

Modification of sediment redox potential by three contrasting macrophytes: implications for phosphorus adsorption/desorption

Kane T. Aldridge^{A,C} and George G. Ganf^{A,B}

^ASchool of Earth and Environmental Sciences, Environmental Biology,
The University of Adelaide, SA 5005, Australia.

^BCooperative Research Centre for Freshwater Ecology.

^CCorresponding author; email: kane.aldridge@adelaide.edu.au

Abstract. Freshwater macrophytes may increase sediment redox potential and the affinity of sediments for phosphorus through radial oxygen loss from their below-ground biomass. This study demonstrated that the ability to alter sediment redox potential differs between macrophytes, according to their capacity to transport oxygen. Of the emergent macrophytes, *Typha domingensis* increased sediment redox potential (218 mV above bare sediment) to a greater extent than *Bolboschoenus caldwellii* (41 mV above bare sediment). However, the inhibition of convective flow in *T. domingensis* reduced its oxidizing ability by 78 mV. In contrast, *Potamogeton crispus*, a submerged macrophyte, had no influence on sediment redox potential. The presence of *T. domingensis* also increased phosphorus uptake from the water column by $0.88 \text{ mg P m}^{-2} \text{ day}^{-1}$, above that of bare sediments. In addition, inundation predictably decreased sediment redox potential from 175 mV to -176 mV over a 42-day period. Similarly, the addition of cellulose (10 mg L^{-1}) decreased sediment redox potential by 42 mV. Consequently, deposition of organic debris may counteract the oxidizing effects of macrophytes that have a limited capacity to transport oxygen, such as *P. crispus*. Results suggest that macrophytes play an important role in facilitating the restoration of freshwater systems.

Extra keywords: *Bolboschoenus caldwellii*, convective flow, eutrophication, inundation, organic matter, *Potamogeton crispus*, *Typha domingensis*.

Introduction

Many catchment management schemes have failed to control eutrophication of freshwater systems by reducing external nutrient sources (Søndergaard *et al.* 1993; Granéli 1999). Consequently, recent research has focussed on internal nutrient sources, particularly sources of phosphorus, which is often identified as the most limiting element (Hutchinson 1957; Reynolds 1984; Oliver 1993). A major internal source of phosphorus to the overlying water column is desorption from sediments that have become saturated with phosphorus by excessive external loading (Boström *et al.* 1988; Marsden 1989).

Freshwater macrophytes may help control eutrophication by creating oxidized conditions that prevent desorption of phosphorus from otherwise reducing sediments to the overlying water column. This is a result of the loss of oxygen from the below-ground biomass of macrophytes, which oxidizes mineral ions to which phosphorus binds to in the sediment (Carpenter *et al.* 1983; Christensen *et al.* 1994; Moore *et al.* 1994; Sorrell 1994; Jespersen *et al.* 1998). The relative extent of sediment oxidation can be measured by redox potential. The capacity of macrophytes to influence sediment redox potential may vary between species according to the process used to transport gas and plant morphology.

Many macrophytes rely on simple gas phase diffusion of air from their above-ground biomass to the below-ground biomass, whereas others have the capacity to enhance the rate of transport through pressurized convective flow (Dacey 1981; Armstrong and Armstrong 1991; White and Ganf 1998; Sorrell and Tanner 2000). Consequently, the release of oxygen into the surrounding sediments may be greater than through simple diffusion. Owing to a greater leaf area exposed to the atmosphere, emergent macrophytes may be able to obtain, transport and release more oxygen into the surrounding sediment than submerged macrophytes.

This study examined whether three morphologically different species influenced sediment redox potential. *Typha domingensis* (Pers.) Steudel is an emergent macrophyte that grows to 4 m and its internal lacunal system permits convective flow (Brix *et al.* 1992). *Bolboschoenus caldwellii* (V. Cook) Soják is also an emergent macrophyte, although it only grows to 90 cm. Brix *et al.* (1992) demonstrated that *Bolboschoenus medianus* (V. Cook) Soják, a species morphologically similar to *B. caldwellii*, relies on simple diffusion to transport oxygen to its below-ground biomass. *Potamogeton crispus* L. is a submerged macrophyte.

Other *Potamogeton* spp. as well as *Myriophyllum* sp. probably rely on simple diffusion to transport oxygen, however,

individuals with emergent flora spikes are able to generate pressure differentials (3–6 kPa) that drive convective flow (Schuette and Klug 1995; Heilman and Carlton 2001). As *P. crispus* had no floral spikes or emergent tissue during the experimental period, it is unlikely to have exhibited convective flow.

Four hypotheses were developed. First, convective flow in *T. domingensis* allows it to increase sediment redox potential more than *T. domingensis* where convective flow has been inhibited. Second, emergent macrophytes that possess convective flow (*T. domingensis*) raise sediment redox potential more than emergent macrophytes reliant on diffusion (*B. caldwellii*). Third, emergent macrophytes (*T. domingensis* and *B. caldwellii*) raise sediment redox potential more than submerged macrophytes (*P. crispus*). Fourth, *T. domingensis* increases sediment redox potential and immobilizes mineral ions, which causes sediments beneath *T. domingensis* to adsorb greater amounts of phosphorus than bare sediments. These primary objectives were examined in order to analyse the effectiveness of macrophytes in management schemes aiming to restore freshwater systems.

The influence of inundation and the addition of cellulose, a surrogate of organic matter, on sediment redox potential were also examined. This was undertaken to determine to what extent the natural microbial community present in the sediments used was able to reduce the redox potential and whether carbon deposition increases oxygen consumption by microbes, and counteracts the ability of macrophytes to oxidize sediments.

Methods

Potting procedure

Three outdoor pond experiments were conducted at The University of Adelaide. Plastic pots were filled with sandy loam and a slow release fertilizer (8 to 9 month Osmocote) was added at a loading rate equivalent to $100 \text{ g N m}^{-2} \text{ year}^{-1}$ (Morris and Ganf 2001). Sediments were capped with clay (Morris and Ganf 2001) to minimize the loss of nutrients and limit algal growth, and inundated with water. Plant material was collected from Barker Inlet (34°49'S, 130°34'E), transplanted to these pots and allowed to establish before the commencement of the experiments.

Measurements of sediment redox potential

Five Hanna combination platinum oxidation–reduction potential electrodes were calibrated with Hanna redox solution and given 3 min to equilibrate with the sediment before measurements were recorded by a data-taker (Data-taker50). Electrodes were rinsed thoroughly with reverse-osmosis water before further measurements were taken. Redox potential measurements were taken 2 cm below the sediment surface because of the importance of the surface layer to sorption of phosphorus (Jensen and Andersen 1992).

Influence of inundation and organic matter on sediment redox potential

Individual 25-L plastic pots were placed in separate 50-L containers and sediments were inundated with 18 cm of water. Redox potential measurements were taken 3 times weekly for 6 weeks. Seventeen days

after the commencement of the experiment, a suspension of cellulose was injected below the clay surface of three pots at a carbon loading of 10 mg L^{-1} . Deionized water was injected below the surface of the remaining three pots.

Influence of macrophytes on sediment redox potential

Twelve 25-L pots were planted with individual *T. domingensis* ramets; six pots with three *B. caldwellii* ramets; six pots with five *P. crispus* ramets; and six pots remained bare. *Potamogeton crispus* did not have floral spikes throughout the experiment and were unlikely to exhibit convective flow (Heilman and Carlton 2001). Sediments were inundated with 12 cm of water and weekly redox potential measurements were taken. Sixty-eight days after the initial redox potential measurements, all leaves of each *T. domingensis* ramet were pierced twice a week with a hypodermic needle to prevent pressurization and convective flow (White and Ganf 1998). All *T. domingensis* leaves in six of the twelve pots were immediately resealed with a non-toxic marine grade silicon sealant (Sikaflex), to control for the act of piercing. At 117 days after the commencement of the experiment, redox potential measurements were taken using two oxidation–reduction potential electrodes at 0–1 cm and 10–11 cm below the sediment surface. This was carried out in all pots of *T. domingensis* (resealed), *B. caldwellii*, *P. crispus* and bare sediments.

Plant growth during the experimental period was measured for each species by measuring initial and final dry weights and photosynthetic area. Initial dry weights were: *T. domingensis* (pierced) $29.2 \pm 12.73 \text{ g}$; *T. domingensis* (resealed) $26.9 \pm 8.04 \text{ g}$; *B. caldwellii* $2.9 \pm 0.26 \text{ g}$; and *P. crispus* $0.1 \pm 0.01 \text{ g}$. Dry weights were measured after plant portions were separated and dried at 80°C. Relative growth rate (RGR) was calculated using the equation of Harper (1977).

Influence of *Typha domingensis* on sediment adsorption of phosphorus

Two *T. domingensis* ramets were planted in each of six 46-L pots and six pots were disturbed to control for planting, but remained bare. Sediment redox potentials were measured daily, 0–1 cm below the sediment surface. Following this, samples were taken from the overlying water and analysed for soluble reactive phosphorus using the method described by Mackereth *et al.* (1989). Inorganic phosphorus, in the form of di-potassium hydrogen orthophosphate (K_2HPO_4), was added at daily intervals to each pot to maintain a soluble reactive phosphorus concentration of $40 \mu\text{g L}^{-1}$. This concentration was chosen to mimic those found in many Australian waterways (Oliver *et al.* 1993). Initial and final sediment samples (5 mL) were collected from the sediment surface of three vegetated and three bare pots and analysed for total phosphorus. Initial and final measurements of the photosynthetic area, number of culms, number of leaves and leaf lengths were also measured for each pot containing *T. domingensis*.

Statistical analyses

All statistical analyses were performed using JMP-IN version 3.2.1 (SAS Institute Inc., Cary, NC, USA). All samples were assessed for normality (Shapiro–Wilk test) and homogeneity (O'Brien test). Errors were calculated and are reported as standard deviations. Statistical differences were analysed using *t*-tests, one-way and two-way ANOVAs, and Tukey's honestly significant difference test. Wherever an α of less than 0.05 is reported, a Bonferroni adjustment has been applied to α to maintain the experiment-wise error rate (Day and Quinn 1989).

Results

Influence of inundation and organic matter on sediment redox potential

Within 24 h of inundation, the sediment redox potential had dropped from $175 \pm 35.1 \text{ mV}$ to $89 \pm 16.5 \text{ mV}$ and reached

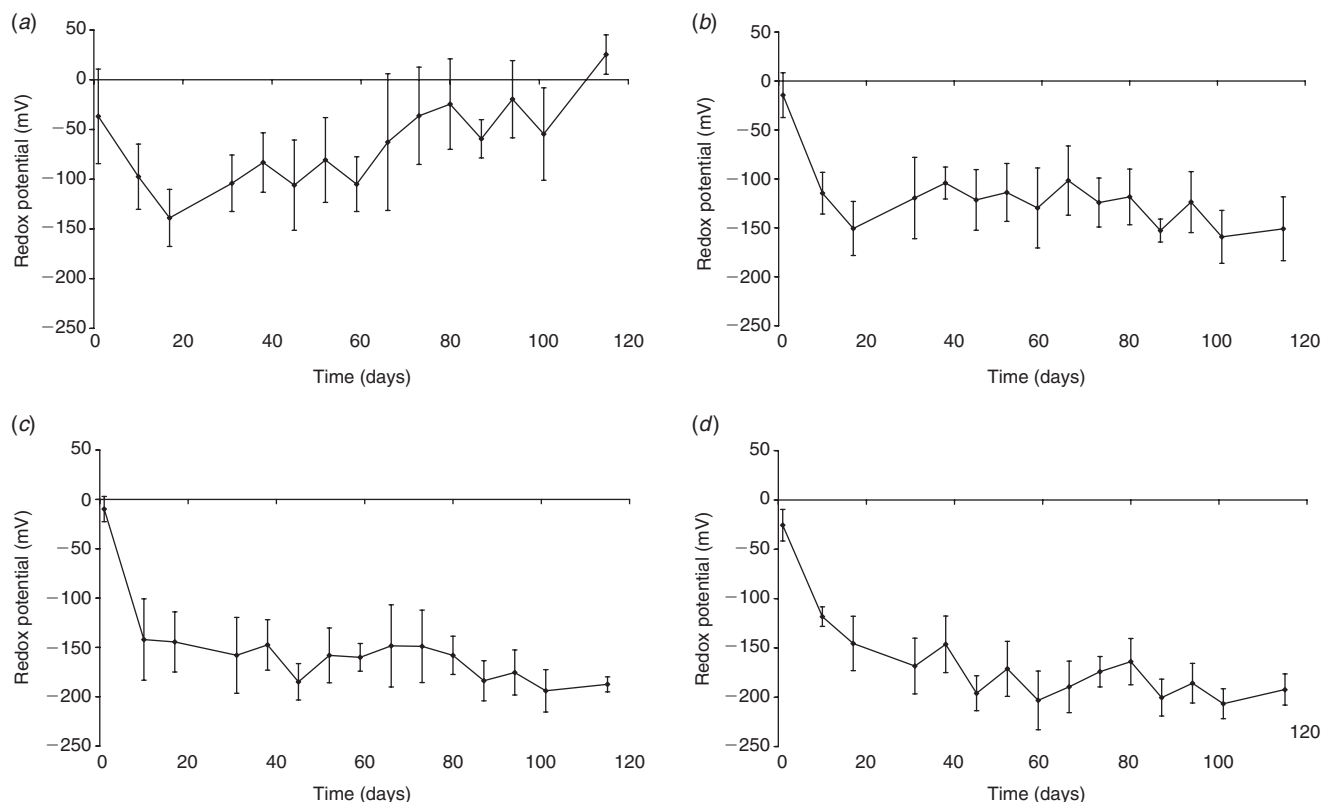


Fig. 1. Change in sediment redox potential beneath (a) *Typha domingensis*, (b) *Bolboschoenus caldwellii*, (c) *Potamogeton crispus* and (d) bare sediments. Redox potential measurements taken at depth of 2 cm. Error bars represent standard deviations ($n = 6$).

negative values (-6 ± 24.8 mV) by Day 13. After 42 days, the redox potential had reached -176 ± 35.7 mV. The addition of cellulose decreased the redox potential of sediments further. Before the addition of cellulose, the redox potentials were -64 ± 40.6 mV and -52 ± 23.8 mV for the control and cellulose treatment, respectively, and were not significantly different ($P = 0.4621$, $n = 3$, $\alpha = 0.025$). Six days after the addition of cellulose, the redox potential was significantly lower in the sediments that had cellulose added (-121 ± 16.2 mV) relative to the control sediments (-78 ± 2.1 mV) ($P = 0.008$, $n = 3$, $\alpha = 0.025$).

Influence of macrophytes on sediment redox potential

Initially, sediment redox potential fell in all treatments until Day 17, when the redox potential of the bare and all of the vegetated sediments did not significantly differ and were approximately -145 mV (Fig. 1) ($P = 0.9157$, $n = 6$, $\alpha = 0.05$). The rate and magnitude of the decrease in redox was similar to the response observed following inundation (see above). After Day 17, the redox potential of the four treatments followed contrasting paths (Fig. 1).

At the completion of the experiment, there was a difference in the sediment redox potential between the various

treatments ($P < 0.0001$, $n = 6$, $\alpha = 0.05$) (Fig. 1). The redox potential of bare sediments and those under *P. crispus* continued to fall and reached -192 ± 15.8 mV and -187 ± 7.6 mV, respectively, and were not significantly different. The redox potential beneath *B. caldwellii* increased to -101 ± 35.4 mV and eventually stabilized at -151 ± 32.6 mV, which was significantly greater than the redox potential of the bare sediments and those beneath *P. crispus*. In contrast, the redox potential beneath *T. domingensis* continued to increase and reached 25 ± 19.8 mV, which was significantly higher than all other treatments, and some 218 mV higher than the bare sediments at the termination of the experiment.

Convective flow

The curtailing of convective flow, through leaf piercing, significantly decreased the redox potential of sediments beneath *T. domingensis* (Fig. 2). Before the piercing procedure began, there was no difference between the two treatments ($P = 0.7974$, $n = 6$, $\alpha = 0.025$). However, at the completion of the experiment, the sediment redox potential beneath *T. domingensis* with pierced, unsealed leaves was -53 ± 42.7 mV, as compared with 25 ± 19.8 mV beneath *T. domingensis* with resealed leaves ($P = 0.0046$, $n = 6$, $\alpha = 0.025$).

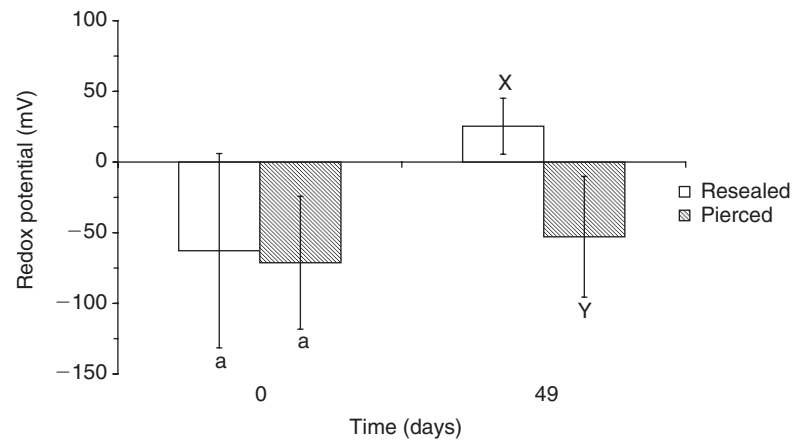


Fig. 2. Influence of leaf piercing on the sediment redox potential beneath *Typha domingensis*. Redox potential measurements were taken at depth of 2 cm before (Day 0) and after (Day 49) the piercing procedure began, with resealed treatment leaves immediately resealed. Error bars represent standard deviations. Shared letters of the same case represent values not significantly different ($n = 6$, $\alpha = 0.025$).

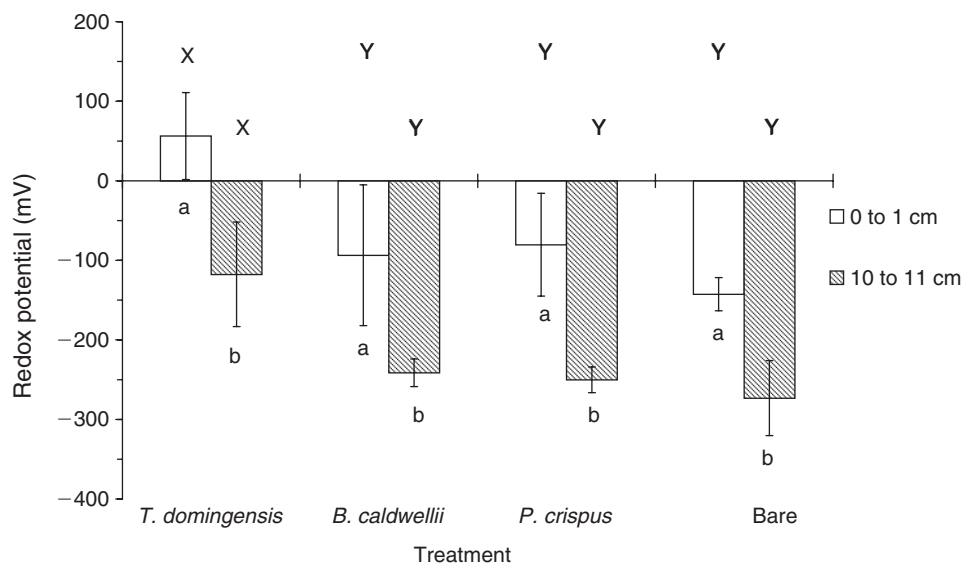


Fig. 3. Influence of *Typha domingensis*, *Bolboschoenus caldwellii*, *Potamogeton crispus* and bare sediments on redox potential at the sediment surface and at a depth of 10 cm. Error bars represent standard deviations. Shared lower case letters between two depths of the same treatment represent values that are not significantly different, according to Tukey's HSD test ($n = 6$, $\alpha = 0.0125$). Shared upper case letters between treatments of the same depth represent values that are not significantly different, according to Tukey's HSD test ($n = 6$, $\alpha = 0.025$).

Vertical redox potential profiles

The redox potential was influenced by both depth ($P < 0.0001$, $n = 6$, $\alpha = 0.05$) and species ($P < 0.0001$, $n = 6$, $\alpha = 0.05$), but there was no interaction between these primary factors ($P = 0.73$, $n = 6$, $\alpha = 0.05$) (Fig. 3). The redox potential was always greater at 0–1 cm than at 10–11 cm, irrespective of the treatment ($P = 0.0004$, 0.0035 , <0.0001 and <0.0001 for *T. domingensis*, *B. caldwellii*, *P. crispus*, and bare sediments, respectively, $n = 6$, $\alpha = 0.0125$).

In addition, the redox potential beneath *T. domingensis* was always greater than the other treatments, irrespective of depth ($P = 0.0004$ and <0.0001 for 0–1 cm and 10–11 cm, respectively, $n = 6$, $\alpha = 0.025$) (Fig. 3). Indeed, the mean redox potential at 0–1 cm for *T. domingensis* was 199 mV greater than that of the bare sediments. However, there was no difference between the redox potentials beneath *B. caldwellii*, *P. crispus* or bare sediments at the sediment surface or at a depth of 10–11 cm.

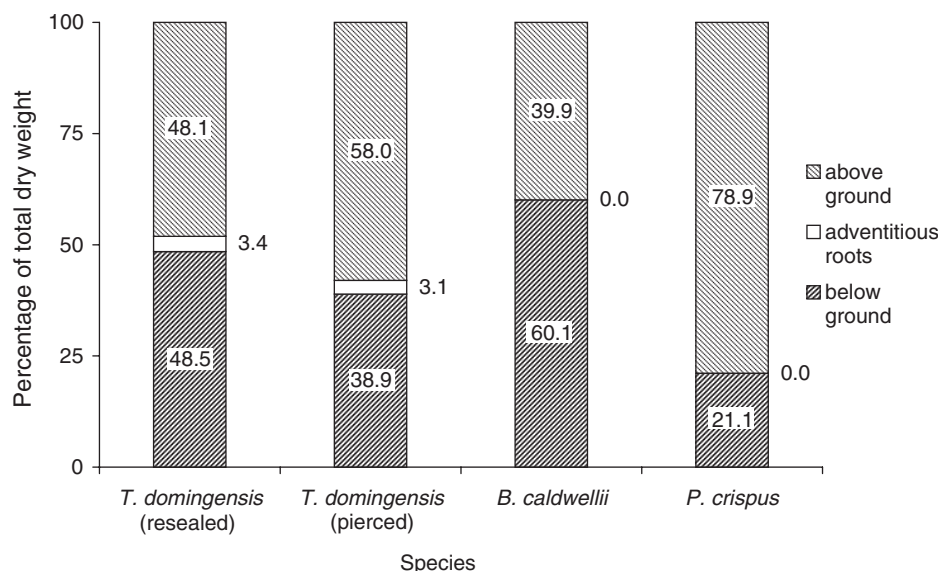


Fig. 4. Resource allocation in *Typha domingensis* (resealed and pierced), *Bolboschoenus caldwellii* and *Potamogeton crispus*. Reported values are percentages of total weight. Leaves of *T. domingensis* (resealed) were resealed following piercing; leaves of *T. domingensis* (pierced) plants were not.

Plant growth

The RGR was different ($P < 0.0001$, $n = 6$, $\alpha = 0.05$) between treatments, with the RGR of *B. caldwellii* ($38 \pm 1.4 \text{ mg g}^{-1} \text{ day}^{-1}$) being greater than resealed and pierced *T. domingensis* treatments (27 ± 2.8 and $28 \pm 2.1 \text{ mg g}^{-1} \text{ day}^{-1}$ respectively). In turn, both *T. domingensis* treatments had a higher RGR than *P. crispus* ($21 \pm 1.5 \text{ mg g}^{-1} \text{ day}^{-1}$). There was also a difference in photosynthetic area ($P < 0.0001$, $n = 6$, $\alpha = 0.05$) with *P. crispus* ($788 \pm 179.9 \text{ cm}^2/\text{pot}$) having a much lower photosynthetic area than resealed and pierced *T. domingensis* (17749 ± 6009.7 and $15762 \pm 1324.3 \text{ cm}^2/\text{pot}$, respectively) and *B. caldwellii* ($16795 \pm 2732.1 \text{ cm}^2/\text{pot}$). The final total dry weight varied between species ($P < 0.0001$, $n = 6$, $\alpha = 0.05$), with the weight of resealed and pierced *T. domingensis* treatments ($1236 \pm 107.8 \text{ g/pot}$ and $1091 \pm 242.6 \text{ g/pot}$, respectively) greater than *B. caldwellii* ($572 \pm 78.2 \text{ g/pot}$), which in turn was greater than *P. crispus* ($2 \pm 0.5 \text{ g/pot}$).

The species also allocated various amounts to above-ground biomass ($P < 0.0001$, $n = 6$, $\alpha = 0.05$), with *P. crispus* allocating a far greater proportion (78.9%) to its above-ground biomass than any other species (Fig. 4). Resealed *T. domingensis* allocated a greater proportion to its above-ground biomass than *B. caldwellii* (39.9%), but pierced *T. domingensis* did not. However, resealed and pierced *T. domingensis* plants did not allocate significantly different amounts to their above-ground biomass (48.1% and 58.0%, respectively). Each species also allocated different amounts to below-ground biomass ($P < 0.0001$, $n = 6$, $\alpha = 0.05$), with *Bolboschoenus caldwellii* allocating a greater proportion (60.1%) than all other species (Fig. 4). The allocation

to below-ground biomass between resealed and pierced *T. domingensis* treatments did not differ (48.5% and 38.9%, respectively). However, they allocated a significantly greater proportion to their below-ground biomass than *P. crispus* (21.1%). Both *T. domingensis* treatments allocated similar proportions to adventitious roots ($P = 0.8286$, $n = 6$, $\alpha = 0.05$).

Influence of *Typha domingensis* on sediment adsorption of phosphorus

The amount of phosphorus required to maintain a water column concentration of $40 \mu\text{g P L}^{-1}$ reflected the disappearance of soluble reactive phosphorus, presumably to the sediment. In the vegetated pots, a total of $2.7 \pm 0.24 \text{ mg P/pot}$ was added, whereas $2.0 \pm 0.25 \text{ mg P/pot}$ was added to the bare pots ($P = 0.0007$, $n = 6$, $\alpha = 0.05$) over the experimental period. At the conclusion of the experiment, cumulative uptake of phosphorus had reached $20.9 \pm 2.26 \text{ mg P m}^{-2}$ in the vegetated pots and $13.8 \pm 3.57 \text{ mg P m}^{-2}$ in the bare pots ($P = 0.0021$, $n = 6$, $\alpha = 0.05$) (Fig. 5). This was equivalent to $2.6 \pm 0.28 \text{ mg m}^{-2} \text{ day}^{-1}$ for vegetated pots and $1.7 \pm 0.45 \text{ mg m}^{-2} \text{ day}^{-1}$ for bare pots ($P = 0.002$, $n = 6$, $\alpha = 0.05$).

At the commencement of the experiment, the total phosphorus concentration in the vegetated sediments ($257 \pm 5.8 \text{ mg P kg}^{-1}$) was not significantly different from that of the bare sediments ($243 \pm 5.8 \text{ mg P kg}^{-1}$) ($P = 0.0474$, $n = 3$, $\alpha = 0.025$). Similarly, there was no significant difference between total phosphorus concentration of bare ($240 \pm 10.0 \text{ mg P kg}^{-1}$) and vegetated ($260 \pm 10.0 \text{ mg P kg}^{-1}$)

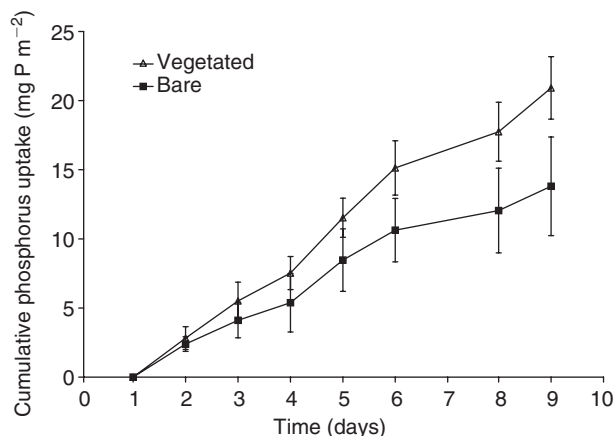


Fig. 5. Influence of *Typha domingensis* on phosphorus uptake (cumulative) from water column. Vegetated represents sediments with *T. domingensis* present; bare represents sediments with *T. domingensis* absent. Error bars represent standard deviations ($n = 6$).

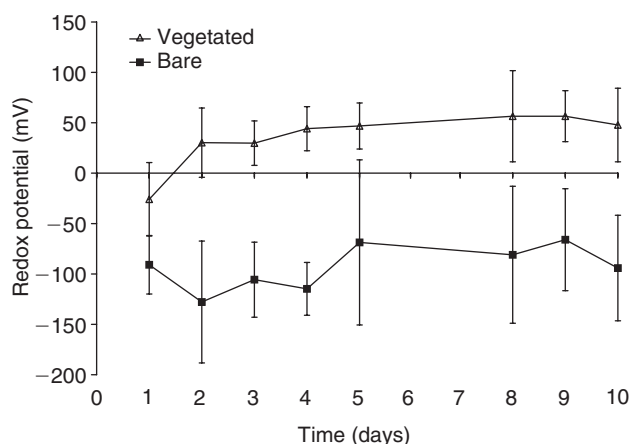


Fig. 6. The redox potential of sediments beneath *Typha domingensis* (vegetated) and bare sediments. Redox potential measurements were taken at sediment surface. Error bars represent standard deviations ($n = 6$).

sediments at the completion of the experiment ($P = 0.0705$, $n = 6$, $\alpha = 0.025$).

The sediment redox potential beneath *T. domingensis* was maintained above that of the bare sediments (Fig. 6). The average redox potential of bare and vegetated sediments was -93 ± 53.8 mV and 36 ± 38.7 mV, respectively, equivalent to an average difference of -129 mV ($P < 0.0001$, $n = 6$, $\alpha = 0.05$). At the completion of the experiment, the redox potential of vegetated sediments was 48 ± 38.7 mV, which was 142 mV above that of the bare sediments ($P = 0.0003$, $n = 6$, $\alpha = 0.05$) (Fig. 6).

Growth of *T. domingensis* during the experimental period was not significant. Initially, there were 13 ± 1.9 culms in each pot and 8 ± 0.5 culms per shoot. This was not significantly different from the final measurements, which were

15 ± 1.8 culms in each pot and 8 ± 0.7 culms per shoot ($P = 0.12$ and 0.58 , respectively, $n = 6$, $\alpha = 0.05$). Similarly, the average leaf length did not significantly change ($P = 0.11$, $n = 6$, $\alpha = 0.05$), with the average leaf length 99 ± 9.3 cm at the beginning of the experiment and 110 ± 12.2 cm at the completion of the experiment. Also, the photosynthetic area did not significantly change between 2315 ± 377.6 cm²/pot and 2879 ± 518.6 cm²/pot during the experimental period ($P = 0.06$, $n = 6$, $\alpha = 0.05$).

Discussion

The redox potential of freshwater sediments is dependant on a number of factors. This study has shown that sediment redox potential decreases immediately following inundation and gradually continues to fall as theoretically suggested by Ponnampetuma (1972). Although the decline in redox potential is likely to be a result of oxygen consumption by microbial metabolism (Ruttner 1963; Spiro and Stigliani 1996), the degree to which redox potential decreases is also a function of sediment oxygen demand. An increased carbon supply promotes additional oxygen consumption by microbes and use of alternative electron donors. Consequently, macrophytes with limited capabilities to transport oxygen may not overcome the reducing effects of inundation and organic matter deposition. In eutrophic systems with high oxygen demands, macrophytes with a limited ability to oxidize sediments may have little influence on the ability of the sediments to adsorb phosphorus (Flessa 1994). Callaway and King (1996) also showed that the ability of *Typha latifolia* L. to increase redox potential was diminished through increasing sediment oxygen demand by increasing temperature.

In this study, the supply of oxygen to the sediment from *T. domingensis* appears to override the reducing effects of both inundation and carbon addition. Callaway and King (1996) also demonstrated that *T. latifolia* could significantly increase sediment oxygen concentrations in comparison with bare sediments. *Typha domingensis* strongly oxidized the surrounding sediment to beyond 10 cm, which suggests that these sediments had a higher affinity for phosphorus than the bare sediments. This was supported by the greater phosphorus uptake from the water column. However, it was not demonstrated that the difference in phosphorus uptake was owing to adsorption onto the sediment surface, most likely because of the insignificant concentrations added to the water column (approximately 2.5 mg P/pot) in comparison to the sediment concentrations (approx. 250 mg P kg⁻¹ of sediment).

The difference in phosphorus uptake from the water column may have also been owing to direct uptake by macrophytes (Chen and Barko 1988; Maine *et al.* 1999) or microorganisms (Van Luijn *et al.* 1995). Chen and Barko (1988) suggest that uptake by macrophytes reduce phosphorus concentrations in porewater, such that desorption from vegetated sediments to the surrounding water column is

lower. Despite plant growth not accounting for the difference in phosphorus uptake from the water column in this study, it appears that macrophytes are capable of taking up phosphorus at a rate of $8.2 \text{ mg P m}^{-2} \text{ day}^{-1}$ (Brix 1997), which is higher than the rate observed in this study.

It is difficult to assess the influence of microorganisms on phosphorus desorption since there is conflicting evidence. Van Luijn *et al.* (1995) suggest that benthic diatoms also decrease the flux of nutrients from sediments by taking up nutrients, thus reducing the concentrations in the water column. On the other hand, Brunberg (1995) suggests that benthic colonies of *Microcystis* sp. increase the flux of phosphorus from the sediments.

Other studies have suggested that oxygenation of sediments by macrophytes enhances microbial activity and mineralization, which may increase phosphorus desorption (Boström *et al.* 1988; Stephen *et al.* 1997; Karjalainen *et al.* 2001). However, a majority of studies agree with the conclusions of the present study, suggesting that macrophytes increase the adsorption capacity of sediments and reduce phosphorus concentrations in water columns (Jaynes and Carpenter 1986; Boon and Sorrell 1991; Moore *et al.* 1994; Christensen and Andersen 1996; Wigand *et al.* 1997). The higher redox potential suggests that the vegetated sediments contain a greater number of insoluble mineral ions (Mortimer 1941, 1942; Oliver 1993; Webster *et al.* 2001), which would promote phosphorus adsorption.

The ability of macrophytes to oxidize sediments is primarily dependant on the process used to transport gas. When convective flow in *T. domingensis* was inhibited, its oxidizing ability was reduced despite no differences in plant morphology between treatments. Therefore, the difference in redox potential beneath the two *T. domingensis* treatments can only be attributed to the ability of the resealed treatment to carry out convective flow. Likewise, the principal reason for the difference in the ability of *T. domingensis* and *B. caldwelii* to increase redox potential is the ability of *T. domingensis* to carry out convective flow. However, some of the difference may be attributed to morphology since *T. domingensis* had a higher final dry weight and allocated a greater proportion of resources to its above-ground biomass. Callaway and King (1996) suggest that the extent of sediment oxidation is dependant on leaf areas for photosynthetic generation or stomatal conductance of oxygen. On the other hand, Chen and Barko (1988) suggest that the extent of sediment oxidation is dependant on root mass. Certainly both hypotheses are plausible. However, since the two macrophytes have similar photosynthetic areas, below-ground biomass appears to be a morphological factor contributing to the difference in sediment oxidation. Greater below-ground biomass would demand greater oxygen supply and may permit greater oxygen release.

Submerged macrophytes, such as *P. crispus*, depend on emergent floral spikes to initiate a pressure differential to

allow convective flow (Schuette and Klug 1995; Heilman and Carlton 2001). Since *P. crispus* did not have emergent floral spikes during the experimental period, it is unlikely that convective flow would have been a significant pathway for oxygenation of the sediments. However, the inability of *P. crispus* to alter the redox potential also appears to be dependent on morphology, a conclusion that is supported by previous studies (Chen and Barko 1988; Boon and Sorrell 1991), with emergent macrophytes oxidizing sediments to a greater extent. This is because redox potential beneath *P. crispus* was below that of *B. caldwelii*, despite both species relying on diffusion. Additional studies have suggested that submerged macrophytes can increase sediment redox potential (Flessa 1994; Christensen and Andersen 1996; Christensen 1999). However, Flessa (1994) showed that the oxidized region did not extend further than 1 mm from root tips. On the other hand, Christensen (1999) and Christensen and Andersen (1996) have shown that the isoetid plant, *Littorella uniflora* (L.) Ascherson, has the ability to oxidize underlying sediments and promote phosphorus adsorption onto those sediments, which may be attributed to their well-developed root biomass. It is likely that *P. crispus* does oxidize the surrounding sediments, but on a much smaller scale than is important for phosphorus adsorption because of its limited below-ground biomass.

The greater phosphorus uptake from the water column owing to the presence of macrophytes has important implications for management strategies of eutrophic freshwater systems. In this study, it was demonstrated that the presence of *T. domingensis* increases phosphorus uptake by $328.5 \text{ kg P km}^{-2} \text{ year}^{-1}$. A reduction in the amount of phosphorus available in the water column in freshwater systems is likely to limit excessive phytoplankton growth and decrease the occurrence of many toxic cyanobacterial blooms. Furthermore, phosphorus uptake may be one of the many benefits of macrophytes that help shift eutrophic freshwater systems back from turbid phytoplankton-dominated systems to clear, macrophyte-dominated systems.

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References

- Armstrong, J., and Armstrong, W. (1991). A convective through-flow of gases in *Phragmites australis* (Cav.) Trin. ex Steud. *Aquatic Botany* **39**, 75–88.
- Boon, P. I., and Sorrell, B. K. (1991). Biogeochemistry of billabong sediments. I. The effect of macrophytes. *Freshwater Biology* **26**, 209–26.

- Boström, B., Andersen, J. M., Fleischer, S., and Jansson, M. (1988). Exchange of phosphorus across the sediment-water interface. *Hydrobiologia* **170**, 229–44.
- Brix, H. (1997). Do macrophytes play a role in constructed treatment wetlands? *Water Science and Technology* **35**, 11–17.
- Brix, H., Sorrell, B. K., and Orr, P. T. (1992). Internal pressurization and convective gas flow in some emergent freshwater macrophytes. *Limnology and Oceanography* **37**, 1420–33.
- Brunberg, A. K. (1995). Microbial activity and phosphorus dynamics in eutrophic lake sediments enriched with *Microcystis* colonies. *Freshwater Biology* **33**, 541–55.
- Callaway, R. M., and King, L. (1996). Temperature-driven variation in substrate oxygenation and the balance of competition and facilitation. *Ecology* **77**, 1189–95.
- Carpenter, S. R., Elser, J. J., and Olson, K. M. (1983). Effects of roots of *Myriophyllum verticillatum* L. on sediment redox conditions. *Aquatic Botany* **17**, 243–9.
- Chen, R. L., and Barko, J. W. (1988). Effects of freshwater macrophytes on sediment chemistry. *Journal of Freshwater Ecology* **4**, 279–90.
- Christensen, K. K. (1999). Comparison of iron and phosphorus mobilization from sediments inhabited by *Littorella uniflora* and *Sphagnum* sp. at different sulfate concentrations. *Archiv für Hydrobiologie* **145**, 257–75.
- Christensen, K. K., and Andersen, F. Ø. (1996). Influence of *Littorella uniflora* on phosphorus retention in sediment supplied with artificial porewater. *Aquatic Botany* **55**, 183–97.
- Christensen, P. B., Revsbech, N. P., and Sand-Jensen, K. (1994). Microsensor analysis of oxygen in the rhizosphere of the aquatic macrophyte *Littorella uniflora* (L.) Ascherson. *Plant Physiology* **105**, 847–52.
- Dacey, J. W. H. (1981). Pressurized ventilation in the yellow waterlily. *Ecology* **62**, 1137–47.
- Day, R. W., and Quinn, G. P. (1989). Comparisons of treatments after an analysis of variance in ecology. *Ecological Monographs* **59**, 433–63.
- Flessa, H. (1994). Plant-induced changes in the redox potential of the rhizospheres of the submerged vascular macrophytes *Myriophyllum verticillatum* L., and *Ranunculus circinatus* L. *Aquatic Botany* **47**, 119–29.
- Granéli, W. (1999). Internal phosphorus loading in Lake Ringsjön. *Hydrobiologia* **404**, 19–26.
- Harper, J. L. (1977). 'Population Biology of Plants.' (Academic Press: London.)
- Heilman, M. A., and Carlton, R. G. (2001). Ebullitive release of lacunar gases from floral spikes of *Potamogeton angustifolius* and *Potamogeton amplifolius*: effects on plant aeration and sediment CH₄ flux. *Aquatic Botany* **71**, 19–33.
- Hutchinson, G. E. (1957). 'A Treatise on Limnology: Geography, Physics and Chemistry.' (John Wiley and Sons, Inc.: New York.)
- Jaynes, M. L., and Carpenter, S. R. (1986). Effects of vascular and nonvascular macrophytes on sediment redox and solute dynamics. *Ecology* **67**, 875–82.
- Jensen, H. S., and Andersen, F. Ø. (1992). Importance of temperature, nitrate, and pH for phosphate release from aerobic sediments of four shallow, eutrophic lakes. *Limnology and Oceanography* **37**, 577–89.
- Jespersen, D. N., Sorrell, B. K., and Brix, H. (1998). Growth and root oxygen release by *Typha latifolia* and its effects on sediment methanogenesis. *Aquatic Botany* **61**, 165–80.
- Karjalainen, H., Stefansson, G., Tuominen, L., and Kairesalo, T. (2001). Do submersed plants enhance microbial activity in sediment? *Aquatic Botany* **69**, 1–13.
- Mackereth, F. J. H., Heron, J., and Talling, J. F. (1989). 'Water Analysis: Some Revised Methods for Limnologists.' (Titus Wilson and Son Ltd: Kendal.)
- Maine, M. A., Suñe, N. L., Panigatti, M. C., Pizarro, M. J., and Emiliani, F. (1999). Relationships between water chemistry and macrophyte chemistry in lotic and lentic environments. *Archiv für Hydrobiologie* **145**, 129–45.
- Marsden, M. W. (1989). Lake restoration by reducing external phosphorus loading: the influence of sediment phosphorus release. *Freshwater Biology* **21**, 139–62.
- Moore, B. C., Lafer, J. E., and Funk, W. H. (1994). Influence of aquatic macrophytes on phosphorus and sediment porewater chemistry in a freshwater wetland. *Aquatic Botany* **49**, 137–48.
- Morris, K., and Ganf, G. G. (2001). The response of an emergent sedge *Bolboschoenus medianus* to salinity and nutrients. *Aquatic Botany* **70**, 311–28.
- Mortimer, C. H. (1941). The exchange of dissolved substances between mud and water in lakes. *Journal of Ecology* **29**, 280–29.
- Mortimer, C. H. (1942). The exchange of dissolved substances between mud and water in lakes. *Journal of Ecology* **30**, 147–201.
- Oliver, R. L. (1993). Phosphorus dynamics and bioavailability in turbid waters. In 'Proceedings of the National Workshop on Phosphorus in Australian Freshwaters'. (Ed. D. Simon.) pp. 93–103. (Land and Water Resources Research and Development Corporation: Wagga Wagga.)
- Oliver, R. L., Hart, B. T., Douglas, G. B., and Beckett, R. (1993). Phosphorus speciation in the Murray and Darling Rivers. *Chemistry in Australia* **60**, 392–7.
- Ponnamperuma, F. N. (1972). The chemistry of submerged soils. *Advances in Agronomy* **24**, 29–96.
- Reynolds, C. S. (1984). 'The Ecology of Freshwater Phytoplankton.' (Cambridge University Press: Cambridge.)
- Ruttner, F. (1963). 'Fundamentals of Limnology.' (University of Toronto Press: Toronto.)
- Schuette, J. L., and Klug, M. J. (1995). Evidence for mass flow in flowering individuals of the submersed vascular plant *Myriophyllum heterophyllum*. *Plant Physiology* **108**, 1251–8.
- Søndergaard, M., Kristensen, P., and Jeppesen, E. (1993). Eight years of internal phosphorus loading and changes in the sediment phosphorus profile of Lake Søbygaard, Denmark. *Hydrobiologia* **253**, 345–56.
- Sorrell, B. K. (1994). Airspace structure and mathematical modelling of oxygen diffusion, aeration and anoxia in *Eleocharis sphacelata* R. Br. roots. *Australian Journal of Freshwater Research* **45**, 1529–41.
- Sorrell, B. K., and Tanner, C. C. (2000). Convective gas flow and internal aeration in *Eleocharis sphacelata* in relation to water depth. *Journal of Ecology* **88**, 778–89.
- Spiro, T. G., and Stigliani, W. M. (1996). 'Chemistry of the Environment.' (Prentice Hall: Upper Saddle River.)
- Stephen, D., Moss, B., and Phillips, G. (1997). Do rooted macrophytes increase sediment phosphorus release? *Hydrobiologia* **342/343**, 27–34.
- Van Luijn, F., Van der Molen, D. T., Luttmer, W. J., and Boers, P. C. M. (1995). Influence of benthic diatoms on the nutrient release from sediments of shallow lakes recovering from eutrophication. *Water Science and Technology* **32**, 89–97.
- Webster, I. T., Ford, P. W., and Hancock, G. (2001). Phosphorus dynamics in Australian lowland rivers. *Marine and Freshwater Research* **52**, 127–37.
- White, S. D., and Ganf, G. G. (1998). The influence of convective flow on rhizome length in *Typha domingensis* over a water depth gradient. *Aquatic Botany* **62**, 57–70.
- Wigand, C., Stevenson, J. C., and Cornwell, J. C. (1997). Effects of different submersed macrophytes on sediment biogeochemistry. *Aquatic Botany* **56**, 233–44.

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