Relationship between water regime and hummock-building by *Melaleuca ericifolia* and *Phragmites australis* in a brackish wetland

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ABSTRACT

We investigated the relationship between hummock height and depth of inundation in a permanently inundated wetland in south-eastern Australia. Our survey of 318 hummocks, in water ranging from 0 to 70 cm depth, revealed a significant positive linear relationship and strong correlation between hummock height and water depth ($r^2 = 0.53$ and 0.79 for *Melaleuca ericifolia* and *Phragmites australis* hummocks respectively). We also investigated whether water regime affects the decomposition rate of litter on hummocks; specifically, whether constant inundation slows decomposition to an extent that would promote accumulation of litter and hummock-building. On the contrary, we found that constantly submerged *M. ericifolia* litter decomposed faster than dry litter, but at a similar rate to litter that experienced intermittent inundation (decay rates (k) $0.0015\,d^{-1}$, $0.0010\,d^{-1}$ and $0.0008\,d^{-1}$ for submerged, intermittent and dry treatments respectively). Submerged *P. australis* litter also decomposed faster ($k = 0.0024\,d^{-1}$) than dry litter ($k = 0.0011\,d^{-1}$). We discuss the interaction of water regime and decomposition of organic material and implications for the maintenance of hummock and hollow topography.

1. Introduction

Topographical heterogeneity is important for maintaining biodiversity because it enables the coexistence of species with different habitat requirements (Vivian-Smith, 1997; Larkin et al., 2006). Hummocks are a common form of topographical heterogeneity in wetlands and consist of clumps of vegetation on mounds, surrounded by sediments of lower elevation ('hollows'; Stribling et al., 2007). Hummocks supporting woody vegetation are also known as tree islands (Wetzel, 2002). Hummocks facilitate plant survival in waterlogged environments by providing refuge from the effects of anoxia and salinity (Bertness et al., 1992; Herr-Turoff and Zedler, 2007).

Plants can initiate hummock formation (Bertness et al., 1992; Saur et al., 1998; Wetzel, 2002; Langlois et al., 2003; Stribling et al., 2007; Herben and Novoplansky, 2008) and certain morphological traits may facilitate hummock building through the accumulation of organic matter. Plants that have been described as hummock-builders often have dense adventitious roots and/or densely spaced shoots in both freshwater (Werner and Zedler, 2002; Crain and Bertness, 2005; Ervin, 2005; Peach and Zedler, 2006; Herr-Turoff and Zedler, 2007) and coastal/brackish wetlands

(Bertness et al., 1992; Windham, 1999; Langlois et al., 2003; Fogel et al., 2004). Plants with this morphology may trap water column sediments or leaf litter, especially low-nutrient, senescent litter that tends to decompose slowly and accumulate (Troxler and Childers, 2009).

Decomposition of organic matter may also contribute to the development of topographical heterogeneity (Troxler and Childers, 2009). In wetlands, the rate of decomposition is often greater when litter has been subjected to wetting and drying, compared to litter that is constantly submerged (Reddy and Patrick, 1975; Brinson et al., 1981; Battle and Golladay, 2001). Therefore, organic matter may decompose more slowly and accumulate to a greater height on hummocks that are submerged for longer periods of time than on hummocks that are exposed to periodic inundation. In addition, deeper water may encourage plants to grow more adventitious roots towards the surface of the water (Fogel et al., 2004; Crain and Bertness, 2005), providing further opportunities to trap sediment and organic material and increase hummock height.

The decomposition of plant litter is influenced by factors other than water regime. These include intrinsic properties of the litter, such as toughness, nutrient content, and the presence of inhibitory chemicals (Boon and Johnstone, 1997; Quinn et al., 2000); and environmental conditions, such as water chemistry, temperature and biota (Brinson et al., 1981). In addition, the physical fragmentation of material and leaching of soluble components can be important decomposition processes that influence the formation of hummocks.

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In this study we investigated the formation of hummocks by two emergent wetland plant species: a woody shrub, *Melaleuca ericifolia* Sm. (Swamp paperbark) and a reed, *Phragmites australis* (Cav.) Trin. ex Steud. (Common Reed). Specifically, we investigated whether hummock height is related to water depth by surveying the height of *M. ericifolia* and *P. australis* hummocks occurring across a range of water depths. We also conducted an experiment using litter bags positioned on hummocks where they experienced different water regimes (dry, submerged, or intermittently inundated). This experiment was used to test the hypothesis that the decomposition rate of organic matter on hummocks is influenced by water regime: particularly, that constantly submerged litter decomposes relatively slowly and contributes to the accumulation of organic matter on hummocks. The carbon and nitrogen content of litter was measured along with environmental characteristics that may influence decomposition rates, including temperature, electrical conductivity, dissolved oxygen and pH. We also conducted a leaching experiment to determine the percentage mass loss of litter that could be attributed to rapid leaching of soluble components.

2. Methods

2.1. Site description

The study took place at Dowd Morass (38°30′S, 147°51′E), a large (1500 ha) brackish wetland located adjacent to the mouth of the LaTrobe river and on the south-western shore of Lake Wellington in central Gippsland, Victoria, Australia. The morass is densely vegetated with *M. ericifolia* and *P. australis*, with fringing zones of *Typha domingensis* and *Juncus* spp. (Bailey et al., 2003). *M. ericifolia* hummocks are breeding sites for ibises, cormorants, spoonbills and egrets and the reserve is listed under the Ramsar Convention for its internationally significant water bird habitat.

Dowd Morass has a catchment area of about 65 km² and receives fresh water from the LaTrobe River, overland flow from the surrounding agricultural area and brackish water from Lake Wellington. Historically, the morass would have experienced fluctuating water levels and dried completely every 3–5 years (Bailey et al., 2003). A series of levees were constructed within the wetland between 1973 and 1975 that separated the wetland into two discrete areas. Dowd Morass has been artificially inundated almost continuously since 1975. A drawdown of water levels across the morass occurred in 1997–1998 and the wetland was dry for 173 d. Since re-flooding in 1998, water levels in Dowd Morass have been maintained between 0.3 and 0.8 m, even deeper than pre-drawdown levels (typically 0.2–0.6 m).

2.2. Study species

M. ericifolia is a small (<8 m), woody shrub that commonly dominates coastal and near-coastal wetlands of south-eastern Australia (Costermans, 1998). It grows mostly in poorly drained soils, swamps and stream flats (Bird, 1962; Costermans, 1998), although it can also tolerate well-drained soil (Bowkett and Kirkpatrick, 2003). Seedlings and young plants of many *Melaleuca* species are known to be highly tolerant of waterlogging (Ladiges et al., 1981; Salter et al., 2007) and are capable of active root growth in waterlogged soils through the production of aerenchyma in the roots (Ladiges et al., 1981). Although established seedlings can survive for extended periods fully submerged, plants that extend above the water line and have a greater proportion of their foliage above water are more likely to survive (Raulings et al., 2007). *M. ericifolia* also reproduces vegetatively and ramets are spaced >5 cm apart. Flooded plants of *M. ericifolia* often produce aerial roots that are positioned above or at the water's surface.

P. australis is a cosmopolitan, flood tolerant grass that grows 1–4 (–6) m high (Sainty and Jacobs, 1994; Roberts and Marston, 2000). It grows in wet soils along the edges of rivers and wetlands and on raised hummocks in flooded sites. *P. australis* is a rhizomatous perennial that can produce culms that are spaced centimetres apart when space is limited (Morris et al., 2008) or further apart under field conditions. In southern Australia, it exhibits a distinctly seasonal growth pattern and dies down over the Austral winter, leaving swards of emergent brown culms. In a glasshouse experiment, buds did not emerge from flooded soils and density, height and biomass are known to be negatively affected by salinity and flooding (Hellings and Gallagher, 1992). Once established, *P. australis* can persist under flooded conditions through the development of aerenchyma and by pressurised convective gas flow (Brix et al., 1992).

2.3. Hummock survey

To establish whether there was a relationship between hummock height and water depth, we conducted surveys at Dowd Morass on four separate occasions (April 6, May 20, July 19 and August 29, 2004). We measured hummock height and surrounding water depth of all hummocks located within eleven, 120 m long, 10 m wide belt transects. Transects were placed perpendicular to the shoreline, and included the minimum and maximum water depths (0–70 cm) that existed within the wetland during the study period. Hummock heights were calculated by measuring the distance between the bottom sediments and the uppermost surface of the hummock. Water depth was measured as the distance from the bottom sediments to the water surface adjacent to each hummock. Three replicate measurements (to nearest cm) of hummock height and water depth were taken from different sides of each hummock. Initially, hummocks were to be classified as dominated by either *M. ericifolia* or *P. Australis*. However, we identified variations on these two hummock types during the initial survey, and expanded the classification system to include hummocks with both *M. ericifolia* and *P. australis* ('Mixed' hummocks) and *M. ericifolia* hummocks with water bird nests ('Nest' hummocks). The measured height of Nest hummocks excluded relatively undecomposed nesting material (sticks, *P. australis* litter). The depth of nesting material on Nest hummocks was measured and recorded separately from hummock height. Because the water level changed between survey dates, we standardised all water depths in relation to the water level on 20th May 2004: the date when we measured the largest number of hummocks.

2.4. Decomposition experiment

The decomposition experiment was conducted between May and August 2004. The experiment was arranged in a completely randomised block design, with water regime as a fixed factor, and hummock (block) as a random factor. We haphazardly selected 28 *M. ericifolia*-dominated and 20 *P. australis*-dominated hummocks located in the deeper regions of the wetland, in order to minimise fluctuations in water depth. We avoided hummocks with water bird nests because the presence of bird faeces may have influenced the decomposition rate of litter on the hummocks. Air-dried plant litter was confined in nylon mesh bags because the use of unconfined litter packs can lead to an overestimation of decomposition rates in wetlands due to the physical fragmentation of the litter (Yates and Day, 1983). Litter bags measured 18 cm × 15 cm with 0.5 mm mesh size. The bags were sewn on three sides and closed with a fishing line drawstring on the fourth side, which facilitated filling and allowed invertebrates into the bag [exclusion of invertebrate detritivores could lead to an underestimation of the decomposition rate (van Dokkum et al., 2002)]. The mass of litter in each bag was

similar to the density of natural litter fall recorded in the literature (Greenway, 1994; Asaeda et al., 2002). Leaves of *M. ericifolia* are very small (ca. 1 mm) and difficult to separate from stem material, and stem and leaf material are often shed together from the plant. Therefore, we combined leaves and stems in the same bag to simulate their natural release. Each litter bag contained ~15 g of *M. ericifolia* leaves and stems or ~25 g of *P. australis* leaves and stems. We filled litter bags with a 3:1 ratio of brown to green *Melaleuca* leaves to emulate natural litter fall observed in seed traps (funnel trap design) that were used in another study at Dowd Morass (Hamilton-Brown et al., 2008). The ratio of leaves:stems was approximately the same in each bag.

It was necessary to calculate a fresh to dry weight correction factor in order to compare the initial fresh weight to the final dry weight of retrieved litter bags. A handling correction factor was also applied to the final dry weight of all litter. This was necessary because *M. ericifolia* leaves and some *P. australis* fragments were small, and it was observed that a small amount of material escaped from the bags during handling. The handling correction was calculated by measuring the weight loss of litter from five *M. ericifolia* and five *P. australis* litter bags that were carried to the field site and immediately transported back to the laboratory. The difference between the initial dry weight and the final dry weight was assumed to be weight loss due to handling (-0.33 ± 0.06 g *M. ericifolia*, -1.95 ± 0.28 g *P. australis*). Environmental data, including water temperature, electrical conductivity, dissolved oxygen and pH were collected during litter bag deployment and collection times.

There were three treatments in the *M. ericifolia* decomposition experiment: 'dry', 'submerged', and 'intermittently inundated' water regimes. In the dry treatment, mesh bags containing *M. ericifolia* litter were placed on top of *M. ericifolia* hummocks, where they remained constantly above the water line but were exposed to rainfall. Litter bags in the intermittently inundated water regime treatment were also placed on top of the hummocks but in a position where they would become inundated following the anticipated increase in water level during the experiment and exposed again as the water receded (i.e. a wetting and drying treatment). Litterbags in the submerged treatment remained constantly submerged ca. 0.1 m below the water surface. Each bag in the submerged treatment was attached to a polystyrene float, which was tied to a bamboo stake and pushed into the sediment immediately adjacent to the side of the hummock. The experiment examining litter breakdown in *P. australis* was conducted in the same way as the *M. ericifolia* experiment, except only the dry and submerged treatments were applied. This was because the smaller top surface of the *P. australis* hummocks made it difficult to position litter bags so that they would be differentially inundated.

Litter bags were retrieved from the field after 9, 15 and 24 weeks. Before drying, the content of each litter bag was gently rinsed through sieves with 500 and 250 μm mesh size to remove all invertebrates, leaving attached biofilms intact. The invertebrates were briefly examined and identified to family level according to (Gooderham and Tsyrlin, 2002). *M. ericifolia* litter bags were classified according to the presence or absence of invertebrate detritivores. Litter was dried to constant weight at 50 °C (typical drying duration was 2–3 d). The results of the field experiments were expressed as the mean percentage mass loss of plant material in each water regime treatment group. Decomposition rates (k, natural log units d^{-1}) were calculated using the exponential loss decay model, $M_t = M_0\,e^{-kt}$, where M_t is the final dry mass after t days and M_0 is the initial dry mass (Enriquez et al., 1993).

Because litter quality has been identified as a factor contributing to decomposition rate, carbon, nitrogen concentrations (%) and C:N ratio were measured at the beginning of the experiment and at each retrieval time (Enriquez et al., 1993). A 2 g sub-sample of dry plant material was removed from four randomly selected litter bags from each of the treatments at each time point and ground to a fine, homogeneous powder talcum powder-like consistency for carbon and nitrogen analysis (LECO CHN 2000 analyser).

2.5. Leaching experiment

The purpose of the leaching experiment was to determine the percentage mass loss of *M. ericifolia* and *P. australis* litter that could be attributed to rapid leaching of soluble components. Twenty five litter bags were filled with 5 g of *M. ericifolia* and 25 bags were filled with 5 g of *P. australis* litter. Individual bags were placed in separate plastic buckets filled with ~9 L of tap water and randomly arranged on an outdoor bench. Five replicate litter bags for each species were retrieved after 6 h, 24 h, 48 h, 72 h and 1 week. The contents of each litter bag were rinsed through sieves with 500 and 250 μm mesh sizes, and dried to constant weight at 50 °C. The difference between the initial and final dry mass of litter at each time period was calculated as the percentage mass loss due to leaching.

2.6. Statistical analysis

Statistical analyses were conducted using R (version 2.10.1) statistical package for Windows. We carried out linear regression and correlation analyses on the survey data to quantify the relationships between hummock height and water depth for each hummock type. Box-plots and residual plots were used to check that the assumptions of normality, homogeneity of variances and linearity were met (Quinn and Keough, 2002).

Analysis of covariance (ANCOVA) was used to test the null hypothesis that there was no difference in the mean height of hummocks of different types, adjusting for water depth. There was no evidence of a violation of the assumption of homogeneity of slopes because there was no significant interaction between hummock type and water depth ($F_{4,320} = 2.172$, $P = 0.072$). Following the global ANCOVA, planned comparisons were used to determine specific height differences among hummock types.

Decomposition experiment data were analysed as a completely randomised block analysis of variance (ANOVA), with water regime (submerged, intermittently inundated and dry) and hummock (block) as main effects. Due to the loss of some replicates, all three treatments did not occur on all hummocks. Therefore, the dry and intermittently inundated treatments were compared to the submerged treatment separately. This was necessary because treatments must occur on the same hummock to be comparable in a randomised block design (G. Quinn, personal communication). The response variable was the mean percentage mass loss of *M. ericifolia* or *P. australis* litter from litter bags after 9, 15 or 24 weeks in the wetland. The percentage mass loss from submerged *M. ericifolia* litter bags with and without invertebrate detritivores was compared with a Student's *t*-test. Invertebrates were not deliberately excluded from litter bags; rather this was a comparison between litter bags with and without observed invertebrate colonisation.

One-way ANOVA was used to compare differences in C (%), N (%), and C:N between water regime treatments in the decomposition experiment, and differences in mean mass loss (%) from litter bags retrieved at different times during the leaching experiment. Significant differences in a group means were further investigated using Tukey's Honestly Significant Difference (HSD) test.

3. Results

3.1. Water characteristics

At the beginning of our study in April 2004, the median water depth was 44.5 cm, which increased to 65 cm in late June and decreased to 59 cm by the end of August (Fig. 1). During this time
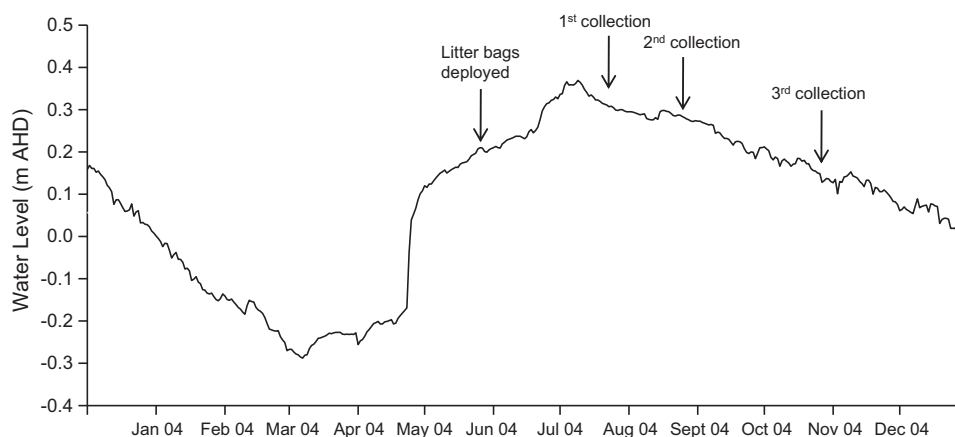
Fig. 1. Surface water depth (metres above Australian Height Datum) at Dowd Morass in 2004.

the recorded water temperature ranged from 9.5 to 26 °C; electrical conductivity of the surface water ranged from 8.5 to 12 mS cm^{-1} and dissolved oxygen from 8.7 to 13.7 mg L^{-1}. The pH of surface water surrounding the hummocks ranged from 5.5 to 6.8.

3.2. Relationship between hummock height and water depth

A total of 318 hummocks were measured during the field survey (Table 1). There was a significant linear relationship between water depth and hummock height for all hummock types (Table 1). Hummocks were smaller and occurred at higher densities closer to the shoreline and became larger (in height and width) and further spaced as the water became deeper (Fig. 2). All hummock types occurred across the water depth gradient, except for Nest hummocks, which did not occur in water depth <26 cm (Table 1).

There was a significant difference in the height of different types of hummocks, adjusted for water depth ($F = 48.4$, $P < 0.001$; Table 1). *P. australis* hummocks (60.5 ± 2.2 cm) were significantly taller than *M. ericifolia* hummocks (45.9 ± 1.1 cm) ($F = 89.2$, $P < 0.001$), but there was no significant difference in height between *P. australis* and Mixed hummocks. *M. ericifolia* hummocks with nests (68.1 ± 2.3 cm) were significantly taller than *M. ericifolia* hummocks without nests (45.9 ± 1.1 cm) ($F = 6.1$, $P = 0.014$). In addition, Nest hummocks were covered with an average of 11.5 ± 1.1 cm of nesting material (i.e. branches, twigs and grasses) that was not counted as part of hummock height.

3.3. Decomposition of litter on hummocks

An unexpectedly large flooding event occurred in July 2004 between the 9 and 15 week retrieval times (~20 cm increase in depth) and completely inundated many of the hummocks, which eliminated the dry treatment on those hummocks (Fig. 1). This reduced the number of *M. ericifolia* hummocks with the dry treatment from 28 to 9 hummocks and the number of replicate *P. australis* hummocks from 20 to 8 hummocks. Conversely, levee banks within the wetland prevented three *M. ericifolia* hummocks from being inundated sufficiently to create the intermittently inundated treatment (i.e. all litter bags on top of the hummock remained dry), and the number of hummocks with the intermittently inundated treatment was reduced from 28 to 25. This prevented the statistical comparison of some pairs of treatments.

Mass loss from *M. ericifolia* litter bags averaged $18.8 \pm 4.2\%$, $14.7 \pm 1.6\%$ and $13.2 \pm 6.4\%$ for submerged, intermittent and dry treatments respectively over the 24 week decomposition experiment (Table 2). After 9 weeks, submerged *M. ericifolia* litter had lost greater mass than dry *M. ericifolia* litter ($F = 20.8$, $P = 0.004$); however, there was no difference in % mass loss between the submerged and intermittently inundated treatments (Table 2). Differences in mass loss of *M. ericifolia* litter between water regime treatments were not statistically significant after 15 and 24 weeks in the field. Decay rates (k) for *M. ericifolia* litter were 0.0015 ± 0.0005 d^{-1}, 0.0010 ± 0.0001 d^{-1} and 0.0008 ± 0.0004 d^{-1} for submerged, intermittent and dry treatments respectively over the 24 week experiment.

Mass loss from *P. australis* litter bags averaged $21.9 \pm 4.7\%$ for the submerged treatment and $10.6 \pm 4.3\%$ for the dry treatment after 15 weeks (Table 2). There were too few *P. australis* litter bags remaining after 24 weeks to analyse this time point, because many bags had been washed away. After 9 weeks, submerged *P. australis* litter experienced significantly greater mass loss than dry litter ($F = 139.7$, $P < 0.001$; Table 2), however, the difference in mass loss between water regime treatments was no longer statistically significant after 15 weeks in the field. The decay rate (k) for *P. australis* litter was 0.0024 ± 0.0007 d^{-1} and 0.0011 ± 0.0005 d^{-1} for the submerged and dry treatments respectively.

We evaluated differences in final carbon and nitrogen levels between treatments due to decomposition. For *M. ericifolia* litter, % C decreased over the period of the experiment, while % N generally increased, although there was a slight decrease in % N around 15 weeks (Table 3). *M. ericifolia* litter exposed to intermittent inundation had higher % N ($F = 5.8$, $P = 0.036$; Table 3) and lower C:N ratio ($F = 4.9$, $P = 0.047$) compared to dry litter after 24 weeks in the field. There was no difference in % C in *M. ericifolia* litter among water regime treatments.

For *P. australis* litter, % C of submerged litter decreased rapidly after 9 weeks, resulting in a significant difference in % C ($F = 10.7$, $P = 0.017$; Table 3) and C:N ratio ($F = 8.2$, $P = 0.029$) between submerged and dry treatments after 15 weeks in the field. There was no difference in % N of *P. australis* litter between water regime treatments (Table 3).

3.4. Invertebrates in litter bags

The diversity of invertebrates found in the litter bags was low, and was dominated by chironomid larvae (bloodworms, *Chironomus* sp.). Chironomids were found on approximately 50% of the submerged *M. ericifolia* litter bags, but were rarely found on *P. australis* litter. There was no significant difference in the percentage mass loss of submerged *M. ericifolia* litter with and without chironomid larva ($P = 0.114$).

Table 1
Summary of linear regression of hummock height with water depth for four hummock types. 'Mixed' refers to hummocks with both *M. ericifolia* + *P. australis* and 'Nest' hummocks are those with water bird nests *P* values indicate significance level of regression coefficient. Heights are mean hummock height (cm) ± S.E., adjusted for water depth using analysis of covariance (different letters indicate significant differences in height between hummock types at *P* < 0.05).

Hummock type	n	F	P	r^2	Height (cm) (SE)	Water depth (cm)
Melaleuca ericifolia	203	223.1	<0.0001	0.53	45.9 (1.1)[a]	0–58
Phragmites australis	51	188.5	<0.001	0.79	60.5 (2.2)[b]	0–60
Mixed	35	53.0	<0.001	0.62	64.3 (1.8)[b]	0–57
Nest	29	9.8	0.004	0.26	68.1 (2.3)[b]	26–59

Table 2
Mean percentage mass loss (±standard error) over time of *M. ericifolia* litter and *P. australis* litter under different water regimes on hummocks.

Species	Water regime treatment	Mass loss (%)		
		9 weeks	15 weeks	24 weeks
M. ericifolia	Submerged	15.9 ± 1.2	15.8 ± 0.9	18.8 ± 4.2
	Intermittent	16.6 ± 0.8	18.4 ± 1.0	14.7 ± 1.6
	Dry	9.6 ± 1.1	11.3 ± 1.7	13.2 ± 6.4
P. australis	Submerged	16.6 ± 1.3	21.9 ± 4.7	
	Dry	4.7 ± 0.7	10.6 ± 4.3	

3.5. Leaching experiment

There was no significant difference between times (i.e. 6 h, 24 h, 48 h, 72 h and 1 week time points) in the percentage mass loss of *M. ericifolia* litter ($F = 0.9$, $P = 0.462$) or *P. australis* litter ($F = 1.1$, $P = 0.372$). Therefore, most of the mass loss occurred within the first 6 h of submersion. On average, *M. ericifolia* litter lost $8.7 \pm 1.5\%$ SE dry weight and *P. australis* lost $5.5 \pm 1.5\%$ dry weight due to leaching after submersion for one week.

4. Discussion

4.1. Hummock-building

Our study demonstrated a positive relationship between hummock height and water depth in a permanently flooded wetland. This result is consistent with a survey of three wetlands in Wisconsin, USA, where *Carex stricta* tussocks were found to be taller, wider and spaced further apart in the wetland with deepest standing water (Peach and Zedler, 2006). Similarly, in experiments involving *C. stricta*, taller tussocks developed under constantly high water levels (18 cm above the soil surface) while constantly low water levels (18 cm below the soil surface) produced shorter hummocks (Lawrence and Zedler, 2008, in press).

The positive relationship between hummock height and water depth implies increased accumulation of organic or inorganic material at greater depth. For organic material, this entails decreased decomposition and/or increased production with increasing depth. Although we detected a difference in decomposition rates among water regimes, the direction was in contrast to our expectations. Submerged litter had a faster decomposition rate than litter that remained dry or was intermittently inundated. The difference between water regime treatments may be attributed to differences in mass loss due to leaching. *M. ericifolia* litterbags did not lose substantial mass after the first 9 weeks in the field. Both submerged and intermittently inundated treatments were inundated by 9 weeks,
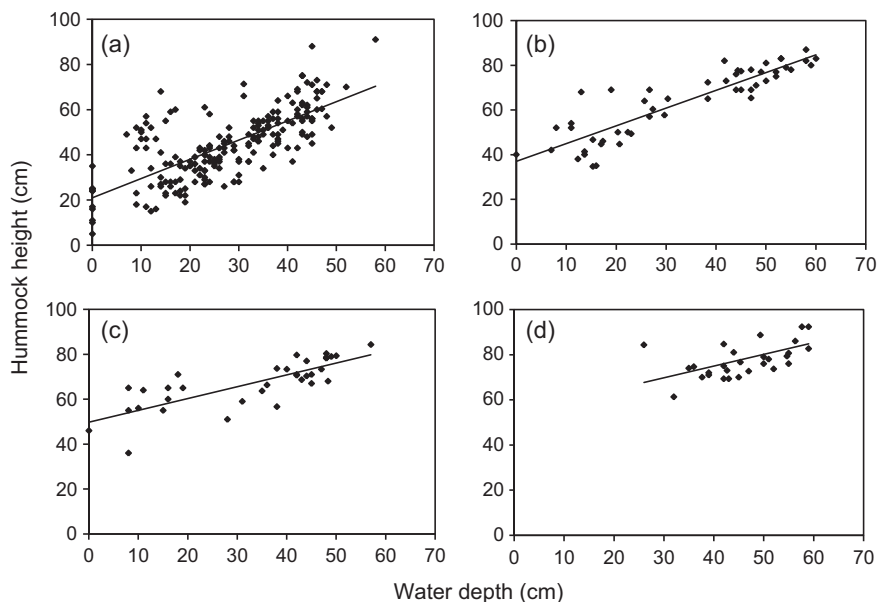
Fig. 2. Relationship between hummock height and water level (with linear regression line) for different hummock types: (a) *Melaleuca ericifolia* (*n* = 203), (b) *Phragmites australis* (*n* = 51), (c) Mixed (*M. ericifolia* + *P. australis*, *n* = 35) and (d) Nest (*M. ericifolia* with water bird nests, *n* = 29).

Table 3

Carbon, nitrogen concentrations and C:N ratio of decomposing *M. ericifolia* and *P. australis* litter exposed to constantly submerged, intermittently inundated or dry water regimes.

Species	Water regime treatment		Dry mass (%) and ratio of C and N			
			0 week	9 weeks	15 weeks	24 weeks
M. ericifolia	Submerged	C	51.6 ± 0.2	52.4 ± 0.3	49.7 ± 0.6	48.4 ± 0.9
		N	1.9 ± 0.0	2.3 ± 0.1	2.1 ± 0.1	2.3 ± 0.0
		C:N	27.2 ± 0.4	23.1 ± 0.6	23.7 ± 1.3	20.9 ± 0.28
	Intermittent	C	51.6 ± 0.2	52.7 ± 0.3	50.1 ± 0.3	48.6 ± 2.5
		N	1.9 ± 0.0	2.2 ± 0.1	2.0 ± 0.1	2.4 ± 0.0
		C:N	27.2 ± 0.4	24.2 ± 0.9	24.7 ± 1.2	20.2 ± 0.6
	Dry	C	51.6 ± 0.2	51.9 ± 0.3	50.8 ± 0.4	49.4 ± 1.0
		N	1.9 ± 0.0	2.2 ± 0.0	2.1 ± 0.1	2.2 ± 0.0
		C:N	27.2 ± 0.4	23.2 ± 0.1	24.1 ± 0.6	22.6 ± 0.6
P. australis	Submerged	C	42.2 ± 0.3	42.5 ± 0.3	33.3 ± 2.1	
		N	2.3 ± 0.4	2.2 ± 0.1	2.3 ± 0.0	
		C:N	20.7 ± 4.7	19.1 ± 0.8	14.2 ± 0.8	
	Dry	C	42.2 ± 0.3	42.1 ± 0.5	40.1 ± 0.1	
		N	2.3 ± 0.4	2.2 ± 0.0	2.3 ± 0.1	
		C:N	20.7 ± 4.7	18.8 ± 0.3	17.5 ± 0.9	

so there was opportunity for leaching of soluble components to occur. In contrast, the 'dry' litter would have experienced only a small amount of leaching by rainfall. The difference in mass loss between the dry and submerged/intermittent treatments in the field was ~7% after 9 weeks, similar to the 8.7% mass loss recorded for litter bags after submergence for one week in the leaching experiment. For *P. australis* litter, the difference between the dry and submerged treatments was consistent at ~11% after both 9 and 15 weeks in the field. In the leaching experiment, we detected 5.5% mass loss after one week of submergence. This suggests that leaching of soluble components may account for much of the difference in mass loss between exposed and submerged litter in the field. Leaching can be substantial, accounting for loss of up to 25% of the initial dry weight of leaves within the first 24 h of submergence (Webster and Benfield, 1986). The slow rate of decomposition of *M. ericifolia* and *P. australis* litter means that the initial mass loss due to leaching was large compared to any further decomposition that occurred during the study. Alternatively, litter that experienced drying may have decomposed more slowly due to desiccation of microbial and fungal communities. Studies over longer time frames may be required to elucidate differences in decomposition rates among water regime treatments.

It is plausible that increased production of organic material with increasing water depth may account for increased hummock height in deeper water. *P. australis* is known to increase allocation of biomass to aboveground structures with increasing water depth (Vretare et al., 2001), so it is possible that aboveground production could exceed decomposition to a greater extent in deeper water, resulting in greater accumulation of organic material with increasing water depth. Christensen et al. (2009) observed that *Typha glauca* had high production and low decomposition rates in the deepest and shallowest water depths in a marsh in Canada, and this resulted in increased accumulation of litter at those depths. However, they found that *P. australis* had lower rates of production and decomposition rates in deeper water and higher production and decomposition at dry or shallow sites, so overall litter accumulation did not differ among water depths (Christensen et al., 2009).

The accumulation of sediment trapped by plant roots is a common explanation for hummock formation (e.g. *Ira frutescens*, Bertness et al., 1992; *Puccinellia maritima*, Langlois et al., 2003). Other studies describe hummocks that are a combination of sediment and decaying litter [e.g. *Juncus effuses* (Ervin, 2007), *C. stricta* (Lawrence and Zedler, 2008)]. At Dowd Morass, the accumulation of organic matter makes up at least a portion of hummock eleva-

tion, because the presence of additional sources of organic matter, such as *P. australis* litter or ibis nesting material, increased the height of *M. ericifolia* hummocks for a given water depth. *P. australis* hummocks were on average 15–20 cm taller than *M. ericifolia* hummocks. This height difference might reflect the high annual litter fall of *P. australis* (Asaeda et al., 2002), because increased input of organic matter should build higher hummocks if this material is retained. *P. australis* can effectively retain its own decaying litter and more than 50% of deposition in *Phragmites* dominated marshes can be organic material (Rooth and Stevenson, 2000; Asaeda *et al.,* 2002). In our study, 'Mixed' hummocks (with both *M. ericifolia* and *P. australis* growing on them) were taller than *M. ericifolia* hummocks, and the same average height as *P. australis* hummocks. This suggests that the presence of *P. australis* on Mixed hummocks increased their average height.

The activities of nesting waterbirds may have also contributed to hummock-building. 'Nest' hummocks were the tallest hummocks recorded, and were taller than expected for a given water depth. In the Florida Everglades, guano deposits by nesting waterbirds have been linked to elevated phosphorus levels on tree islands (Givnish et al., 2008), which stimulate plant production and increase the rate of peat accretion (Craft and Richardson, 1998). Another way in which waterbirds may contribute to hummock-building is by the direct addition of organic nesting material. At Dowd Morass, water birds return to the same hummocks every year, building new nests on top of the old nests, and we observed that decomposed nesting material contributed to hummock height. This process is likely to be facilitated by the large amount of guano deposited during the breeding season. Consequently, bird nesting activities may help to maintain breeding hummocks at a height that reduces the risk that nests will be inundated.

4.2. Conclusion and implications of study

Our study demonstrated that hummock height increased with increasing water depth for the two dominant plant species in the wetland, *P. australis* and *M. ericifolia*. In this study, increased hummock height in deeper water was not a consequence of different decomposition rates of organic matter under variable water regimes, although a longer period of study may be required to further distinguish the effects of water regime. We posit that increased accumulation of organic material contributes to the greater height of hummocks in deeper water. Other factors, such as bird nesting material are also likely to be important contributors to hummock formation. Future studies that assess decomposition over longer

time frames and measure rates of organic matter accumulation would further elucidate the processes involved in hummock formation. Given the importance of hummock and hollow topography for the maintenance of plant diversity and breeding habitat for colonially nesting water birds, the maintenance of topographical heterogeneity should be a consideration when making water regime decisions in wetlands.

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References

Asaeda, T., Nam, L., Hietz, P., Tanaka, N., Karunaratnes, S., 2002. Seasonal fluctuations in live and dead biomass of *Phragmites australis* as described by a growth and decomposition model: implications of duration of aerobic conditions for litter mineralization and sedimentation. Aquat. Bot. 73, 223–239.

Bailey, P., Watkins, S., Morris, K., Boon, P., 2003. Do *Melaleuca ericifolia* S.M. leaves suppress organic matter decay in freshwater wetlands? Arch. Hydrobiol. 156, 225–240.

Battle, J.M., Golladay, S.W., 2001. Hydroperiod influence on breakdown of leaf litter in cypress-gum wetlands. Am. Midl. Nat. 146, 128–145.

Bertness, M.D., Wikler, K., Chatkupt, T., 1992. Flood tolerance and the distribution of *Iva-frutescens* across New-England salt marshes. Oecologia 91, 171–178.

Bird, E.C.F., 1962. The swamp paper-bark. Vic. Nat. 79, 72–81.

Boon, P.I., Johnstone, L., 1997. Organic matter decay in coastal wetlands: an inhibitory role for essential oil from Melaleuca alternifolia leaves? Arch. Hydrobiol. 138, 433–449.

Bowkett, L., Kirkpatrick, J., 2003. Ecology and conservation of remnant *Melaleuca ericifolia* stands in the Tamar Valley, Tasmania. Aust. J. Bot. 51, 405–413.

Brinson, M., Lugo, A., Brown, S., 1981. Primary productivity, decomposition, and consumer activity in freshwater wetlands. Annu. Rev. Ecol. Syst. 12, 123–161.

Brix, H., Sorrell, B.K., Orr, P.T., 1992. Internal pressurization and convective gas-flow in some emergent fresh-water macrophytes. Limnol. Oceanogr. 37, 1420–1433.

Christensen, J.R., Crumpton, W.G., van der Valk, A.G., 2009. Estimating the breakdown and accumulation of emergent macrophyte litter: a mass-balance approach. Wetlands 29, 204–214.

Costermans, L.F., 1998. Native Trees and Shrubs of South-eastern Australia. Landsdowne Publishing, Sydney.

Craft, C.B., Richardson, C.J., 1998. Recent and long-term organic soil accretion and nutrient accumulation in the everglades. Soil Sci. Soc. Am. J. 62, 834–843.

Crain, C.M., Bertness, N.D., 2005. Community impacts of a tussock sedge: is ecosystem engineering important in benign habitats? Ecology 86, 2695–2704.

Enriquez, S., Duarte, C., Sand-Jensen, K., 1993. Patterns in decomposition rates among photosynthetic organisms: the importance of detritus C:N:P content. Oecologia 94, 457–471.

Ervin, G.N., 2005. Spatio-temporally variable effects of a dominant macrophyte on vascular plant neighbors. Wetlands 25, 317–325.

Ervin, G.N., 2007. An experimental study on the facilitative effects of tussock structure among wetland plants. Wetlands 27, 620–630.

Fogel, B.N., Crain, C.M., Bertness, M.D., 2004. Community level engineering effects of *Triglochin maritima* (seaside arrowgrass) in a salt marsh in northern New England, USA. J. Ecol. 92, 589–597.

Givnish, T.J., Volin, J.C., Owen, V.D., Volin, V.C., Muss, J.D., Glaser, P.H., 2008. Vegetation differentiation in the patterned landscape of the central Everglades: importance of local and landscape drivers. Global Ecol. Biogeogr. 17, 384–402.

Gooderham, J., Tsyrlin, E., 2002. The Waterbug Book. CSIRO Publishing, Melbourne.

Greenway, M., 1994. Litter accession and accumulation in a *Melaleuca quinquenervia* (Cav.) S.T. Blake wetland in south-eastern Queensland. Aust. J. Mar. Freshw. Res. 45, 1509–1519.

Hamilton-Brown, S., Boon, P., Raulings, E., Morris, K., Robinson, R., 2008. Aerial seed storage in *Melaleuca ericifolia* Sm. (Swamp Paperbark): environmental triggers for seed release. Hydrobiologia.

Hellings, S.E., Gallagher, J.L., 1992. The effects of salinity and flooding on *Phragmites australis*. J. Appl. Ecol. 29, 41–49.

Herben, T., Novoplansky, A., 2008. Implications of self/non-self discrimination for spatial patterning of clonal plants. Evol. Ecol. 22, 337–350.

Herr-Turoff, A., Zedler, J.B., 2007. Does morphological plasticity of the *Phalaris arundinacea* canopy increase invasiveness? Plant Ecol. 193, 265–277.

Ladiges, P., Foord, P.C., Willis, R.J., 1981. Salinity and waterlogging tolerance of some populations of *Melaleuca ericifolia* Smith. Aust. J. Ecol. 6, 203–215.

Langlois, E., Bonis, A., Bouzille, J., 2003. Sediment and plant dynamics in saltmarshes pioneer zone: *Puccinella maritima* as a key species? Estuar. Coast. Shelf Sci. 56, 239–249.

Larkin, D., Vivian-Smith, G., Zedler, J., 2006. Topographical heterogeneity theory and ecological restoration. In: Falk, D., Palmer, M., Zedler, J. (Eds.), Foundations of Restoration Ecology; the Science and Practice of Ecological Restoration. Island Press.

Lawrence, B., Zedler, J., 2008. Restoring an ecological engineer: Carex stricta tussock composition and formation. In: 93rd ESA Annual Meeting , Milwaukee, Wisconsin.

Lawrence, B., Zedler, J. Formation of tussocks by sedges: effects of hydroperiod and nutrients. Ecol. Appl., in press.

Morris, K., Boon, P.I., Raulings, E.J., White, S.D., 2008. Floristic shifts in wetlands: the effects of environmental variables on the interaction between *Phragmites australis* (Common Reed) and *Melaleuca ericifolia* (Swamp Paperbark). Mar. Freshw. Res. 59, 187–204.

Peach, M., Zedler, J.B., 2006. How tussocks structure sedge meadow vegetation. Wetlands 26, 322–335.

Quinn, G., Keough, M., 2002. Experimental Design and Data Analysis for Biologists. Cambridge University Press, Cambridge.

Quinn, J.M., Burrell, G.P., Parkyn, S.M., 2000. Influences of leaf toughness and nitrogen content on in-stream processing and nutrient uptake by litter in a Waikato, New Zealand, pasture stream and streamside channels. N. Z. J. Mar. Freshw. Res. 34, 253–271.

Raulings, E., Boon, P., Bailey, P., Roache, M., Morris, K., Robinson, R., 2007. Rehabilitation of Swamp Paperbark (*Melaleuca ericifolia*) wetlands in south-eastern Australia: effects of hydrology, microtopography, plant age and planting technique on the success of community-based revegetation trials. Wetlands Ecol. Manag. 15, 175–188.

Reddy, K., Patrick, W., 1975. Effect of alternate aerobic and anaerobic conditions on redox potential, organic matter decomposition and nitrogen loss in a flooded soil. Soil Biol. Biochem. 7, 87–94.

Roberts, J., Marston, F., 2000. Water Regime of Wetland and Floodplain Plants in the Murray-Darling Basin. CSIRO Land and Water, Canberra.

Rooth, J., Stevenson, J., 2000. Sediment deposition patterns in *Phragmites australis* communities: implications for coastal areas threatened by rising sea level. Wetlands Ecol. Manag. 8, 173–183.

Sainty, G.R., Jacobs, S.W.L., 1994. Waterplants in Australia. A Field Guide. Sainty and Associates, Sydney.

Salter, J., Morris, K., Bailey, P.C.E., Boon, P.I., 2007. Interactive effects of salinity and water depth on the growth of *Melaleuca ericifolia* Sm. (Swamp paperbark) seedlings. Aquat. Bot. 86, 213–222.

Saur, E., Bonheme, I., Nygren, P., Imbert, D., 1998. Nodulation of pterocarpus officinalis in the swamp forest of Guadeloupe (Lesser Antilles). J. Trop. Ecol. 14, 761–770.

Stribling, J.M., Cornwell, J.C., Glahn, O.A., 2007. Microtopography in tidal marshes: ecosystem engineering by vegetation? Estuar. Coasts 30, 1007–1015.

Troxler, T.G., Childers, D.L., 2009. Litter decomposition promotes differential feedbacks in an oligotrophic southern Everglades wetland. Plant Ecol. 200, 69–82.

van Dokkum, H.P., Slijkerman, D.M.E., Rossi, L., Costantini, M.L., 2002. Variation in the decomposition of *Phragmites australis* litter in a monomictic lake: the role of gammarids. Hydrobiologia 482, 69–77.

Vivian-Smith, G., 1997. Microtopographical heterogeneity and floristic diversity in experimental wetland communities. J. Ecol. 85, 71–82.

Vretare, V., Weisner, S., Strand, J., Graneli, W., 2001. Phenotypic plasticity in *Phragmites australis* as a functional response to water depth. Aquat. Bot. 69, 127–145.

Webster, J., Benfield, E., 1986. Vascular plant breakdown in freshwater ecosystems. Annu. Rev. Ecol. Syst. 17, 567–594.

Werner, K., Zedler, J., 2002. How sedge meadow soils, microtopography, and vegetation respond to sedimentation. Wetlands 22, 451–466.

Wetzel, P.R., 2002. Tree island ecosystems of the world. In: Sklar, F.H., van der Valk, A. (Eds.), Tree Islands of the Everglades. Kluwer Academic Publishers, Dordrecht.

Windham, L., 1999. Microscale spatial distribution of *Phragmites australis* (common reed) invasion into *Spartina patens* (salt hay)-dominated communities in brackish tidal marsh. Biol. Invasions 1, 137–148.

Yates, R., Day, F., 1983. Decay rates and nutrient dynamics in confined and unconfined leaf litter in the Great Dismal Swamp. Am. Midl. Nat. 110, 37–45.