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Changing Carbon Partitioning in Some *Eucalyptus* Species at the Seedling Stage Under Salinity

[1]*Loutfy Ibrahim El-Juhany,* [2]*Ibrahim Mohamed Aref and* [2]*Abdullah Ismaiel M. Ahmed*

[1]Prince Sultan Institute for Environmental, Water and Desert Research, Saudi Arabia
[2]Department of Plant Production, Faculty of Food Sciences and
Agriculture King Saud University, P.O. Box: 2454 Riyadh 11451, Saudi Arabia

Abstract: Soil salinity is a common problem in arid and semi-arid regions. Plants cope with soil salinity and salinity in irrigation water in several different ways. A pot experiment was carried out in the greenhouse to study the mechanism by which *Eucalyptus* species cope with salinity at the seedling stage. Partitioning of carbon into structural (SCC) and non-structural compounds (NSCC) was determined using a modified ethanol and water extraction process with oven-dried leaves, stems and roots of the seedlings that were harvested after four months of treatment. The results showed that increasing salinity level in the irrigation water significantly increased the NSCC in leaves and stems of the seedlings. These increases in NSCC were concomitant with decreases in SCC. The ratio of NSCC/SCC increased in leaves and stems of *Eucalyptus* seedlings with increasing salinity concentration in irrigation water. On the other hand, this ratio was greater in the roots of *E. camaldulensis* seedlings than in those of either *E. microtheca* or *E. intertexta* seedlings. The results indicated that *Eucalyptus* seedlings adapt to changes in salinity by adjusting their carbon partitioning. This study, therefore, provides further understanding of how seedlings deal with salt stress through physiological responses.

Key words: *Eucalyptus* · Structural · Non-structural compounds · Ethanol · Water extraction · Saline water · Salt tolerance · Seedling

INTRODUCTION

Soil salinity is a common problem in arid and semi-arid regions, where poor irrigation water often contains a considerable amount of salts. Indeed, 25% of the irrigated land is affected by salts in arid and semi-arid areas, making the effects of salinity more conspicuous [1]. Some climatic parameters, such as temperature, precipitation and wind, can worsen the salinity problem by increasing evaporation rates that in return increase the soil's salt concentration. Soil salinization is one of the major factors of soil degradation, reaching an impressive 19.5% of the irrigated and 2.1% of the dry agricultural land worldwide [2].

Salinity is considered to be one of the most limiting factors for plant growth. Many studies have reported reductions of seed germination and seedling growth with increasing salinity [3-7]. Inhibition of plant growth due to salinity results from osmotic and ionic effects [8]. Studies on salt tolerance during seedling stage could probably provide insights for enhancing tolerance throughout the plant life cycle [9].

Because increased salt concentration lowers the osmotic potential of the soil, root zone salinity is thought to affect plant growth by lowering cell turgor. In fact, sudden decreases in turgor pressure have been shown to inhibit growth [10].

The accumulation of compatible solutes to maintain turgor is one of the different morphological and physiological processes plants use to increase their salt tolerance in salt-affected soils. Upon exposure to osmotic stress as a result of drought, high salinity and low temperature, these metabolically benign solutes, collectively known as compatible solutes or osmolytes, whose primary function is turgor maintenance, accumulate in plants [11]. This increase in soluble content of the

Corresponding Author: Prof. Loutfy I. El-Juhany, Prince Sultan Institute for Environmental, Water and Desert Research, King Saud University, P.O. Box: 2454 Riyadh 11451, Saudi Arabia.

cytoplasm is regarded as a mechanism to balance the osmotic potential between the cytoplasm and the vacuole of cells under salt stress conditions [12].

Woody plants adapt to salinity by tolerating and/or avoiding salt. In some plants, osmotic adjustment results from synthesis of compatible organic solutes in the cytoplasm, including proline, glycine, betaine and other amino acids, as well as sugars [13]. Studying carbon partitioning in terms of dry matter partitioning into structural and non-structural compounds may provide a new approach that considers the physiological activity of each plant organ as well as its morphological characteristics [14]. By convention, both starch and non-structural carbohydrates are considered non-structural carbon compounds.

The objective of the present study was to evaluate the role of carbon partitioning into structural and non-structural compounds in the tolerance of *E. microtheca*, *E. camaldulensis* and *E. intertexta* under salt stress conditions at the seedling stage.

MATERIALS AND METHODS

Plant Material and Treatments: Seedlings of *Eucalyptus camaldulensis* Dehn., *Eucalyptus intertexta* R. T. Baker and *Eucalyptus microtheca F. Muell were* grown in a pot experiment conducted in the greenhouse at the Research and Experiments Station of the Faculty of Food Sciences and Agriculture, King Saud University, Riyadh City, Saudi Arabia. One-month-old seedlings were irrigated with water with varying levels of salinity for four months. The seedlings were treated with varying salinity levels using sodium chloride solutions with EC = 1, 4, 8 and 16 dS/m, denoted as control, low, medium and high salinity, respectively [7]. At the end of five months, the leaves, stems and roots of the plants were dried in an oven for analysis.

Quantification of Structural and Non-Structural Carbon Compounds: The measurement of structural and non-structural carbon compounds in the leaves, stems and roots was carried out using an extraction procedure previously described by Browning [15] and modified according to Ibrahim [14]. Non-structural carbon compounds included both starch and non-structural carbohydrates.

Preparation of Samples: Oven-dried samples of leaves, stems and roots of the trees grown in different salinity conditions were ground in an electric grinder. The ground material was then sieved through a set of laboratory sieves. The particles that passed the 40-mesh sieve and remained on the 60-mesh sieve were dried in an oven at 60-70°C until weight constancy was achieved. Three grams of the dried ground material was transferred into a white winceyette sack that was 2 × 5 cm in size. Empty sacks were tested for leachability by being subjected to the extraction procedure.

Extraction Procedure: A sample of 2-5 g with 40-60-mesh particle size was weighed in a glass thimble and placed into a 100 cm^3 Soxhlet extractor. Then, 125 mL of 95% ethanol was placed in a 250 mL round bottom distillation flask. Extraction was carried out for a period of 4-8 h. After extraction, the thimble was removed from the extractor and placed upright on an absorbent tissue for approximately three days to air dry the sample at room temperature. After the drying period, the thimble and its contents were weighed and the ethanol soluble extractives were calculated.

The ethanol-extracted contents of the thimble were transferred to a 250 mL Pyrex glass beaker. After the addition of 100 mL of distilled water, the beaker was placed in a boiling water bath for 3 h. After the hot water extraction, the contents of the beaker were filtered through a medium-fast filter paper (Whatman No. 1) and washed with small amounts of hot water. The filter paper and the precipitate were then placed in an aluminum can and dried at 105±1°C to constant weight.

Calculations: The weight of structural carbon compounds (SCC) was obtained by subtracting the can weight from the oven dry weight of the can and its contents. The weight of the non-structural carbon compounds (NSCC) is equal to the difference between the dry weight and SCC weight. SCC can also be obtained from the dry weight minus the sum of both ethanol and water extractives, which represent the NSCC weight.

Statistical Design and Analysis: A complete randomized design (CRD) with a factorial arrangement was used as previously described [16], including four salinity levels and three *Eucalyptus* species (i.e. 12 treatment combinations). The experiment was carried out with seven replicates.

Data were analyzed with analysis of variance (ANOVA) using SAS software [17]. The differences between the means were determined using Fisher's least significant difference (LSD) test at $p < 0.05$. Data were log or arcsine transformed when necessary.

RESULTS

In order to determine how three species of *Eucalyptus* trees cope with salinity levels of irrigation water, a pot experiment was performed in the greenhouse. *Eucalyptus camaldulensis* Dehn., *Eucalyptus intertexta* R. T. Baker and *Eucalyptus microtheca* F. Muell seedlings were treated with water with four levels of salinity from one month to five months of age. The leaves, stems and roots were then analyzed for non-structural carbon compounds (NSCC) and structural carbon compounds (SCC) components. ANOVA analysis revealed a significant increase in the percentage of NSCC of the leaves with increasing levels of salinity in the irrigation water across all *Eucalyptus* species ($p = 0.0024$), ranging from 34% in the control to 44% in the high-salinity treatment (Table 1). On the other hand, SCC of the leaves of the seedlings decreased with increasing salinity levels across all *Eucalyptus* species ($p < 0.0001$), ranging from 66% in the control to 55% in the high-salinity treatment (Table 2).

The NSCC percentage of the stem increased with increasing salinity levels in irrigation water across all *Eucalyptus* species ($p < 0.0024$); control treatment resulted in 23% NSCC in the stem, while the high-salinity treatment led to 36.74% (Table 1). Significant differences were also found in the percentage of SCC in the stem between the various treatments ($p = 0.0368$); 76.58% SCC level in the control group decreased to 58.23% with the high-salinity treatment (Table 2).

Increasing salinity level in the irrigation water had no significant effect on carbon partitioning in the roots of the *Eucalyptus* seedlings. However, the NSCC and SCC levels varied significantly between species ($p = 0.0003$). The roots of *E. intertexta* and *E. camaldulensis* had similar root NSCC levels, which were significantly lower than those of *E. microtheca*. On the other hand, the root SCC levels of both *E. intertexta* and *E. camaldulensis* were similar and significantly greater than those of *E. microtheca* (Table 2).

There were no significant differences between *Eucalyptus* species (across treatments) in their content of either structural or non-structural carbon compounds.

However, *E. intertexta* stems had a significantly higher NSCC percentage, which was double that of *E. microtheca* stems and more than double that of *E. camaldulensis* stems ($p < 0.01$, Table 1). On the other hand, *E. microtheca* had a significantly higher stem SCC percentage than *E. camaldulensis* and *E. intertexta*, in decreasing order ($p < 0.01$, Table 2).

Most importantly, the ratio of NSCC/SCC increased in *Eucalyptus* leaves with increasing salinity levels of the irrigation water ($p = 0.0103$). It increased from 0.52 in the control to 0.69 in low to 0.78 in medium to 0.82 in high salt concentration treatment. A similar trend in the stems was observed (Table 3). However, this ratio varied significantly among the roots of *Eucalyptus* species ($p < 0.0008$). Across treatments, the NSCC/SCC ratio was greater in the roots of *E. camaldulensis* seedlings than the other two species (Table 3).

Table 1: Distribution of non-structural carbon compounds (NSCC) (per cent) to leaves, stem and roots of *E. microtheca*, *E. intertexta and E. camaldulensis* under saline irrigation water treatments

		Species			
NSCC (%)	Treatments (dS m^{-1})	*E. microtheca*	*E. intertexta*	*E. camaldulensis*	Treatment means
Leaves	1	29.50	38.18	34.21	*33.96[b]
	4	39.53	44.93	36.64	40.37[a]
	8	47.51	42.85	40.76	43.71[a]
	16	41.12	45.73	46.15	44.33[a]
	Species means	39.42[a]	42.92[a]	39.44[a]	
Stem	1	20.76	27.54	21.67	23.32[c]
	4	18.66	32.78	31.03	27.49[bc]
	8	21.08	55.64	35.07	37.26[a]
	16	19.93	44.51	45.77	36.74[ab]
	Species means	20.11[b]	40.12[a]	33.39[ab]	
Roots	1	47.94	29.96	24.78	34.23[a]
	4	50.08	19.02	21.08	30.06[a]
	8	44.49	26.57	27.89	32.98[a]
	16	29.12	22.64	38.22	29.99[a]
	Species means	42.91[a]	24.55[b]	27.99[b]	

*Means followed by the same superscript letters within each three sequential boxes (horizontal for species and vertical for treatments) are not statistically different according to L.S.D Test

Table 2: Distribution of structural carbon compounds (SCC) (per cent) to leaves, stem and roots of *E. microtheca*, *E. intertexta and E. camaldulensis* under saline irrigation water treatments

		Species			
SCC (%)	Treatments (dS m^{-1})	*E. microtheca*	*E. intertexta*	*E. camaldulensis*	Treatment means
Leaves	1	*70.50	61.81	65.78	*66.03[a]
	4	60.46	55.06	63.36	59.63[b]
	8	52.49	57.14	59.24	56.29[b]
	16	58.87	54.26	53.86	55.66[b]
Species means		60.58[a]	57.07[a]	60.56[a]	
Stem	1	79.24	72.46	78.03	76.58[a]
	4	81.33	67.21	68.97	72.50[ab]
	8	68.92	44.35	64.93	59.40[c]
	16	65.06	55.49	54.23	58.26[b]
Species means		73.64[a]	59.88[b]	66.54[ab]	
Roots	1	52.06	70.04	75.22	65.77[a]
	4	49.92	80.98	78.92	69.94[a]
	8	55.51	73.43	72.10	67.01[a]
	16	70.88	77.36	61.78	70.01[a]
Species means		57.09[b]	75.45[a]	72.01[a]	

*Means followed by the same superscript letters within each three sequential boxes (horizontal for species and vertical for treatments) are not statistically different according to L.S.D Test

Table 3: Non-structural/ structural carbon compounds ratio (NSCC/SCC) in the leaves, stem and roots of *E. microtheca*, *E. intertexta and E. camaldulensis* under saline irrigation water treatments

		Species			
NSCC ratio	Treatments (ds m^{-1})	*E. microtheca*	*E. intertexta*	*E. camaldulensis*	Treatment means
Leaves	1	0.42	0.62	0.52	[a]0.52[b]
	4	0.65	0.84	0.57	0.69[ab]
	8	0.92	0.75	0.68	0.78[a]
	16	0.71	0.88	0.87	0.82[a]
	Species means	0.68[a]	0.77[a]	0.66[a]	
Stem	1	0.26	0.49	0.28	0.34[b]
	4	0.23	0.53	0.47	0.41[ab]
	8	0.48	0.61	0.58	0.56[a]
	16	0.26	0.89	0.84	0.66[a]
	Species means	0.31[a]	0.63[a]	0.54[a]	
Roots	1	1.02	0.49	0.33	0.61[a]
	4	1.35	0.24	0.28	0.62[a]
	8	1.03	0.36	0.39	0.59[a]
	16	0.41	0.31	0.62	0.45[a]
	Species means	0.95[a]	0.35[b]	0.41[b]	

*Means followed by the same superscript letters within each three sequential boxes (horizontal for species and vertical for treatments) are not statistically different according to L.S.D Test

DISCUSSION

The growth of most of plants is inhibited under saline conditions, which can be attributed to several factors. The ability of a plant to cope with salinity stress is an important determinant of its growth and productivity and therefore it is important to understand the mechanisms by which the plant can tolerate salinity.

The results of the present study showed that *Eucalyptus* seedlings employ carbon partitioning to tolerate increasing levels of salinity in irrigation water. The role of carbon partitioning as a mechanism by which plants can cope with salinity has been previously noted. Poljakoff-Mayber and Lerner [18] asserted that the different growth responses to salinity can result from changes in the allocation and partitioning of photoassimilates. Photoassimilates produced under salt stress are used to support crucial, mutually exclusive processes, such as growth, maintenance and osmotic adjustment [19].

Our results revealed significant increases in NSCC in the leaves and stems of *Eucalyptus* seedlings with increasing salinity at the expense of SCC. Similar results were obtained by Balibrea *et al*. [19] and Nemati *et al*. [20]. In addition, De Lacerda *et al*. [21] found increased carbohydrate content in plant parts with increasing salt stress, which they attributed to salt tolerance. However, it seems that such an increase in NSCC is not a universal plant mechanism for coping with increased salinity, as the total soluble carbohydrate concentrations in the leaves of *Prosopis alba* Griseb. seedlings were unaffected by salinity [22]. Nevertheless, an increase in carbohydrate and organic solute content would in general reduce the osmotic potential and allow plants to maintain turgor pressure [23, 13].

Many studies have reported the accumulation of sugars in different parts of plants in response to a variety of environmental stresses, such as salt and water stress [24-32]. Adaptation to these stresses has been attributed to the stress-induced increase in carbohydrate levels, as salinity and water stress induce soluble sugar accumulation [33, 34, 35]. In addition, the accumulation of soluble carbohydrates under salt stress was reported for woody species at the seedling stage [36-39]. Moreover, the total soluble carbohydrate concentration in *Prosopis alba* seedling roots increased sharply in relation to the stress intensity, as the seedlings accumulated more total soluble carbohydrates in their roots than in their leaves [22].

In this study, we investigated the role of carbon partitioning into structural and non-structural compounds within the plant organs as a potential salt tolerance mechanism. The NSCC/SCC ratio was measured in each organ to evaluate the change in this ratio in response to increased salinity in irrigation water. An increase in the NSCC/SCC ratio in an organ indicates an increase in NSCC at the expense of SCC. We found that the NSCC/SCC ratio increased significantly in the leaves and stems of *Eucalyptus* seedlings with increasing salinity. This is in agreement with the results obtained by Ghosh *et al*. [40] and Amirjani [41]. On the other hand, *E. camaldulensis* seedling roots had significantly higher NSCC/SCC ratios than those of *E. microtheca* and *E. intertexta*. This concurs with the results obtained by Meloni *et al*. [22] where they found root total soluble carbohydrate concentration in *Prosopis alba* seedlings increased sharply in relation to the stress intensity, as the seedlings accumulated more total soluble carbohydrates in their roots than in their leaves.

Importantly, the three *Eucalyptus* species in the present study tolerated salinity stress in different manners. They adapted to salinity stress by accumulating ions and other organic compounds and changing their carbon partitioning. In addition, El-Juhany *et al*. [7] found that these species cope with increasing salinity by modifying their leaf area and number. Our results suggest that the *Eucalptus* species tested can moderately and highly tolerate changes in salinity. Previous studies have reported different results for the degree to which these three *Eucalyptus* species could tolerate salinity. Benyon *et al*. [42] reported that *E. camaldulensis* demonstrated moderate salt tolerance and Hamilton [43] considered *E. intertexta* salt tolerant, because it is known to grow near salt pans. On the other hand, the Department of Natural Resources of New South Wales Government [44] placed both *E. camaldulensis* and *E. microtheca* within a class of plants that can tolerate high saline conditions (8 dS/m). In contrast, the Ecocorp Data Sheets of FAO [45] reported that *E. intertexta* can only tolerate low to medium salinity.

Our results indicate that changing carbon partitioning is one mechanism by which *Eucalyptus* species adapt to salinity stress at the seedling stage, though at different degrees.

The accumulation of organic compounds, such as sugars, amino acids and quaternary ammonium compounds plays an important role in osmoregulation in *Eucalyptus* plants under high salinity conditions. Our results are supported by the fact that glucose and sucrose are the major organic solutes in salt-tolerant *E. camaldulensis* [46] and *E. microtheca* exhibit an increase in sugar concentration in response to salt stress [47, 36]. Moreover, when the accumulation of soluble carbohydrates in different *Eucalyptus* species under saline stress was compared, the sugar content was higher in *E. microtheca* than in either *E. alba* (Reinw. ex Blume) or *E. camaldulensis* [36], which is in agreement with our findings.

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