

Does salinity reduce the tolerance of two contrasting wetland plants, the submerged monocot *Vallisneria australis* and the woody shrub *Melaleuca ericifolia*, to wetting and drying?

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Abstract. Adverse hydrological regimes and secondary salinisation are ubiquitous stressors to wetland plants in south-eastern Australia. To test whether salinity stress interacts with hydrological stress to affect the growth and survival of aquatic plants, we examined the responses of *Melaleuca ericifolia* Smith, a shrub favouring drained sites, and the obligately submerged monocot *Vallisneria australis* (S.W.L. Jacobs & D.H. Les) to different hydrological regimes under freshwater and saline conditions. Under freshwater conditions both species recovered from water regimes that were considered *prima facie* unsuitable to their growth form: *M. ericifolia* from 5 and 10 weeks of submersion, and *V. australis* from a simulated water-level drawdown and exposure to air. Salinity, however, markedly compromised the survival of *M. ericifolia* after it was re-exposed following submersion. Salinity not only reduced the recovery of *V. australis* after its release from a period of drying that desiccated aboveground organs, but prohibited recovery when the soil dried out. We conclude that *M. ericifolia* and *V. australis* can tolerate short periods of submergence and drying, respectively, under freshwater conditions, but that salinity compromises the ability of both taxa to recover from water regimes that, based on the plant's growth form, would be considered unsuitable for long-term survival and growth.

Additional keywords: drawdown and flooding patterns, wetland conservation and management.

Introduction

Allowing temporary wetlands to episodically flood and dry is increasingly recognised as vital to the maintenance and restoration of wetland functioning and diversity in Australia (Casanova and Brock 2000). Submerged, amphibious and terrestrial wetland plants are able to tolerate hydrological conditions that would otherwise be unsuitable for growth or survival by means of a wide range of morphological and physiological adaptations. For example, many wetland plant communities can persist during periods of hydrologically adverse conditions because of the existence of dormant seeds, spores or vegetative propagules in the seed bank (Brock 1998; Brock *et al.* 2003), or by virtue of their clonal life history, which allows for resource sharing across ramets (Hatton *et al.* in press). Other taxa, especially woody plants, rely on the existence of an aerial seedbank to regenerate following environmentally adverse conditions (Lamont *et al.* 1991). As a plant's ability to tolerate periods of flooding or drying is limited to the life expectancy of the adult plants, seeds or propagules (Leck and Brock 2000), prolonged periods of inundation or of desiccation may limit the suite of plant growth forms that occur in a given wetland. Several studies have shown, for example, that chronic flooding favours submerged aquatic taxa and excludes most emergent species, whereas an alternation in wetting and drying cycles allows both growth forms to co-exist, but separated in time or space (Van der Valk *et al.* 1994; Casanova and Brock 2000). Conversely, chronic desiccation has

well documented adverse impacts on the structure and function of wetlands (Boulton and Brock 1999).

To better manage and rehabilitate degraded wetlands, the interactive effects of wetting and drying need to be examined in concert with changes that take place simultaneously in other key environmental variables. In Australia, the most important of these is likely to be salinity, as secondary salinisation is not only responsible for pervasive environmental degradation, but is almost always a consequence of altered hydrological regimes (Bailey *et al.* 2006). Although the interactive effect of salinity and waterlogging on Australian plants is reasonably well researched (Froend *et al.* 1987; Van der Moezel *et al.* 1988; Craig *et al.* 1990; Akilan *et al.* 1997; Bell 1999; Salter *et al.* 2007), few studies have examined how salinity alters a plant's ability to tolerate fluctuating water regimes. A seedbank study has suggested, however, that the effect of salinity is more pronounced for plants under fluctuating water regimes than under continual flooding (Brock *et al.* 2005). We posited that high salinities would interact with hydrology to reduce the suite of plant growth forms that are able to persist under a variable water regime and tested this prediction with two taxa of aquatic plants that differed markedly in their life histories.

Melaleuca ericifolia Sm. (Myrtaceae) and *Vallisneria australis* (S.W.L. Jacobs & D.H. Les) (Hydrocharitaceae) are two plant species with contrasting growth forms that provide an ideal contrast for examining the interactive effects of dynamic

hydrological regimes and secondary salinisation on plant performance. *Melaleuca ericifolia* is a native shrub or small tree distributed extensively across freshwater and brackish-water wetlands in southern Australia (Bird 1962). It stores seeds in an aerial seedbank (Bowkett and Kirkpatrick 2003), but can also spread and reproduce clonally via root suckers (Ladiges *et al.* 1981; Walsh and Entwisle 1993). Although *M. ericifolia* is tolerant of intermittent flooding (Bird 1962) and adults can even survive long-term (>30 years) inundation, seedlings grow best under drained conditions (Raulings *et al.* 2007; Salter *et al.* 2007). Although seeds may germinate underwater (Ladiges *et al.* 1981), the growth of *M. ericifolia* seedlings is severely inhibited by inundation even at low salinities (Salter *et al.* 2007). We have previously reported dramatic reductions in growth and survival of *M. ericifolia* seedlings when subject to waterlogging or submergence at high salinities (~20% below seawater and approximating seawater) (Salter *et al.* 2007). The degree to which salinity may affect the response of this species to a dynamic water regime is not known because prior studies on this and related species (e.g. *Melaleuca halmaturorum*: Denton and Ganf 1994; *Melaleuca quinquenervia*: Lockhart *et al.* 1999) have examined only submersion and re-exposure in fresh water.

In contrast to *M. ericifolia*, the submerged monocot *V. australis* (formerly classified as *V. americana* var. *americana* Michx.) (Les *et al.* 2008) favours aquatic systems that are permanently flooded with relatively deep and stable fresh water (Blanch *et al.* 1999). Although to our knowledge, the salinity tolerance of *V. australis* has not been examined in Australia, *V. americana* var. *americana* in North America reportedly tolerates salinities up to ~23 dS m⁻¹ (15 mg L⁻¹) (Doering *et al.* 1999; Kraemer *et al.* 1999). *Vallisneria australis* is found widely in coastal and inland areas of south-east Australia (Jacobs and Frank 1997) and reproduces both sexually via seed and vegetatively via stolons (Cunningham *et al.* 1992). A drawdown of water level, where the soil remains moist, should desiccate the leaves of submerged taxa such as *V. australis*, which have poorly developed mechanisms for minimising water loss. Although populations of submerged plants can often recover from drying events when their wetland refloods (via regeneration from vegetative organs, such as rhizomes and turions, or germination of sediment-based seedbanks: Leck 1989; Casanova and Brock 2000; Brock *et al.* 2003; Combroux and Gudrun 2004), prolonged desiccation could destroy even the belowground organs and compromise the species' ability to recolonise vegetatively after re-flooding. Indeed, prolonged drawdown of water levels is one of the favoured methods to control submerged angiosperms, including *Vallisneria* spp., in the northern hemisphere (Cook 1980; Seagrave 1988).

In the present study, we expand on our earlier observations of the response of *M. ericifolia* to static water regimes at high salinity levels (Salter *et al.* 2007) by testing whether a lower salinity treatment could compromise the ability of two plant taxa with contrasting life histories to tolerate contrasting and fluctuating water regimes that would be considered nominally unsuitable for the growth of either species. To answer this question, we compared the responses of *M. ericifolia* to inundation and *V. australis* to desiccation under fresh water (0.1 dS m⁻¹) and saline (18 dS m⁻¹) conditions. Conductivity values of 0.1 dS m⁻¹ and 18 dS m⁻¹ represent salinities of

~0.06 and 11.5 g L⁻¹, respectively, if we assume a conductivity–salinity conversion factor of 0.64 (Hart *et al.* 1990). The higher salinity (equivalent to approximately one-third seawater) is not uncommon in brackish-water wetlands that support extensive stands of *M. ericifolia* (e.g. Sinclair Knight Mertz 2001; Hatton *et al.* in press). In addition to survival, several non-destructive plant performance variables were measured for each species to assess responses over time and to identify which variables were useful indicators of plant stress.

On the basis of responses reported for *Melaleuca halmaturorum* by Denton and Ganf (1994), we predicted that *M. ericifolia* seedlings would survive complete submergence in fresh water, but would experience considerable mortality after being re-exposed when water levels fell. We predicted also that increasing the period for which *M. ericifolia* was submerged would increase mortality after re-exposure; moreover, progressively fewer plants would survive submergence for longer periods under saline water, and the most severe responses would be seen when plants were re-exposed after having been inundated previously with saline water. In the case of *V. australis*, we predicted that, as the severity of drying increased, survival following re-submergence would decline and that salinity would further reduce tolerance to earlier desiccation, resulting in poor growth and reduced survival of plants following re-flooding with saline water.

Materials and methods

Experimental design

The response of *M. ericifolia* and *V. australis* to temporary submergence and drying, respectively, was examined under fresh (0.1 dS m⁻¹) and saline (18 dS m⁻¹) conditions using a split-plot design. Plants were grown in three replicate outdoor mesocosms (9000 L) at each salinity and contrasting hydrological regimes were applied for the different species to represent a range of 'optimal' and 'stressful' wetting and drying cycles. *Melaleuca ericifolia* plants were grown under four water regimes in each mesocosm: (i) constantly exposed for 21 weeks; (ii) constantly exposed for 26 weeks; (iii) exposed for 2 weeks, submerged for 5 weeks and re-exposed for 14 weeks; and (iv) exposed for 2 weeks, submerged for 10 weeks and re-exposed for 14 weeks. The two submerged treatments represent conditions that would be regarded as *prima facie* unsuitable for this species, whereas constant exposure would represent a condition to which *M. ericifolia* was well adapted. The responses of plants that were submerged for 5 weeks were compared with plants of the same age, but which had been constantly exposed for 21 weeks, and plants that were submerged for 10 weeks were compared with plants that were constantly exposed for 26 weeks. The exposed and submerged treatments represent water depths from the soil surface of -15 cm and +55 cm respectively. Plants in the submerged treatments were placed on the floor of the mesocosm and those in the exposed treatment were placed on raised platforms to elevate them in the water column. Because of variation in plant height, the tips of the shoots of the most submerged plants sat at the water surface, whereas the tips of shorter plants were up to 20 cm below the water surface. Following submergence for 5 or 10 weeks, plants were returned to the platforms and re-exposed to air for 14 weeks, then harvested at Weeks 21

and 26, respectively, together with a subset of constantly exposed plants.

Vallisneria australis plants in each mesocosm were also subjected to four water regimes: (i) constantly submerged for 20 weeks; (ii) constantly submerged for 26 weeks; (iii) submerged for 2 weeks, moderately dried until the leaves were desiccated (7 weeks) and re-submerged for 11 weeks; and (iv) submerged for 2 weeks, severely dried until the soil cracked (13 weeks) and re-submerged for 11 weeks. The two desiccation regimes represent conditions that would be regarded as *prima facie* unsuitable for this species, whereas constant submergence would represent a condition to which *V. australis* was well adapted. The responses of plants that were moderately dried were compared with plants of the same age, but which had been constantly submerged for 20 weeks, and plants that had been severely dried were compared with plants that were constantly submerged for 26 weeks. Following moderate and severe drying, plants were re-submerged for 11 weeks and then harvested at Weeks 20 and 26, respectively, together with a subset of constantly submerged plants.

Plant establishment

Ninety *M. ericifolia* seedlings were grown from seed collected at Dowd Morass, a brackish-water wetland in south-eastern Victoria (38°09'S, 147°12'E). The mean monthly salinity in this site can vary from 0.1 to nearly 20 dS m⁻¹, or ~40% seawater (Sinclair Knight Mertz 2001). Five-month-old plants were used in the experiment. One hundred and twenty *V. australis* ramets were collected from Lauriston Reservoir, a freshwater lake near Kyneton, Victoria (37°15'S, 144°22'E) in November 2004. Plants were established for 6 months in an outdoor mesocosm before being used in the experiment. By this time, the *V. australis* plants had reached maturity and were flowering. On 20 April 2005, 78 *M. ericifolia* and 90 *V. australis* plants were selected for uniformity for use in the experiment.

All plants were potted into 5-L plastic potting bags filled with a mix of 70% sand and 30% loam, with 2.5 g of Osmocote (Scotts Australia, Baulkham Hills, NSW) formulated specifically for native plants (17 N: 8.7 K: 1.6 P, 6 months nominal release period). The soil surface was overlain with 1 cm of clay to stimulate the development of anaerobic soil and prevent the loss of Osmocote beads and soil into the water column. Numerous holes were pierced in the sides and base of the pots to allow free movement of salt and water within the soil profile.

Six plants of each species selected for the experiment were harvested at the beginning of the experiment. Of the 84 remaining *V. australis* plants, 12 were randomly allocated to each of the three replicate fresh and three replicate saline mesocosms. Within each mesocosm, three plants were allocated to each of the two constantly submerged treatments (20 or 26 weeks) and three plants were allocated to each of the two 'stressful' water regime treatments (moderately or severely dried followed by 11 weeks re-submergence). In addition, one extra plant was allocated only to the moderate and severe drying treatments within each of the six mesocosms to provide a sample to harvest immediately after drying. Of the 72 remaining *M. ericifolia* plants, 12 were randomly allocated to each of the three replicate fresh and three replicate saline mesocosms. Within each mesocosm, three plants

were allocated to each of the two constantly exposed treatments (21 or 26 weeks) and three plants were allocated to each of the two 'stressful' water regime treatments (submerged for 5 weeks or submerged for 10 weeks followed by 14 weeks re-exposure).

Salinity treatment

Conductivity has been used to estimate salinity and is reported as dS m⁻¹. Over the range of salinities used in this experiment there exists a linear relationship between conductivity and salinity (Williams and Sherwood 1994). Conductivity units in dS m⁻¹ can be approximately converted to salinity units (g L⁻¹) by applying a factor of 0.64 (Hart *et al.* 1990). The higher salinity of 18 dS m⁻¹ (~30% seawater) was chosen because it is slightly less than the estimated salinity tolerance of *V. americana* in North America (Doering *et al.* 1999), but is similar to the mean highest salinities observed in Dowd Morass, a site where *M. ericifolia* forms extensive swamp-scrub communities (Sinclair Knight Mertz 2001). Water with the appropriate salinity was made up using ocean water from Sorrento, Victoria. Although there is some variation in the ionic composition of NaCl-dominated inland waters (Radke *et al.* 2002, 2003), seawater is likely to be similar in composition to the saline water within most inland systems in south-eastern Australia (Williams 1967) and to coastal systems, such as Dowd Morass, and particularly to those subjected to seawater intrusion.

Four weeks after the plants were placed in the mesocosms, seawater was added to three mesocosms (11 May 2005) in instalments of 6 dS m⁻¹ every 3 days until 18 dS m⁻¹ was reached (17 May 2005) at Week 1. Salt was added by pumping 3000 L of water out of each 9000-L mesocosm and replacing it with seawater in each of the three saline mesocosms, and with Melbourne tap water in the three freshwater mesocosms, which is both low in salt and in chemicals known to be toxic to plants (Handreck and Black 1984). To ensure that the salinity was uniform throughout the mesocosm, the water column was manually mixed in all mesocosms after each seawater addition.

Water regime treatments

All *M. ericifolia* plants were initially placed in an exposed position using raised platforms on 20 April 2005. At Week 2 (23 May 2005), 6 days after the saline mesocosms reached the target salinity of 18 dS m⁻¹, *M. ericifolia* seedlings allocated to the submerged treatments were removed from the platforms and immediately placed on the floor of the mesocosm. After 5 weeks of submergence, three *M. ericifolia* seedlings from each mesocosm were immediately returned to the exposed condition for 14 weeks and then harvested at Week 21 (3 October) along with three constantly exposed *M. ericifolia* seedlings from each mesocosm. After 10 weeks submergence, the remaining *M. ericifolia* seedlings were re-exposed for 14 weeks. At Week 26 (7 November), these plants were harvested together with the three constantly exposed plants from each mesocosm.

All *V. australis* plants selected for the experiment were initially flooded 55 cm above the soil surface with fresh water. At Week 2, plants allocated to the two drying treatments were placed in an unheated glasshouse to dry. Seasonally low air temperatures, particularly at night (8°C), and high humidity in the glasshouse prevented the shoots from drying completely, so plants were subsequently dried in the laboratory at 22–25°C from

Week 7 to Week 9. At Week 9, after 7 weeks of air-drying, the shoots had dried and three *V. australis* plants were re-submerged in their original mesocosm. In addition, three moderately dried plants that had been taken from each of the fresh and saline mesocosms were harvested to retrieve any belowground biomass. Plants in the severely dried treatment were placed in an oven at 30°C and dried for a further 6 weeks, until Week 15, when the soil had cracked in all pots. Plants were then either re-submerged in their original mesocosm or harvested as described for the moderately dried plants. After 11 weeks re-submergence, moderately and severely dried plants were harvested along with three constantly submerged plants at Week 20 and Week 26 respectively. Plants were separated into aboveground and belowground material, dried to a constant weight at 60°C and weighed.

Soil moisture content

The moisture content of the soil in the *V. australis* pots was measured to assess the severity of the various drying treatments. The soil moisture content of *M. ericifolia* was not quantified because plants were not dried. At the end of the *V. australis* desiccation period, soil samples were obtained from six moderate and six severely dried *V. australis* pots, one from each of the replicate mesocosms. To minimise disturbance to the plants, three small soil samples were taken from each pot using a 5-mm diameter corer to a depth of ~7 cm and pooled. Soil samples were weighed before and after drying in an oven at 105°C to derive soil moisture content. Additional data on soil moisture were obtained across all treatments from samples collected for soil salinity as described below.

Soil salinity

Soil salinity was measured for each species at each harvest. For each species, one replicate pot in each water regime treatment nested within each of the three fresh and three saline mesocosms was sampled. Soil samples (~40 mL) were collected within the root zone, ~7 cm below the soil surface. Fresh weights of each soil sample were taken before samples were oven-dried (105°C) to a constant weight. Dry soil samples were re-weighed and then ground using a pestle and mortar to pass through a 1-mm mesh size sieve. The conductivity of a 1 : 5 soil : de-ionised water extract was measured with a WP-81 Conductivity–Salinity–pH–Temperature meter (TPS instruments, Brisbane, Australia) after the samples had been shaken for 12 h. Soil moisture content was then used to calculate *in situ* soil salinity.

Physicochemical variables

Water-column temperature, salinity and pH in each mesocosm were measured weekly with the WP-81 Conductivity–Salinity–pH–Temperature meter (TPS Instruments). Water depths were maintained at 75 cm by additions of water as necessary, and the salinity of the water column was adjusted with additions of seawater or tap water as required. As with the initial establishment of the salinity regimes in the various mesocosms, the water column was mixed manually every week or following any addition of water to ensure that the salinity was uniform throughout each mesocosm.

Plant responses

Survivorship, height and the number of living growth points (terminal branches) of *M. ericifolia* were measured every 2–4 weeks. Growth points were considered living if greater than 50% of the stem was green; *M. ericifolia* were considered dead if they had no live growth points. Survivorship was calculated as the number of plants that exhibited green growth, as a percentage of all the plants in the treatment. At the end of the experiment, the diameter of *M. ericifolia* stems was measured 5 cm above the soil surface using calipers. For *V. australis*, survivorship, maximum living leaf length (cm) per pot and the number of ramets per pot were measured every 2–4 weeks; plants were considered dead if they had no green (living) tissue. All harvested plants were washed and separated into aboveground and belowground biomass, dried to a constant weight (60°C) and weighed.

Statistical analyses

Measurements on replicate plants in each mesocosm were averaged before analysis. Data for both species were analysed with a split-plot, two-way ANOVA using SYSTAT (Version 10) for Windows (SPSS, Chicago, IL), with salt and flooding effects treated as fixed factors. Survival of both species at Weeks 21 and 26 could not be analysed because all constantly exposed and constantly submerged plants survived.

If the two-way ANOVA revealed no significant interaction between salinity and water regime, planned comparisons between the various water regime treatments were carried out using the statistical software package R (Ihaka and Gentleman 1996). For *M. ericifolia*, planned comparisons compared the growth responses of plants subjected to 5 and 10 weeks submergence with plants subjected to constant exposure for 21 and 26 weeks respectively. For *V. australis*, planned comparisons compared plant responses to moderate and severe drying with constant submergence for 20 and 26 weeks respectively. If the two-way ANOVA revealed a significant interaction between salinity and water regime, the effect of water regime was tested separately for the fresh and saline treatments using a split-plot ANOVA. If a significant effect of water regime was revealed, differences between water regime treatments for each species were tested using planned comparisons for fresh and salinised plants.

Normality and homogeneity of variance were examined with box-plots using SYSTAT (Version 10) for Windows and R. Data were transformed where necessary; transformations are described in the text. A significance value of $P < 0.05$ was used for all analyses. Sphericity was tested using Greenhouse–Geisser (G–G) epsilon; values less than 1 indicate non-sphericity and require adjustment of the P value (Quinn and Keough 2002). The Greenhouse–Geisser adjustment was used when epsilon values fell below 0.75. When epsilon values were close to 0.75 or greater, the Greenhouse–Geisser adjustment is overly conservative (Quinn and Keough 2002) and the more liberal Huynh–Feldt (H–F) adjustment was used.

Results

Physicochemical properties of the water column and soil

In the freshwater treatment, water-column conductivity was ~0.07 dS m⁻¹ and soil conductivity was ~2 dS m⁻¹. In the

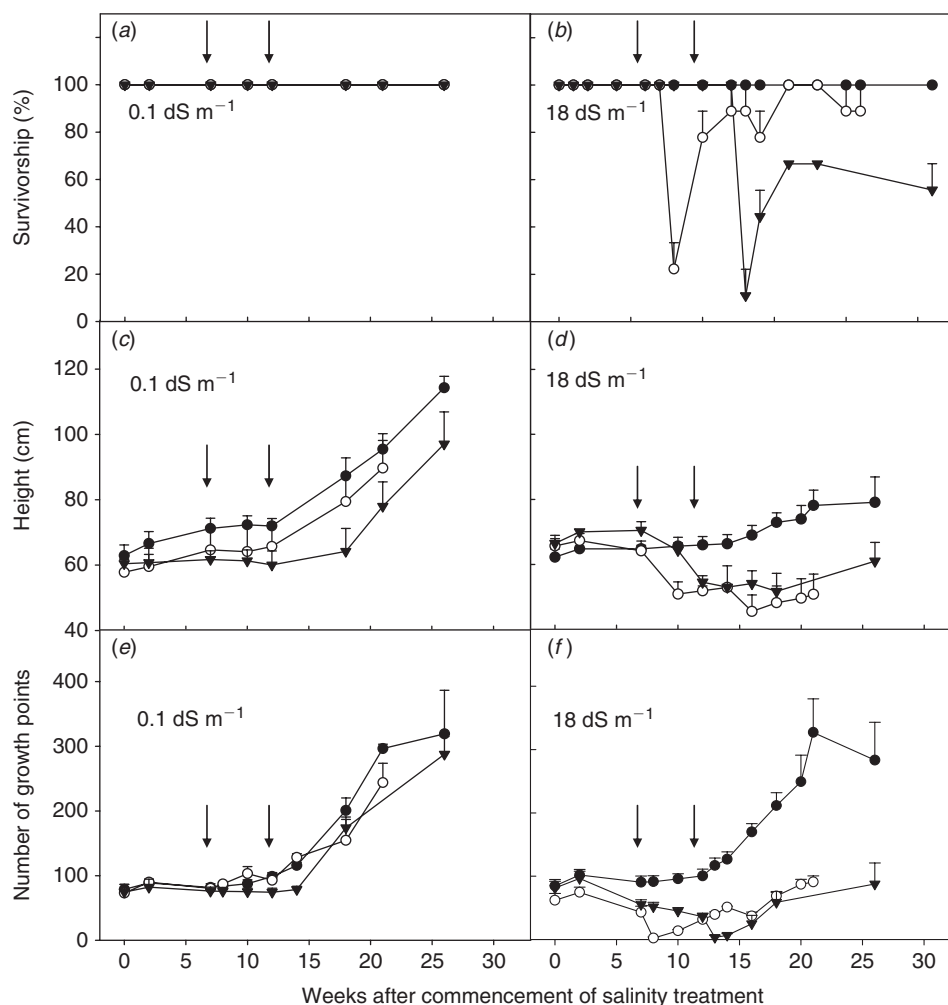


Fig. 1. Changes in (a, b) survivorship, (c, d) plant height and (e, f) number of growth points of *Melaleuca ericifolia* seedlings at salinities of 0.1 dS m^{-1} (a, c, e) and 18 dS m^{-1} (b, d, f) for three water regime treatments: constantly exposed (black circle); submerged 5 weeks then re-exposed 14 weeks (open circle) and submerged 10 weeks then re-exposed 14 weeks (black triangle). Plants in the two submergence treatments were submerged at Week 2, two weeks after salt additions commenced; arrows indicate the times when these plants were re-exposed. Data represent means ($n = 3$) and bars represent s.e. In some instances the s.e. are smaller than the symbol.

saline treatment, water-column conductivity was within 15% of the target salinity of 18 dS m^{-1} . Soil conductivity varied from 21 to 24 dS m^{-1} for *M. ericifolia* and from 13 to 20 dS m^{-1} for *V. australis*. The mean soil moisture content of constantly submerged *V. australis* pots ranged from 0.37 to $0.42 \text{ mL g soil dry weight (DW)}^{-1}$; this was not altered by air drying. However, oven-drying reduced the mean soil moisture content to $0.13 \pm 0.01 \text{ mL g soil DW}^{-1}$.

The water column of the saline mesocosms was slightly more alkaline than that of the freshwater mesocosms. Over the course of the experiment, daytime water-column temperatures ranged from 8.1°C to 17.5°C and monthly rainfall for Melbourne averaged 47 mm (Bureau of Meteorology Climate Averages Data for Dandenong, available from: http://www.bom.gov.au/climate/averages/tables/cw_086224.shtml). Average air temperatures declined throughout the first 3 months of the experiment, and reached the lowest value in July 2005

(max. 15.3°C , min. 8.4°C), and then subsequently increased to a mean maximum of 24.4°C (min. 13.9°C) in November 2005.

Melaleuca ericifolia responses

Survival

All plants in the constantly exposed and freshwater treatments survived (Fig. 1a, b). Nevertheless, the stems of submerged *M. ericifolia* plants were thin and brittle and those submerged in saline mesocosms had very few leaves. Following 1 week of re-exposure, the number of plants that were recorded 'alive' (i.e. exhibiting any green growth) in the saline mesocosms was lower for plants submerged for 10 weeks (11% of the total) than for plants submerged for only 5 weeks (22%). Surprisingly, many plants that were considered 'dead' 1 week after re-exposure had recovered after 14 weeks. These plants had short, bushy stems

Table 1. Results of a split-plot ANOVA for the height, number of growth points and total biomass of *Melaleuca ericifolia* seedlings and for the longest leaf length, number of ramets and total biomass of *Vallisneria australis* plants in response to salinity and water regime treatments

Species	Variables	Source	d.f.	F-ratio	P
<i>M. ericifolia</i>	Height	Salinity	1	20.7	0.009
		Water regime	3	6.97	0.010 ^B
		Salinity × water regime	3	1.30	0.264 ^B ns
	No. growth points	Salinity ^A	1	117	<0.0001
		Water regime ^A	3	8.02	0.011 ^B
		Salinity × water regime ^A	3	5.39	0.031 ^B
	Total biomass	Salinity	1	144	<0.0001
		Water regime	3	26.5	<0.0001
		Salinity × water regime	3	0.90	0.472 ^C ns
<i>V. australis</i>	Longest leaf length	Salinity	1	44.7	0.002
		Water regime	3	134	<0.0001
		Salinity × water regime	3	15.5	0.002 ^B
	No. ramets	Salinity	1	0.54	0.504 ns
		Water regime	3	201	<0.0001
		Salinity × water regime	3	18.4	0.005 ^B
	Total biomass	Salinity	1	183	0.007
		Water regime	3	31.8	<0.0001
		Salinity × water regime	3	19.9	0.010 ^B

^AData were log transformed. ^BGreenhouse–Geisser corrected *P*-values. ^CHuynh–Feldt corrected *P*-values. ns, no significant difference.

after their period of re-growth. Approximately 90% and 56%, respectively, of plants previously submerged for 5 and 10 weeks had living tissue.

Stem thickness

Stem diameter was measured at the end of the experiment. Plants in the exposed treatment at $\sim 0.1 \text{ dS m}^{-1}$ had the thickest stems ($1.2 \pm 0.1 \text{ cm}$) and both submergence and salinity reduced stem diameter by $\sim 25\%$. Plants submerged at 18 dS m^{-1} had the smallest stem diameters ($0.8 \pm 0.0 \text{ cm}$).

Plant height

Plants increased in height only a little over the first 12 weeks of the experiment. After this initial 3 months, however, the height of the exposed plants in freshwater mesocosms increased rapidly and reached 114 cm by Week 26 (Fig. 1c). In contrast, the height of the exposed plants at 18 dS m^{-1} increased very slowly throughout the experiment and they were 30% shorter than their freshwater counterparts by the end of the experiment at Week 26 (Fig. 1d).

After 14 weeks of re-exposure, the height of the plants that had been submerged for 5 weeks in fresh water was similar to that of constantly exposed plants, whereas plants that had been submerged for 10 weeks in fresh water remained $\sim 15\%$ shorter (Fig. 1c). In the salinised treatment, the height of re-exposed plants increased slowly, and after 14 weeks the plant height of plants submerged for 5 and 10 weeks remained $\sim 25\%$ and $\sim 35\%$ lower, respectively, than plants in the exposed treatment. Although salinity and submergence both significantly reduced plant height (Table 1), the interaction term was not significant; planned comparisons of final plant heights (pooled across

salinity treatments) indicated that submergence for both 5 and 10 weeks reduced plant height after 14 weeks of re-exposure (Table 2).

Number of growth points

As observed for plant height, the number of growth points did not increase rapidly until after Week 12. Submergence in fresh water for 10 weeks, but not 5 weeks, reduced the number of growth points compared with constantly exposed plants. The number of growth points on submerged plants quickly increased after re-exposure in freshwater conditions, and after 14 weeks the number of growth points of plants submerged for 5 and 10 weeks was only $\sim 18\%$ and 10% lower, respectively, than the constantly exposed plants (Fig. 1e).

Although salinity had little effect on the number of growth points when plants were exposed, the response was quite different when the plants were submerged (Fig. 1e, f). At 18 dS m^{-1} , submergence for 5 and 10 weeks lowered the number of growth points by $\sim 47\%$ and 63% , respectively, compared with constantly exposed plants in fresh water (Fig. 1f). One week after re-exposure, however, almost all growth points were lost from plants at 18 dS m^{-1} . Plants submerged for 5 and 10 weeks began to recover 2 weeks later, but after 14 weeks re-exposure they still had $\sim 70\%$ fewer growth points than their constantly exposed counterparts.

Both salinity and the water regime treatment significantly affected the final number of growth points (Table 1). In this case the interaction term was significant and data were not pooled. A subsequent split-plot ANOVA applied separately for plants in the freshwater and saline water treatments indicated that the number of growth points was significantly altered by the water regime

Table 2. Results of a planned comparison of the effect of water regime on the height and total biomass of *Melaleuca ericifolia* seedlings for combined salinity data and on the number of growth points at 0.1 dS m⁻¹ and 18 dS m⁻¹, and for the effect of water regime on the number of ramets, longest leaf length and total biomass of *Vallisneria australis* at 0.1 dS m⁻¹

Water regime treatments for *M. ericifolia* seedlings: constantly exposed for 21 weeks (Exp₂₁) and 26 weeks (Exp₂₆); exposed 2 weeks–submerged 5 weeks–exposed 14 weeks (Exp₂-Sub₅-Exp₁₄) and exposed 2 weeks–submerged 10 weeks–exposed 14 weeks (Exp₂-Sub₁₀-Exp₁₄). Water regime treatments for *V. australis*: constantly submerged 20 weeks (Sub₂₀) and 26 weeks (Sub₂₆); submerged 2 weeks–moderately dried 7 weeks–submerged 11 weeks (Sub₂-MD₇-Sub₁₁) and submerged 2 weeks–severely dried 13 weeks–submerged 11 weeks (Sub₂-s.d.₁₃-Sub₁₁)

Species	Variables	Salinity	Planned contrast	d.f.	F-ratio	P
<i>M. ericifolia</i>	Height (cm)	Combined	Exp ₂ -Sub ₅ -Exp ₁₄ v. Exp ₂₁	1	14.9	0.002
			Exp ₂ -Sub ₁₀ -Exp ₁₄ v. Exp ₂₆	1	3.93	0.021
	Total biomass (g DW)	Combined	Exp ₂ -Sub ₅ -Exp ₁₄ v. Exp ₂₁	1	35.6	<0.0001
			Exp ₂ -Sub ₁₀ -Exp ₁₄ v. Exp ₂₆	1	9.73	0.009
	No. growth points	0.1 dS m ⁻¹ A	Exp ₂ -Sub ₅ -Exp ₁₄ v. Exp ₂₁	1	0.53	0.495 ns
			Exp ₂ -Sub ₁₀ -Exp ₁₄ v. Exp ₂₆	1	1.25	0.307 ns
		18 dS m ⁻¹ A	Exp ₂ -Sub ₅ -Exp ₁₄ v. Exp ₂₁	1	6.41	0.045
			Exp ₂ -Sub ₁₀ -Exp ₁₄ v. Exp ₂₆	1	3.27	0.120 ns
<i>V. australis</i>	Longest leaf length (cm)	0.1 dS m ⁻¹ B	Sub ₂ -MD ₇ -Sub ₁₁ v. Sub ₂₀	1	63.0	0.0002
			Sub ₂ -s.d. ₁₃ -Sub ₁₁ v. Sub ₂₆	1	35.2	0.001
	No. ramets	0.1 dS m ⁻¹	Sub ₂ -MD ₇ -Sub ₁₁ v. Sub ₂₀	1	70.2	<0.0001
			Sub ₂ -s.d. ₁₃ -Sub ₁₁ v. Sub ₂₆	1	81.0	<0.0001
	Total biomass (g DW)	0.1 dS m ⁻¹	Sub ₂ -MD ₇ -Sub ₁₁ v. Sub ₂₀	1	81.0	<0.0001
			Sub ₂ -s.d. ₁₃ -Sub ₁₁ v. Sub ₂₆	1	83.6	<0.0001

A Data were log transformed. B Data were square-root transformed. DW, dry weight; ns, no significant difference.

treatments at 18 dS m⁻¹ ($P = 0.044$, G–G adjusted), but not at 0.1 dS m⁻¹ ($P = 0.572$, G–G adjusted). Under the 18 dS m⁻¹ treatment, submergence for 5 weeks followed by 14 weeks re-exposure significantly lowered the number of growth points compared with constantly exposed plants (Table 2). Surprisingly, no significant difference was found between plants submerged for 10 weeks and re-exposed for 14 weeks and plants constantly exposed for 26 weeks at 18 dS m⁻¹. This result is most likely because of high within-treatment variability and a lack of statistical power to unequivocally separate the two treatments.

Biomass

Submergence in fresh water for 5 or 10 weeks followed by 14 weeks re-exposure reduced the total biomass of *M. ericifolia* seedlings by ~30% compared with constantly exposed plants (Table 3). Salinity reduced the total biomass of plants constantly exposed for 21 and 26 weeks by 48% and 41%, respectively, compared with plants in fresh water. Statistical analysis showed that both salinity and water regime significantly affected plant total biomass (Table 1). Although submergence at 18 dS m⁻¹ reduced plant biomass to a greater extent (~70%) than did submergence in fresh water (~30%), the response to submergence was not significantly altered by salinity (Table 1). This result is most likely a reflection of poor statistical power. Planned comparisons revealed that total biomass was significantly lowered by 5 and 10 weeks submergence compared with constantly exposed plants (Table 2).

Aboveground to belowground biomass

The ratio of aboveground to belowground biomass of all constantly exposed plants increased ~20% between Weeks 21 and 26 (Table 3), a pattern that reflects a shift in resource allocation from roots to shoots as the plants matured. While submerged

in freshwater, *M. ericifolia* grew roots that protruded above the sediment. Plants submerged for 5 and 10 weeks followed by 14 weeks re-exposure in freshwater treatments had aboveground to belowground ratios that were 89% and 8% higher, respectively, than constantly exposed plants; this result is a reflection of a greater decrease in belowground than aboveground biomass (Table 3). The reduction in belowground biomass associated with submergence was exacerbated by salinity, which caused the aboveground to belowground biomass ratio to increase by 89% and 67% for plants submerged for 5 and 10 weeks, respectively, compared with plants constantly exposed for 21 and 26 weeks in fresh water (Table 3).

Vallisneria australis responses

Survivorship

All constantly submerged *V. australis* plants survived in fresh water and at 18 dS m⁻¹ (Fig. 2a, b). Although no plants appeared to be alive following the moderate or severe drying treatments, all moderately dried plants re-grew after 3 weeks of re-submergence in fresh water (Fig. 2a). In contrast, only 11% of severely dried plants re-grew after 11 weeks of re-submergence in fresh water. Salinity markedly reduced the ability of plants to recover from drying; only 56 ± 11% of moderately dried plants, and no severely dried plants, had re-grown after 11 weeks of re-submergence in saline water (Fig. 2b). The effect of drying on growth could not be analysed for plants in the saline mesocosms because of the death of all the severely dried plants in this treatment.

Maximum leaf length

Salinity and water regime both significantly affected the final values of maximum leaf length, and the interaction term was

Table 3. Total biomass, aboveground biomass, belowground biomass and ratio of aboveground:belowground biomass of *Melaleuca ericifolia* seedlings and *Vallisneria australis* plants in response to salinity and water regime treatments

Water regime treatments for *M. ericifolia* seedlings: constantly exposed for 21 weeks (Exp₂₁) and 26 weeks (Exp₂₆); exposed 2 weeks–submerged 5 weeks–exposed 14 weeks (Exp₂-Sub₅-Exp₁₄) and exposed 2 weeks–submerged 10 weeks–exposed 14 weeks (Exp₂-Sub₁₀-Exp₁₄). Water regime treatments for *V. australis*: constantly submerged 20 weeks (Sub₂₀) and 26 weeks (Sub₂₆); submerged 2 weeks–moderately dried 7 weeks–submerged 11 weeks (Sub₂-MD₇-Sub₁₁) and submerged 2 weeks–severely dried 13 weeks–submerged 11 weeks (Sub₂-s.d.₁₃-Sub₁₁)

Species	Salinity (dS m ⁻¹)	Water regime	Total biomass (g DW)	Aboveground biomass (g DW)	Belowground biomass (g DW)	Aboveground:belowground ratio
<i>M. ericifolia</i>	0.1	Exp ₂₁	50 ± 2.6	22 ± 3.3	28 ± 0.8	0.9 ± 0.1
		Exp ₂ -Sub ₅ -Exp ₁₄	34 ± 4.5	20 ± 2.2	15 ± 2.7	1.7 ± 0.3
		Exp ₂₆	53 ± 0.6	28 ± 2.5	25 ± 2.5	1.2 ± 0.2
		Exp ₂ -Sub ₁₀ -Exp ₁₄	36 ± 1.6	20 ± 1.6	17 ± 2.0	1.3 ± 0.1
	18	Exp ₂₁	28 ± 3.6	15 ± 1.2	13 ± 2.4	1.3 ± 0.1
		Exp ₂ -Sub ₅ -Exp ₁₄	9.3 ± 1.6	5.5 ± 0.5	3.8 ± 1.3	1.7 ± 0.3
		Exp ₂₆	31 ± 4.7	19 ± 3.5	13 ± 1.6	1.6 ± 0.1
		Exp ₂ -Sub ₁₀ -Exp ₁₄	6.0 ± 2.3	4.2 ± 1.4	2.2 ± 0.8	2.0 ± 0.1
<i>V. australis</i>	0.1	Sub ₂₀	54 ± 2.9	36 ± 1.6	21 ± 1.7	2.1 ± 0.4
		Sub ₂ -MD ₇ -Sub ₁₁	1.1 ± 0.2	0.1 ± 0.0	1.0 ± 0.2	0.1 ± 0.02
		Sub ₂₆	51 ± 7.0	35 ± 4.7	15 ± 2.5	1.8 ± 0.6
		Sub ₂ -s.d. ₁₃ -Sub ₁₁	0.1 ± 0.1	0.02 ± 0.02	0.1 ± 0.1	0.3 ± 0.0
	18	Sub ₂₀	27 ± 1.0	19 ± 0.4	7.3 ± 0.6	2.8 ± 0.3
		Sub ₂ -MD ₇ -Sub ₁₁	0.3 ± 0.2	0.02 ± 0.01	0.3 ± 0.2	0.9 ± 0.7
		Sub ₂₆	26 ± 0.7	19 ± 2.8	7.3 ± 0.7	3.2 ± 1.0
		Sub ₂ -s.d. ₁₃ -Sub ₁₁	0.0 ± 0	0.0 ± 0.0	0 ± 0.0	ND

Data represent mean ± standard error ($n = 3$). DW, dry weight; ND, no data.

significant (Table 1). A split-plot ANOVA of data from the freshwater treatment revealed that water regime significantly altered leaf length ($P = 0.003$, G–G adjusted). The leaf length of plants in freshwater was significantly reduced by drying (Table 2); the leaves of moderately and severely dried plants in freshwater were only 10% and 24% as long, respectively, as the leaves of constantly submerged plants after 11 weeks re-submergence (Fig. 2c). Salinity reduced leaf length across all water regime treatments (Fig. 2d). For example, leaf length was reduced by 41% and 65% for plants constantly submerged at 18 dS m⁻¹ for 21 and 26 weeks, respectively, compared with those in fresh water (Fig. 2c, d). Furthermore, the leaf length of constantly submerged plants at 18 dS m⁻¹ declined ~44% between Weeks 21 and 26 (Fig. 2d). Salinity further exacerbated the decline in leaf length associated with drying. For example, the leaf length of moderately dried plants at 18 dS m⁻¹ was 76% shorter than the length in fresh water (Fig. 2c, d).

Number of ramets

Submerged plants produced few ramets over the first 18 weeks (Fig. 2e). After three more weeks (Week 21), the number of ramets had increased substantially; increases were greater in the freshwater than in the saline mesocosms (Fig. 2e, f). After Week 21, ramet numbers declined in the freshwater treatment, but continued to increase in the saline treatment. Few of the original ramets re-grew after moderate drying, especially in the saline treatments. The decline in the number of ramets associated with drying was significantly exacerbated by salinity (Table 1).

Water regime, but not salinity, significantly affected the final number of *V. australis* ramets per pot (Table 1). The interaction between salinity and water regime was significant and a subsequent split-plot ANOVA undertaken for plants in fresh water

revealed that water regime significantly altered ramet number per pot ($P = 0.007$, G–G adjusted). In freshwater treatments, dried plants had a significantly lower number of ramets per pot than constantly submerged plants (Table 2). In freshwater treatments, drying reduced the number of ramets in moderate (86%) and severe drying (96%) treatments compared with constantly submerged plants at Weeks 20 and 26 respectively (Fig. 2e). Salinity reduced the number of ramets for plants in moderately dried treatments by 74% compared with those in fresh water, and completely prohibited regeneration of severely dried plants (Fig. 2e, f).

Biomass

Water regime significantly affected the biomass of *V. australis* (Table 1). In freshwater mesocosms, moderate and severe drying reduced the total biomass by over 95% compared with submerged plants (Table 3). Salinity also significantly reduced total biomass; constantly submerged plants at 18 dS m⁻¹ had half the total biomass of plants submerged in fresh water (Table 3). A significant effect of water regime and salinity on total biomass was evident (Table 1). At 18 dS m⁻¹, moderately dried plants had only 1% of the biomass of constantly submerged plants in fresh water (Table 3), and no biomass was recovered from severely dried plants. A split-plot ANOVA of the freshwater treatment found that biomass was significantly altered by water regime ($P = 0.011$, G–G adjusted).

Aboveground to belowground biomass

Salinity reduced the aboveground biomass of constantly submerged *V. australis* plants and resulted in the lowering of the aboveground to belowground ratio by ~25% and ~44% at Weeks 20 and 26, respectively, compared with plants grown in fresh

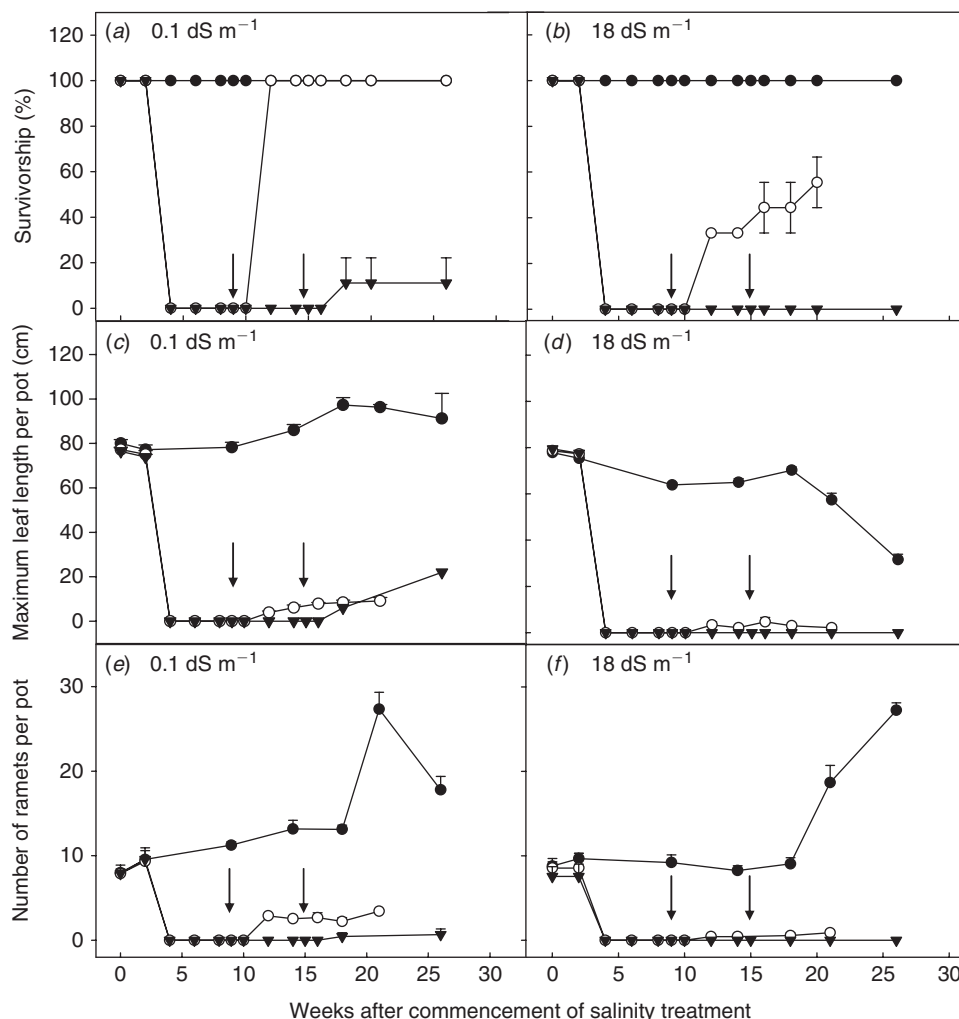


Fig. 2. Changes in (a, b) survivorship, (c, d) leaf length (cm) and (e, f) number of ramets per pot of *Vallisneria australis* at salinities of 0.1 dS m⁻¹ (a, c, e) and 18 dS m⁻¹ (b, d, f) for three water regime treatments: constantly submerged (black circle); moderately dried then re-submerged for 11 weeks (open circle) and severely dried then re-submerged for 11 weeks (black triangle). Plants in the two drying treatments were removed for drying at Week 2, 2 weeks after salt additions commenced; arrows indicate the times when these plants were re-submerged. Data represent means ($n = 3$) and bars represent s.e. In some instances the s.e. are smaller than the symbol.

water (Table 3). As all the aboveground tissue had died after drying and only started to re-grow approximately 9 weeks before the end of the experiment, the aboveground to belowground ratio was reduced by >80% in both the moderately and severely dried treatments compared with their submerged counterparts.

Discussion

Although plants of temporary wetlands are generally considered to be well adapted to dynamic water regimes, human-induced changes, such as secondary salinity, may impose a new set of limits on the ability of a given species to tolerate fluctuating water levels or markedly different wetting and drying cycles. The experiment reported in this paper tested the proposal that salinity could reduce the ability of the wetland shrub *M. ericifolia* and the submerged monocot *V. australis* to recover from wetting

and drying cycles that would be considered *prima facie* to be unsuitable to their growth form.

Melaleuca ericifolia

We found that submergence followed by re-exposure significantly reduced the biomass of *M. ericifolia* seedlings, but extending the period of submergence under freshwater conditions from 5 to 10 weeks had little effect on plant survivorship or growth. The experiment was undertaken in winter/spring, and it may be that slow growth of *M. ericifolia* plants early in the experiment contributed to the lack of differences in response to the two periods of submergence. Certainly *M. ericifolia* seedlings grew very slowly over the first 3 months of the experiment (i.e. between May and August), the coldest months of the year in southern Australia. As temperatures rose from August to November, the plants in fresh water started to grow rapidly (Fig. 1c, e).

Although the effects of submergence are likely to have been reduced by submerging plants over a winter period, this timing was deliberate because it coincides with the natural pattern of wetland inundation in south-eastern Australia (e.g. Briggs 1988).

Our results clearly show that *M. ericifolia* seedlings can recover rapidly after long periods of flooding in winter if water levels were to recede over the following spring, a season of potentially rapid growth. In contrast to Denton and Ganf's (1994) findings that survival of *M. halmaturorum* seedlings declined following re-exposure after flooding, we found that *M. ericifolia* seedlings submerged in fresh water grew rapidly following re-exposure. In addition, *Melaleuca quinquenervia* saplings in sub-tropical USA have been reported to show a growth spurt after water levels receded (Lockhart *et al.* 1999). The capacity for rapid growth following re-exposure may represent an important adaptation of *M. ericifolia* seedlings to withstanding seasonal floods, a hydrological condition that is likely to be common across wetlands in south-eastern Australia. Their adaptation to a variable water regime in fresh water is also supported by field evidence that demonstrates good survivorship of 4-year-old *M. ericifolia* saplings subject to extremes of drought and flooding (de Jong 2000).

The response of *M. ericifolia* to inundation and subsequent re-exposure was, however, affected markedly by the salinity of the water that inundated them. We have previously reported that *M. ericifolia* seedlings were highly salt tolerant and that, for example, 90% of *M. ericifolia* seedlings survived when soil was exposed to the air despite soil salinities reaching 76 dS m^{-1} (Salter *et al.* 2007). The current study confirms these earlier findings that *M. ericifolia* is highly tolerant of salinity under drained conditions. Indeed, as shown in Fig. 1b, no exposed seedlings in this mesocosm experiment died even when soil salinities reached $\sim 24 \text{ dS m}^{-1}$. Moreover, although a water-column salinity of 18 dS m^{-1} reduced the total biomass of constantly exposed *M. ericifolia* seedlings, this pattern was not reflected in the number of growth points, which continued to increase until Week 21.

Despite these indications of the general salt tolerance of *M. ericifolia* seedlings, the impact of salinisation was most evident when salinity stress was combined with water-level fluctuations that, based on the plant's growth form, would be considered unsuitable for its long-term survival and growth. This synergistic effect supports several earlier papers that have shown that a combined effect of flooding and salinity had a much greater negative effect on the performance of woody plant species than did either factor applied in isolation (Van der Moezel *et al.* 1988; Allen *et al.* 1996; Akilan *et al.* 1997). Although we found that *M. ericifolia* seedlings submerged in fresh water re-grew rapidly when re-exposed, a very different response was observed when the plants were inundated with saline water and, in this case, the survival of *M. ericifolia* seedlings submerged with saline (18 dS m^{-1}) water declined rapidly following re-exposure.

A range of non-destructive variables were used in our study to assess the responses of *M. ericifolia* to combined hydrological and salinity regimes, and to identify those measurements that were good indicators of flooding or salt stress. Although total biomass declined when plants were submerged with fresh water and when they were grown under exposed saline conditions, the number of growth points did not significantly alter. In contrast, both salinity and submergence resulted in shorter

seedlings, which suggests that height, rather than growth points, is a more sensitive indicator of salt and flooding stress. Submergence and re-exposure in saline water imposed the greatest stress on *M. ericifolia*, resulting in very low biomass and survival. After re-exposure, the number of growth points declined rapidly and remained significantly lower than constantly exposed plants even after 14 weeks re-exposure. Plant height was a less sensitive indicator of stress in this treatment. These responses may indicate that the number of terminal branches of *M. ericifolia* declines only when the plant is highly stressed. Had *M. ericifolia* been harvested immediately following re-exposure, and the aboveground biomass divided into shoots and stems, as advocated by Poorter and Nagel (2000), a dramatic loss of leaves following re-exposure of saline submerged seedlings would have been apparent. Such a stress response would be reflected in a change in the number of growth points with time and the very low aboveground biomass recorded for plants in this treatment. The production of short, bushy stems following re-exposure led to plants exhibiting many growth points, but low biomass, highlighting the importance of measuring both variables.

Vallisneria australis

Although all moderately dried *V. australis* plants recovered when plants were re-submerged in fresh water, they attained only 2% of the biomass of constantly flooded plants after 11 weeks. The severe stress imposed by moderate drying on *V. australis* was evident also in the data for leaf length and ramet number, both of which were significantly lower for moderately dried plants than those constantly submerged at Week 20, following 11 weeks re-submergence of dried plants. Given these results, it is likely that during the phase of re-growth after drying, *V. australis* communities under natural conditions would be highly vulnerable to other environmental stresses, such as high turbidity, increased water depth or feeding by water birds.

In contrast to the effects of moderate drying, severe drying resulted in an almost complete loss of belowground biomass of *V. australis* and largely prevented plants from regenerating when they were subsequently re-flooded. This result highlights the importance of maintaining moist sediments in *Vallisneria* beds to preserve the belowground components of this nominally obligate submerged species. It is likely that submerged species with larger and more robust underground storage organs would be more tolerant of soil drying. For example, Rea and Ganf (1994) reported that the substantial tubers of *Triglochin procerum* (Juncaginaceae) allowed this species to withstand prolonged (9 months) soil drying. *Vallisneria australis* does not possess such robust underground storage organs and would be far more susceptible to severe sediment desiccation.

Among the reported responses of *Vallisneria* to salinity is a decrease in leaf length (Lores and Sprecht 2001). Although the leaf length of plants submerged at 18 dS m^{-1} declined between Weeks 20 and 26 in our experiment, the number of ramets per pot increased during this period. A re-allocation of biomass could account for the similar final biomass values of submerged plants at Weeks 20 and 26 in the saline mesocosms. *Bolboschoenus medianus* (Cyperaceae) also has been shown to re-allocate biomass in response to salinity, by producing fewer leaves and shorter culms and simultaneously increasing tuber

biomass (Morris and Ganf 2001). A shift in biomass allocation from leaf growth to vegetative reproduction may represent a tolerance mechanism, which would allow *V. australis* to persist in saline environments. In support of this contention, we note that Bengtsson and Ceplitis (2000) proposed that plants in saline environments may increase vegetative reproduction to bypass the uncertainties of seedling establishment. Given the difference in response shown by leaf length and ramet number, we conclude that leaf length is a better indicator of salinity stress than ramet density for constantly submerged *V. australis*.

Despite this species' apparent tolerance to salinity when growing under conditions of permanent submersion, our results show clearly that high salinity strongly compromised the ability of *V. australis* to recover from an episode of sediment desiccation. An illustration of this effect is that the survival of moderately dried plants was halved under the 18 dS m⁻¹ treatment and that no severely dried plants survived under these high-salinity conditions. This mesocosm-based result is broadly supported by our field observations at Dowd Morass, where extensive loss of *V. australis* was observed following a 'moist soil' draw-down during the summer of 2004, when soil salinities reached ~30 dS m⁻¹ (J. Salter, unpubl. data).

Ecological and management implications

Our findings demonstrate that wetland plants that represent extremes in growth form can nevertheless demonstrate considerable tolerance to fluctuating wetting and drying cycles that would be considered outside of their preferred water regime. Tolerance may be higher in species more adapted to water level changes, such as amphibious tolerators and responders (see Brock and Casanova 1997). This resilience indicates that a variable water regime would allow the long-term persistence of both *M. ericifolia* and *V. australis* in a freshwater wetland, despite the former being a woody shrub that performs best under drained conditions and the latter a submerged angiosperm that is largely intolerant of desiccation. Under freshwater conditions, *M. ericifolia* seedlings are tolerant of short periods of submergence and re-exposure, and *V. australis* plants are somewhat tolerant of shoot desiccation. *Vallisneria australis* plants, however, are unlikely to recover vegetatively if the soils dry substantially, even in fresh water, because belowground organs are lost.

This resilience to fluctuating or seemingly adverse water regimes is, however, strongly compromised under saline conditions. The growth and survival of *M. ericifolia* seedlings is markedly reduced when re-exposed following saline flooding, and *V. australis* can be lost from a wetland completely if water levels are drawn down to the point that sediments are fully desiccated before being flooded with saline water. Such a response could be taken to indicate that water levels should not be allowed to fluctuate in saline wetlands. A reduction in the variability of water-level fluctuations in saline wetlands may not be warranted because continual flooding of temporary wetlands may reduce species richness and fluctuating wetting and drying cycles tend to promote a variety of growth forms in temporary wetlands (Casanova and Brock 2000). Whether water levels should be allowed to fluctuate would depend strongly on the management targets for a given wetland and whether the resultant changes in salinity regimes would be likely to compromise those key plant

species targeted for conservation. Furthermore, persistence is determined not only by the response of adult plants, but also by the capacity of any soil-based seedbank, aerial seedbank or vegetative propagules to facilitate recolonisation.

We caution that our results are derived from a single life stage of two species that are at opposite ends of the growth-form spectrum; it is likely that both species may persist during unfavourable water regimes via another life-history stage, such as seeds (*V. australis*) or clonal spread of adults (*M. ericifolia*). Even so, the results demonstrate clearly that secondary salinisation strongly compromises the ability of both taxa to recover from water regimes that, based on the plant's growth form, would be considered unsuitable for long-term survival and growth.

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