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Source: *Wetlands*, 25(3):594-606. 2005.

Published By: The Society of Wetland Scientists

DOI: 10.1672/0277-5212(2005)025[0594:FAAOSP]2.0.CO;2

URL:

<http://www.bioone.org/doi/full/10.1672/0277-5212%282005%29025%5B0594%3AFAAOSP%5D2.0.CO%3B2>

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FORMS AND ACCUMULATION OF SOIL P IN NATURAL AND RECENTLY RESTORED PEATLANDS—UPPER KLAMATH LAKE, OREGON, USA

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Abstract: Forms, amounts, and accumulation of soil phosphorus (P) were measured in natural and recently restored marshes surrounding Upper Klamath Lake located in south-central Oregon, USA to determine rates of P accumulation in natural marshes and to assess changes in P pools caused by long-term drainage in recently restored marshes. Soil cores were collected from three natural marshes and radiometrically dated to determine recent (¹³⁷Cs-based) and long-term (²¹⁰Pb-based) rates of peat accretion and P accumulation. A second set of soil cores collected from the three natural marshes and from three recently restored marshes was analyzed using a modification of the Hedley procedure to determine the forms and amounts of soil P. Total P in the recently restored marshes (222 to 311 μg cm⁻³) was 2–3 times greater than in the natural marshes (103 to 117 μg cm⁻³), primarily due to greater bulk density caused by soil subsidence, a consequence of long-term marsh drainage. Occluded Fe- and Al-bound P_i, calcium-bound P_i and residual P were 4 times, 22 times, and 5 times greater, respectively, in the recently restored marshes. More than 67% of the P pool in both the natural and recently restored marshes was present in recalcitrant forms (humic-acid P_o and residual P) that provide long-term P storage in peat. Phosphorus accumulation in the natural marshes averaged 0.45 g m⁻² yr⁻¹ (¹³⁷Cs) and 0.40 g m⁻² yr⁻¹ (²¹⁰Pb), providing a benchmark for optimizing P sequestration in the recently restored marshes. Effective P sequestration in the recently restored marshes, however, will depend on re-establishing equilibrium between the P-enriched soils and the P concentration of floodwaters and a hydrologic regime similar to the natural marshes.

Key Words: Upper Klamath Lake, eutrophication, wetland restoration, phosphorus, phosphorus fractionation, phosphorus accumulation, nutrient accumulation, peat accretion, peatland, radiometric dating, Cesium-137, Lead-210

INTRODUCTION

Eutrophication of freshwater ecosystems is a major environmental problem that is frequently linked to human activities. Upper Klamath Lake, a large, shallow, naturally productive lake in Oregon, USA is one such case. Although paleolimnological studies suggest that Upper Klamath Lake has been naturally eutrophic for at least a thousand years (Sanville et al. 1974, Eilers

et al. 2001), biological changes in sediment chronology suggest progressive cultural eutrophication of the lake since the late 1800s, when Europeans first settled the area (Bradbury et al. 2004). For the past 50 years, nuisance blooms of the cyanobacteria *Aphanizomenon flos-aquae* (L.) Ralfs. have plagued Upper Klamath Lake, reducing dissolved oxygen (<2 mg L⁻¹) and increasing ammonia, pH (>9.5), and turbidity (Bortleson and Fretwell 1993) and have led to the lake's recent

classification as a hypereutrophic system (Eilers *et al.* 2001). While there is general agreement that declining water quality in Upper Klamath Lake coincides with the settlement of Upper Klamath Basin (Bortleson and Fretwell 1993, Snyder and Morace 1997, Eilers 2001, Bradbury *et al.* 2004), the causal mechanism is yet unclear. Several hypotheses have been proposed to explain the eutrophication of Upper Klamath Lake during the last century, including the release of nutrients resulting from marsh drainage, increased nutrient loads caused by agricultural activities in the basin and on reclaimed marshland, and changes in flushing patterns caused by reservoir regulation (Bortleson and Fretwell 1993). Another hypothesis suggests that marsh drainage has reduced the transfer of organic compounds (limno-humic acids) to the water column, thereby increasing light availability and promoting the growth of bluegreen algae, such as *A. flos-aquae* (National Research Council 2004, Stan Geiger pers. comm.).

Overall, central to the issue of eutrophication of Upper Klamath Lake is marsh drainage. Prior to European settlement of the basin, about 19,500 ha of marsh surrounded Upper Klamath Lake (Snyder and Morace 1997). Since the late 1800s, approximately 64% (12,500 ha) of this marshland has been diked, ditched, and drained for agricultural use. This has led to increased aerobic decomposition of peat, N and P mineralization in marsh soils converted to agriculture, and the estimated release of approximately 3,900 metric tons of P (Snyder and Morace 1997). However, because Upper Klamath Lake is naturally productive, there has been considerable debate as to the causal relationship of increased P loading from marsh drainage and associated agriculture activities and declining water quality. There is additional debate as to whether marsh restoration activities currently underway in the Upper Klamath Basin will have any significant impact on water quality because of 1) the high internal P load from lake sediments (Gahler and Sanville 1971, Laenen and LeTourneau 1996) and 2) subsidence that has lowered the soil surface elevation of reflooded marshland and altered the hydrology and plant communities. Also, because soils in the recently restored marshes have been highly altered from years of agricultural activity, forms and amounts of soil P may differ from those wetlands that have never been drained.

The objective of this study was to determine the amount P sequestered annually in the marshes of Upper Klamath Lake by measuring recent and long-term rates of P accumulation based on radiometrically (^{137}Cs and ^{210}Pb) dated peat cores from three natural marshes and to estimate potential P sequestration by recently restored marshes. We also measured forms and amounts of soil P in three natural marshes and in three recently restored marshes to quantify changes in soil

P pools caused by long-term drainage and agricultural activities.

Methods

Site Description

Upper Klamath Basin is situated in a large, flat valley east of the Cascade Mountain Range in south-central Oregon and spans two geologic provinces: the Basin and Range to the east and the Sierra-Cascade Mountains to the west. Upper Klamath Lake has a surface area of about 360 km², making it the largest lake in Oregon (Figure 1). Despite its large surface area, the lake is very shallow, with average and maximum depths of 2.4 m and 17.7 m, respectively (U.S. Army Corps of Engineers 1979). The watershed of Upper Klamath Lake encompasses an area of approximately 9,800 km², and the primary source waters for the lake are the Wood and the Williamson Rivers. Prior to entering the lake, the Sprague River flows into the Williamson River, and together, they account for approximately one half of the inflow to Upper Klamath Lake. Secondary water sources include spring flow and ground-water seepage. Upper Klamath Lake is drained by the Link River to the south, where water levels are controlled by the Link River Dam, constructed in 1921, replacing the natural rock sill.

The naturally eutrophic condition of Upper Klamath Lake is attributed to the geology of the basin (Walker 2001). Volcanic ash and pumice deposited throughout the Upper Klamath Basin from the eruption of Mount Mazama (Crater Lake) some 6,800 years ago are rich in P. As a result, the background concentration of total P in Upper Klamath Lake water is estimated to be 60 $\mu\text{g L}^{-1}$ (Boyd *et al.* 2001), more than enough to support dense populations of phytoplankton. Early accounts (1906) from settlers of the basin reported ice supplies contaminated with algae and organic matter (Bortleson and Fretwell 1993). At that time, however, the dominant algae were diatoms, and it was not until 1933 that *A. flos-aquae* were first reported in Upper Klamath Lake. Dominance was established by this bluegreen in the 1950s (Bortleson and Fretwell 1993), and today, *A. flos-aquae* is responsible for annual chlorophyll *a* concentrations that exceed 100 $\mu\text{g L}^{-1}$ (National Research Council 2004).

Upper Klamath Lake was once surrounded by marsh. Today, only about 7,000 ha (36%) of Upper Klamath's marshes still exist in their natural state (Snyder and Morace 1997). Emergent plant communities in these marshes are dominated by hardstem bulrush (*Schoenoplectus/Scirpus acutus* Muhl.), bur-reed (*Sparganium eurycarpum* Engelm.), creeping spike-rush (*Eleocharis palustris* L.), broadleaf cattail (*Typha*

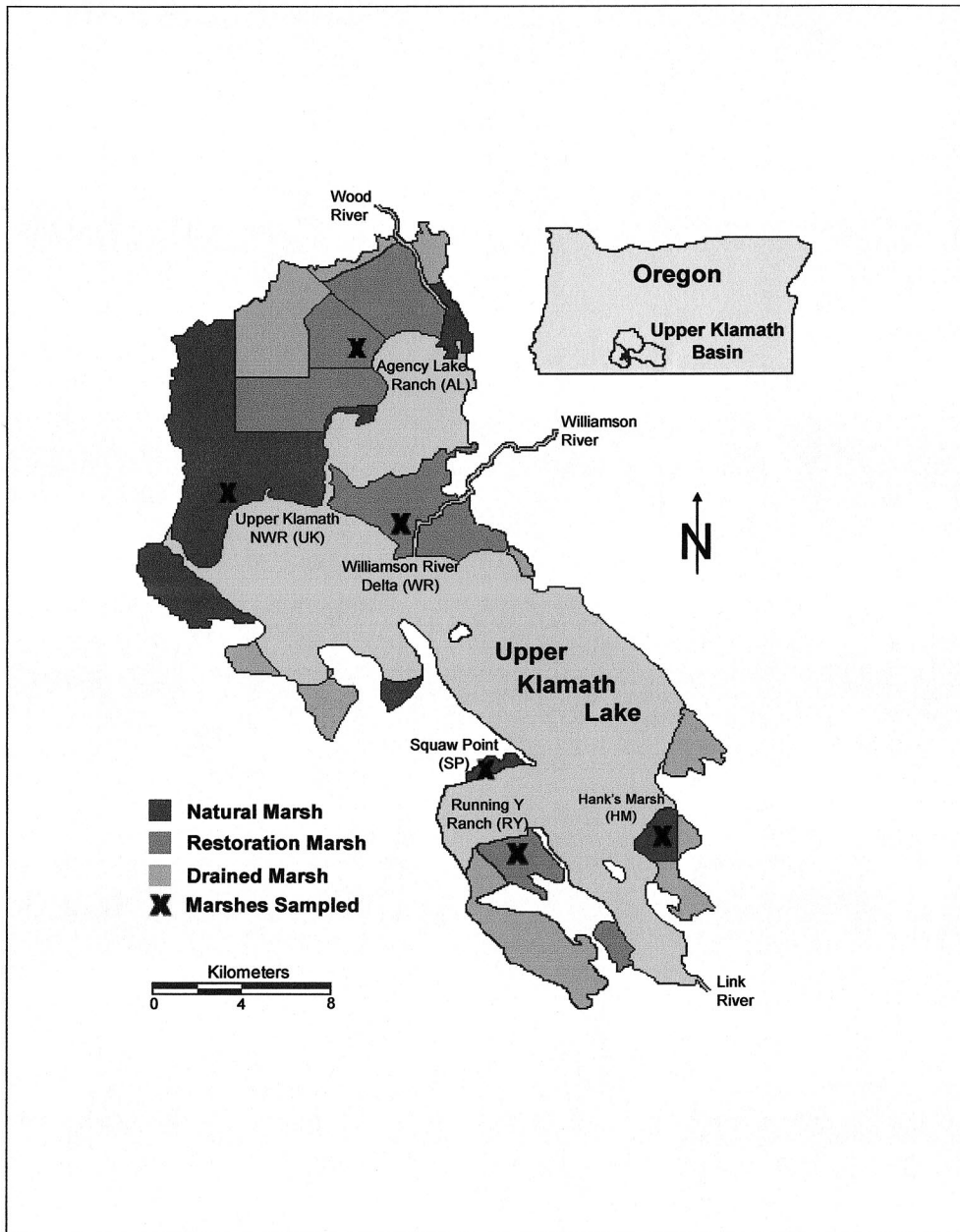


Figure 1. Map of Upper Klamath Lake showing adjacent marshes and sampling locations.

latifolia L.), western yellow pond lily or wocus (*Nuphar lutea* (L.) Sm. ssp. *Polysepala* (Engelm.) E. O. Beal). Less common species include water smartweed (*Polygonum amphibium* L.), arumleaf arrowhead (*Sagittaria cuneata* Sheldon), chairmaker's bulrush (*Schoenoplectus pungens* (Vahl) Palla), cosmopolitan bulrush (*Schoenoplectus/Scirpus maritimus* L.), American water-plantain (*Alisma plantago-aquatica* L.), various sedges (*Carex* spp. L.), and common mare's tail (*Hippuris vulgaris* L.).

Both natural and recently restored marsh soils are classified as Histosols. The recently restored marsh

soils are classified as Lather series (Coprogenous, euc Limnic Borohemists) (USDA 1985). The natural marsh soils were not classified below the level of soil order. Histosol formation at Upper Klamath Lake is the result of organic matter deposition from emergent wetland vegetation, as well as volcanic ash, alluvial materials (volcanic rocks), and lacustrine (diatomaceous and organic) sediments (Snyder and Morace 1997). Based on our organic C and bulk density data in Figure 2a,d, our natural and restored marshes soils, respectively, contain approximately 35% and 65% organic matter by weight to a depth of 30 cm.

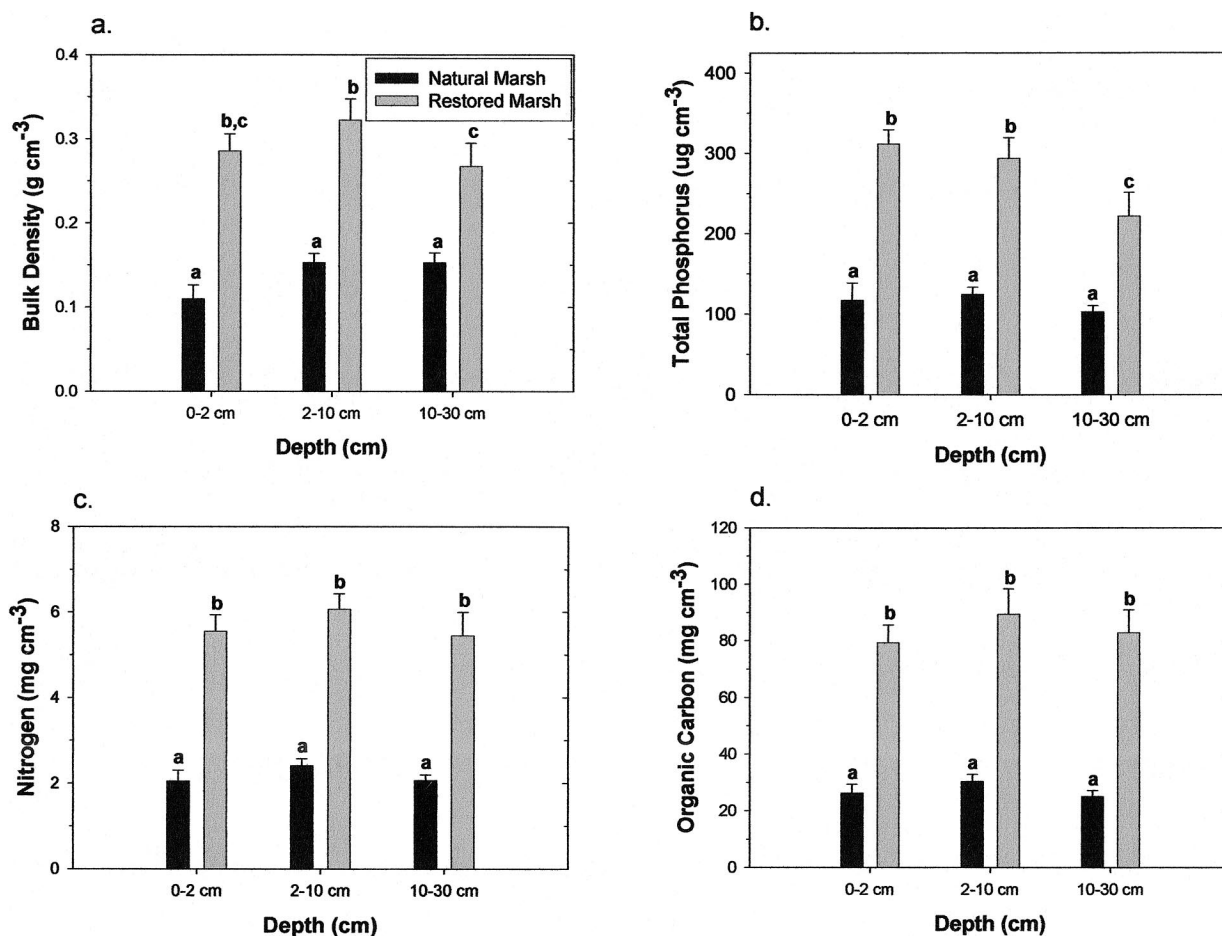


Figure 2. (a) Bulk density, (b) total phosphorus, (c) total nitrogen, and (d) organic carbon in natural ($n = 9$) and recently restored ($n = 9$) marsh soils adjacent to Upper Klamath Lake. Means separated by different letters are significantly different ($p \leq 0.05$) according to the Ryan-Einot-Gabriel Welsh Multiple Range Test.

Upper Klamath Lake Marsh drainage began in 1889 and continued through 1971 to provide land for agriculture (Snyder and Morace 1997). Agricultural activities on drained marshes include crop (potatoes, barley, wheat, and hay) cultivation and livestock (cattle and sheep) grazing. The application of phosphorus and nitrogen fertilizers was common where crops were grown, as was the use of soil amendments, such as lime to raise soil pH (Snyder and Morace 1997).

Activities to restore the drained marshes began in 1993 and have been different for every project, depending on the goals and objectives of the agencies or organizations conducting the restoration (Table 1). Approximately 6,200 ha of drained marsh adjacent to Upper Klamath Lake have been purchased for reflooding. Reflooding of this former farmland began in 1995 to restore one or more of the following: natural hydrologic conditions, lake water-storage capacity, wetland plant communities, wildlife habitat, or nutrient storage capacity, especially P. As of 2004, approximately 5,100 ha of farmland had been reflooded. Species com-

position in these recently restored marshes is similar to the natural marshes, but vegetation is sparse and open water is more prevalent because of soil subsidence.

Field Sampling

Soil cores were collected from three natural and three recently restored marshes surrounding Upper Klamath Lake on July 14–17, 2002 using an 8.5-cm-diameter stainless steel piston soil corer (Figure 1). Two soil cores, each 60 cm long, were collected from representative sampling locations in three natural marshes (Hank's Marsh, Shoalwater Bay Wildlife Area at Squaw Point, and Upper Klamath National Wildlife Refuge) adjacent to Upper Klamath Lake. Soil cores were sectioned into 2-cm increments and analyzed separately for determination of recent (~30 yr) and historic (~100 yr) rates of peat accretion and P accumulation.

Three additional soil cores, each 30-cm long, were

Table 1. Marsh restoration at Upper Klamath Lake. The area given indicates restored area and not necessarily the total site area. Land use is prior to site drainage. Lead agency is the agency primarily responsible for implementing the restoration activities.

Site Name	Area (ha)	Year Drained (Land Use)	Restoration Activities (Year)	Lead Agency
Wood River Ranch (not sampled)	1,300	1940-1957 (cattle grazing)	<ul style="list-style-type: none"> ● Restoration of ≈ 10 km of meandering channels (1997) ● Began seasonal flooding of 650 ha and permanent flooding of 485 ha of emergent marsh habitat (1998) ● Reconstruction of 2.7 km of the lower Wood River channel to create ≈ 10 ha of floodplain marsh (1997-1999) ● Restoration of historic Wood River channel to reconnect 40 ha of marsh to its original delta (2000-2001) 	Bureau of Land Management
Williamson River Delta	800	1920 (crop cultivation)	<ul style="list-style-type: none"> ● Flooded ≈ 800 ha allowing colonization of marsh vegetation without active planting (1998) ● Purchased an additional 1,500 ha with plans to relood 1,100 ha in 2006 (1999) 	The Nature Conservancy
Running Y Ranch	100	1916 (cattle grazing/crop cultivation)	<ul style="list-style-type: none"> ● Graded, seeded, planted and relooded ≈ 40 ha (1997) ● Relooded an additional 60 ha following similar restoration strategies (2000) 	Running Y Ranch
Agency Lake Ranch	2,900	1962, 1968-1971 (cattle grazing)	<ul style="list-style-type: none"> ● Seasonal flooding to store up to 15,000 m³ of water (1999) ● Soils are kept moist to maintain anaerobic conditions ● Colonization of native marsh vegetation without active planting 	Bureau of Reclamation

collected from representative sampling locations in each of the three natural marshes and three marshes being restored (Williamson River Delta Preserve, Running Y Ranch, and Agency Lake Ranch). Each core was sectioned into 0–2 cm, 2–10 cm, and 10–30 cm increments. Cores were analyzed separately for forms and amounts of P. All cores were transported to the lab on ice, where they were kept refrigerated at 4 °C until analysis.

Peat Accretion and Phosphorus Accumulation

Each field-moist 2-cm depth increment was air dried, weighed to determine bulk density, then ground using a mortar and pestle and sieved through 2-mm mesh. Subsamples were packed into petri dishes (50 mm \times 9 mm) and ¹³⁷Cs and ²¹⁰Pb activity measured in each soil depth increment by gamma spectrometry at 661.62 keV and 46.54 keV, respectively, using a high purity germanium detector (Canberra GL2820R, Canberra Industries, Meriden, CT) to determine recent (1964) and long-term (ca. 1900) rates of peat accretion.

Cesium-137 is a byproduct of nuclear fission with no natural sources (Ritchie and McHenry 1990). Because ¹³⁷Cs adsorbs tightly to clay and organic matter ion exchange sites (Davis 1963), biological uptake is

low and chemical diffusion is limited (Wise 1980). The ¹³⁷Cs maximum in the soil profile corresponds to the period of maximum deposition (ca. 1964) resulting from aboveground thermonuclear testing. Accumulation of soil above the ¹³⁷Cs maximum represents the net accretion over the past 38 years, from 1964 to 2002.

Lead-210 is naturally occurring and a member of the ²³⁸U radionuclide decay series that accumulates in soil and sediment through atmospheric deposition and sedimentation (excess or unsupported ²¹⁰Pb activity) and by the decay of ²²⁶Ra present in the soil/sediment matrix (supported ²¹⁰Pb activity) (Brenner et al. 1994). Excess ²¹⁰Pb in soil is produced by the radioactive decay of ²²⁶Ra in rocks and soils to gaseous ²²²Rn. The radon gas escapes to the atmosphere and decays rapidly through a series of short-lived radionuclides to ²¹⁰Pb and is eventually re-deposited on the land surface with precipitation or as dryfall. Lead-210 can be used to estimate accretion rates to approximately 100 yr before present.

Excess ²¹⁰Pb was estimated from measured total ²¹⁰Pb by assuming that activity in the bottom depth increments of each core was representative of supported ²¹⁰Pb. The constant activity (CA) model (Oldfield and Appleby 1984) was applied to those cores that displayed a monotonic decrease in total ²¹⁰Pb,

Table 2. Extraction procedure for sequential phosphorus fractionation.

P Fraction	Extraction Procedure
Labile P _i (plant available)	0.5 M NaHCO ₃ extraction
Labile total P	0.5 M NaHCO ₃ extraction + persulfate digestion
Labile P _o	0.5 M NaHCO ₃ total P less 0.5 M NaHCO ₃ P _i
Microbial bound P	CHCl ₃ + 0.5 M NaHCO ₃ + persulfate digestion
Surface Al and Fe bound P _i	0.1 M NaOH extraction
Occluded Al and Fe bound P _i	0.1 M NaOH extraction + sonication
Humic acid-bound P _o	Residual NaOH fraction + nitric and perchloric acid digestion
Calcium bound P _o	1 M HCl extraction
Residual P	Nitric and perchloric acid digestion
Total P	Sum of all P fraction

whereas the constant rate of supply (CRS) model was applied to cores that showed non-monotonic decrease with depth (Appleby and Oldfield 1978, Bricker-Urso *et al.* 1989).

A subsample from each depth increment was also oven-dried at 70 °C, weighed for bulk density, and analyzed for organic C and total N using a Perkin-Elmer 2400 CHN Analyzer. Total P was measured colorimetrically as ortho-P using the ascorbic acid method (APHA 1998), following digestion in nitric and perchloric acid (Sommers and Nelson 1972).

Phosphorus Fractionation

Extraction of P forms was carried out on a subsample from each field-moist soil depth increment (0–2 cm, 2–10 cm, and 10–30) using a modification of the Hedley procedure (Hedley *et al.* 1982). Table 2 outlines the procedures used to extract inorganic (P_i) and organic (P_o) forms of P sequentially. The Hedley fractionation is a sequential extraction using increasingly reactive reagents to extract increasingly recalcitrant P fractions. We acknowledge that these P fractions are operationally defined (e.g., NaOH extractable). However, the procedure provides a measure of the relative reactivity/availability of each fraction. For a detailed description of these procedures, see Qualls and Richardson (1995).

All P extracts were filtered through 2.5- μ m filter paper and analyzed colorimetrically using the ascorbic acid method (APHA 1998). Total P was compared with the sum of all P fractions to obtain percent recovery. Average recovery of total P from the fractionation procedure was 88.6%.

The P fractionation data are presented on a volume basis (μ g cm⁻³) as opposed to a mass basis (μ g g⁻¹). Our reasoning for this is based on the following: 1) plant roots explore a volume of soil, and plant uptake of soil P occurs on a volume basis; 2) inundation of the marsh soil by lake water occurs over a given area to a given depth, therefore P flux occurs on volume

basis; and 3) expression of soil P on a volumetric basis is necessary to calculate area-based rates of P accumulation. Conversion of the P fractionation data to mass units can be achieved by dividing by the bulk density.

A second subsample from each field-moist depth increment was mixed at a 1:1 ratio with deionized water to determine soil pH. Measurements of pH were performed using an Orion (model 250A) pH meter and an Orion (model 9107) low maintenance triode. A third subsample from each increment was oven-dried at 70 °C and weighed to determine bulk density. Oven-dried subsamples were also analyzed for organic C, total N, and total P as described above.

Statistical Analyses

Analysis of Variance (ANOVA) was used to test for differences between marsh types (natural vs. recently restored), sampling location, and depth (SAS 2001). Means were separated using the Ryan-Einot-Gabriel-Welsch multiple range test (SAS 2001). All tests of significance were made at $p \leq 0.05$.

RESULTS AND DISCUSSION

Bulk Density, Phosphorus, Nitrogen, and Carbon

Soil bulk density and total P, total N, and organic C (volume basis) were 2–3 times greater in the recently restored marshes compared to the natural marshes (Figure 2a–d). Soil moisture content was similar in recently restored marshes (68–86%) and natural marshes (72–85%) but lower than that found by Eilers *et al.* (2001) for Upper Klamath Lake sediments (87–94%). Total P concentrations in the recently restored marshes were greatest in the top 10 cm of soil and decreased with depth, whereas in the natural marshes, total P concentrations did not vary with depth (Figure 2b). Total N and organic C did not vary with depth in either the recently restored or natural marshes (Figure

2c–d). Greater bulk density and volume-based nutrient concentrations in recently restored marshes were attributed to soil subsidence and compaction caused by long-term drainage.

On a mass basis, total P did not differ between the natural (681–1054 $\mu\text{g g}^{-1}$) and recently restored marshes (821–1143 $\mu\text{g g}^{-1}$). Total N and organic C in the recently restored marshes, however, were significantly greater at the subsurface depths (2–10 cm and 10–30 cm) compared to natural marshes. Soil N and organic C concentrations decreased from 20 mg N g^{-1} and 252 mg C g^{-1} (0–2 cm) to 14 mg N g^{-1} and 171 mg C g^{-1} (10–30 cm) in the natural marshes, while not varying with depth (19–21 mg N g^{-1} and 281–313 mg C g^{-1}) in the recently restored marshes.

Peat Accretion and P, N, and Organic C Accumulation

Rates of peat accretion in the natural marshes based on interpretable ^{137}Cs profiles (Figure 3a, d) ranged from 2.4 to 6.1 mm yr^{-1} . Peat accretion determined by ^{210}Pb (Figure 3b, c, e, f) was similar, 3.2 to 6.6 mm yr^{-1} . For the three natural marshes, the average rate of ^{210}Pb -based peat accretion was 3.7 mm yr^{-1} , compared to 3.8 mm yr^{-1} based on ^{137}Cs (Table 3). One of the six cores indicated a variable ^{210}Pb accretion rate over time. Accretion at Upper Klamath National Wildlife Refuge (NWR) was substantially greater during the past 30 yr (4.7 mm yr^{-1}) than it was 100 yr ago (1.3 mm yr^{-1}) (Figure 3e, f). Calculation of increment age as a function of depth using the CRS model indicates that the locally accelerated rate of accretion began at this site around 1972. Cesium-137-based accretion at Upper Klamath NWR also displayed a similarly high rate (6.1 mm yr^{-1}) since circa 1964. However, the cause for locally accelerated accretion at Upper Klamath NWR is unknown.

Phosphorus, N, and organic C accumulation, based on accretion rates and depth-averaged measurements of bulk density and nutrient concentrations, showed trends similar to peat accretion (Table 3). Hank's Marsh had the lowest rates of accretion and P, N, and C accumulation, whereas higher rates were measured at Upper Klamath NWR and Squaw Point. Average ^{137}Cs -based accumulation rates were 0.45 g P $\text{m}^{-2} \text{yr}^{-1}$, 8.6 g N $\text{m}^{-2} \text{yr}^{-1}$, and 105 g C $\text{m}^{-2} \text{yr}^{-1}$ compared to 0.40 g P $\text{m}^{-2} \text{yr}^{-1}$, 9.1 g N $\text{m}^{-2} \text{yr}^{-1}$, and 116 g C $\text{m}^{-2} \text{yr}^{-1}$ based on ^{210}Pb . The similarity between recent and long-term rates of nutrient accumulation in Upper Klamath Lake's natural marshes suggests that these wetlands have been sequestering nutrients at relatively constant rates since the turn of century (Table 3).

Although P accumulation in wetlands is generally low, usually $< 1 \text{ g m}^{-2} \text{yr}^{-1}$ (Craft and Richardson

1998, Richardson and Qian 1999), large areas of wetlands have the potential to store significant amounts of P. Based on our analysis and in accordance with the ^{137}Cs -based P accumulation rate of 0.45 g $\text{m}^{-2} \text{yr}^{-1}$ measured herein, the 7,000 ha of natural marsh surrounding Upper Klamath Lake store approximately 31.5 metric tons P yr^{-1} . Further, between 1964 and 2002, these marshes sequestered about 1200 metric tons of P. Based on the calculated ^{210}Pb phosphorus accumulation rate of 0.40 g $\text{m}^{-2} \text{yr}^{-1}$, the remaining natural marshes of Upper Klamath Lake have sequestered almost 2,900 metric tons of P since the turn of the last century.

The 2002 TMDL (Total Maximum Daily Load) water quality goal for Upper Klamath Lake is to reduce the current external P load by 40% or 73 metric tons yr^{-1} , and the restoration of lake-fringe wetlands is considered an important element of plans to improve water quality by reducing the P load to Upper Klamath Lake (Boyd et al. 2002). The P storage potential associated with establishing naturally functioning marshes on the 5,100 ha of re-flooded farmland considered here is approximately 23 metric tons yr^{-1} , based on the ^{137}Cs -based P accumulation rate. However, this estimated 23 metric ton yr^{-1} reduction in P loading to the lake represents a best-case scenario where the recently restored marshes function as though they were never disturbed. Soil subsidence following long-term drainage and land-use conversion has increased soil bulk density, which may reduce or, in some areas, inhibit the P-sequestration capabilities of the recently restored marshes. Because the recently restored marshes have been drained for several decades, up to a meter of soil subsidence has occurred in some places. For example, at the Williamson River Delta site an estimated 150 to 500 ha of marsh, depending on lake level, will become lake bottom because water levels will be too deep to support marsh vegetation. Consequently, soil will accumulate in a manner that resembles lake sediment rather than marsh peat and reduce the rate of P accumulation in these areas. The magnitude of soil subsidence may make the restoration of emergent marsh impossible unless the levees separating these lands from the lake are maintained and water levels are controlled. The cost of installing and maintaining this infrastructure is not inconsequential and must be considered when weighing the water quality benefits gained from a managed wetland against other watershed strategies for P reduction.

The type of vegetation that colonizes the recently restored marshes may also be influenced by the degree of soil subsidence and affect the rate of P accumulation. For example, Upper Klamath NWR and Squaw Point, which are dominated by hardstem bulrush (*Schoenoplectus/Scirpus acutus*), had much higher

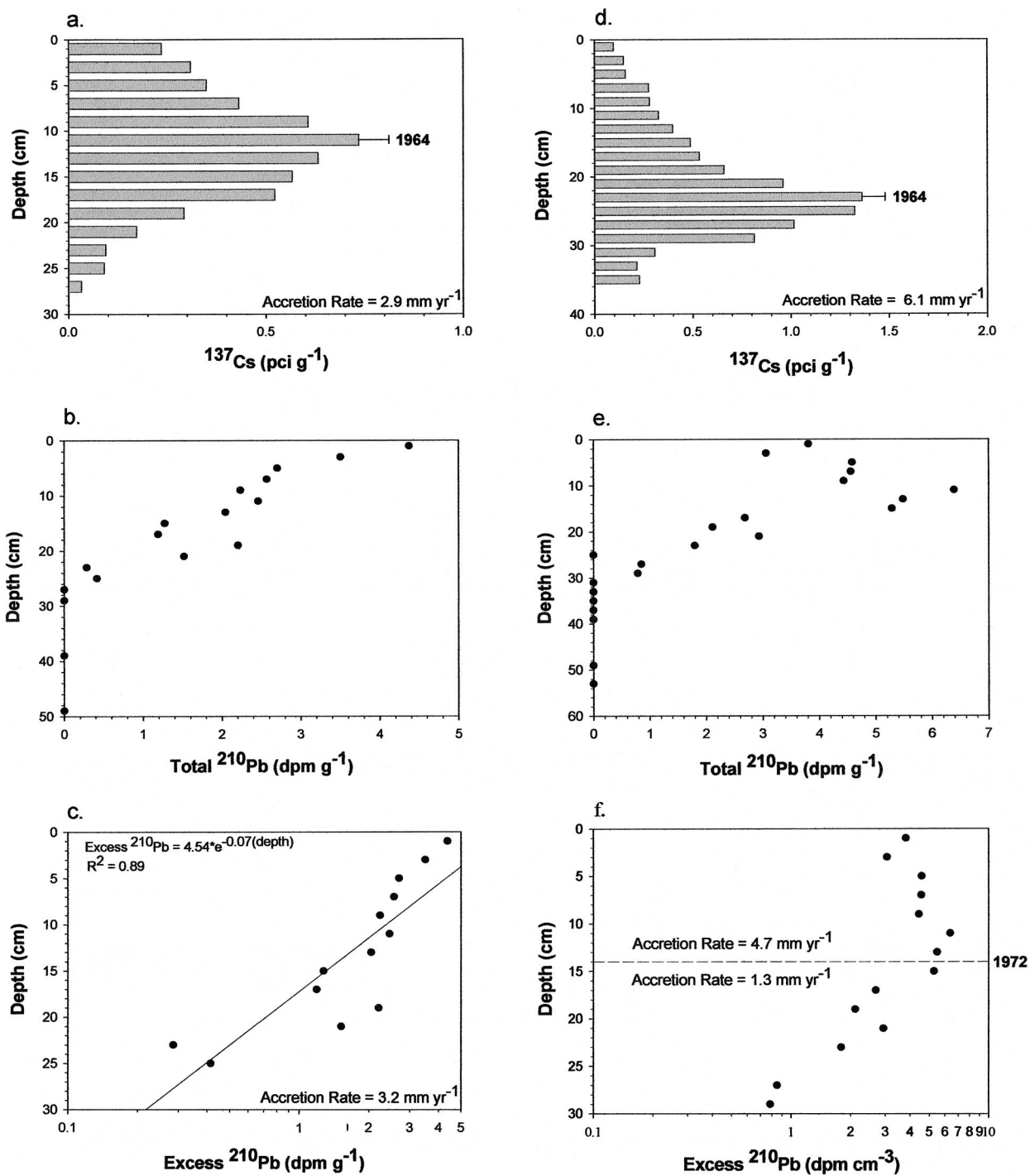


Figure 3. Representative ^{137}Cs and ^{210}Pb profiles for natural marshes adjacent to Upper Klamath Lake. Hank's Marsh (south core) is displayed in a-c and is representative of the constant activity (CA) model, whereas Upper Klamath NWR (south core) is displayed in d-f and is representative of the constant rate of supply (CRS) model.

^{137}Cs -based P accumulation rates than Hank's Marsh where wocus (*Nuphar lutea ssp. polysepala*) is a co-dominant component of the plant community and open water is more prevalent (Table 3). Soft-stem species such as *Nuphar* decompose faster because of their low cellulose and lignin content (Odum and Heywood

1978) and therefore may sequester P in peat at a lower rate. Thus, in areas where some subsidence has occurred, establishment of a wocus community may occur, resulting in reduced peat accretion and P accumulation as compared to a bulrush-dominated marsh.

Table 4 displays rates of peat accretion and nutrient

Table 3. Cesium-137 and ²¹⁰Pb-based peat accretation and P, N, and organic C accumulation in natural marshes adjacent to Upper Klamath Lake. Two cores were analyzed from each site unless otherwise indicated. Values are reported as the average of each site (\pm range) and the average of all sites (\pm SE).

	Accretion Rate (mm yr ⁻¹)	Total Phosphorus (g m ⁻² yr ⁻¹)	Total Nitrogen (g m ⁻² yr ⁻¹)	Organic Carbon (g m ⁻² yr ⁻¹)
¹³⁷ Cs Model (1964 to present)				
Hank's Marsh	2.4 (\pm 0.6)	0.24 (\pm 0.07)	5.1 (\pm 1.5)	67 (\pm 24)
Upper Klamath NWR ¹	6.1	0.64	12.8	158
Squaw Point	4.2 (\pm 0.3)	0.57 (\pm 0.02)	10.0 (\pm 1.7)	116 (\pm 21)
Average	3.8 (\pm 0.7)	0.45 (\pm 0.09)	8.6 (\pm 1.7)	105 (\pm 20)
²¹⁰ Pb Model (ca. 1900 to present)				
Hank's Marsh	3.2 (\pm 0.1)	0.29 (\pm 0.03)	7.5 (\pm 0.8)	101 (\pm 18)
Upper Klamath NWR (1972-present) ^{1,2}	4.7	0.49	9.0	115
Upper Klamath NWR (1868-1972) ^{1,2}	1.3	0.12	2.8	33
Squaw Point ¹	6.6	0.75	17.3	209
Average	3.7 (\pm 1.0)	0.40 (\pm 0.14)	9.1 (\pm 2.9)	116 (\pm 34)

¹ Sites with only one interpretable core.

² This ²¹⁰Pb profile had a variable accretion rate (CRS model). A time weighted average of the two rates (1:3.5) was used to calculate the overall average of the three sites.

accumulation from various peatlands across the United States. Comparison of Upper Klamath Lake marshes with these North American peatlands shows a trend of enhanced peat accretion and P, N, and organic C accumulation in response to P enrichment. In fact, the rate of phosphorus accumulation in Upper Klamath Lake marshes is nearly the same as that found in eutrophic areas of the Lake Tahoe Basin, the Upper St. John's River Basin, and the Florida Everglades.

Forms and Amounts of Soil Phosphorus

Occluded Fe- and Al-P_i, Ca-P_i, humic-acid P_o (0–2 cm depth increment only), and residual P were significantly greater in the recently restored marshes as compared to the natural marshes (Table 5). Occluded Fe- and Al-P_i was four times greater, Ca-P_i twenty-two times greater, humic-acid P_o two times greater, and residual P five times greater. Labile P_i and P_o, microbial P, and surface Fe- and Al-P_i did not differ between marsh types.

When expressed as a percentage of total P, labile P_i and P_o, microbial P, surface Fe- and Al-P_i, and humic-acid P_o were significantly greater in the natural marshes compared to the recently restored marshes. Labile P_i (9%) was nine times greater, labile P_o (2%) and microbial P (7%) five times greater, and surface Fe- and Al-P_i (10%) and humic-acid P_o (53%) two times greater in the natural marshes. In contrast, occluded Fe- and Al-P_i (5%), Ca-P_i (16%), and residual P (46%) were significantly greater in the recently restored marshes compared to the natural marshes (occluded

Fe- and Al-P_i = 3%, calcium-bound P_i = 2%, and residual P = 25–29%).

Forms and amounts of soil P did not vary with depth in the natural marshes, and there was little difference among the three sites. In the recently restored marshes, however, labile P_i and P_o, surface Fe- and Al-P_i, Ca-P_i, humic-acid P_o, and residual P were significantly different among sites. Additionally, the surface 0–2 cm depth increment in the recently restored marshes had significantly more labile P_i, labile P_o, and surface Fe- and Al-P_i as compared to the subsurface (10–30 cm) depth increment (Table 5). Residual P also decreased with depth and was significantly greater in the 0–2 cm and 2–10 cm depth as compared the deeper, 10–30 cm depth.

Although humic-acid P_o is the largest natural marsh soil P fraction (on a volume basis), a substantial portion of the P pool on a weight basis is associated with the inorganic soil matrix. Based on the data presented in Figure 2, the calculated natural marsh soil depth averaged organic matter content is approximately 350 g kg⁻¹. Therefore, about 65% of the soil dry weight is inorganic material. Since Upper Klamath Lake is near Crater Lake, at least some of the inorganic soil P originates from volcanic materials. Volcanically derived soils typically have a high P sorption capacity, which is likely the source of the large amounts of P retained in non-labile Fe- and Al-P_i and residual P (Table 5).

Overall, greater soil P concentrations in the recently restored marshes compared to the natural marshes are primarily the result of greater bulk density (Table 5). When organic soils are drained, not only does physical compaction occur, but the decomposition of organic

Table 4. Peat accretion and P, N, and organic C accumulation in various P-enriched and unenriched freshwater peatlands of the USA.

	Accretion Rate (mm yr ⁻¹)	Phosphorus (g m ⁻² yr ⁻¹)	Nitrogen (g m ⁻² yr ⁻¹)	Org. Carbon (g m ⁻² yr ⁻¹)	Source
Unenriched					
Maryland, Pennsylvania and West Virginia Bogs	1.4–3.1	0.07–0.16	1.4–3.1	64–89	Wieder <i>et al.</i> (1994), Wieder (1985)
Minnesota Bog	2.4	—	—	79	Wieder <i>et al.</i> (1994), Wieder (1985)
Massachusetts Bog	4.3	—	1.2	90	Hemond (1980, 1983)
Michigan Fens	0.9	0.11	3	42	Craft and Richardson (1998), Richardson <i>et al.</i> (1978)
Michigan Fen	—	0.3	—	—	Richardson and Marshall (1986)
North Carolina Pocosin	2.6	0.06	3	127	Craft and Richardson (1998), Bridgham and Richardson (1993)
Okefenokee, Georgia	—	0.15	3.8	82	Schlesinger (1978)
Florida Everglades	1.4	0.06	4.7	65	Craft and Richardson (1998)
Lake Tahoe Basin	1.0–1.2	0.11–0.26	2.7–4.3	42–69	Kim <i>et al.</i> (2001)
P Enriched					
Upper Klamath Lake					This study
¹³⁷ Cs	3.8	0.45	8.6	104	
²¹⁰ Pb	3.7	0.4	9.1	116	
Lake Tahoe Basin	1.7–2.3	0.47–0.65	5.6–9.0	88–97	Kim <i>et al.</i> (2001)
Anderson Marsh, California	4.5	1.25	12.9	138	Kim (2003)
Florida Everglades	6.7	0.46	16.6	223	Craft and Richardson (1998)
Upper St. Johns River Basin	5.3	0.40	15.3	202	Brenner <i>et al.</i> (2001)
Michigan Fen	—	0.9	—	—	Richardson and Marshall (1986)

matter takes place at a much faster rate as well. Under natural conditions, organic residue coats the surface of soil colloids, restricting the activity of soil Al and Fe in sorbing P (Iyamuremye *et al.* 1996). During agricultural production, the drained marsh soils at Upper Klamath Lake oxidized, accelerating the rate of decomposition and exposing more of the soil inorganic matrix (Fe and Al). This provided added sorption capacity for the P liberated through decomposition and resulted in greater concentrations of occluded Fe and Al-P_i at the recently restored marshes compared to the natural marshes (Table 5). Soil pH and Ca-P_i also were greater in recently restored marshes (Williamson River, Running Y Ranch), possibly as a result of lime and fertilizer (P) additions during past cultivation (Table 5).

CONCLUSION

Cesium-137 and ²¹⁰Pb-based measurements of P accumulation in natural marshes of Upper Klamath Lake suggest that these wetlands are sequestering 4.0–4.5 kg P ha⁻¹ yr⁻¹ and that most P (>67%) is being sequestered in recalcitrant forms such as humic-acid P_o and residual P. The natural marshes are storing approximately 31.5 metric tons of P yr⁻¹. If it is possible to re-establish natural hydrology and restore the pre-

viously drained marsh around Upper Klamath Lake to naturally functioning conditions, the 5,100 ha of marsh undergoing restoration can potentially store up to 23 metric tons of P annually. However, our findings show that physical changes have occurred in the recently restored marshes, namely soil subsidence resulting from long-term drainage. Soil subsidence could prevent the establishment of marsh vegetation, slow recolonization rates, or induce a shift from emergents to floating aquatic species over large areas in the recently restored marshes, thereby slowing peat accretion.

Subsidence, long-term drainage, and land-use conversion have also resulted in soil P concentrations on a volume basis that are more than two times greater in the recently restored marshes as compared to the natural marshes. However, most soil P is present in forms that are not readily solubilized. Of concern though are the high Ca-P_i concentrations measured in the recently restored marsh soils. If marsh hydrology is restored, soil pH of the restored marshes will likely approach that of the natural marsh (pH 4.9–5.6) with time, resulting in the dissolution of some of the Ca-P_i fraction. Upon dissolution, some soil P will likely be lost to the water column. However, given sufficient time and successful establishment of vegetation, the high P soils of the recently restored wetlands will be

Table 5. Forms and amounts of soil P in natural vs. recently restored wetlands at 0-2 cm, 2-10 cm, and 10-30 cm. Bulk density, pH, and soil P concentrations are displayed for site means (n = 3) and type mean (n = 9) ± SE at each depth increment. An asterisk indicates a statistically greater (p ≤ 0.05) type mean by depth according to the Ryan-Einot-Gabriel-Welsh Multiple Range Test.

Depth (cm)	Type ¹	Site ²	Soil pH	Bulk Density (g cm ⁻³)	Labile		Labile P _o	Microbial P	Surface		Occluded		Ca P _i	Humic-acid P _o	Residual P	Total P (Sum P)
					P _i	P _o			Fe- and Al-P _i	Fe- and Al-P _i						
0-2	NAT	UK	4.7 ± 0.7	0.10 ± 0.01	5.5 ± 3.7	2.2 ± 0.7	4.1 ± 1.2	7.9 ± 0.3	3.2 ± 0.1	1.7 ± 0.1	31.9 ± 8.0	20.0 ± 3.2	76.5 ± 6.0			
		SP	5.3 ± 0.7	0.13 ± 0.04	13.0 ± 8.0	3.7 ± 1.6	7.6 ± 0.9	14.9 ± 5.4	4.4 ± 1.5	3.2 ± 1.9	42.9 ± 15.1	47.7 ± 24.2	137.5 ± 52.7			
		HM	4.7 ± 0.1	0.10 ± 0.03	4.1 ± 2.6	0.8 ± 0.3	7.2 ± 3.7	6.8 ± 1.2	1.9 ± 0.5	1.0 ± 0.3	36.5 ± 9.3	18.4 ± 1.9	76.7 ± 14.1			
	RES	AVG	4.9 ± 0.3	0.11 ± 0.02	7.5 ± 3.0	2.2 ± 0.7	66.3 ± 1.3	9.9 ± 2.0	3.2 ± 0.6	2.0 ± 0.6	114.5 ± 19.9	28.7 ± 8.5	96.9 ± 18.8			
		WR	6.5 ± 0.2	0.30 ± 0.04	1.9 ± 0.7	1.4 ± 0.5	4.1 ± 2.6	16.1 ± 4.2	16.1 ± 7.3	56.3 ± 23.0	126.2 ± 7.7	336.7 ± 33.1				
		AL	4.8 ± 0.1	0.23 ± 0.02	5.8 ± 2.5	2.9 ± 0.3	8.8 ± 2.1	26.4 ± 5.2	15.6 ± 3.3	17.9 ± 3.0	67.6 ± 6.1	143.0 ± 21.5	288.1 ± 25.6			
2-10	NAT	RY	6.5 ± 0.1	0.32 ± 0.02	0.6 ± 0.1	0.4 ± 0.2	2.3 ± 0.4	6.7 ± 0.7	8.3 ± 0.3	54.7 ± 6.9	82.0 ± 16.4	205.4 ± 13.6				
		AVG	6.0 ± 0.3*	0.29 ± 0.02*	2.8 ± 1.1	1.6 ± 0.4	5.1 ± 1.4	16.4 ± 3.4	13.3 ± 2.6*	43.0 ± 9.4*	77.5 ± 11.7*	117.1 ± 12.2*	276.7 ± 23.0*			
		UK	5.5 ± 0.4	0.17 ± 0.01	0.6 ± 0.2	1.4 ± 0.3	9.2 ± 2.7	11.1 ± 2.2	3.4 ± 0.9	2.2 ± 0.5	50.5 ± 14.2	21.8 ± 4.2	100.2 ± 17.4			
	RES	SP	5.9 ± 0.2	0.16 ± 0.02	2.3 ± 0.3	2.3 ± 0.9	4.1 ± 2.0	13.3 ± 2.2	4.1 ± 0.8	1.8 ± 0.4	61.8 ± 5.1	27.0 ± 2.6	116.7 ± 8.0			
		HM	5.2 ± 0.1	0.13 ± 0.02	1.1 ± 0.4	2.8 ± 1.5	5.1 ± 0.8	5.8 ± 0.7	1.9 ± 0.3	1.2 ± 0.2	44.1 ± 9.9	26.8 ± 5.1	88.9 ± 15.8			
		AVG	5.5 ± 0.2	0.15 ± 0.01	1.4 ± 0.3*	2.2 ± 0.6	6.1 ± 1.3	10.1 ± 1.4	3.1 ± 0.5	1.8 ± 0.2	52.1 ± 5.8	25.2 ± 2.2	101.9 ± 8.0			
10-30	NAT	WR	6.5 ± 0.3	0.32 ± 0.02	0.7 ± 0.3	1.0 ± 0.3	1.5 ± 0.3	11.3 ± 1.1	11.6 ± 1.9	37.9 ± 5.3	127.0 ± 21.8	124.9 ± 10.2	316.0 ± 14.4			
		AL	5.1 ± 0.2	0.24 ± 0.02	0.3 ± 0.2	1.5 ± 0.4	4.9 ± 1.4	14.2 ± 1.4	10.3 ± 2.8	9.5 ± 2.0	43.0 ± 9.7	117.8 ± 17.1	201.6 ± 21.2			
		RY	7.0 ± 0.1	0.40 ± 0.03	0.7 ± 0.1	0.3 ± 0.2	11.1 ± 9.6	6.1 ± 1.5	9.8 ± 0.9	68.3 ± 5.4	67.9 ± 10.3	111.9 ± 16.4	276.1 ± 35.4			
	RES	AVG	6.2 ± 0.3	0.32 ± 0.03*	0.6 ± 0.1	0.9 ± 0.2	5.8 ± 3.1	10.5 ± 1.4	10.6 ± 1.1*	38.6 ± 8.8*	79.3 ± 14.5	118.2 ± 7.7*	264.6 ± 21.0*			
		UK	5.6 ± 0.2	0.19 ± 0.01	0.4 ± 0.2	1.0 ± 0.4	6.3 ± 5.1	7.6 ± 1.8	3.2 ± 0.5	2.5 ± 1.0	67.6 ± 12.0	24.1 ± 4.9	112.7 ± 16.5			
		SP	5.5 ± 0.1	0.16 ± 0.01	2.8 ± 2.5	1.2 ± 0.5	2.8 ± 1.6	9.1 ± 0.5	4.0 ± 0.9	1.9 ± 0.4	66.1 ± 3.7	24.1 ± 4.5	111.9 ± 7.2			
RES	HM	5.6 ± 0.2	0.11 ± 0.003	0.3 ± 3.6	0.5 ± 0.1	1.0 ± 0.3	4.2 ± 0.9	1.9 ± 0.3	1.6 ± 0.3	29.2 ± 9.5	28.9 ± 2.5	67.6 ± 9.8				
	AVG	5.6 ± 0.1	0.15 ± 0.01	1.1 ± 0.8	0.9 ± 0.2	3.3 ± 1.7	7.0 ± 0.9	3.0 ± 0.4	2.0 ± 0.3	54.3 ± 7.7	25.7 ± 2.2	97.4 ± 9.5				
	WR	6.4 ± 0.4	0.31 ± 0.02	0.7 ± 0.2	0.9 ± 0.1	0.8 ± 0.4	9.5 ± 1.2	11.5 ± 1.6	40.1 ± 4.5	116.1 ± 28.9	112.8 ± 16.4	292.4 ± 19.3				
RES	AL	5.1 ± 0.1	0.17 ± 0.02	1.1 ± 0.6	1.2 ± 0.3	1.6 ± 0.6	9.9 ± 2.4	8.1 ± 1.3	6.2 ± 2.6	34.5 ± 6.9	54.1 ± 13.3	116.6 ± 9.7				
	RY	7.1 ± 0.1	0.32 ± 0.02	0.4 ± 0.1	0.2 ± 0.1	1.0 ± 0.4	4.2 ± 0.7	7.4 ± 1.8	56.8 ± 10.2	49.3 ± 7.8	75.8 ± 5.6	195.1 ± 13.4				
AVG	6.2 ± 0.3	0.27 ± 0.03*	0.7 ± 0.2	0.8 ± 0.2	1.1 ± 0.3	7.8 ± 1.2	9.0 ± 1.0*	34.4 ± 8.1*	66.6 ± 15.4	80.9 ± 10.6*	201.4 ± 26.5*					

¹ Marsh type abbreviations: NAT = natural marsh, RES = recently restored marsh

² Site abbreviations: UK = Upper Klamath NWR, SP = Squaw Point, HM = Hank's Marsh, WR = Williamson River Delta Preserve, AL = Agency Lake Ranch, RY = Running Y Ranch, AVG = marsh type mean

buried by the deposition of plant detritus, making the P less accessible to the water column.

ACKNOWLEDGMENTS

Project funding was provided by the U.S. Fish and Wildlife Service Klamath Basin Ecosystem Restoration Office. We thank Chad Ferguson for assistance in the field, Jim Rhodes, Bill Rutherford, and Dave Mauer with the Klamath Basin Wildlife Refuges for airboat transportation, and Christina Pruett and Sara Butler for their help preparing samples and assisting with chemical analyses. We also thank Wedge Watkins, Stan Geiger, Christine Karas, and Bob Davis for providing information on marsh restoration activities and two anonymous reviews whose insightful comments greatly improved the quality of this manuscript.

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Manuscript received 5 April 2004; revisions received 7 September 2004 and 28 March 2005; accepted 28 April 2005.