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Influence of soft rush (*Juncus effusus*) on phosphorus flux in grazed seasonal wetlands

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ABSTRACT

Livestock significantly affect wetland soils and vegetation but their impacts on wetland nutrient dynamics are poorly understood. We set up a full factorial laboratory experiment to assess the effects of *Juncus effusus*, grazing exclusion, and flooding on P flux from intact cores collected from seasonal wetlands in cattle pastures in south Florida. We collected intact cores from *Juncus* tussocks and plant interspaces inside and outside 4-year grazing exclosures in five replicate wetlands. We incubated the cores for 50 days under continuous flooding or weekly 1-day flooding cycles and measured P concentrations in surface and pore water. Grazing exclosures had less *Juncus* (17%) and bare ground (2%) than adjacent grazed areas (*Juncus*, 48%; bare ground, 12%), but did not affect P fluxes. Initial fluxes of soluble reactive P (SRP) were much higher in cores with *Juncus* ($242 \pm 153 \text{ mg P m}^{-2} \text{ day}^{-1}$) than without *Juncus* ($14 \pm 20 \text{ mg P m}^{-2} \text{ day}^{-1}$). In weekly flooded cores P fluxes fell to $19.7 \pm 13.4 \text{ mg P m}^{-2} \text{ day}^{-1}$ in cores with and 2.7 ± 2.6 in cores without *Juncus*. The strong effect of *Juncus* on P flux was an indirect effect of cattle grazing, but 4 years of grazing exclusion did not have a significant effect on P fluxes.

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1. Introduction

Concern over eutrophication of Lake Okeechobee has stimulated interest in best management practices (BMPs) to control non-point sources of phosphorus (P) in the surrounding watershed (Florida State Legislature 373.4595; South Florida Water Management District, 2004). Freshwater wetlands are important for storage of nutrients in this watershed and are being considered for their potential to ameliorate nutrient runoff (James et al., 2006; Dunne et al., 2007). One promising approach is to increase the ability of wetlands to retain water, for example by plugging drainage ditches, thereby storing more P in wetlands and reducing runoff from the adjacent land use (Hiscock et al., 2003; Zhang et al., 2006; Capece et al., 2007). Although retaining water in wetlands would be a relatively

easy and inexpensive practice to implement, its efficacy is uncertain because of the wide variety of factors, both natural and anthropogenic, that influence P storage and release in these systems (Reddy et al., 1995). Therefore, it is necessary to increase our understanding of factors influencing P storage and release from soils in these wetlands.

Cattle ranching is the dominant land use (36% by area) in the Lake Okeechobee watershed and wetlands on ranches have been considered for their potential to store water and nutrients in the landscape (Hiscock et al., 2003; Gathumbi et al., 2005). Management practices associated with ranching, including fertilizer use, introduction of exotic grasses, increased cattle stocking densities, and artificial drainage have the potential to influence biogeochemical cycling in seasonally inundated wetlands, which account for about 15% of

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pasture area in this region (Gathumbi et al., 2005; Dunne et al., 2007). Wetlands in improved pastures (i.e. pastures planted with forage species, fertilized and maintained for high productivity) contribute substantially to soil P storage in this watershed, and it is possible that this storage could be increased by reflooding drained wetlands or otherwise increasing wetland hydroperiods (Dunne et al., 2007).

In addition to being influenced by drainage and other water management practices, wetlands on ranches are strongly affected by cattle. Cattle can bring more P to wetlands by depositing manure rich in organic P (Graetz and Nair, 1999; Bottcher et al., 1999; Alloush et al., 2003), but they also remove P from wetlands and deposit it in the uplands. Grazing can increase the nutrient content of re-growing shoots and influence the decomposition of shoot tissues (Semmartin et al., 2008). Cattle can also disturb wetland soil and sediments through trampling and increase levels of suspended solids and nutrients (McDowell et al., 2005; Turner et al., 1979). Additionally, cattle trampling can increase soil bulk density, decrease soil porosity and can also increase the turnover rate of nutrients in wetland plants by trampling wetland vegetation (McDowell et al., 2005; Naeth et al., 1991; Palmer et al., 2000). Trampling can increase physical breakdown of litter as well as increasing contact of litter with mineral particles, stimulating enhanced decomposition of litter.

Cattle grazing influences plant species composition in wetlands because cattle selectively graze certain species and allow less palatable plant species, such as *Juncus effusus* L. subsp. *solutus* (Fernald and Wiegand) Hämet-Ahti (hereafter referred to as *Juncus*) to proliferate in grazed wetlands (Steinman et al., 2003; Marty, 2004; Bohlen and Gathumbi, 2007). Changes in plant species composition can alter the total amount of P stored in plant biomass, detritus and soil organic matter (Naeth et al., 1991). Grazing-induced shifts in wetland plant species composition may have consequences for the total amount of P stored in vegetation and its subsequent turnover during decomposition, because wetland plant species differ in their P content and uptake (Reddy et al., 1995). The nutrient content of plant tissue, or concentration of secondary plant compounds, can in turn influence P release and decomposition rates, which can vary greatly among plant species (Reddy and DeBusk, 1985; Richardson, 1999; Balcer, 2006). Thus by shifting plant species composition, cattle may indirectly influence rates of decomposition and nutrient release.

In addition to being affected by ranch management practices, phosphorus storage and flux in wetland on cattle ranches are influenced by natural water table fluctuations that occur seasonally, as well as during isolated rainfall events (Steinman et al., 2003; Bohlen and Gathumbi, 2007). Water table fluctuation influences P biogeochemistry in a variety of indirect ways (Richardson, 1985; Reddy et al., 1995). Continuous flooding leads to anaerobic conditions, which generally lead to increased concentrations of soluble reactive phosphorus (SRP) (Wright et al., 2001; Nair et al., 1999). One cause for increases in SRP under anaerobic conditions is the dissolution of ferrous phosphates (Richardson, 1999; Patrick and Khalid, 1974; Ponnampereuma, 1972), but concentrations of P may also increase during flooding due to microbial cell lysis (Wright et al., 2001) and a decrease in P demand resulting

from plant dormancy (Gambrell and Patrick, 1978; Mitsch and Gosselink, 2003). However, P concentrations may also decrease under anaerobic conditions from an increase in surface area of P-binding molecules (Corstanje and Reddy, 2004; Richardson, 1999; Olila and Reddy, 1997). The complex interactions among these multiple factors determine how the fluctuating water table affects P flux from wetland soils to overlying water.

In this study we investigated the influence of vegetation and flooding on P fluxes from intact cores collected from small seasonal wetlands in improved Bahia grass (*Paspalum notatum* Flugge) pastures on a cattle ranch in the Okeechobee watershed. Most P flux studies from wetland and aquatic systems focus on flux from soil, but in this experiment we examined fluxes from cores collected from bare soil areas created by cattle trampling and from *Juncus* tussocks, offering a more complete picture of fluxes from the whole soil–plant–detritus system. The direct effects of cattle on these processes was examined by comparing fluxes from cores collected within and outside 4-year grazing exclosures, and the indirect effects of cattle were inferred by their influences on the wetland vegetation community, in particular their effects on the distribution of *Juncus* tussocks and intervening bare soil areas.

2. Methods

2.1. Site description

The study sites were at the MacArthur Agro-ecology Research Center at Buck Island Ranch (27° 09' N, 81° 11' W) near Lake Placid, Florida, a 4250-ha cow–calf operation (Swain et al., 2007). Cattle-stocking densities on the ranch range from 0.74 to 1.73 cows ha⁻¹, and are typical of cow–calf operations in this region. Wetlands selected for this study were in improved Bahia grass pastures (52% of the ranch area). These improved pastures are typically fertilized annually in spring with N (~52 kg ha⁻¹), and were fertilized regularly with NPK (40 kg ha⁻¹ P₂O₅) for 15–20 years until 1987, and only occasionally with NPK thereafter, such as following sod harvesting (Swain et al., 2007). The pastures were intensively ditched in past decades to promote drainage during the wet season, and are occasionally mowed to control weeds.

Soils at the site are acidic sands consisting primarily of Spodosols, Entisols, and Alfisols. Upland soils in improved pastures are sandy hyperthermic Haplaquods, whereas wetland soils consist of varying proportions of hyperthermic Spodic Psammaquents and hyperthermic Typic Humaqupts, commonly known as Bassinger depressional fine sand and Placid depressional fine sand, respectively (USDA, 1989). Mean annual precipitation is 1300 mm, of which over 69% falls during the wet season (June–October). Annual temperatures average 22 °C, with summer maximums of 33 °C.

The small seasonal wetlands on the ranch range from 0.01 to 41.9 hectares (mean: 0.86 ± 2.42 ha) and account for ~15% of the ranch area, which is typical for ranches in this region (Dunne et al., 2007). These wetlands are typically flooded in the rainy season, but hydroperiods can vary from less than three to more than ten months depending on rainfall. In improved

pastures the wetland ecotone, or transition zone, is dominated by *J. effusus*, a plant species that forms dense tussocks and that proliferates in grazed wetlands because cattle avoid eating it, while preferentially grazing its competitors (Gathumbi et al., 2005). Areas between the *Juncus* tussocks are typically bare soil due to heavy trampling by cattle as they walk between the tussocks. Deeper areas of these wetlands are dominated by emergent macrophytes such as *Pontederia cordata* L. and *Sagittaria lancifolia* L. as well as floating vegetation such as *Pistia stratiotes* L. and algal mats during flooded periods, although some shallow wetlands are dominated by *Juncus* throughout.

2.2. Experimental design

The experiment included a full factorial design applied to intact cores with three main factors, each of which had two levels: (1) *Juncus* (cores collected from *Juncus* tussocks or from interspaces between *Juncus* tussocks) (2) grazing exclusion (cores collected from within or outside 4-year grazing exclosures) and (3) flooding (cores subjected to continuous flooding or weekly, 1-day flooding). The cores were incubated for a total of 50 days and water samples were collected at 1 h and 1 day after initial flooding and weekly thereafter until the end of the 50-day experiment, as described below. Soils were harvested from the cores for analysis at the end of the experiment. Details on core construction and the *Juncus* and flooding treatments are provided in the following sections. The grazing exclosures referred to in the grazing treatment were established in 2002, by installing 10 m × 10 m fenced areas at the edges of five small freshwater wetlands (1.29 ± 0.25 ha) in improved pastures, and were constructed by securing standard galvanized fence panels to T-posts. Paired plots were also marked in adjacent 10 m × 10 m areas, but remained accessible to cattle.

2.2.1. Soil core collection and construction

A total of 40 intact cores were collected, eight from each of the five wetlands with grazing exclosures (April 11–12, 2006). In each wetland, cores were collected from within two randomly selected *Juncus* tussocks and from areas of bare soil immediately adjacent to the sampled tussocks, both inside and outside the grazing exclosure (2 core types × 2 cattle grazing treatments × 2 flooding treatments × 5 wetlands = 40 total cores). The cores were made of clear acrylic tube (10.2 cm i.d. × 45 cm long), and sharpened at the bottom edge. At each sampling location, a core was placed on the soil surface and cut around with a knife to sever roots and detritus, and then was driven to a soil depth of 25 cm with a rubber mallet, protecting the top of the core with a block of wood. Cores taken from within *Juncus* tussocks were slid over the top of *Juncus* stems and driven through the detritus layer and into the mineral soil to 25 cm. Thus the plant interspace cores were essentially soil cores (with detritus, if present) and the *Juncus* cores included the whole soil–plant–detritus environment. Once the target depth was reached, the cores were gently removed, capped at the bottom of the core, and returned to the lab. Because of the limited space for the *Juncus* plants within cores, some stems were removed at the base using a razor blade. All but 3–5 live *Juncus* stems per core were removed to prevent stem die-

off. Cores were kept outdoors, watered regularly and allowed to equilibrate for 3 weeks prior to moving them into controlled laboratory conditions. Once indoors, plants were kept under a mixture of artificial and natural light and steady daytime temperatures (~26 °C). Cores were allowed to adjust for two additional weeks before applying experimental treatments.

After the pre-incubation period, soil cores were drained and outfitted with pore water sampling ports at the bottom of the core and 5 cm below the soil surface. Bottom caps were filled with 400 mL of acid-washed sand to facilitate drainage and collection of drainage water. Sampling ports were constructed of 1.3 cm × 4 cm air diffusers (Sweetwater AS1; Aquatic Eco-Systems, Inc.) connected through a rubber stopper, and clamped with pinch valves. The original description of this pore water extraction method (Winger and Lasier, 1991) used the vacuum created by a sampling syringe to extract pore water. In our setup, the vacuum was not necessary because water drained freely through the ports when the clamps were opened.

Platinum redox probes were installed at the 5 cm depth to monitor the redox status of the soil throughout the experiment. The redox probes were constructed of 1.3 cm of 0.51 mm diameter 99.95% pure platinum wire (Fisher Scientific), that had been soaked overnight in a 1:1 mixture of nitric and hydrochloric acids to remove any oxidation that may have formed (Patrick et al., 1996). Probes were inserted through a small hole drilled in the acrylic core 5 cm below the soil surface, and were sealed with a non-conductive superglue. Redox measurements were made using a Thermo Orion 420A+ pH/mV meter, a redox probe (Thermo Orion 96–78) inserted in the surface water, and a test clip attached to the platinum wire (Villapando and Graetz, 2001). The redox probe was used as a reference electrode by using only the wire from the reference portion of the electrode, and splicing a wire into the center of the cable. Prior to each sampling, the reference electrode (E_c) was calibrated using pH 4 and pH 7 quinhydrone buffers as described by Patrick et al. (1996). All readings were adjusted to a hydrogen standard (E_h) by adding 245 mV. A more detailed description of probe construction and calibration can be found in Patrick et al. (1996).

2.2.2. Flooding treatment and water sampling

Each of the two flooding treatments included one set of 20 cores (2 *Juncus* treatments × 2 grazing treatments × 5 replicates) that were flooded for the whole 50-day experiment, and a second set of 20 cores that were flooded weekly for 1 day each week. Cores were flooded with DI water to a depth of approximately 15 cm above the surface, which amounted to 600 mL. This volume was used as the standard flooding volume above the soil surface for the rest of the cores. Because core porosity varied, the volume of water needed to reach the soil surface of each core was recorded. This same-volume approach was chosen over same-depth flooding because of the concern that same-depth flooding would expose the columns to differing amounts of solute, thus confounding water concentration data. Approximately 100 mL of DI water was added to the continuously flooded cores once per week to maintain the initial flooding volume.

Water samples were collected from surface water, upper ports, and bottom ports of all cores at 1 and 24h after initial flooding, and then weekly thereafter up to 50 days. Cores undergoing the weekly flooding treatment were immediately drawn down after 1 day of flooding and remained drained until the next week when they were reflooded and sampled the following day. Soil and detritus in periodically flooded cores remained moist between flooding events. Continuously flooded cores were sampled on the same day as the periodically flooded cores. Surface water samples were collected by syringe and immediately gravity filtered through a 0.45 μm filter. Pore water samples were filtered in the same manner as surface water samples, but were not analyzed for TP, because they were collected through diffusers with 140 μm pores. Redox readings accompanied all water sampling.

Soluble reactive phosphorus (SRP) was analyzed colorimetrically using an ascorbic acid method originally developed by Murphy and Riley (1962), and modified for micro-scale analysis by Pote and Daniel (2000a). Water TP was analyzed using a persulfate digestion followed by the ascorbic acid method (Pote and Daniel, 2000b). All samples were analyzed in a microplate spectrophotometer (μQuant Microplate Spectrophotometer, Bio-Tek Instruments, Winooski, Vermont).

2.2.3. Soil analysis

The cores were drained after 50 days by allowing water to drain out the bottom port. The cores were then disassembled for soil physicochemical analysis. Soil horizons were clearly visible, and cores were sub-divided into detritus, organic, and mineral layers. Layer thickness and bulk density were measured for each soil layer. Soil samples from each layer of each core were homogenized and passed through a 2 mm sieve and refrigerated prior to analysis. Mehlich-1 extractable P was determined by the dilute double acid method originally developed by Mehlich (1953) and modified by Sims (2000). Soil subsamples were dried, weighed and organic matter levels were determined by loss-on-ignition (450 °C for 16h). These ashed samples were then used to determine total soil P by extracting with aqua regia (3HCl + HNO₃). Mehlich-1 P and aqua regia extracts were analyzed colorimetrically using the ascorbic acid method described previously. Soil pH was also determined on a 1:1 mixture of fresh soil and deionized water incubated at room temperature for 30 min.

2.3. Data analysis

Soil data were analyzed in a full factorial analysis of variance (ANOVA), using *Juncus*, grazing and flooding treatments as main factors with wetland site as a covariate using JMP® 6 Statistical Discovery Software (SAS Institute, Cary, NC). All data were tested for normality using the Shapiro-Wilk test. Water nutrient concentration and P flux data were not normally distributed and were analyzed using a repeated-measures ANOVA (Friedman’s test), with wetland site as a covariate, using rank-transformed data. These data were also analyzed in a Friedman’s test weighted by soil physicochemical parameters. Soil data transformations used in particular tests are indicated in Table 3.

Table 1 – Percent ground cover of *Juncus effusus*, *Panicum hemitomon*, and bare ground in grazed and 4-year ungrazed areas along the edges of isolated subtropical wetlands in improved cattle pastures (mean ± 1 S.E.)

	Percentage ground cover		
	<i>Juncus effusus</i> ^a	<i>Panicum hemitomon</i> ^a	Bare ground ^b
Grazed ^c	47.9 ± 5.9	3.8 ± 2.5	16.7 ± 6.4
Ungrazed ^d	12.0 ± 4.9	51.6 ± 13.5	1.8 ± 1.0

^a p < 0.05.
^b p = 0.052.
^c 0.74–1.73 cows ha⁻¹.
^d Plots inside 4-year grazing exclosures.

3. Results

3.1. Vegetation in grazing exclosures and adjacent ungrazed plots

J. effusus dominated the wetland plant community outside the grazing exclosures but was out competed by other plants such as *Panicum hemitomon* Schultes (maidencane) within the grazing exclosures after a period of only 3–4 years after (Table 1). Grazed areas also had more bare ground (16%) due to heavy traffic and trampling by cattle between *Juncus* clumps; there was less than 2% bare ground within the grazing exclosures.

3.2. Surface and pore water

Flux rates of SRP were an order of magnitude higher in cores with *Juncus* than in cores without *Juncus* (Table 2). In continuously flooded cores highest flux rates occurred during the first day of flooding. After 15 days fluxes in cores with *Juncus* were negative indicating net uptake of previously released P, and in cores without *Juncus* fluctuated between low positive and negative values until the end of the experiment. In weekly flooded cores flux rates were highest during the first flooding and decreased thereafter. Flux rates in weekly flooded cores from *Juncus* tussocks remained an order of magnitude higher than rates in cores from plant interspace areas throughout the study (Table 2).

Mean TP concentrations were nearly 10-fold greater in surface water of *Juncus* cores than in cores without *Juncus* (*Juncus* = 2.83 mg L⁻¹ ± 0.30 S.E.; non-*Juncus* = 0.29 mg L⁻¹ ± 0.47 S.E.; N = 20). The temporal pattern of SRP concentrations varied considerable with the flooding treatments, increasing to a maximum in surface water and organic layer pore water in about 15 days in continuously flooded cores with *Juncus* (Fig. 1). Phosphorus concentrations in surface water and organic layer pore water were similar, but concentrations in the mineral layer were much lower (Fig. 1). In cores containing *Juncus*, P concentrations were much greater under continuous flooding than under periodic flooding (Fig. 1). Concentrations of both SRP and TP in surface water of continuously flooded *Juncus* cores increased for the first 15 and 20 days, respectively, and then declined continuously until the end of the experiment (Fig. 1 for SRP, TP data not shown). Phosphorus concentrations in soil pore water of continuously flooded *Juncus* cores sta-

Table 2 – Flux rates from soil and soil–plant–detritus in cores from *Juncus* tussocks or plant interspaces subjected to continuous flooding or flooded once per week for 24 h over a 50-day period

Days	Continuously flooded ^a		Flooded weekly ^b	
	<i>Juncus</i> tussock	Plant interspace	<i>Juncus</i> tussock	Plant interspace
P flux $\text{mg m}^{-2} \text{ day}^{-1}$				
1	253 ± 101	10.9 ± 16.1	231 ± 197	17.4 ± 24.0
8	6.7 ± 8.5	1.8 ± 2.5	122 ± 107	10.8 ± 11.5
15	5.1 ± 4.7	1.3 ± 1.9	84.7 ± 84.1	8.7 ± 10.4
22	−3.8 ± 2.7	0.1 ± 0.9	60.3 ± 57.0	6.4 ± 8.6
29	−4.4 ± 2.4	−0.2 ± 0.8	37.1 ± 35.7	3.1 ± 4.8
36	−0.9 ± 3.6	0.1 ± 0.4	27.8 ± 22.8	1.8 ± 2.4
43	−5.1 ± 3.4	1.1 ± 2.0	37.5 ± 24.0	6.6 ± 4.9
50	−2.4 ± 2.7	−0.8 ± 1.5	19.7 ± 13.4	2.7 ± 2.6

Values are means ± 1 standard deviation (N = 10). Flux rates for continuously flooded cores are based on changes in P concentration in surface water between sampling dates, and for weekly flooded cores are 1-day flux rates for each flooding event.

^a Time (F-value = 71.4, $p < 0.0001$) and *Juncus* (F value = 56.8, $p < 0.0001$) significantly affected P flux in continuously flooded cores (repeated measures MANOVA, N = 5).

^b Time (F value = 18.5, $p < 0.0007$) and *Juncus* (F value = 12.7, $p = 0.003$) significantly affected P flux in weekly flooded cores (repeated measures MANOVA, N = 5).

bilized after 15 days in the organic soil layer, and increased throughout the incubation in the mineral layer (Fig. 1b, c). By contrast, in periodically flooded *Juncus* cores P concentrations in surface water and organic layer pore water decreased with each flooding event, with most of the decline occurring dur-

ing the first three events (Fig. 1). Phosphorus concentrations in the mineral layer of these same cores increased after the second flooding event and then decreased gradually over time (Fig. 1c).

In cores from plant interspace areas, SRP concentrations in the surface water and organic soil layer were significantly greater in continuously flooded cores than in periodically flooded cores (Fig. 1). The SRP concentrations in the continuously flooded cores from plant interspace areas increased throughout the 50-day flooding treatment, and were greatest on the final sample date in the organic soil layer (mean = $1.70 \text{ mg L}^{-1} \pm 0.29 \text{ S.E.}$). The SRP concentrations in weekly flooded cores from plant interspace areas yielded low but relatively steady SRP concentrations at each flooding, with the highest values occurring after the first flooding event. The ratios of SRP to TP were consistently higher in cores with *Juncus* than in cores without *Juncus* ($p < 0.0001$), and these ratios decreased steadily with time irrespective of other treatments ($p < 0.0001$).

3.2.1. Redox potential

Redox potential (Eh) in continuously flooded cores declined steadily for 22 days, and then stabilized at about -110 mV , showing that anaerobic status in these cores was maintained throughout the remainder of the experiment (Fig. 2). Redox readings in periodically flooded cores began to increase after the second flooding event, resulting in final redox potentials about 80 mV higher than readings taken 24 h after the first flooding. Although the flooding treatment clearly affected redox readings (repeated-measures ANOVA, $p = 0.0003$), the *Juncus* and grazing exclusion treatments did affect redox potential.

3.3. Soil properties in cores at the end of the experiment

The presence of *Juncus* was associated with significantly increased concentrations of P in detritus, as well as the min-

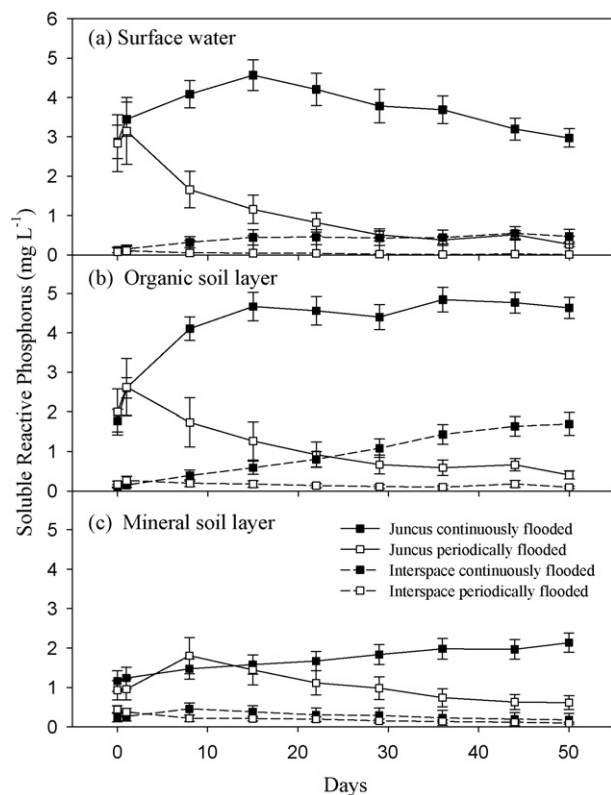


Fig. 1 – Soluble reactive phosphorus (SRP) concentrations (mean ± 1 S.E., N = 20) in soil cores with (solid lines) or without (dashed lines) *Juncus*, and with continuous (solid squares) or periodic (open squares) flooding in surface water (a), organic layer porewater (b), and mineral soil porewater (c).

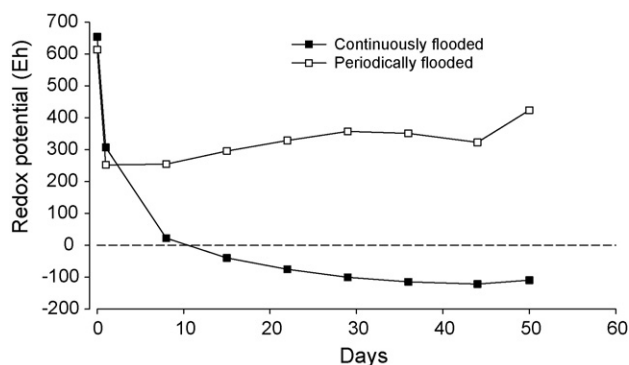


Fig. 2 – Changes in redox potential (Eh) with time. Solid squares: continuously flooded cores, open squares: periodically flooded cores (mean ± 1 S.E.).

eral soil layer (Table 3, $p < 0.0001$). There were also significant interactions between the grazing treatment and the presence of *Juncus* ($p = 0.0003$), in which the exclusion of cattle did not affect TP and organic matter in *Juncus* tussocks, but significantly reduced detritus organic matter and detritus TP in the plant interspace areas in the detrital layer. Cores from plant interspace areas lacked a detritus layer in grazed plots, but had $6.4 \pm 3.2 \text{ kg/m}^2$ of detritus inside the grazing exclosures, which was 60–75% of the detritus present in *Juncus* tussocks (grazed: $8.5 \pm 3.1 \text{ kg/m}^2$; ungrazed: $11.4 \pm 9.6 \text{ kg/m}^2$). The organic mat-

ter and P content of mineral soil was not affected by grazing exclosures (Table 3, significance column).

Periodic flooding decreased Mehlich-1 P in both soil layers over time (ANOVA: organic, $p = 0.0140$; mineral, $p = 0.0024$). Soil TP was not affected by the flooding treatment. The pH of the organic soil layer was greater in continuously flooded cores (ANOVA, $p = 0.0251$), as would be expected from the inverse relationship between pH and redox values (Mitsch and Gosselink, 2003).

4. Discussion

4.1. The dominant role of *Juncus* tussocks in P flux

Phosphorus flux rates were much greater from *Juncus* tussocks than from plant interspace areas, indicating that the tussocks are a major source of P flux in these wetlands during seasonal flooding events. Flux estimates based on fluxes from mineral soil would greatly underestimate actual P flux rates in the field, which are likely to be dominated by the concentrations of detritus and decaying litter within the tussocks, at least in wetland areas dominated by *Juncus*. A study in 2005 in the same sampling sites showed that detritus associated with *Juncus* tussocks accounted for 63% of the total detritus organic matter within the *Juncus* hydrologic zone (Smith, 2006). Our results indicate that this large pool of organic matter is a major source of P release during flooding events.

Table 3 – Soil physicochemical properties of cores with or without *Juncus* plants and subjected to different flooding treatments (N = 10, mean ± 1 S.E.)

Soil parameter	<i>Juncus</i>		Interspace		$p < 0.05^a$
	Continuous flooding	Periodic flooding	Continuous flooding	Periodic flooding	
Mehlich-1 P ($\mu\text{g/g}$)					
Organic layer	9.8 ± 0.8	7.9 ± 1.1	6.8 ± 0.4	5.4 ± 0.7	J, F ^b
Mineral layer	1.9 ± 0.2	1.4 ± 0.3	1.1 ± 0.1	0.7 ± 0.1	J, F ^b
Total P ($\mu\text{g/g}$)					
Detritus	596.3 ± 62.4	577.1 ± 78.1	236.6 ± 86.0	223.5 ± 86.2	G, J, G × J, G × J × F ^c
Organic layer	186.0 ± 14.6	200.4 ± 21.3	158.5 ± 11.2	146.0 ± 11.4	J
Mineral layer	6.4 ± 0.9	6.2 ± 0.9	4.6 ± 0.5	4.2 ± 0.6	J
Organic matter (%)					
Detritus	51.5 ± 5.8	47.6 ± 6.2	19.0 ± 6.9	18.9 ± 7.7	G, J, G × J ^c
Organic layer	18.9 ± 1.5	19.0 ± 2.5	15.3 ± 0.9	13.8 ± 1.2	J ^b
Mineral layer	1.2 ± 0.2	1.9 ± 0.7	0.8 ± 0.1	0.7 ± 0.1	J ^b
Total P (mg)					
Detritus	46.29 ± 7.43	34.52 ± 3.03	10.64 ± 3.92	11.527 ± 4.53	G, J, G × J
Organic layer	115.07 ± 15.75	129.63 ± 10.59	126.08 ± 8.97	122.99 ± 7.64	G × F
Mineral layer	6.574 ± 0.70	5.9166 ± 1.18	5.1881 ± 0.663	4.4564 ± 0.66	–
Organic Matter (g)					
Detritus	40.83 ± 1.10	28.65 ± 2.69	8.54 ± 3.15	9.38 ± 3.62	G, J, G × J
Organic layer	117.05 ± 16.47	122.21 ± 11.84	120.61 ± 4.31	116.19 ± 7.53	G × F
Mineral layer	10.134 ± 1.62	12.051 ± 2.49	9.082 ± 1.60	7.3186 ± 1.04	–

Significance values are given for the main treatments of *Juncus*, (J), flooding (F) and grazing (G).

^a ANOVA.

^b Data log-transformed prior to analysis.

^c Data rank-transformed prior to analysis.

The SRP flux rates in cores from plant interspace areas in our experiment were within the range of values summarized by Malecki et al. (2004) from a variety of studies examining SRP flux rates from riverine sediments (−0.37 to 53.0). However, the initial flux from *Juncus* tussock cores in our study were much higher than that reported range (Table 2). Most flux studies are performed with soil or sediment cores in the absence of significant plant structures (e.g. Malecki et al., 2004; Fisher and Reddy, 2001). We are unaware of flux studies from intact soil–plant–detritus systems, such as those represented by our *Juncus* tussock cores, but our data suggest that these tussocks could be a major source of P flux during flooding events.

The effects of *Juncus* on P flux can be viewed as an indirect effect of grazing because cattle have a strong influence on composition of the plant communities in these wetlands. Higher grazing intensity during the growing season fosters proliferation of areas dominated by *Juncus* and other “weedy” species, and lower intensity grazing in the dormant season is associated with a more diverse plant community containing more native species (Gathumbi et al., 2005; Bohlen and Gathumbi, 2007). At the upland-wetland ecotone of grazed wetlands at our study site, *Juncus* comprised 48% of ground cover, and there was considerable bare ground due to cattle trampling between tussocks (Table 1). By contrast, in small fenced plots where cattle had been excluded for four years, *Juncus* accounted for only 12% of cover and there was little bare ground. *Panicum hemitomon*, a preferred forage grass, accounted for 65% of ground cover inside cattle enclosures but only 4% in grazed areas, showing that this species out competes *Juncus* in the absence of grazing (Table 1).

The shift towards dominance by *Juncus* in grazed wetlands may alter wetland P cycling not only because of the increased heterogeneity in the distribution of soil P, but also because of differences between *Juncus* and other species in P release from decaying plant litter. A recent study comparing P release from the senescent tissues of various wetland plants showed that *Juncus* decomposed more quickly and released more P to water than *P. hemitomon*, indicating that *P. hemitomon* may provide more effective P storage in detritus (Balcer, 2006). In our study, the detritus that had built up between *Juncus* tussocks in the grazing enclosures was not associated with elevated concentrations of SRP or TP in surface water of soil cores collected from the interspace areas. Thus, this newly accumulated detritus contributed additional P storage with lower risk of P release when compared with *Juncus* detritus. It is possible that given greater time to accumulate in the absence of grazing, this detritus build up could lead to greater P release. This hypothesis could be tested in areas that have had long-term grazing enclosures in which the soil conditions had reached a new equilibrium in the absence of cattle. However, available data suggest that the plant species that develop in the absence of grazing produce detritus with lower P release than *Juncus* detritus.

Detritus in *Juncus* tussocks consisted of a mixture of recently senesced stems and a thick layer of plant material in various stages of decomposition, and it is not known whether P release was greater from more recently deposited or more highly decomposed material. Rewetting of fen soils

from northern Germany resulted in greater P release from more highly decomposed material than from less decomposed material (Zak and Gelbrecht, 2007). It is possible that there is greater release of P from more highly decomposed material within *Juncus* clumps, which contributes to greater P release upon rewetting as this detritus becomes more highly decomposed.

We expected that *Juncus* would maintain aerobic conditions longer than similar cores without *Juncus*, due to oxygenating effects in the *Juncus* rhizosphere, but the anaerobic status of *Juncus* cores was indistinguishable from cores without *Juncus*. It is possible that the large quantities of detritus stored in *Juncus* tussocks supported high heterotrophic activities associated with decomposition, which consumed available oxygen and maintained an anaerobic status.

Although we observed indirect effects of grazing on wetland-scale P release, due to changes in plant community composition and the heterogeneity created by *Juncus* tussocks and bare soil, we expected that there would be a greater direct effect of excluding cattle from the enclosure areas for four years. The lack of a large direct effect of cattle on P dynamics, when compared to other studies, may be attributed to the relatively low stocking densities in our study (0.74–1.73 cows ha^{−1}), which were much lower than densities reported by McDowell et al. (2005) (80–556 cows ha^{−1}, short-term) or Turner et al. (1979) (400 sheep ha^{−1}). Another reason may be that the grazing enclosures in our study had not been in place long enough as discussed above. Our study design was not ideal for examining the direct effects of cattle on P fluxes; for example, we did not specifically examine the effects of cattle trampling, which could have been simulating by disturbing the soil surface in the cores or in confined mesocosms in the field. Our study was not designed to test for the influence of manure deposition, which may have an influence on P release to the water column in the field. Although these direct effects of cattle may be very important, our study focused more in indirect effects of cattle due to shifts in the plant community and long-term changes in the soil environment.

4.2. Influence of flooding treatments on P dynamics

Flooded conditions contribute to P release due to the inverse relationship between P release and soil redox conditions (Moore et al., 1998; Fisher and Reddy, 2001). The rhizosphere of aquatic macrophytes is more susceptible to increased P release during long-hydroperiods since rhizosphere soil is typically more ferric than surrounding soils (Weiss et al., 2004). Iron-related P release is considered to be a consequence of the reduction of Fe³⁺ to the more soluble Fe²⁺, which has been shown to increase SRP concentrations (Reddy et al., 1999; Patrick and Khalid, 1974; Richardson, 1985).

Although we did not measure Fe, redox data from our cores show that reduced conditions were created under continuous flooding, and these low redox conditions were associated with P release (Fig. 2). Other data from wetlands in improved pastures on Buck Island Ranch showed that Fe–Al–P accounted for about 12% of total P in the upper 8 cm of mineral soil, and that Al concentrations (355.8 mg/kg) were much greater than Fe concentrations (13.2 mg/kg) (Hill, 2003). By contrast, organic

P in these wetland soils accounted for 61% of total P, indicating that mineralization or release of organically bound P may have been the most likely source of inorganic P released during flooding. Hydrolytic cleavage of particulate organic matter is believed to be an important process for P release from peaty soils (Turner et al., 2003). Thus the microbial activity involved in decomposition of *Juncus* detritus may have made the largest contribution to P mobilization. In addition to redox conditions, biotic factors, such as changes in microbial activity, and release from cell lysis, can affect P release during inundation and may have been important in our study (Wright et al., 2001).

The decrease in water column SRP, pore water SRP in mineral soil, and Mehlich-1 P concentrations in periodically flooded cores could have been due to a loss of P in drainage water or conversion of P to less available forms due to P adsorption. Draw down of water below the soil surface is associated with oxidation of soils (Busnardo et al., 1992), and the soil in periodically flooded cores remained oxic throughout the experiment. The redox values were relatively stable throughout the experiment but were only measured after the weekly flooding events and may have fluctuated to higher levels after draining the cores.

5. Conclusions

Our results show that *Juncus* tussocks are both an important source and sink of P in isolated wetlands, and that their distribution is strongly influenced by cattle. Cattle increase the heterogeneity of P storage and release in these wetlands by shifting the plant community from one dominated by dense marsh vegetation with continuous soil cover to one dominated by *Juncus* tussocks separated by bare, heavily trampled soil. This heterogeneity must be taken into account when assessing P flux from wetland soil and detritus to surface water in grazed wetlands. If the main effect of cattle is to decrease soil OM storage and shift the plant community towards species that have greater P release from decaying tissues, then it may be difficult to increase the P sink strength of wetlands in cattle pastures without altering cattle stocking regimes.

Possible goals for BMPs in isolated wetlands in cattle pastures would be to minimize release of P from wetland soils and maximize build up of detritus with low P release characteristics. Soil accumulation represents the major long-term sink for P in wetlands, but natural wetlands are not particularly effective as nutrient sinks, particularly at high nutrient concentrations (Howard-Williams, 1985). Furthermore, cattle may reduce the ability of wetlands to achieve maximum nutrient storage in the soil–plant–detritus system because cattle reduce soil organic matter storage and detritus by trampling, and may also increase P release due to sediment suspension during flooded conditions. Keeping cattle out of wetlands in pasture or limiting access to certain time periods would be impractical in most cases due to the large number of small wetlands and the cost of building and maintaining fences. Providing economic incentives to landowners for implementing such management options could encourage their adoption. A greater understanding of the effects

of grazing and ranch management practices on P dynamics in these wetlands is needed to clarify the potential of these systems to act as nutrient sinks or sources in the landscape.

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