Hydrologic Regime Controls Soil Phosphorus Fluxes in Restoration and Undisturbed Wetlands

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Abstract

Many wetland restoration projects occur on former agricultural soils that have a history of disturbance and fertilization, making them prone to phosphorus (P) release upon flooding. To study the relationship between P release and hydrologic regime, we collected soil cores from three restoration wetlands and three undisturbed wetlands around Upper Klamath Lake in southern Oregon, U.S.A. Soil cores were subjected to one of three hydrologic regimes—flooded, moist, and dry—for 7.5 weeks, and P fluxes were measured upon reflooding. Soils from restoration wetlands released P upon reflooding regardless of the hydrologic regime, with the greatest releases coming from soils that had been flooded or dried. Undisturbed wetland soils released P only after drying. Patterns in P release can be explained by a combination of physical and biological processes, including the release of iron-bound P due to anoxia in the flooded treatment and the mineralization of organic P under aerobic conditions in the dry treatment. Higher rates of soil P release from restoration wetland soils, particularly under flooded conditions, were associated with higher total P concentrations compared with undisturbed wetland soils. We conclude that maintaining moist soil is the means to minimize P release from recently flooded wetland soils. Alternatively, prolonged flooding provides a means of liberating excess labile P from former agricultural soils while minimizing continued organic P mineralization and soil subsidence.

Key words: hydrologic regime, lake eutrophication, phosphorus, soils, Upper Klamath Basin, Oregon, wetland restoration.

Introduction

Restoration of agricultural land that was previously wetland is an increasingly common practice in North America where economic incentives and policy initiatives support restoration to recoup lost ecosystem functions (e.g., Wetland Reserve Program 2002). These lands typically have a history of row crop agriculture and/or livestock grazing, with associated soil disturbances including nutrient enrichment from fertilizers and animal excrement, loss of organic matter, compaction and subsidence, and disruption of the soil profile from tillage (Knops & Tilman 2000; Bruland et al. 2003; Zedler 2003).

Because of these soil disturbances, it is challenging to restore wetland biogeochemical functions in the short term (Kusler & Kentula 1990; Zedler 2000, 2003). In particular, a history of nitrogen (N) and phosphorus (P) enrichment can upset the nutrient cycle balance in ecosystems whose plant and microbial communities likely were limited historically by one of these elements (Wisheu et al. 1990; Bedford et al. 1999). A typical desired outcome for wetland restoration projects is resumption of the ecosystems' nutrient storage functions. However, recent studies of wetland restoration on land drained for agriculture show an initial release of P once the land is reflooded (D'Angelo & Reddy 1994; Phillips 2001; Pant & Reddy 2003). The focus of such studies has been to develop management strategies that minimize these releases and maximize P storage efficiency.

Wetland restoration on reclaimed agricultural land is a critical watershed restoration strategy in the Upper Klamath Basin in southern Oregon. Since 1899, approximately 85–90% of original wetlands in the Upper Klamath Basin have been drained for agriculture (Akins 1970; USFWS 1991). This land use conversion, in addition to erosion from forest-clearing activities in the watershed, is believed to have accelerated P loading to Upper Klamath Lake, resulting in a hypereutrophic state characterized by massive summertime cyanobacterial blooms and associated fish kills (Kann & Smith 1999; Saiki et al. 1999). Wetland restoration is viewed as an important tool for reducing nutrient levels in Upper Klamath Lake because of the nutrient sequestration properties associated with these ecosystems (Boyd et al. 2002). However, these efforts are tempered by concern that excessive soil P release from restoration wetlands may further exacerbate water quality problems in the lake.

Predicting whether and how much P will be lost from newly flooded wetlands is complicated by the intricacies of the P cycle but likely depends greatly on hydrology.

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In particular, the flooding regime imposed on these ecosystems influences many physical and biotic properties that affect P mobility and availability. For example, soil and water pH and redox status control the forms of metals such as iron that will bind or release P (Frossard et al. 1995; Schlesinger 1997), and biologically mediated processes such as organic matter decomposition may contribute to P release (Koerselman et al. 1993). On the other hand, P uptake and release may be a product of edaphic properties related to the previous land use (e.g., fertilization and soil organic P [P_o] mineralization) and beyond management control. Regardless of what controls P fluxes in these wetlands, it is important to predict the effects of restoration on surface water P concentrations, as well as to identify management actions that might minimize P release.

The objective of this study was to compare P fluxes from undisturbed and restoration marsh soils from around Upper Klamath Lake, Oregon, which were exposed to different hydrologic regimes. We tested two hypotheses: (1) soils from restoration wetlands disturbed by agriculture will release P upon flooding, whereas soils from wetlands that had never been drained will be in equilibrium with the surface water and thus will not release P and (2) the hydrologic regime will have a significant effect on P uptake or release through its controls on peat decomposition and soil and water redox status. These results will be used to guide water management strategies for restoration wetlands around Upper Klamath Lake and to assess the potential for these projects to affect lake water quality.

Methods

Site Characteristics

Six wetlands around Upper Klamath Lake were sampled (Table 1). Three were drained and converted to agriculture during the past century and currently are being restored to wetland. Caledonia Marsh at the Running Y Ranch (lat 42°17'15"N, long 121°54'5"W) and the Williamson River Delta (lat 42°29'41"N, long 121°58'22"W) were drained in the 1910s and 1940s, respectively, and farmed

until the end of the century. These properties were first reflooded in 1997 and 1998, respectively, although restoration at some sites in the form of dike, levee, and drain removal is ongoing. The Agency Lake Ranch (lat 42°34'54"N, long 121°57'30"W) was drained in the 1960s and grazed until 1998 when it was purchased by the U.S. Bureau of Reclamation and flooded seasonally to increase water storage in the lake. The other three wetlands never were drained, although they are impacted by lake-level management, which is controlled to support water withdrawals for irrigation. Both Upper Klamath Lake National Wildlife Refuge (lat 42°28'17"N, long 122°3'22"W) and Squaw Point (lat 42°21'28"N, long 121°53'38"W) have little or no open water, whereas Hank's Marsh (lat 42°18'45"N, long 121°49'46"W) is more open, with vegetation in clusters separated by open water. We refer to the drained and reflooded wetlands as restoration wetlands, to reflect the ongoing process of restoration, and to the sites that never were drained as undisturbed wetlands, although we acknowledge that the latter are affected by lake-level management.

Plant communities at all sites are dominated by emergent species, such as Cattail (*Typha latifolia*), Hard-stem bulrush (*Schoenoplectus acutus*), and Simple-stem burreed (*Sparganium eurycarpum*); undisturbed wetlands also contain patches of the floating macrophyte Yellow pond lily (*Nuphar lutea* spp. *polysepala*). The undisturbed sites are more densely vegetated, whereas the restoration sites have bare ground interspersed with vegetation, probably because the plants have not had sufficient time to colonize.

Restoration wetlands have hydrologic regimes controlled by dikes and pumps that flood and drain the wetlands. Most of these sites dry out by mid- to late summer and are reflooded to depths ranging from several centimeters to over 1 m in the winter and spring. Water levels in undisturbed wetlands fluctuate with lake levels, with maximum and minimum depths occurring in March and September, respectively. These wetlands remain flooded for much of the year.

Soils at all the sites are Lather-Histosols, which are very deep, very poorly drained muck soils that formed in organic matter (National Cooperative Soil Survey 1985).

Table 1. Study site and land use; soil characteristics; and SRP concentrations midway through the experiment.

Site Name (ha)	Year Drained (Agricultural Use)	Bulk Density (g/cm³)	Total Soil Carbon (mg/cm³)	Total Soil P (µg/cm³)	SRP (mg/L)
Hank's Marsh (490)	n/a	0.13 (0.01)	26.54 (2.33)	97.44 (3.12)	0.025
Squaw Point (150)	n/a	0.15 (0.02)	27.75 (2.82)	147.71 (5.92)	0.036
Upper Klamath Lake National Wildlife Refuge (5,590)	n/a	0.15 (0.01)	34.46 (4.27)	124.81 (11.77)	0.039
Agency Lake Ranch (1,050)	1962 (grazing)	0.24 (0.02)	79.50 (7.70)	235.87 (27.80)	2.38
Running Y Ranch (1,010)	1916 (crops)	0.38 (0.03)	116.17 (4.27)	302.33 (29.30)	0.275
Williamson River Delta (3,040)	1920 (crops)	0.32 (0.02)	66.52 (8.21)	353.80 (15.01)	1.81

Soil samples were taken from the upper 10 cm of the soil profile. Values are means of three replicates (±SE). Concentrations of SRP were taken on day 18; samples from each location were composites of the flooded treatment cores, and there was no replication. Cores had been replenished with lake water approximately 1 week prior to sampling and were replenished again immediately after sampling. n/a = not drained.

All the restoration sites have experienced significant soil subsidence as a result of peat compaction and oxidation. Data on physical and chemical soil properties are given in Table 1.

P Flux Study

In July 2002, triplicate 20-cm soil cores were collected from three randomly selected locations at each of the six sites, for a total of 54 cores. Cores were collected using 20-cm tall and 10-cm-diameter polyvinyl chloride (PVC) tubes, each with a beveled end that was pushed into the soil. A bread knife was used to cut into the soil around the core to minimize compaction. The bottom of the core was cut flush with the bottom of the tube, which was then sealed with a fitted PVC cap using nonleachable glue approved for drinking water. Each core was placed in a slightly larger polyethylene container capable of holding water (see flooded treatment below). The containers were assigned randomly to tubs to keep the containers off the bare ground, with six containers per tub. The tubs were kept outside in a shaded area for the duration of the experiment, and an overhead tarp prevented rainwater from reaching the cores. There was a small amount of algal growth in the containers, which was removed with tweezers.

The nine cores from each site were assigned randomly to one of the three hydrologic treatments: (1) dry (cores allowed to dry out completely); (2) moist (cores remained moist with all pore spaces filled but with no standing water above the soil surface); and (3) flooded (cores maintained with 5 cm of standing water). Cores were replenished with lake water as needed, which had total P concentrations ranging from 0.170 to 0.577 mg P/L and soluble reactive P (SRP) concentrations ranging from 0.090 to 0.412 mg SRP/L. Due to a small amount of leakage from the flooded cores, water levels in the larger polyethylene containers were maintained at the same level as those in the PVC tubes. We assumed that little mixing occurred between the water in the tube and that in the surrounding container because the head was equal in both and the amount of leakage was slight.

Cores were maintained under these hydrologic treatments for 7.5 weeks (53 days) from mid-July to mid-September 2002. All the surface water in the flooded cores was removed midway through the experiment (day 18), and subsampled for SRP, which is the most bioavailable form of P (APHA 1998). Because we sampled prior to water replenishment, we pooled samples from each site to obtain sufficient volume for the analysis. Samples were filtered through a 0.45-μm filter, chilled, and analyzed for SRP within 48 hours at a private lab (Aquatic Research, Inc., Seattle, WA, U.S.A.), using the automated ascorbic acid reduction method.

On day 54, surface water was drained from the flooded cores, and the dry cores were wetted to a saturated state with lake water. Wetting the dry cores was done to ensure that all the water added afterward stayed as surface water rather than simply filling soil pores. On day 55, 300 ml of lake water was added to each core to achieve a standing water depth of approximately 5 cm. After 24 hours (day 56), the surface water was sampled from all cores and replaced with an additional 300 ml of fresh lake water. This water was collected on day 60. All water samples were filtered immediately upon collection and analyzed for SRP as above. Half the cores from Hank's Marsh (an undisturbed site) expanded during the experiment, and we were only able to add 100 ml to these cores.

P fluxes were estimated by calculating the difference in SRP concentrations between lake water and standing water after 24 hours or 4 days. This value was divided by the core surface area and the elapsed time between water addition and sampling to calculate the flux (reported in mg SRP m^{-2} day^{-1}).

Soil Chemistry

To quantify the forms and amounts of soil P, three soil cores of 8.5-cm diameter × 10 cm deep were collected at the same locations from each of the six marshes on 14–17 July 2002. Cores were transported to the lab on ice where they were kept refrigerated at 4°C while awaiting analysis. Each field moist core was weighed and a 10-g (wet weight) subsample dried at 70°C. Bulk density was estimated by multiplying the weight of the core by the dry:wet weight ratio and dividing by the core volume.

Forms of P were sequentially extracted using a modification of the Hedley procedure (Hedley et al. 1982; Qualls & Richardson 1995). Labile inorganic P (P_i) was extracted with 0.5 M NaHCO$_3$. A subsample from each NaHCO$_3$ extract was digested with potassium persulfate to determine amounts of labile total P (APHA 1998). Labile organic P (P_o) was calculated by subtracting labile P_i from labile total P. A second set of soils was fumigated with chloroform, then extracted with sodium bicarbonate, and digested with potassium persulfate. Microbial-bound P was calculated as phosphate in the chloroform-extracted soils minus P in the unfumigated soil. Surface Fe- and Al-bound P_i was extracted using 0.1 M NaOH followed by NaOH + sonication to extract occluded Al- and Fe-bound P_i. Humic acid–bound P_o was precipitated from both the unsonicated and sonicated NaOH extracts using 6 M HCl. The precipitate was oven dried at 70°C, ground, and digested with nitric and perchloric acid (Sommers & Nelson 1972). Calcium-bound P_i was extracted with 1 M HCl. The remaining soil residue was oven dried at 70°C, ground, and digested with nitric and perchloric acid to estimate residual P.

A second set of soils from each increment was oven dried at 70°C and analyzed for organic C (Perkin-Elmer 2400 CHN Analyzer, Perkin-Elmer, Norwalk, CT, U.S.A.) and total P by nitric and perchloric acid digestion (Sommers & Nelson 1972). Total P was compared with the sum of all P fractions to obtain percent recovery. All P

extracts were analyzed colorimetrically using the ascorbic acid method (APHA 1998).

Statistical Analysis

Flux data were log transformed to meet assumptions of homoscedasticity and normality. The data were analyzed using a general linear model (SYSTAT Software, Inc. 2002). The response variables were SRP flux from the cores at 24 hours and 4 days. Predictor variables were "class" (restoration vs. undisturbed), "site" (nested within class), "treatment" (the hydrologic regime), and their interactions. To test for significant differences among treatment means, we used a test of pairwise comparisons with a Bonferroni adjustment.

Results

Soil P Fluxes

Midway through the experiment, standing water SRP concentrations of flooded cores from the restoration wetlands were greater than those from undisturbed wetlands (Table 1). However, this difference was not statistically significant because of the relatively low concentrations for the Running Y cores, which were higher than that for the undisturbed wetlands but almost 10-fold less than those for the other two restoration sites.

At the end of the experiment, nearly all soil cores released SRP into the water column 24 hours and 4 days after flooding. In particular, soils from the restoration wetlands had positive net SRP fluxes (Fig. 1a). After 24 hours, mean P fluxes from the restoration wetland soils were 32.07 (±11.99) (dry), 15.03 (±4.93) (moist), and 55.52 (±16.84) (flooded) mg SRP m^{-2} day^{-1} (±SE). Net SRP fluxes dropped for these cores after 4 days but were still significantly positive at 26.63 (±7.86) (dry), 8.56 (±2.73) (moist), and 19.93 (±5.60) (flooded) mg SRP m^{-2} day^{-1}. Flux rates for the flooded cores might have been underestimated because the surface water was removed once in the middle of the experiment and any removed P could not be accounted for in the final P flux estimates. We did not compare the 24-hour and 4-day data statistically because the amount of incubation time differed for each, making comparisons of daily flux rates not statistically valid. Flux rates from Running Y Ranch soils were lower in all treatments than those from the two other restoration wetlands and were within the range of those from undisturbed wetlands.

In contrast to the restoration wetlands, soil cores from the undisturbed wetlands responded very differently to the hydrologic treatments (Fig. 1b). Cores in the dry treatment had net positive SRP fluxes from the soils to the water column, similar to the restoration wetlands at 18.10 (±7.61) (24 hours) and 10.30 (±3.55) (4 days) mg SRP m^{-2} day^{-1}. For the moist and flooded treatments, net SRP fluxes were not significantly different from 0, at both 24
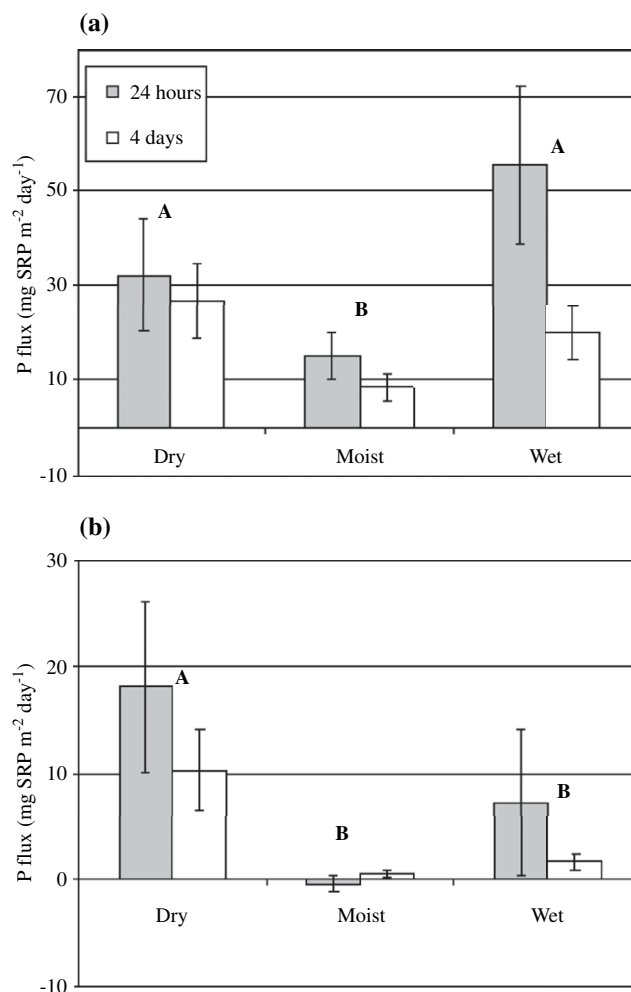

Figure 1. P fluxes from wetland soils, 24 hours and 4 days after flooding. (a) Restoration wetlands and (b) undisturbed wetlands. Treatment means with the same uppercase letter are not significantly different ($p < 0.05$) using a test of pairwise comparisons with a Bonferroni adjustment. Note different scales on y-axes.

hours and 4 days. However, similar to the restoration wetlands, the P flux rates for the flooded cores might have been underestimated because of potential P removal halfway through the experiment.

Soils from restoration and undisturbed wetlands responded differently to the hydrologic treatments as evidenced by a significant drainage class-by-treatment effect in the repeated measures general linear model ($p < 0.05$, both wetland types). For the restoration wetlands, the flooded and dry treatments had significantly greater P fluxes than the moist treatment (Fig. 1a). In the undisturbed wetlands, dry soils released significantly more P than either moist or flooded soil (Fig. 1b). The lack of a significant main effect for wetland class was attributed to the extremely low flux rates for Running Y soils compared with other restoration wetlands.

The only soil cores to show a net P uptake, indicated by a negative flux, both after 24 hours and 4 days, were predominantly from undisturbed wetlands that were either moist or flooded. However, this net negative SRP flux was not statistically different from 0.

Soil Chemistry

Total P in soil cores from the restoration wetlands was more than two times greater than that from the undisturbed wetlands (Table 1). Most of the excess P in the restoration wetlands was held in the residual-P pool, the Ca-P pool, and the humic-P pool (Table 2). Concentrations of occluded Fe- and Al-P were significantly greater in the restoration wetlands; however, surface-bound Fe- and Al-P were similar in both wetland classes. Although accounting for less than 10% of the sum of all P fractions, two of the most labile forms of P, labile P_o and microbial P, were significantly greater in the undisturbed wetlands than in the restoration sites.

Organic C was greater in the restoration site cores than in the undisturbed ones (Table 1). The same was true for bulk density, which can be accounted for by soil compaction from agricultural practices at the restoration sites.

Discussion

Our results demonstrate that flooded soils in the restoration areas will initially be a source of P, regardless of the hydrologic management regime. We measured P fluxes ranging from -2 to $+135$ mg P m^{-2} day^{-1} after 24 hours and from -0.2 to $+67$ mg P m^{-2} day^{-1} after 4 days. The daily flux rates likely decreased for the 4-day measure because we expected an asymptotic flux curve over time as the water and soil reached equilibrium.

These flux rates are similar to those documented elsewhere for newly flooded agricultural soils. In a lakeside wetland in central Florida, fluxes from previously drained agricultural soils averaged 5.5 mg P m^{-2} day^{-1} for the first month of flooding but decreased 2- to 9-fold over the next 10 months (D'Angelo & Reddy 1994). In another constructed wetland on agricultural soils in south-central Florida, Pant and Reddy (2003) measured fluxes ranging from 3 to 93 mg P m^{-2} day^{-1}. They estimated that the constructed wetland would continue to release P for up to 3 years before reaching equilibrium with surface waters. Using soils from an Australian *Melaleuca* wetland, Phillips (2001) measured fluxes of 1–1,175 mg P m^{-2} day^{-1} over 21 days.

P fluxes between wetland soils and the water column are controlled by a combination of geochemical, hydrological, and biological processes (Richardson 1985; Walbridge & Struthers 1993; Frossard et al. 1995). Under oxidizing conditions associated with shallow or mixed water, iron is in the ferric form (Fe^{3+}), which binds P_i in oxyhydroxide flocs. Once the redox potential drops, iron is reduced to ferrous Fe^{2+}, releasing P from the flocs. P release under reducing conditions caused by continuous flooding has been measured numerous times in many types of wetlands (e.g., Richardson & Marshall 1986; Koerselman et al. 1993; Walbridge & Struthers 1993; Appan & Ting 1996; Moore et al. 1998; Phillips 2001). The importance of redox-controlled P release from these soils is supported by the P fractionation data, which show the presence of occluded Fe-bound P in all soils and significantly higher concentrations in restoration wetlands. Assuming that the flooded treatment cores went anoxic at the water/soil interface, release of P from this fraction would explain the relatively high P fluxes for both restoration and undisturbed soils. Although we did not measure the redox potential during this experiment, the cores were covered continuously with water for 7.5 weeks and kept in a sheltered area with little wind, so anoxia easily could have developed. Indeed, data from one of the restoration wetlands (Williamson River Delta) indicate that anoxia can develop in shallow water in less than 24 hours (The Nature Conservancy, unpublished data).

A second mechanism of P release that is generally important for peat soils is organic matter hydrolysis. This process is accelerated under aerobic conditions and may explain high P releases observed for dry cores following reflooding. All samples were peat soils, with organic C greater than 20 mg/cm^3 and with humic-P accounting for 30–50% of P fractions. This organically bound P could be liberated by soil drying and oxidation. Furthermore, the combined concentrations of humic-P and residual-P were greater in the restoration cores, which also had significantly greater P fluxes. Indeed, peat oxidation and the associated release of nonvolatile nutrients from drained wetland soils is thought to be partly responsible for the current eutrophic conditions in Upper Klamath Lake (Snyder & Morace 1997) and elsewhere (Sinke et al. 1990; Kadlec & Knight 1996).

The moist treatment soils showed the lowest P fluxes. Soils from this treatment possibly had higher redox potentials and so did not experience the same Fe reduction as the flooded cores. Nor did they experience the enhanced organic matter decomposition and P mineralization associated

Table 2. Forms and amounts of soil P in the top 10 cm of undisturbed and restoration wetlands.

P Forms	Undisturbed Wetlands	Restoration Wetlands
Residual P_o	**5.9 (2.3)**	**118.0 (8.1)**
Humic acid-bound P_o	52.0 (4.2)	78.9 (13.4)
Ca-bound P_o	**1.9 (0.3)**	**39.5 (8.5)**
Occluded Fe- and Al-bound P_i	**3.1 (0.5)**	**11.1 (1.2)**
Surface Fe- and Al-bound P_i	10.0 (1.4)	11.7 (1.7)
Microbial-bound P_o	**6.2 (1.0)**	**3.3 (0.8)**
Labile P_o	**2.2 (0.4)**	**1.1 (0.3)**
Labile P_i	2.6 (0.7)	1.0 (0.2)

All fractions are reported in μg P/cm^3. Values for each wetland type are means ($\pm$SE) of nine samples (three sites $\times$ three samples per site). Significant differences between wetland types are indicated in bold.

with the dry treatment. From these results we conclude that the optimum hydrologic management scenario for minimizing P release is to maintain wet, but not flooded, soils.

The significant class-by-treatment interaction, showing that the restoration and undisturbed wetlands responded in unique ways to the hydrologic regimes, indicates that some edaphic properties not controlled by hydrology influenced P fluxes to surface waters. Drainage and cultivation caused the restoration wetland soils to have greater total P and organic C on a per mass basis because compaction from agricultural practices increased the bulk density at these sites. These soil properties likely had a significant effect on the quantity of P released. Altered soil profiles are common for drained wetland soils and can significantly affect the stability and release of stored P (Kadlec & Knight 1996). However, differences in bulk density and total P chemistry did not explain the markedly lower P flux rates from Running Y soils compared to other restoration wetlands because these characteristics were similar for all restoration wetlands. It is possible that different original soil types or differences in past agricultural land use practices would significantly influence P flux rates. For example, Running Y soils had the greatest Ca-P fraction ($65.6\ \mu g/cm^3$) compared to the mean for restoration wetlands ($39.5\ \mu g/cm^3$) or the mean for undisturbed wetlands ($1.9\ \mu g/cm^3$). Although soils of this region are Ca poor, gypsum ($CaSO_4$) was commonly used as a soil amendment to correct the pH (D. Renne 2002, The Nature Conservancy, personal communication). The Ca-P bond is strong and thus might have lowered P fluxes from these soils. Additionally, the Fe- and Al-P fractions were lower at Running Y ($6.2\ \mu g/cm^3$) than the mean for restoration sites ($11.7\ \mu g/cm^3$), which may have contributed to the particularly low P fluxes in the wet treatment cores.

One interesting effect of soil disturbances from agriculture on P fluxes was with the moist treatment. At the undisturbed sites, there was little P exchange between soils and surface water. Soils in the lake fringe wetlands usually remain moist at low lake elevations due to the wicking properties of intact peat. P sorption/desorption processes likely are in equilibrium with the lake water that was used in the treatments. This is in contrast with the restoration wetlands, which under moist conditions still released P into the water column.

Although positive P fluxes from flooding wetland soils are expected regardless of hydrologic regime, this effect might be minimized by controlling water levels to maintain moist soils, thus preventing the alternating oxidizing and reducing conditions and associated enhanced organic matter oxidation and Fe reduction, which we believe to be factors controlling P release. But a highly controlled water management scenario is unrealistic because hydroperiods will differ in the wetlands according to variation in soil surface elevation, individual water management manipulations, and climate. Furthermore, stable water levels are not desirable for promoting wetland development on these lands. A more natural hydroperiod for emergent marshes is one that fluctuates, and native wetland plant communities and other wetland organisms are specifically adapted to a fluctuating hydroperiod. Such a regime would mimic that found in undisturbed Upper Klamath Lake wetlands, which are exposed only for a short period of time each fall and maintain moist surfaces because the undisturbed peat can wick water upward even when the water level has dropped.

Given current lake-level management and the conditions of the soils in the restoration wetlands, our results suggest three management recommendations. (1) During the restoration process, wetlands should not dry out for prolonged periods of time. (2) Soils should be kept moist while vegetation is establishing. In addition to minimizing P fluxes, net primary production and thus P sequestration might be maximized by moist soils (Brinson et al. 1981). (3) Prolonged deep flooding should be avoided in areas prone to stagnation, to prevent anoxia-driven release of Fe-bound P.

Where wetlands are restored on soil that was farmed, it is perhaps inevitable that there will be an initial period of equilibration. For the first several years, it is likely that they will not behave as their undisturbed counterparts and that soil biogeochemistry will be one of the most difficult components to restore. However, in landscapes such as the Upper Klamath Basin where many wetlands have been lost, the negative impacts of releasing loosely bound P must be weighed against the tremendous benefits of providing habitat for fish, aquatic birds, and other wildlife.

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