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Full Length Research Paper

Ecophysiological responses of *Melaleuca* species to dual stresses of water logging and salinity

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The combined effects of salinity and water logging on growth and ecophysiological characteristics of three *Melaleuca* species were investigated in a glasshouse study. Salinity treatments were imposed from day 28 at 0.3, 0.8, 2 and 5 g NaCl kg^{-1} soil. Shoot Na^+ concentration and Na^+/K^+ ratio for *M. thyiodes* at all salt level and of *M. nesophila* at 5.0 g NaCl kg^{-1} were higher under waterlogged as compared with non-waterlogged conditions. The concentration of Cl^- was double in *M. thyiodes* and *M. nesophila* shoots after 2 weeks of water logging at 5 g NaCl kg^{-1} soil, but not in *M. halmaturorum*. Final dry weights of shoots and roots of the three *Melaleuca* species decreased with increased salinity levels. Shoot dry weight of plants grown at 5.0 g NaCl kg^{-1} soil decreased to 30, 50 and 11% of those achieved at 0.3 g NaCl kg^{-1} soil for *M. halmaturorum, M. thyoides, and M. nesophila*, respectively. The results indicated different salinity resistance within *Melaleuca* species.

Key words: Sodium, potassium, chloride, Na^+/K^+ ratio, water logging.

INTRODUCTION

Soil salinity is an important constraint on plant growth. Negative effect of salinity on plant growth is due to the direct toxic effects of ions and osmotic stress that may hamper a range of physiological and biochemical processes in plants (Al-Karaki, 2000; Munns, 2002; Barrett-Lennard, 2003; Ashraf and Harris, 2004; Munns, et al., 2006). Salinity can directly affect plant uptake of nutrients and may cause nutrient imbalances, due to the competion of Na^+ and Cl^- with other nutrients such as K^+, Ca^{2+}, and NO_3^- (Hu and Schmidhalter, 2005). Both Na^+ and K^+ ions have similar chemical properties and such similarity causes competition in uptake of these ions by plants (Amtmann et al., 2004). This was also stated by Schachtman and Liu (1999) that in saline soils the excess Na^+ will reduce K^+ uptake due to competitive effects. Therefore, high ratios of $K^+ : Na^+$ will also improve the resistance of the plant to salinity (Asch et al., 2000), and has been used to evaluate the selectivity of ion uptake under saline conditions and thus the ability of plants to tolerate salt stress.

Large proportion of saline land is also subject to water logging (saturation of the soil) because of the presence of the shallow water-table or decreased infiltration of surface water (Barret-Lennard, 2003, Teakle et al., 2006). Detrimental effects of water logging on plant growth are predominantly due to the low oxygen concentration around roots in water-saturated soils. This is caused by either the continuous oxygen consumption by roots and micro-organisms present in the soil or a severely hampered rate of oxygen diffusion from the atmosphere to the roots (Vartapetian and Jackson, 1997; Barret-Lennard, 2003; Teakle et al., 2006).

Different plant families, genera, species and provenances show vary in their salinity and water logging tolerance. However, their tolerance is inhibited by exposure either to salinity or water logging especially when both stresses happen simultaneously (Van der Moezel et al., 1988). Unfortunately, in many field situations, water

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logging is usually associated with salinity. Therefore, it is necessary to study the adaptation of plants to combined stresses of salinity and water logging. Barrett-Lennard (2003) stated that three possible strategies of plant adaptations to the water logging/salinity interaction are by avoiding hypoxia through the formation of aerenchym, reducing stomatal conductance, or by protecting metabolism through the implementaton of salt removal strategies.

Melaleuca species are generally more salt-tolerant than the most salt-tolerant *Eucalyptus* and *Casuarina* species (Van der Moezel et al., 1988). Many *Melaleuca* species grow in saturated soils near water bodies, often in swamps and estuaries or in seasonal streams in arid areas that are occasionally subjected to inundation (Holliday, 1989; Naidu et al., 2000).

The objectives of this study were: 1) to evaluate ecophysiological responses of three *Melaleuca* species to salinity, water logging and the combined stresses; and 2) to examine relationships among salt levels in the soil, ion accumulation in shoots and roots, and biomass production.

MATERIALS AND METHODS

Soil and plant materials

Virgin brown sandy soil (Uc4.22, Northcote, 1979) was collected from a bushland site in Western Australia (31°56' S, 115°20' E). The soil was air-dried, sieved through a 2-mm sieve and thoroughly mixed. The soil analyses showed that it contents 1 mg NO_3^--N, 57 mg K ($NaHCO_3$-extractable) and 10.3 g organic carbon per kg soil and had a pH buffering capacity of 0.56 cmol H^+ kg^{-1} pH^{-1} (Tang, 1998). The soil was then placed in polyvinyl chloride pots.

The pots (410 mm deep, 90 mm diameter) had a 20 mm layer of gravel at the bottom. An 8 mm diameter hole was drilled through the bottom of the pot and a piece of transparent hose was glued into the hole. Each pot contained 3 kg of soil.

Basal nutrients were added in solution to each pot at the following rates (mg per kg soil): KH_2PO_4 (91), K_2SO_4 (174), $CaCO_3$ (300), $MgSO_4.7H_2O$ (49), $CuSO_4.5H_2O$ (2.5), $MnSO_4.H_2O$ (3.4), H_3BO_3 (0.6), $Na_2MoO_4.2H_2O$ (0.2), $ZnSO_4.7H_2O$ (2.9), and NH_4NO_3 (40). After air-drying, nutrients were thoroughly mixed with the soil by shaking in a plastic jar. NH_4NO_3 was added as basal fertilisation initially as well as every 2 weeks starting in week 5 after transplanting. Soil was watered to field capacity [11% (w/w)] with deionised water and incubated for 2 days before planting.

Plant materials used in this experiment were three *Melaleuca* species that is, (1) *Melaleuca halmaturorum*, a deep-rooted species commonly found around salt lakes and brackish swamps on soils with high clay content and with NaCl as dominant salt; it is expected to have high tolerance to water logging and salinity; (2) *Melaleuca thyoides*, a shallow-rooted species occurring at the interface between sand dunes and salt flats; it is expected to have high tolerance to salinity and moderate tolerance to water logging; and (3) *Melaleuca nesophila*, commonly found on sandy soils in coastal areas; it is expected to tolerate high NaCl concentration, but not water logging (Holliday, 1989; Wrigley and Fagg, 1993).

Experimental design and treatments

For each plant species under study, treatments were arranged in a randomised block design, involving four salt and two water logging levels as treatments. Uniform seedlings were transplanted into pots. In order to reduce the variation between replicate pots, two seedlings were grown in each pot. Soil surface was covered with alkathene beads to minimise water loss by evaporation. Pots were weighed and soil was watered to field capacity with deionised water every second day. Plants were grown in a glasshouse with temperature maintained at around 23°C.

Four salt levels were used for the study, *viz*. 0.3, 0.8, 2.0 and 5.0 g NaCl kg^{-1} soil. Salt treatments were introduced gradually by adding the NaCl solution every second day starting on day 28 after transplanting. After the salt treatments were fully established at the levels planned (6th week), pots were watered to field capacity with deionised water every second day. Water logging treatment was imposed on day 91 by connecting a hose at the bottom of pot to a container filled with deionised water; the water level was maintained at 2 cm above the soil surface.

Plant growth and ion content measurements

Shoot height was measured weekly starting from the first week after transplanting. Plants were harvested 105 days (*M. thyoides*) and 119 days (*M. halmaturorum* and *M. nesophila*) after transplanting. Roots were separated from the soil by sieving through a 4-mm sieve. Roots were then rinsed with deionised water and dried at 70°C for 48 h. Shoot fresh weight was determined after drying at 70°C for 48 h.

Concentration of Na^+ and K^+ in dried shoots and roots were determined using atomic absorption spectrometry (AAS) after digestion in hot concentrated nitric acid as outlined by Reuter et al. (1986). Sub-samples of 0.5 g each were placed in 50 mL flasks and 10 mL of concentrated nitric acid added. The mixture was first heated on fry pans to 90°C for 30 min, and then temperature increased to 140°C to remove excess nitric acid. De-ionised water was added to make up to the 23 mL volume of the primary extract. An aliquot of this primary extract was diluted for determination of sodium (Na^+), potassium (K^+) and calcium (Ca^{2+}) concentration using the AAS (Perkin Elmer AAnalyst 300, USA). To minimize ion interferences, a solution of lanthanum oxide (La_2O_3) was added to each diluted extract to give a lanthanum content of 0.1% (w/w). The Na^+/K^+ and Na^+/Ca^{2+} ratios were calculated for shoots and roots under different salinity levels. Chloride was extracted in hot water by shaking for 48 h followed by measurement using a chloride-sensitive electrode.

Statistical analysis

A two-way analysis of variance (ANOVA) was conducted using GENSTAT VI (Genstat VI Committee, 2002) statistical package to compare the main effects and interactive effects combined salinity and water logging stress on shoot biomass, root biomass, plant height and Na^+/K^+ ratios of plant tissues. Differences among the treatments were separated by the Fisher's protected least significant difference (LSD) test at a significance level of 5%.

RESULTS

Growth response

By the time of harvest, dry weights of shoots and roots of the three *Melaleuca* species decreased with increasing salinity levels (Table 1). For example, shoot dry weight of plants grown at 5 g NaCl kg^{-1} soil decreased to 30, 50,

Table 1. Dry weight of shoots and roots of three *Melaleuca* species grown for 105 (*M. thyoides*) or 119 days (*M. halmaturorum* and *M. nesophila*) at various levels of salinity which were commenced on day 28.

Treatment salinity	Shoot dry weight (g/pot)			Shoot dry weight (g/pot)		
(g NaCl kg^{-1} soil)	***M. halmaturorum***	***M. thyoides***	***M. nesophila***	***M. halmaturorum***	***M. thyoides***	***M. nesophila***
0.3	12.34 a	5.95 a	24.0 a	2.08 a	1.02 a	5.04 a
0.8	12.42 a	6.17 a	21.5 a	1.99 a	0.96 a	3.21 b
2	8.53 b	5.12 a	12.3 b	1.56 b	0.91 a	1.27 c
5	3.68 c	3.00 b	2.6 c	1.02 c	0.61 b	0.64 c

Values in a column followed by different letter showed significantly different at $P = 0.05$.

and 11% of the 0.3 g NaCl kg^{-1} treatment for *M. halmaturorum, M. thyoides, and M. nesophila*, respectively. Comparable values were obtained for the root growth decrease as a consequence of increasing salinity (Tabel 1). *Melaleuca* species were not affected by water logging treatment, except that *M. thyoides* died after 1 week of being subjected to water logging at high salt level (5 g NaCl kg^{-1} soil).

Tissue mineral concentration

The three *Melaleuca* species differed in their response to water logging and salinity. Significant interaction between water logging and salinity was observed for sodium (Na^+) and chloride (Cl^-) tissue concentration in *M. halmaturorum, M. thyoides*, and *M. nesophila*. Generally, shoots of *Melaleuca* species accumulated more Na^+ and Cl^- when grown in water logging soil compared with non-waterlogged one (Table 2)

Na^+ concentration in shoots and roots of *M. halmaturorum* and *M. thyoides* increased significantly with increasing salinity level (Table 2). Na^+ concentration in shoots grown at 5 g NaCl kg^{-1} soil increased approximately 5, 7 and 4 times fold as compared with values obtained at 3 g NaCl kg^{-1} soil for *M. halmaturorum, M. thyoides*, and *M. nesophila*, respectively. However, for *M. nesophila* there was no difference in root concentration of Na^+ regardless the NaCl treatment, with shoot Na^+ concentration increasing only at 5 g NaCl kg^{-1} soil compared with those for the 0.3 g NaCl kg^{-1} salt treatment (Table 2). In general, Na^+ accumulation was greater in the root than the shoot tissue of *M. halmaturorum* and *M. thyoides*.. In contrast, *M. nesophila* shoots had higher Na^+ concentration compared with the root tissue. The shoots of *M. halmaturorum*, *M. thyoides* and *M. nesophila* had greater Na^+ concentration in the water logging compared to the non-waterlogged treatment, especially at 2 and 5 g NaCl kg^{-1} soil tratments.

Interactive effects of salinity and water logging were evident for the Cl^{-1} concentrations in shoots and roots of *M. halmaturorum*, *M. thyoides,* and *M. nesophila*. The Cl^{-1} concentrations in roots and shoots of *Melaleuca* species significantly increased with increasing salinity levels, both for water logging or non-waterlogged treatment (Table 2). Higher Cl^{-1} concentration was observed in shoot of three *Melaleuca* species compared with roots.

The shoot K^+ concentration was affected by the interaction between salinity and water logging (Table 2). For example, shoot K^+ in *M. halmaturorum* under water logging did not differ among NaCl treatments, whereas under the non-waterlogged treatments shoot K^+ concentration in the 2 and 5 g NaCl treatments were significantly lower than those in the 0.3 and 0.8 g NaCl treatments. For *M. thyoides*, the shoot K^+ concentration under water logging treatment were similar for the 0.3, 0.8, 2 and 5 g NaCl treatments Under the non-waterlogged condition the shoot K^+ concentration showed a gradual decrease with increased NaCl level. The trend in shoot K^+ concentration in *M. nesophila* was reversed compared with the other two *Melaleuca* species. Under both waterlogged and non-waterlogged conditions the shoot K^+ concentration in the 5 g NaCl treatment was much greater than those in other NaCl treatments. The concentration of K^+ in roots differed among salinity treatments only in *M. thyoides*, with the 5 g NaCl treatment having the lowest K^+ concentration compared with other treatment.

The significant interaction between water logging and salinity with respect to the Na^+/K^+ ratio in shoots were observed in shoot of *M. halmaturorum*, *M. thyoides* and *M. nesophila* The shoot Na^+/K^+ ratio in *M. halmaturorum*, *M. thyoides* and *M. nesophila* at all NaCl levels ware higher when plants were grown in the waterlogged

Table 2. Sodium (Na^+) Chloride (Cl^-), and potassium (K^+) concentration in shoots and roots of three *Melaleuca* species grown under different salinity (NaCl) levels at field capacity or with water logging (WL).

Water logging	Salinity (g NaCl/kg soil)	Shoot Na^+ ($mg.g^{-1}$ dw)	Shoot Cl^- ($mg.g^{-1}$ dw)	Shoot K^+ ($mg.g^{-1}$ dw)	Root Na^+ ($mg.g^{-1}$ dw)	Root Cl^- ($mg.g^{-1}$ dw)	Root K^+ ($mg.g^{-1}$ dw)
				M. halmaturorum			
Field capacity	0.3	2.99 c	12.18 bc	8.46 a	4.94 c	11.10 b	7.93 a
	0.8	4.40 c	14.81 b	8.11 a	9.92 b	19.00 ab	7.12 a
	2	7.82 bc	18.75 ab	6.03 b	14.73 a	21.90 ab	6.36 a
	5	10.59 b	22.84 a	5.81 b	17.99 a	25.60 a	6.45 a
Water logging	0.3	2.80 c	7.12 c	6.54 b	8.11 bc	9.10 b	8.04 a
	0.8	4.61 c	9.53 c	6.21 b	8.83 bc	11.50 b	8.02 a
	2	9.53 bc	13.38 bc	6.32 b	13.30 ab	15.90 b	6.61 a
	5	18.85 a	20.07 a	6.40 b	17.71 a	17.90 ab	6.12 a
				M. thyoides			
Field capacity	0.3	1.49 d	6.65 c	9.66 a	5.94 a	5.04 b	8.19 a
	0.8	2.66 d	8.39 c	8.46 b	9.75 a	7.77 b	7.65 a
	2	6.63 c	11.11 bc	7.21 c	11.49 a	9.78 ab	7.12 a
	5	10.05 bc	14.31 b	6.41 c	15.13 a	11.34 ab	4.23 b
Water logging	0.3	3.63 cd	6.13 c	7.98 bc	8.22 a	5.65 b	9.09 a
	0.8	5.54 cd	8.28 c	8.38 bc	11.34 a	8.00 ab	7.68 a
	2	11.77 b	13.61 b	6.19 c	14.25 a	11.83 a	3.53 bc
	5	25.55 a	26.39 a	7.25 c	14.16 a	11.40 ab	1.80 c
				M. nesophila			
Field capacity	0.3	6.8 c	12.82 d	7.23 c	6.46 a	4.01 b	4.18 ab
	0.8	13.5 bc	17.62 cd	7.63 c	6.36 a	6.08 b	4.18 ab
	2	16.4 bc	22.28 bc	6.50 c	11.29 a	7.42 b	3.74 ab
	5	17.3 bc	27.01 b	11.96 a	12.47 a	14.66 a	3.02 ab
Water logging	0.3	12.4 bc	16.37 cd	6.57 c	8.19 a	7.03 b	4.62 ab
	0.8	15.4 bc	20.58 c	6.05 c	6.15 a	6.93 b	4.35 ab
	2	21.2 b	24.50 bc	6.13 c	9.67 a	9.39 ab	4.69 a
	5	54.1 a	45.19 a	9.88 b	7.25 a	11.95 ab	2.34 b

Within the eight combinations of salt x water logging treatments for each species, means followed by different letter indicated significant difference at 0.05 significance level.

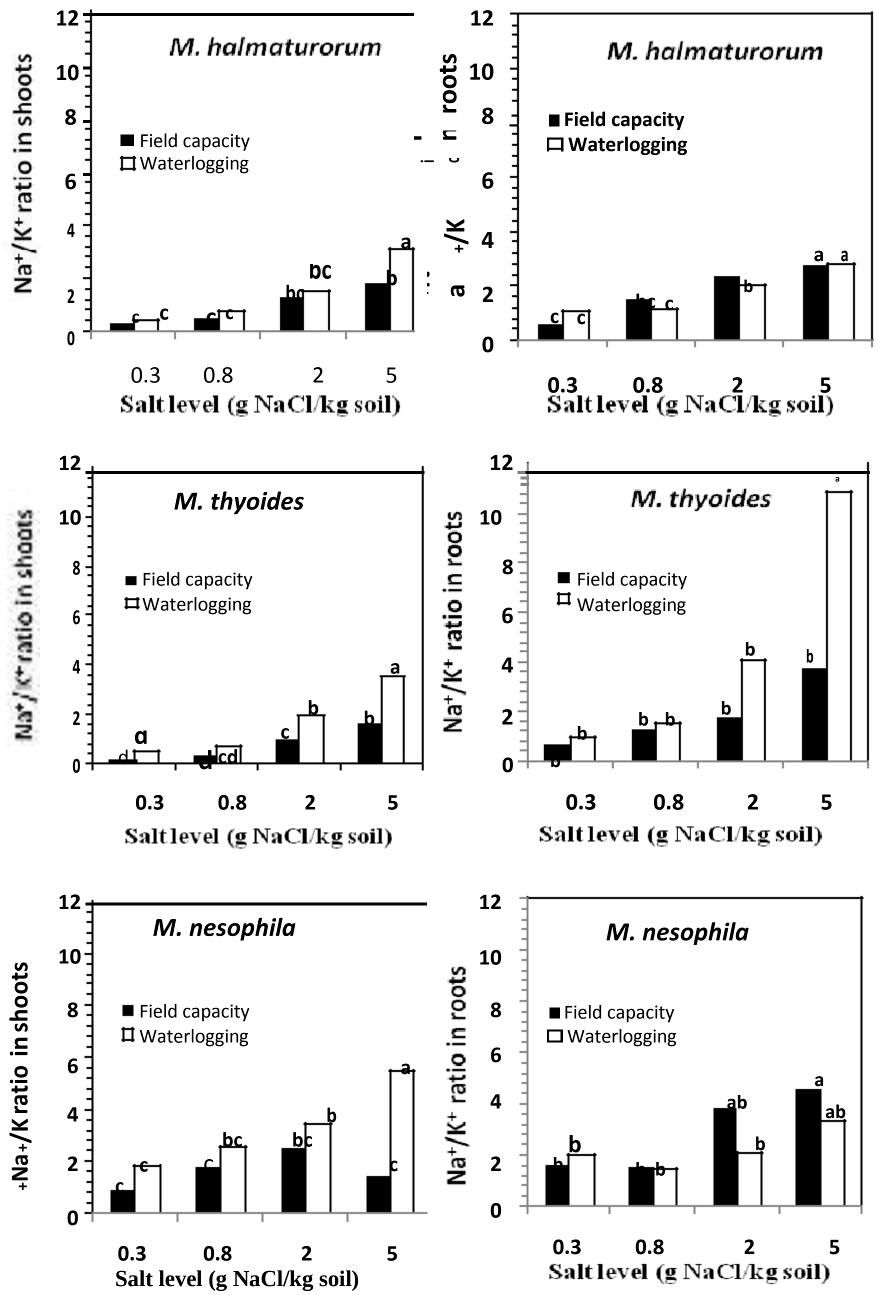

Figure 1. Interactive effects of salinity and water logging on Na^+/K^+ ratio in shoots and roots of *Melaleuca thyoides* (grown for 105 days), *Melaleuca halmaturorum* and *Melaleuca nesophila* grown for 119 days, respectively, in soil columns. Salinity treatments commenced on day 28 and water logging commenced on day 91. Values followed by the same letter are not different at *P*=0.05

compared with the control (field capacity) soil (Figure 1). This interactive effect also observed in *M. thyoides* root.

DISCUSSION

This study demonstrated that *Melaleuca* species were differentially affected by the interaction of water logging and salinity. This interaction affected the accumulation of Na^+, Cl^- and Na^+/K^+ ratio in *M. Halmaturorum*, *M. thyoides* and *M. nesophila* shoots. Similar studies on other plant species have shown that the combination of water logging and salinity is considerably more detrimental than the single stress alone, especially at increasing salinity (Meddings et al., 2001, Barrett – Lenard, 2003, Teakle et al., 2006).

The Na^+/K^+ ratio in *M. Halmaturorum, M. thyoides* and *M. nesophila* shoots increased with increasing salinity and was higher in water logging compared with non-water logging treatment. This could be due to reduced control of Na^+ intake as a result of the damage to the cell membrane structures and the energy generation mechanisms, especially under high NaCl concentration. Such disruptions might also have decreased selectivity for K^+ compared with Na^+, thus facilitating accumulation of Na^+ without equivalent uptake of K^+ required to maintain an optimum ion balance for metabolic processes. The increase in salt accumulation due to salinity and water logging was likely to be caused by increased passive uptake of Na^+ through damaged membranes (Drew and Dikumwin, 1985) and as a result of breakdown in active exclusion mechanisms (Thomson et al., 1989). However, this was not the case for *M. halmaturorum* and *M. nesophila* roots, indicating that different species of *Melaleuca* have different responses to salinity and water logging.

In this study, all the *Melaleuca* species survived, even though the stem elongation and dry matter accumulation were reduced with increasing saline levels. This result supports the previous studies reporting an adverse effect on stem elongation due to increasing NaCl concentration (Tozlu et al., 2000). *M. thyoides* appeared relatively more tolerant to salinity than *M. halmaturorum* and *M. nesophila*. The more tolerance of M thyoides might be due to genetically characteristric of the plant (Marcar et al., 1995). The plant height of *M. thyoides* was not influenced by salinity treatment, whereas *M. halmaturorum* and *M. nesophila* were significantly stunted at 5 g NaCl kg^{-1} soil. The decline in shoot biomass of *M. thyoides* occurred only at the highest salinity level, whereas root growth was not affected. However, biomass production of *M. halmaturorum* and *M. nesophila* was decreased even under low salinity (2 g NaCl kg^{-1} soil).

Na^+ and Cl^- concentration in roots and shoots of three *Melaleuca* species increased with increasing salinity, except in *M. nesophila* roots. These results suggest that there is no blocking or exclusion mechanism for accumulation of Na^+ and Cl^-. In general, the accumulation of Na^+ was greater in roots of *M. halmaturorum* and *M. thyoides* than in the shoots. Hence, these two species had the capacity to sequester salt in roots, thus minimizing the exposure of leaf cells (containing photosynthetic apparatus) to high concentration of salt (Garg and Gupta, 1997). On the contrary, this was not the case for *M. nesophila*, supporting differential salinity resistance within *Melaleuca* species.

Beside the increase in Na^+ and Cl^- tissue concentration with increasing salinity, the strongest effect of salinity in this experiment was manifested in the Na^+/K^+ ratio, which increased both in shoots and roots of *Melaleuca* species, except in *M. nesophila* roots. The high Na^+/K^+ ratio reflected ion imbalances caused by salinity. These results are consistent with those reported in *Taxodium distichum* (Allen et al., 1996), *Poncirus trifoliata* (Tozlu et al., 2000) and *Vitis vinifera* (Fisarakis et al., 2001).

Water logging causes hypoxia (low oxygen concentration) and successively lower redox potentials (Barrett-Lennard, 2003). The earliest responses to water logging are reduced water absorption and transpiration. Further responses may include decreased root and shoot growth, reduced mineral uptake, causing premature leaf senescence,abscission, and shoot dieback (Kozlowski and Pallardy, 1997). Our results demonstrated that biomass of three *Melaleuca* species was not affected by water logging for up to 4 weeks, except decreased root growth of *M. halmaturorum* and *M. thyoides* in the water logging treatment. Nevertheless, the Na^+/K^+ ratio for *Melaleuca* shoots, except for *M. halmaturorum,* was significantly higher in waterlogged compared with non-waterlogged treatments. These results indicate that water logging reduces the selectivity for K^+ relative to Na^+. Hypoxia condition also most likely caused a significant efflux of K^+ from the root, as evidenced by lower K^+ concentration in the roots, especially for *M. thyoides*. Similar findings have been reported for *Atriplex amnicola* where 80% loss of K^+ from roots occurred under hypoxia (Galloway and Davidson, 1993).

Conclusion

Melaleuca species exhibit differential salinity resistance. Water logging increased the uptake of Na^+ and Cl^- as reflected in higher shoot concentration. Thus *Melaleuca* species levels of tolerance are drastically reduced when plants are subjected to water logging. This has implications in rehabilitation of saline-waterlogged lands, using *Melaleuca* species.

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