases linearly with increasing salinity. In accordance with these works, the results showed that *Eucalyptus camaldulensis* saplings can tolerate the salt stress up to 16 dS·m^{-1}. Also, there is a trade-off recorded in the aboveground biomass allocation that favours plant height and stem diameter at the expense of the number of leaves and the number of branches.

Effect of salt stress on dry biomass production and allocation

The leaf fresh weight and leaf dry weight remained unaffected under moderate stress, however, they decreased significantly by 24.2% and 22.5% under high salt stress treatment, respectively (Table 3). Stem moisture content decreased significantly under both moderate and high salt stress treatment. Stem fresh weight and dry weight showed no significant change under moderate or high salt stress treatment. It is interesting that root fresh weight increased by 10.6 and 20.2% under moderate and high salt stress treatment, respectively. Root moisture content decreased significantly under moderate and high salt stress treatment. Consequently, root dry weight increased significantly by 20% and 25.4% under moderate and high salt stress, respectively.

The root/shoot (R : S) ratio increased significantly ($P < 0.005$) by 37.7% under high salt stress treatment. Although the leaf and stem dry weight allocation decreased significantly ($P = 0.012$ and $P = 0.015$) under high salt stress treatment (Table 4), the root dry weight allocation increased

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Table 4. Total dry weight production and allocation in *Eucalyptus camaldulensis* saplings examined under three levels of salt stress (2, 8, and 16 dS·m^{-1})

Parameters	Control	Moderate stress	High stress	*F*-value	*P*-value
Total plant dry weight (g)	24.8 ± 1.08^a	25.4 ± 0.92^a	24.0 ± 0.99^a	3.88	$P = 0.082$
R:S ratio	0.33 ± 0.063^a	0.44 ± 0.041^a	0.53 ± 0.034^b	4.42	$P = 0.005$
Leaf biomass allocation (%)	35.6 ± 0.89^a	34.2 ± 0.99^a	28.4 ± 1.22^b	4.12	$P = 0.012$
Stem biomass allocation (%)	39.1 ± 1.21^a	35.3 ± 1.11^b	36.8 ± 1.08^b	4.09	$P = 0.015$
Root biomass allocation (%)	25.0 ± 0.89^a	30.6 ± 0.45^b	34.6 ± 0.22^c	4.87	$P < 0.001$

Variability of parameters was analysed using one-way ANOVA, means are presented with their standard errors and small letters represent differences between treatments tested using *post-hoc* Tukey's test, all tests were taken significant at $P < 0.05$

significantly ($P < 0.001$) by 18.3% and 27.7% under moderate and high salt stress, respectively.

The fresh weight of various plant sections is considered an important indicator for salt stress tolerance in plant species. The species that show higher fresh weight under salt stress show faster growth under saline conditions. Species under salt stress generally show a significantly increased root fresh weight as the increased root development helps in nutrient and water uptake, therefore, species tend to invest more biomass to roots and develop their root system under abiotic stresses (Lynch 1995).

Globally, the root biomass represents almost 32–65% of the worldwide terrestrial net primary production (Abramoff, Finzi 2015) and is exclusively responsible for the transport of water and other important minerals from the soil (Norby et al. 2004). Roots are also involved in nutrient uptake, storage and supply to the other parts of the plants (Ouimet et al. 2008). Therefore, a significant increase in the R : S ratio is a very common response in tree species under increased salinity (Álvarez, Sánchez-Blanco 2014).

Our results are also in line with the previous findings where an increase in root biomass production was reported in *P. deltoides* under increased salt stress (Zafar et al. 2018). Similar results regarding the R : S ratio were reported by Fernández-García et al. (2014) and Glaeser et al. (2016). Furthermore, Zafar et al. (2019) found that the R : S ratio remained similar to the control under moderate salt stress, but a significant decrease of the R : S ratio was found under high salt stress in *Terminalia arjuna* saplings. In this study, the observed increase in root dry weight with an increase in salt stress is in line with the previous results in *P. deltoides* (Zafar et al. 2018).

In this study, total plant dry weight showed no variation across the salt stress treatments ($P = 0.082$; Table 4). Similar results were reported by Zafar et al. (2018), where *P. deltoides* showed a significant decrease in total biomass at an electrical conductance of 12 dS·m^{-1}, and no differences were found in total biomass production at an electrical conductance of 6 dS·m^{-1} of salinity. On the contrary, in *Terminalia arjuna*, although stem and leaf biomass production was reported to decrease even under moderate salt stress, total biomass production in the control and under moderate salt stress treatment was found to be similar (Zafar et al. 2019).

Therefore, results of the present study reaffirm that various plant species have different tolerance levels to salt stress because of varying degrees of ionic usage of salts for osmotic adjustments (Koyro 2006). According to the results of this study, *Eucalyptus camaldulensis* saplings showed a considerable degree of adaptability under moderate salt stress in terms of total dry biomass production and allocation.

Effect of salt stress on physiological attributes

The physiological attributes showed significant variation across the treatments. Net CO_2 assimilation rate remained similar ($P = 0.724$) across the treatments (Figure 1A) and remained at almost 10.1 μmol·m^{-2}·s^{-1} under both moderate and high salt stress treatments. However, salt stress also had a negative impact on stomatal conductance that decreased significantly ($P = 0.007$) under both moderate and high salt stress treatments. The maximum value of 154.2 mmol·m^{-2}·s^{-1} was observed under control conditions which decreased to 101.5 mmo·m^{-2}·s^{-1} under moderate stress and to 79.4 mmol·m^{-2}·s^{-1} under high stress treatment (Figure 1B). Stomatal conductance decreased by 35.2% and 48.4% under moderate and high stress treatments, respectively. The transpiration rate showed a similar trend like

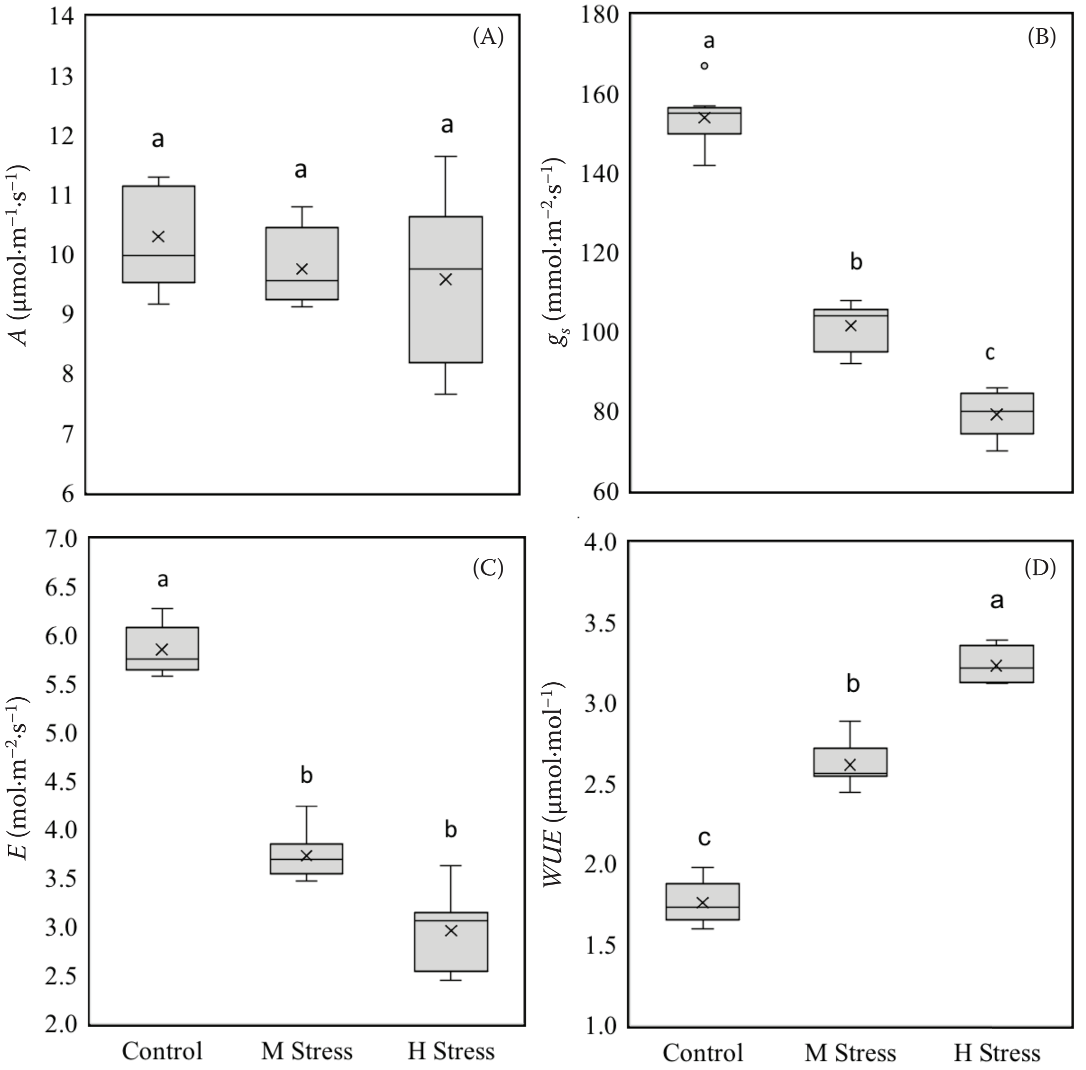

Figure 1. Physiological parameters: *A* – net CO_2 assimilation rate (A); g_s – stomatal conductance (B); *E* – transpiration rate (C); *WUE* – water use efficiency in *Eucalyptus camaldulensis* (D) under Control (2 dS·m^{-1}); moderate (M. Stress – 8 dS·m^{-1}) and high salt stress (H. Stress – 16 dS ·m^{-1}). Parameters were analysed using one-way ANOVA. Lower and upper whiskers represent the minimum and maximum value and lower and upper limits of the box represent the first and the third quartile, respectively. Mean value is indicated with "*x*" and horizontal bar within each box represents the median value for the whole data set. Homogeneous groups defined by Tukey's HSD test are presented with small letters

stomatal conductance and decreased significantly ($P = 0.005$) with an increase in salt stress (Figure 1C). Due to a significant decrease in the transpiration rate under both moderate and high salt stress treatments, water use efficiency (ratio between net CO_2 assimilation rate and transpiration rate) increased significantly under both moderate and high stress treatment (Figure 1D).

It has been well documented that variation of water use efficiency depends upon the relative increase or decrease in net CO_2 assimilation rate and transpiration rate (Rasheed et al. 2013; 2015). In this study, results showed that in *Eucalyptus camaldulensis* saplings, the observed variation in water use efficiency was mainly driven by the variations in transpiration rate rather than in net CO_2 assimilation rate. According to Farquhar and Sharkey (1982), species regulate a water loss through the transpiration rate by adjusting their stomatal aperture and maintain an optimum plant water potential. These adjustments help species to maintain an optimum net CO_2 assimilation rate, however, under extreme conditions, such adjustments may also lead to a significant decrease in the net CO_2 assimilation rate (Zafar et al. 2019). Although in this study stomatal conductance decreased significantly under salt stress, this decrease had no impact on the net CO_2 assimilation rate under either treatment. These results concur with the previous findings where no impact was found in net CO_2 assimilation under salt stress (Rawat, Banerjee 1998; James et al. 2002).

As the plant response to salt stress largely depends upon the duration and intensity of salt stress (Munn et al. 2009), we argue that the salt stress applied in this study was not high enough to cause a decrease in the net CO_2 assimilation rate. However, a significant decrease in the transpiration rate observed in this study clearly indicated that the rapid stomatal response is an important tolerance strategy in *Eucalyptus camaldulensis* to cope with the induced salt stress. These results are in line with the previous results reported by Abbruzzese et al. (2009) in white poplar and Zafar et al. (2019) in *Terminalia arjuna*.

In the present study, water use efficiency increased significantly in both the moderate and high stress treatments, which concurs with the previous studies where increased water use efficiency under saline conditions have been evidenced in needle-shaped as well as broad-leaved species (Ferrio et al. 2003; Adams, Kolb 2004).

However, the observed increase in water use efficiency under salt stress was mainly due to a decrease in the transpiration rate which is in line with the previous studies (Arndt et al. 2001; Zafar et al. 2019). Therefore, we may conclude that young saplings of *Eucalyptus camaldulensis* can tolerate moderate salt stress due to increased production of root biomass and increased water use efficiency under moderate salt stress treatment.

CONCLUSION

The study showed that saplings of *Eucalyptus camaldulensis* under salt stress reduced biomass allocation to leaves and stem in favour of roots, but total plant dry weight produced under all the treatments remained similar. The R : S ratio increased under moderate and high salt stress treatments as compared to the control. The net CO_2 assimilation rate remained unaltered while the transpiration rate decreased significantly under moderate and high salt stress. Consequently, water use efficiency increased significantly under medium as well as high salt stress treatment. Results indicate that a considerable increase in the allocation of biomass to roots in *Eucalyptus camaldulensis* could have significant implications in the breeding strategies, as well as in selection of a suitable species for introduction into salt affected areas.

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