Hydrology and species-specific effects of *Bacopa monnieri* and *Leersia oryzoides* on soil and water chemistry[†]

S. C. Pierce,[1] S. R. Pezeshki,[1]* D. Larsen[2] and M. T. Moore[3]

[1] *Department of Biology, The University of Memphis, Memphis, TN 38152, USA*
[2] *Department of Earth Sciences, The University of Memphis, Memphis, TN 38152, USA*
[3] *USDA-Agricultural Research Service, National Sedimentation Laboratory, Oxford, MS 38655, USA*

ABSTRACT

In an 8-week greenhouse experiment, *Bacopa monnieri* (water hyssop) and *Leersia oryzoides* (rice cutgrass) were compared for nutrient assimilation as well as soil and water chemistry under variable flooding regimes using a nutrient solution rich in nitrogen (N) and phosphorus (P). Soil redox potential decreased in flooded treatments; however, mesocosms containing *B. monnieri* remained aerobic for much of the study, while flooded mesocosms containing *L. oryzoides* became moderately reduced. Soils containing *L. oryzoides* were higher in nitrogen. Generally, effluent concentrations of PO_4^{3-} were higher in *B. monnieri* mesocosms. *B. monnieri* immobilization of N and P was significantly less in below-ground tissues than *L. oryzoides*. P immobilization in *L. oryzoides* generally increased in response to flooding, while *B. monnieri* showed no detectable response. Results indicated that species-specific flood responses in plant nutrient status are due to differing interactions of *B. monnieri* and *L. oryzoides* with the soil environment. Additionally, *L. oryzoides* demonstrated greater P uptake than *B. monnieri* across treatments, resulting in decreased concentrations of PO_4^{-3} in effluent. Although N was also affected by flooding and species, generalizations on N allocation within the system are difficult to describe due to the changes in species of N in response to oxidation–reduction gradients and biotic assimilation. Copyright © 2009 John Wiley & Sons, Ltd.

KEY WORDS   agricultural ditches; wetland plants; phytoremediation; surface water quality; eutrophication; *Leersia oryzoides*; *Bacopa monnieri*

Received 1 October 2008; Accepted 25 February 2009

INTRODUCTION

It has been widely accepted that wetlands can improve water quality and that reversing the trend towards water-quality degradation associated with wetland losses will require a multi-faceted approach, including changes in farm management practices to decrease non-point pollution in agricultural areas (Day *et al.*, 2003). In an effort to establish 'environmentally friendly' guidelines for farmers, three government agencies, the United States Department of Agriculture Natural Resource Conservation Service (USDA-NRCS), United States Department of Agriculture Agricultural Research Service (USDA-ARS), and the National Association of Conservation Districts (NACD), are involved in an ongoing process to develop best management practices to decrease water pollution (as cited by Cooper *et al.*, 2004). Recent research suggests that the presence of vegetation in agricultural ditches could significantly impact water quality (Cooper *et al.*, 2004; Kröger *et al.*, 2007a)

Several studies in constructed wetlands have demonstrated that vegetation substantially reduces nutrient load by a number of potential mechanisms (Cronk and Fennessy, 2001). These mechanisms include physical responses, such as decreased erosion, decreased sediment suspension (Braskerud, 2001), and increased surface areas for microbial growth (Brix, 1997). Plants also alter soil chemistry. Specifically, plant roots exude a number of substances that alter pH and microbial growth (Jones *et al.*, 2004). Under flooded conditions, oxygen may diffuse from wetland plant roots (Armstrong and Beckett, 1987), possibly counteracting the trend towards reduction in the immediate rhizosphere (Reddy *et al.*, 1989). Finally, plants may reduce nutrient load through direct assimilation and immobilization. Although in constructed wetlands designed for high nutrient loads plants account for only a small fraction of nutrient removal, in low-load systems ($0.4–2.0$ N m^{-2} d^{-1}) plants can account for a substantial percentage of N removal (Peterson and Teal, 1996).

In agricultural ditches, seasonal and short-term fluctuations in water level can lead to plant stress either via water deficits or through soil reduction resulting from flooding. This hydrologic variability has also been demonstrated to affect both phosphorus and nitrogen concentrations (Kröger *et al.*, 2007b, 2008; Needelman *et al.*, 2007); however, species-specific plant responses to hydrologic variability and the subsequent changes in soil and water chemistry remain largely understudied, even though it

* Correspondence to: S. R. Pezeshki, Department of Biology, The University of Memphis, Memphis, TN 38152, USA.
E-mail: pezeshki@memphis.edu

is well established that flood-related stress affects wetland plant productivity and nutrient allocation (Pezeshki *et al.*, 2001). Previous research (Deaver *et al.*, 2005) demonstrated that *Leersia oryzoides* can reduce effluent phosphorus concentrations, even when compared to other plants common in agricultural ditches. The present study compares nutrient allocation in two wetland plant species *L. oryzoides*, rice cutgrass, and *Bacopa monnieri*, water hyssop, to a range of water regimes ranging from drained to continuously flooded. We hypothesized that the deeper rooted *L. oryzoides* would have a greater impact on soil chemistry than *B. monnieri*, resulting in comparatively decreased water nutrient concentrations, but that this effect would be decreased under more intensive flooding due to decreased root elongation.

METHODOLOGY

Experimental design

Plants were collected from wild populations found in wetland cells at the Jamie L. Whitten Plant Materials Center in Coffeeville, MS, and grown under natural light in the Life Sciences Greenhouse at the University of Memphis. Plants were grown in pots 60 cm high constructed of 15-cm-polyvinyl chloride pipe filled with a 60 : 40 (v/v) mixture of washed play sand and field soil, to allow for adequate drainage. Field soil was obtained from the A_p horizon of the Waverly Silt Loam Series (Soil Conservation Service, 1989). Although the high sand content of the sand/soil mixture used in this study is not representative of agricultural ditches in the region, the hydraulic conductivity of such soils is so low that a well-drained control was essentially impossible given the hydroperiods under study. After placement in PVC pipes, plants were well-watered and well-drained for a period of 3 weeks prior to treatment initiation. During this time, plants were fertilized weekly with 500 ml of 20-20-20 Peter's fertilizer mixed with tap water at 1·25 g/l. More information about the geochemistry of the municipal water source is available in Larsen *et al.* (2003). The study was terminated 56 days after treatment initiation.

Soil moisture treatments

Flooding treatments followed procedures previously described in Pierce *et al.* (2007). A completely randomized design was employed, examining stress response of *L. oryzoides* across four soil moisture regimes. Each treatment was replicated 12 times, with individual plants being treated as replicates. After treatment initiation, plants were watered daily with approximately 2 l of a nutrient solution containing a maximum of 12 mg/l ammonium nitrate and a maximum of 5 mg/l sodium phosphate. These concentrations approximate the upper expected concentrations for agricultural ditches of the Mississippi River Delta in Arkansas and Mississippi (Bouldin *et al.*, 2004).

Treatments included a (1) well-watered, well-drained control; (2) well-watered, well-drained intermittently flooded treatment; (3) partially flooded treatment; and (4) continuously flooded treatment. Water level was manipulated by placing pots in polyethylene bags and raising or lowering the level of the bag to the appropriate distance from the top of the soil. Other details included:

1. A control with plants that was well-watered and allowed to drain freely.
2. An intermittently flooded treatment that was well-watered and well-drained except on days 7, 14, 19, 28, 35, and 45, when pots were flooded to 5 cm above soil surface for a period of 48 h.
3. A partially flooded treatment with water maintained at 15 cm below soil surface. Water level within the soil was checked periodically using an internal gauge constructed from 1·9 cm perforated PVC pipe.
4. A continuously flooded treatment with water maintained at 5 cm above the soil surface.
5. On days 7, 14, 19, 28, 35, and 45, partially flooded and continuously flooded pots were flooded an additional 15 cm of water for 48 h.

Any excess water was held in overflow buckets and used to maintain water conditions as described above. Standing water in the three flooded treatments was drained overnight and all treatments were refreshed with 7 l of nutrient solution once a week prior to the 48-h intermittent flood. This design was intended to mimic variable hydrologic conditions on both ditch slope and trough as represented by the partially flooded and continuously flooded treatments, respectively.

Soil redox potential (Eh) was monitored using platinum-tipped electrodes, a Model 250 A ORION redox meter and a calomel reference electrode (Thermo Orion, Beverly, MA, USA) as described by Patrick and DeLaune (1977). Redox electrodes (one at each depth) were placed at 10 cm and 30 cm below the soil surface. Measurements were replicated at least eight times per measurement day on days 0, 1, 9, 16, and 30, with measures in each pot at each depth being considered replicates.

Water analysis

Because of variations in evaporation rates, and occasional tears in the polyethylene bags, water for sampling was not consistently available for each replicate throughout the course of the study. Thus, individual experimental units could not be reliably measured over time. Consequently, water samples were collected from experimental units chosen on the basis of water availability in either the flooding apparatus (for intermittently flooded, partially flooded, and continuously flooded) or the overflow container (for the control and open container). Samples were taken 2 days after initiation of pulse flooding on days 16, 30, and 45.

The water pH and specific conductance were measured for samples collected on day 30 and 45 using

a pH Testr 2 double junction (Oaktron Instruments) and YSI 30 SCT, respectively. Raw samples were filtered using 0·47-μm nitrocellulose filter, a portion of the sample was used to measure ammonium concentration, while the remainder of the sample was stored in the dark at 10 °C to await anion testing. Ammonium concentrations were measured using a Hach DR/2000 direct reading spectrophotometer utilizing the low range test'n tube Hach method 10023 (range: 0·02 to 2·5 mg/l, standard deviation: +/−0·03 mg/l). Reactive orthophosphate concentrations were individually analysed with a HACH DR/2000 direct reading spectrophotometer using the PhosVer 3 Hach method 8048 (range: 0 to 2·5 mg/l, standard deviation: +/−0·02 mg/l). Concentrations of Fl^-, Cl^-, NO_2^-, Br^-, NO_3^-, and SO_4^{2-} were all measured using a Dionex DX-120 Ion Chromatograph. Concentrations of Fl^-, NO_2^-, and Br^-, were all near or below detection limits and are not included. Internal standards were used to calculate reproducibility for Cl^-, NO_3^-, and SO_4^{2-}. Concentrations, standard deviations, and % reproducibility were as follows: Cl^- standard: 2·62 +/− 0·35 mg/l (13·3% error); $NO3^-$ standard: 10·16 +/− 0·098 mg/l (0·961% error); SO_4^{2-} standard 14·6 +/− 0·67 mg/l (4·61% error).

Plant and soil nutrient analysis

Six soil cores per treatment were taken to a depth of 30 cm using a 3-cm-diameter soil probe. Each core was divided into a 0- to 15-cm-depth sample and a 15- to 30-cm-depth sample. Samples were air dried for 2 weeks and pulverized using a mortar and pestle, any root tissue greater than 1 mm in diameter was removed. Sub-samples of approximately 0·1 g were prepared using Kjeldahl digestion and analysed for N and P as described below.

Ten randomly chosen plants per treatment were analysed for tissue nutrient analysis. Plants were divided into above-ground and below-ground portions, air dried for 2 weeks, and weighed. Samples were then ground in a Wiley Mill until they passed through a 40 mesh screen. Sub-samples of approximately 0·2 g were prepared using Kjeldahl digestion and analysed for N and P as described below.

Plant and soil samples were digested according to QuikChem Method 10-107-06-2-E (detection limit 0·018 mg/l) for total Kjeldahl nitrogen (TKN) as described by Wendt (1997), and QuikChem Method 10-115-01-1-C (detection limit 0·015 mg/l) for total phosphorus (Lachat Instruments, 1995). Reproducibility for nitrogen and phosphorus using these methods are approximately 5% (Lachat Instruments, 1995; Horneck and Miller, 1998). The Kjeldahl digestion process stabilizes ammonium nitrogen and converts organic nitrogen into ammonium. Nitrate is not converted into ammonium. The phosphate digestion process converts organic and inorganic phosphorus to orthophosphate. Ammonium and orthophosphate were subsequently quantified by colorimetry using Lachat Instruments QuickChem FIA+ 8000 series Colorimeter.

Data analysis

Unless otherwise indicated, statistical analyses used the general linear model for ANOVA using SPSS 14 (SPSS, Inc., 2005), with two species and four levels of water regime as independent factors. Eh was analysed as a repeated measures with MANOVA, with Eh values at 10 and 30 cm depth analysed as correlated dependent variables. Final soil nutrient concentrations were analysed with a factorial MANOVA (water treatment × time), with concentrations at 15 and 30 cm depth as correlated dependent variables. Water chemistry measures were individually analysed with factorial ANOVA tests (water treatment × time). Plant nutrient data were evaluated with MANOVA, with above-ground and below-ground values as correlated dependent variables. Plant nutrient immobilization was calculated by multiplying the respective nutrient concentrations by the biomass of the same plant. Above-ground and below-ground immobilizations were analysed in a multivariate context as previously described.

RESULTS AND DISCUSSION

Results

Plants and soil. Prior to the initiation of the soil moisture treatment, the soil was aerated in all mesocosms at both 10 and 30 cm depth (Eh = 460 +/− 180 mV and 420 +/− 210 mV, respectively). However, following treatment initiation, flooded treatments showed a decline in Eh within 24 h, while drained mesocosms remained aerated. Flooded mesocosms containing *L. oryzoides* were moderately reduced at 10 and 30 cm depth by day 15, while mesocosms containing *B. monnieri* remained aerated at 10 cm depth until day 30. *B. monnieri* demonstrated consistently higher Eh at both depths, as indicated in Figure 1A and B ($F = 8·39$, $p < 0·0005$).

L. oryzoides produced greater total biomass compared with *B. monnieri*, but no treatment effect was observed (Table I). Root : shoot biomass ratios displayed a significant species × treatment interaction. Root : shoot ratios in *B. monnieri* were unaffected by flooding treatments ($F = 1·078$, $p < 0·368$), whereas flooding decreased root : shoot ratios in *L. oryzoides* ($F = 6·82$, $p < 0·0005$). All flooded treatments displayed significantly lower root : shoot ratios than the drained treatment ($p < 0·05$). Root : shoot biomass ratios in *L. oryzoides* were nearly an order of magnitude higher than in *B. monnieri* (Table I, for all pair-wise comparisons $p < 0·0005$).

Final soil nitrogen concentrations (mean at 0−15 cm = 0·149 +/− 0·016 mg/g, mean at 15−30 cm = 0·152 +/− 0·022 mg/g) did not significantly differ from those of initial concentrations (mean at 0−15 cm = 0·149 +/− 0·015 mg/g, mean at 15−30 cm = 0·163 +/− 0·022 mg/g). Nitrogen concentration at 15−30 cm decreased in response to flooding, an effect most pronounced in *L. oryzoides* (Figure 2). Both shallow and deeper samples in mesocosms containing *L. oryzoides* had higher nitrogen

Table I. Biomass, root : shoot ratio, and total plant immobilization of phosphorus and nitrogen.

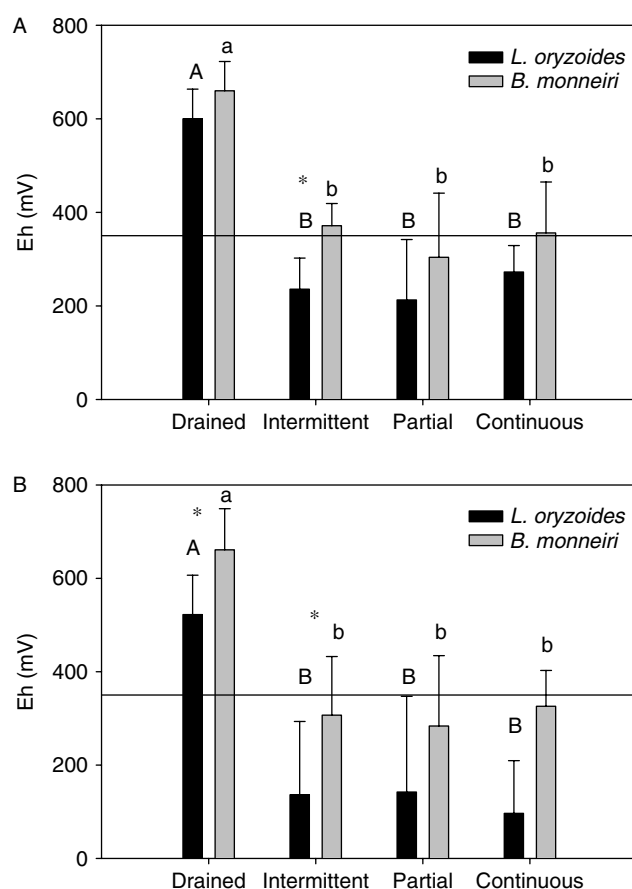| | Biomass (g) | R : S | Total plant immobilization (mg) | | | |
| | | | TP | | TKN | |
			Below-ground	Above-ground	Below-ground	Above-ground
Leersia						
Drained	58·5 + / − 18·4	0·81 + / − 0·039	41·4 + / − 15·8	98·7 + / − 16·0	141 + / − 63·5	341 + / − 79·0
Intermittent flooding	59·5 + / − 14·6	0·59 + / − 0·041	58·4 + / − 29·5	81·5 + / − 25·5	139 + / − 10·2	289 + / − 120
Partial flooding	56·3 + / − 14·7	0·57 + / − 0·039	59·3 + / − 26·7	81·8 + / − 22·2	123 + / − 49·6	294 + / − 102
Continuous flooding	67·6 + / − 17·4	0·43 + / − 0·041	62·4 + / − 16·8	111 + / − 41·5	110 + / − 49·3	356 + / − 136
Bacopa						
Drained	58·5 + / − 18·4	0·096 + / − 0·039	10·8 + / − 8·05	85·5 + / − 27·8	23·2 + / − 10·1	339 + / − 120
Intermittent flooding	40·5 + / − 8·75	0·076 + / − 0·039	6·25 + / − 4·30	87·5 + / − 34·2	19·3 + / − 9·4	324 + / − 153
Partial flooding	39·2 + / − 16·5	0·071 + / − 0·041	7·04 + / − 5·46	76·8 + / − 20·9	25·2 + / − 21·6	291 + / − 73·6
Continuous flooding	39·3 + / − 7·34	0·075 + / − 0·039	4·62 + / − 1·63	68·6 + / − 25·8	17·3 + / − 9·21	270 + / − 93·9

Figure 1. (A and B) Soil redox potential (Eh) on day 30 at 10 and 30 cm depth, respectively. The reference line indicates the approximate Eh at which oxygen is depleted. Species differences within a flooding treatment are indicated by an asterisk ($p < 0.05$). Differing upper-case letters indicate a significant difference from drained conditions for *L. oryzoides*, while differing lower-case letters indicate a significant difference from drained conditions for *B. monnieri* ($p < 0.05$). If no letters are present, no effect of flooding treatments was observed. Error bars indicate +/−1 standard deviation.
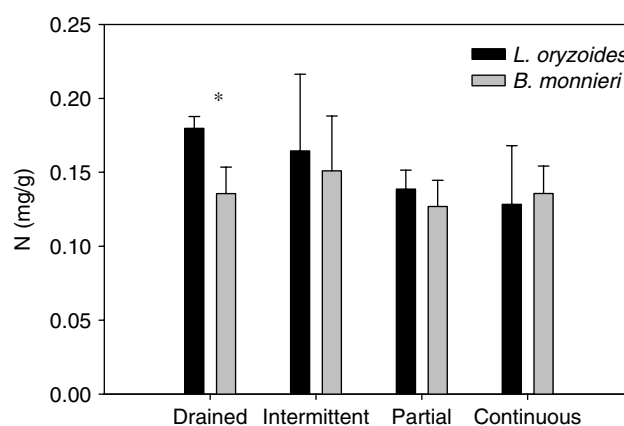

Figure 2. Soil N concentration at 15−30 cm depth on day 56, demonstrating a flood-related decline in soil N for mesocosms containing *L. oryzoides*. Differing upper-case letters indicate a significant difference from drained conditions for *L. oryzoides*, while differing lower-case letters indicate a significant difference from drained conditions for *B. monnieri* ($p < 0.05$). If no letters are present, no effect of flooding treatments was observed. Error bars indicate +/−1 standard deviation.

than those containing *B. monnieri* (F = 6·46, p = 0·003); however, these differences were negated by flooding. Final soil phosphate concentration (mean at 0−15 cm = 0·0178 + / − 0·050, mean at 15−30 cm = 0·153 + / − 0·029) did not significantly differ from those of initial concentration (mean at 0−15 cm = 0·0176 + / − 0·013, mean at 15−30 cm = 0·144 + / − 0·034). Overall, no treatment effect or species effect was observed on soil phosphate concentrations.

In *L. oryzoides*, P immobilization was enhanced in response to flooding ($F = 2·96$, $p = 0·013$), but no differences were observed among individual treatments. *L. oryzoides* immobilized more *P* in both above-ground and below-ground tissues than *B. monnieri* and immobilized more N in below-ground tissues. Total plant N showed no response to flooding in either species (Table I).

Water chemistry. Specific conductance increased over time, with a mean value of 130 µs on day 30 increasing to 168 µs by day 45. This increase was intensified by flooding ($F = 8·36$, $p < 0·0005$). Effluent from mesocosms containing *L. oryzoides* was higher in conductivity than those containing *B. monnieri* ($F = 18·4$, $p < 0·0005$; Figure 3). Effluent pH was neutral to slightly alkaline across treatments (pH = 7·81 + / − 0·46). Generally pH for *B. monnieri* effluent was higher than *L. oryzoides*
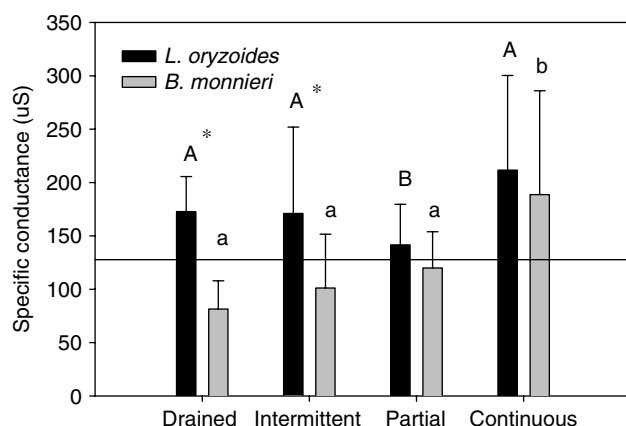
Figure 3. Mean effluent specific conductance. The reference line is the mean specific conductance of reference water that was not exposed to mesocosms. Differing upper-case letters indicate a significant difference from drained conditions for *L. oryzoides*, while differing lower-case letters indicate a significant difference from drained conditions for *B. monnieri* ($p < 0.05$). If no letters are present, no effect of flooding treatments was observed. Error bars indicate $+/-1$ standard deviation.
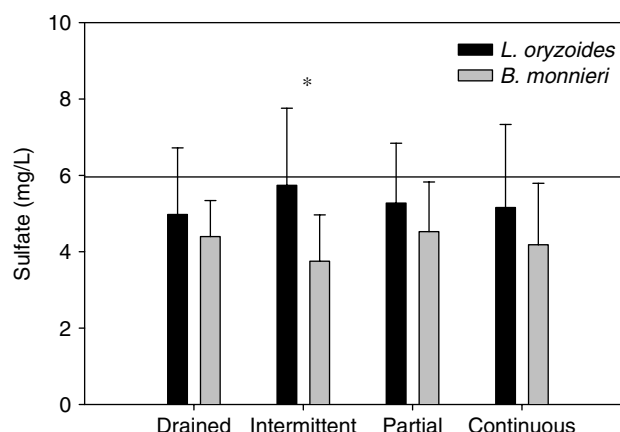

Figure 4. Mean effluent sulfate concentration. The reference line is the mean concentration of sulfate in reference water that was not exposed to mesocosms. Differing upper-case letters indicate a significant difference from drained conditions for *L. oryzoides*, while differing lower-case letters indicate a significant difference from drained conditions for *B. monnieri* ($p < 0.05$). If no letters are present, no effect of flooding treatments was observed. Error bars indicate $+/-1$ standard deviation.

in more intensely flooded treatments, whereas it was lower in effluent from drained and intermittently flooded treatments. *Leersia oryzoides* pH declined in continuous flooding from $7.86 +/- 0.28$ to $7.48 +/- 0.31$ ($F = 5.42$, $p = 0.040$). Effluent pH in *B. monnieri* increased in the partially flooded treatment from $7.70 +/- 0.23$ to $8.72 +/- 0.58$ ($F = 17.85$, $p = 0.002$).

The SO_4^{2-} concentrations ranged from approximately 3 to 6 mg/l. There were no species differences in drained treatments, but effluent SO_4^{2-} was generally higher in *L. oryzoides* than *B. monnieri* in flooded treatments ($F = 18.3$, $p < 0.0005$; Figure 4). Cl^- concentrations ranged from approximately 1 to 6 mg/l and increased in flooded treatment of both species, resulting in higher concentrations compared to controls ($F = 24.1$, $p < 0.0005$; Figure 5). Cl^- concentrations were higher in *L. oryzoides* across all flooded treatments ($F = 3.23$, $p = 0.043$).

Phosphate concentration demonstrated a treatment effect in *L. oryzoides* ($F = 4.277$; $p = 0.009$) with partially flooded values initially higher than other treatments. Initially, effluent phosphate concentrations were higher in *B. monnieri* than in *L. oryzoides* across all treatments. Phosphate concentrations in effluent from flooded mesocosms declined to values similar to *L. oryzoides*, while phosphate concentrations from drained mesocosms with *B. monnieri* were more than triple those of *L. oryzoides* ($F = 4.277$, $p = 0.009$). Effluent from drained mesocosms of *B. monnieri* was higher in PO_4^{3-} than flooded effluent from mesocosms ($F = 9.321$, $p = 0.001$; Table II).

B. monnieri effluent had higher NO_3^- under drained conditions than did *L. oryzoides* ($F = 17.81$, $p < 0.0005$). Additionally, flooded *B. monnieri* demonstrated lower NO_3^- concentrations than drained mesocosms on day 45 ($F = 23.8$, $p < 0.0005$). Ammonium concentrations did not differ between species treatments. An increase was observed in continuously flooded *B.*
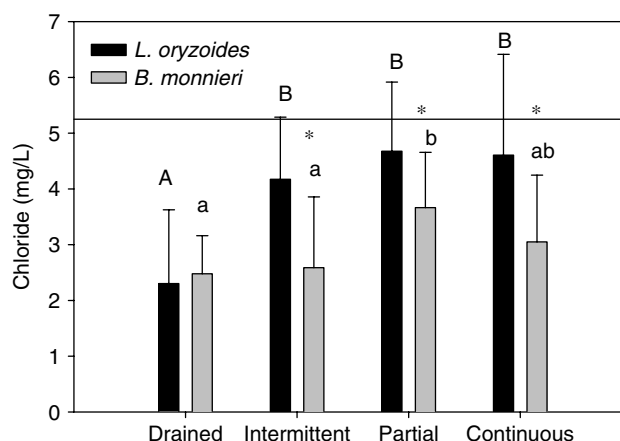

Figure 5. Mean chloride concentration. The reference line is the mean concentration of chloride in reference water that was not exposed to mesocosms. Differing upper-case letters indicate a significant difference from drained conditions for *L. oryzoides*, while differing lower-case letters indicate a significant difference from drained conditions for *B. monnieri* ($p < 0.05$). If no letters are present, no effect of flooding treatments was observed. Error bars indicate $+/-1$ standard deviation.

monnieri mesocosms ($p = 0.033$) on day 30, but not thereafter.

Discussion

Flooded soils generally display decreased Eh as seen in the present study. As oxygen availability declines (at $\sim$Eh = 350 mV), soil microorganisms use alternate electron acceptors in a stepwise fashion with decreasing Eh (e.g. $-$Eh $\approx$ 250: NO_3^- and Eh $\approx$ 100: Fe (III); Mitsch and Gosselink, 2000). The weekly draining of water from all treatments during refreshment of the nutrient solution introduced air into the interstitial soil pores and may have somewhat attenuated this trend towards soil reduction. However, any oxidation occurring during this period would likely last less than a day and would be counteracted by the flooding treatments applied approximately 10 h after initiation of draining. A study

Table II. Summary table of measured nitrate, ammonium and reactive phosphate in mesocosm effluent.

	Effluent concentrations (mg/l)							
	NH$_4^+$		NO$_3^-$			PO$_4^{-3}$		
	Day		Day			Day		
	30	45	16	30	45	16	30	45
Reference water	1·92 +/− 0·82	0·62 +/− 0·16	5·05	9·48 +/− 0·619	5·51 +/− 0·73	3·00	5·35 +/− 0·87	3·29 +/− 0·57
Leersia								
Drained	0·12 +/− 0·09	0·14 +/− 0·06	1·19 +/− 0·89	0·91 +/− 1·25	0·67 +/− 0·45	0·46 +/− 0·42	0·19 +/− 0·16	0·76 +/− 0·58
Intermittent flooding	0·17 +/− 0·16	0·06 +/− 0·10	1·72 +/− 2·66	0·98 +/− 2·09	0·60 +/− 0·65	0·41 +/− 0·29	0·53 +/− 0·61	0·21 +/− 0·28
Partial flooding	0·22 +/− 0·28	0·07 +/− 0·11	0·93 +/− 1·00	2·87 +/− 3·38	1·87 +/− 1·78	**2·01** +/− **1·66**	1·33 +/− 1·02	0·45 +/− 0·59
Continuous flooding	0·29 +/− 0·42	0·03 +/− 0·04	1·67 +/− 3·52	2·48 +/− 3·10	0·28 +/− 041	0·52 +/− 0·63	0·75 +/− 1·55	·075 +/− 0·02
Bacopa								
Drained	0·16 +/− 0·04	0·18 +/− 0·08	1·67 +/− 1·77	2·77 +/− 0·55	2·32 +/− 0·46	1·82 +/− 2·18	1·13 +/− 0·55	2·03 +/− 1·37
Intermittent flooding	0·09 +/− 0·76	0·07 +/− 0·07	0·84 +/− 0·80	1·15 +/− 1·19	**0·72** +/+ − **0·58**	2·61 +/− 2·47	0·73 +/− 0·47	**0·34** +/+ − **0·27**
Partial flooding	0·04 +/− 0·04	0·10 +/− 0·21	1·41 +/− 1·86	1·56 +/− 0·78	·**059** +/− **0·10**	3·03 +/− 1·92	1·65 +/− 0·96	**0·10** +/+ − **0·01**
Continuous flooding	**0·49** +/+ − **0·51**	0·06 +/− 0·08	0·80 +/− 0·58	3·02 +/− 2·74	**0·35** +/− **0·77**	1·68 +/− 2·60	1·05 +/− 0·88	**0·22** +/+ − **0·16**

'Day' indicates number of days from treatment initiation. Bold numbers indicate significant difference from drained treatment. 'Reference water' refers to water that was poured directly into overflow containers without passing through the mesocosms.

examining soil redox response in *Spartina alternaflora* mesocosms utilizing high-resolution time series data found that alternating flooding: draining resulted in periodic Eh fluctuations of 75 mV (Catallo, 1999). The trend towards oxidation that occurred during draining was reversed within a few hours of flooding.

Because the anoxic environment can be stressful for plants, many wetland plants have internal aeration ducts (lacunae) to convey oxygen into the rhizosphere (Reddy *et al*., 1989). Species differences in influencing soil Eh may reflect a greater ability in *B. monnieri* for rhizosphere oxidation. Both root and shoot tissues appeared highly porous compared with *L. oryzoides*. Alternately, these differences may be the result of *L. oryzoides* indirectly promoting soil reduction either through rhizosphere exudation of organic carbon (Neuman and Römhel, 2002; Ehrenfeld *et al*., 2005), or through facilitation of microbial growth (Jones *et al*., 2004). Roots of *L. oryzoides*, for example, have been found to harbor populations of Fe-oxidizing bacteria, which have been implicated in redox reactions in the soil (Emerson *et al*., 1999).

Because there was no unplanted treatment (bare soil) in the present study, it is unclear which of these mechanisms are most likely for the observed species differences in soil Eh. Existing research would imply that plants generally increase Eh in flooded soils (Chen and Barko, 1988; McKee *et al*., 1988; Wright and Otte, 1999). Owing to the high sand content of the soil used in this study, intense reduction would not be expected in unplanted soil (DeLaune *et al*., 1990; Pezeshki and DeLaune 1990). In addition to changes in Eh, flooding can also affect the pH of soils. A series of chemical transformations occurring in response to reducing conditions in the soil often causes acidification, processes that are exacerbated by rhizosphere acidification resulting from plant interactions with reduced forms of nitrogen and iron (Begg *et al*., 1994; Neuman and Römhel, 2002).

The decreased nitrogen concentrations measured in the soils of continuously flooded mesocosms containing *L. oryzoides* were somewhat counterintuitive. It would be expected that soil reduction would increase NH_4^+: NO_3^- ratios, and as the method for determination of nitrogen concentration in the present study does not include NO_3^-, nitrogen values would subsequently increase. However, such conditions may also enhance ammonification of organic nitrogen and denitrification, leading to the production of gaseous or volatile forms of nitrogen that would diffuse into the atmosphere (Mitsch and Gosselink, 2000).

Higher concentrations of NO_3^- and PO_4^{3-} in effluent from *B. monnieri* mesocosms compared with *L. oryzoides* mesocosms are partially due to increased plant immobilization in below-ground tissues of *L. oryzoides* resulting primarily from greater biomass in the latter. Previous studies have demonstrated that *L. oryzoides* may act as a phosphorus source (Kröger *et al*., 2007a) or a sink (Deaver *et al*., 2005). With regard to nitrogen, *L. oryzoides* appears to be more limited in its nutrient removal capability. Whereas two common ditch plants,

Juncus effuses and *Ludwigia peploides*, decreased N in effluent water in a mesocosms experiment (measured as NO_3^- and NH_4^+) when compared to controls, *L. oryzoides* did not (Deaver *et al*., 2005). In the present study, differences in effluent NO_3^- may be indicative of nitrogen species transformation from NO_3^- to reduced forms, as *B. monnieri* remained above the threshold for this transformation (i.e. Eh ≈ 250) through day 30, whereas soils planted with *L. oryzoides* approached this threshold within 9 days of flooding.

Twisk *et al*. (2003) found that flooding lowered effluent Cl^- at very high concentrations (>200 mg/l). For the present study, increases in effluent Cl^- resulting from flooding may be related to plant uptake of NO_3^-. Bar-Tal (1999) observed that uptake of NO_3^- and Cl^- may be regulated to maintain a steady-state value for $NO_3^- + Cl^-$. As plants in drained treatments are likely to use NO_3^- as the predominant form of nitrogen, there may be the added benefit of increased Cl^- uptake; however, low reproducibility of Cl–standards in the present study (i.e. −error + / − 13·3%) preclude further interpretation.

When iron-rich soil, such as the soil used in this study, is flooded for an extended time, the reduction of Fe (III) to soluble Fe (II) results in the dissolution of iron-phosphate complexes in the soil, yielding soluble PO_4^{3-} (Szilas *et al*., 1998). While water concentrations of PO_4^{3-} would generally be expected to increase in response to flood-induced soil reduction, no such response was observed. Concentrations of PO_4^{3-} in *B. monnieri* were actually lower in all flooded treatments than controls. Previous studies suggest that the diffusion of oxygen to the rhizosphere via lacunae may lead to the oxidation of Fe (II) and subsequent co-precipitation of phosphorus along the root epidermis and cortex (Chen *et al*., 2005; Liang *et al*., 2006). This process likely explains higher levels of phosphorus in below-ground tissues of *L. oryzoides*. The mechanisms explaining phosphorus differences in effluent water from *B. monnieri* are not so straightforward, but may involve subtle rhizosphere pH differences between treatments influencing predominant forms of P (Fang *et al*., 2007).

CONCLUSIONS

Whereas previous research has demonstrated that *L. oryzoides* may reduce effluent phosphorus concentrations under saturated conditions, the present study shows that immobilization of phosphorus in below-ground tissues is related to intensity of soil reduction during flooding. The increased uptake of PO_4^{3-} and NO_3^- from *L. oryzoides* effluent compared with *B. monnieri* effluent was mitigated after 45 days of flooding. These results imply that *L. oryzoides* may be more effective than shallow-rooted semi-aquatic species such as *B. monnieri* for remediation of agricultural water when exposed to periodic draw down allowing for soil oxidation. Mesocosms with *B. monnieri*, on the other hand showed decreases in effluent macronutrients only after continuous flooding.

Agricultural management practices employing controlled drainage for enhanced water quality may promote dominance of semi-aquatic species such as *B. monnieri*. The species-specific differences in soil redox potential, pH, and conductivity imply that if hydrological alterations do affect species composition, they may be accompanied by plant-mediated differences in soil and water chemistry.

REFERENCES

Armstrong W, Beckett PM. 1987. Internal aeration and the development of stelar anoxia in submerged roots: A multishelled mathematical model combining axial diffusion of oxygen in the cortex with radial losses to the stele, the wall layers, and the rhizosphere. *New Phytologist* **105**: 221–245.

Bar-Tal A. 1999. The significance of root size for plant nutrition in intensive horticulture. In *Mineral Nutrition of Crops: Fundamental Mechanisms and Implications*, Rengel Z (ed.). Food Products Press: Binghampton, NY.

Begg CBM, Kirk GJD, Mackenzie AF, Neue HU. 1994. Root-induced iron oxidation and pH changes in the lowland rice rhizosphere. *New Phytologist* **128**: 469–477.

Bouldin JL, Farris JL, Moore MT, Cooper CM. 2004. Vegetative and structural characteristics of agricultural drainages in the Mississippi Delta landscapes. *Environmental Pollution* **132**: 403–411.

Braskerud BC. 2001. The influence of vegetation on sedimentation and resuspension of soil particles in small constructed wetlands. *Journal of Environmental Quality* **30**: 1447–1457.

Brix H. 1997. Do macrophytes play a role in constructed treatment wetlands? *Water Science and Technology* **35**: 11–17.

Catallo WJ. 1999. *Hourly and Daily Variations of Sedimen Redox Potential in Tidal Wetland Sediments*, Biological Science Report No. USGS/BRD/BSR-1999-0001. United States Geological Survey, Biological Resources Division. National Wetlands Research Center: Lafayette, LA.

Chen RL, Barko JW. 1988. Effects of freshwater macrophytes on sediment chemistry. *Journal of Freshwater Ecology* **4**: 279–289.

Chen H, Qualls RG, Blank RR. 2005. Effect of soil flooding on photosynthesis, carbohydrate partitioning and nutrient uptake in the invasive exotic *Lepidium latifolium*. *Aquatic Botany* **82**: 250–268.

Cooper CM, Moore MT, Bennett ER, Smith S Jr, Farris JL, Milam CD, Shields FD Jr. 2004. Innovative uses of vegetated drainage ditches for reducing agricultural runoff. *Water Science and Technology* **49**: 117–123.

Cronk JK, Fennessy SB. 2001. *Wetland Plants: Biology and Ecology*. CRC press: Boca Raton, FL.

Day JW Jr, Arancibia AY, Mitsch WJ, Lara-Dominguez AL, Day JN, Ko J, Lane R, Lindsey J, Lomeli DZ. 2003. Using ecotechnology to address water quality and wetland habitat loss problems in the Mississippi basin: a hierarchical approach. *Biotechnology Advances* **22**: 135–159.

Deaver E, Moore MT, Cooper CM, Knight SS. 2005. Efficiency of three aquatic macrophytes in mitigating nutrient runoff. *International Journal of Ecology and Environmental Sciences* **31**: 1–7.

DeLaune RD, Pezeshki SR, Pardue JH. 1990. An oxidation-reduction buffer for evaluating physiological response of plants to root oxygen stress. *Environmental and Experimental Botany* **30**(2): 243–247.

Emerson D, Weiss JV, JMegonigal JP. 1999. Iron-oxidizing bacteria are associated with ferric hydroxide precipitates (Fe-plaque) on the roots of wetland plants. *Applied and Environmental Microbiology* **65**: 2758–2761.

Ehrenfeld JG, Ravit B, Elgersma K. 2005. Feedback in the plant-soil system. *Annual Review of Environment and Resources* **30**: 75–115.

Fang YY, Babourina O, Rengel Z, Yang XE, Pu PM. 2007. Spatial distribution of ammonium and nitrate fluxes along roots of wetland plants. *Plant Science* **173**: 240–246.

Horneck DA, Miller RO. 1998. Determination of total nitrogen in plant tissue. In *Handbook of Reference Methods for Plant Analysis*, Kalra YP (ed.). CRC Press: Boca Raton, FL.

Jones DL, Hodge A, Kuzyakov Y. 2004. Plant and mycorrhizal regulation of rhizodeposition. *New Phytologist* **163**: 459–480.

Kröger R, Holland MM, Moore MT, Cooper CM. 2007a. Plant senescence: a mechanism for nutrient release in temperate agricultural wetlands. *Environmental Pollution* **146**: 114–119.

Kröger R, Holland MM, Moore MT, Cooper CM. 2007b. Hydrological variability and agricultural drainage ditch inorganic nitrogen reduction capacity. *Journal of Environmental Quality* **36**: 1646–1652.

Kröger R, Holland MM, Moore MT, Cooper CM. 2008. Agricultural drainage ditches mitigate phosphorus loads as a function of hydrological variability. *Journal of Environmental Quality* **37**: 107–113.

Lachat Instruments. 1995. *Total Phosphorus in Kjeldahl Digests*, QuikChem Method 10-115-01-1-C. Lachat Instruments: Milwaukee, WI.

Larsen D, Gentry RW, Solomon DK. 2003. The geochemistry and mixing of leakage in a semi-confined aquifer at a municipal well field, Memphis, Tennessee, USA. *Applied Geochemistry* **18**: 1043–1063.

Liang Y, Zhu YG, Xia Y, Li Z, Ma Y. 2006. Iron plaque enhances phosphorus uptake by rice (*Oryza sativa*) growing under varying phosphorus and iron concentrations. *Annals of Applied Biology* **149**: 305–312.

McKee KL, Mendelssohn IA, Hester MW. 1988. Examination of pore water sulfide concentrations and redox potentials near the aerial roots of *Rhizophora mangle* and *Avicennia germinans*. *American Journal of Botany* **75**: 1352–1359.

Mitsch WJ, Gosselink JG. 2000. *Wetlands*. John Wiley and Sons: New York.

Needelman BA, Ruppert DE, Vaughan RE. 2007. The role of ditch soil formation and redox biogeochemistry in mitigating nutrient and pollutant losses from agriculture. *Journal of Soil and Water Conservation* **62**: 207–215.

Neuman G, Römhel V. 2002. Root-induced changes in the availability of nutrients in the rhizosphere. In *Plant Roots: The Hidden Half*, 3rd edn. Waisel Y, Eshel A, Kafkafi U (eds). Marcel Dekker: New York; 617–649.

Patrick WH, DeLaune RD. 1977. Chemical and biological redox systems affecting nutrient availability in the coastal wetlands. *Geoscience and Man* **18**: 131–137.

Peterson SB, Teal JM. 1996. The role of plants in ecologically engineered wastewater treatment systems. *Ecological Engineering* **6**: 137–148.

Pezeshki SR. 2001. Wetland plant responses to soil flooding. *Environmental and Experimental Botany* **46**: 299–312.

Pezeshki SR, DeLaune RD. 1990. Influence of sediment oxidation-reduction potential on root elongation in *Spartina patens*. *Acta Oecologia* **11**: 377–383.

Pierce SC, Pezeshki SR, Moore MT. 2007. Ditch plant response to variable flooding: a case study of *Leersia oryzoides* (Rice Cutgrass). *Journal of Soil and Water Conservation* **62**: 216–224.

Reddy KR, D'Angelo EM, DeBusk TA. 1989. Oxygen transport through aquatic macrophytes: the role in wastewater treatment. *Journal of Environmental Quality* **19**: 261–267.

Soil Conservation Service. 1989. *Soil Survey: Shelby County, Tennessee*. Division of Soil Conservation Service, USDA: Washington, DC; 53.

SPSS, Inc. 2005. SPSS for windows, rel. 14·0·1, Chicago.

Szilas CP, Borggaard K, Hansen HCB, Rauer J. 1998. Potential iron and phosphate mobilization during flooding of soil material. *Water Air and Soil Pollution* **106**: 97–109.

Twisk W, Noordervliet MAW, ter Keurs WJ. 2003. The nature value of ditch vegetation in peat areas in relation to farm management. *Aquatic Ecology* **37**: 191–209.

Wendt K. 1997. *Determination of Total Kjeldahl Nitrogen by Flow Injection Analysis Colorimetry (Block Digestor Method)*, QuikChem Method 10-107-06-2-E. Lachat Instruments: Milwaukee, WI.

Wright DJ, Otte M. 1999. Wetland plant effects on the biogeochemistry of metals beyond the rhizosphere. *Biology and Environment-Proceedings of the Royal Irish Academy* **99B**: 3–10.